THE BIOLOGY AND ABUNDANCE OF THREE CICHLID SPECIES FROM THE KAVANGO AND CAPRIVI REGIONS, NAMIBIA

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by

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ABSTRACT

River-floodplains are highly productive environments capable of supporting large fisheries. In the Kavango and Caprivi Regions in Namibia, artisanal gillnet fisheries catch is dominated by three cichlids: *Oreochromis andersonii*, *Oreochromis macrochir* and *Tilapia rendalli*. Their abundance is declining because of increased fishing pressure and their stocks are becoming vulnerable to overfishing. The aim of this thesis was to provide management recommendations for the three cichlids by investigating and comparing their age, growth, reproduction and relative abundance in Lake Liambezi and the Kavango, Kwando and Zambezi Rivers. These four systems present different scenarios whereby Lake Liambezi is a highly productive but heavily exploited area, the Zambezi River is considered heavily exploited and the samples from the Kavango and Kwando Rivers were collected from protected areas where exploitation was low.

Fish community composition and relative abundance were assessed using experimental gillnet fleets in each system. Gillnet catch composition was similar between the three river systems but differed markedly in Lake Liambezi because of habitat differences. *Schilbe intermedius* dominated gillnet catches in the three river systems, while *Brycinus lateralis* was most abundant in Lake Liambezi. Cichlid abundance was low despite their importance in artisanal fisheries. Catch per unit effort (CPUE) for *O. andersonii* and *O. macrochir* was highest in the unexploited systems and lowest in the exploited systems. *Tilapia rendalli* CPUE was highest in Lake Liambezi and was lowest in the Zambezi River.

Age and growth were estimated using sectioned sagittal otoliths. Growth zone deposition rate was validated as annual using edge analysis (EA) and occurred in summer between October and January. Initial growth rates for each species were fastest in exploited populations, and *O. andersonii* and *O. macrochir* attained larger sizes in the Zambezi River. While the three species attained older ages in protected areas, their growth rates were slower in these areas. This may be a consequence of intra-specific competition as well as of general system productivity. Age-at-50% maturity (tm_{50}) differed significantly between populations of each species as a result of differences in growth rates, but length-at-50% maturity (Lm_{50}) did not differ significantly between populations. Reproduction of the three assessed species peaked between September and April.

These results indicate that cichlid fisheries in the Kavango and Caprivi Regions could be managed using similar exploitation rules in all systems. It was recommended that the legal minimum mesh size be increased from 3” (76 mm) to 3.5” (89 mm) to ensure that juvenile cichlids are not targeted by the fishery. The implementation of this would reduce the risk of overfishing. The establishment of Fish Protection Areas (FPA’s) on the Zambezi River was endorsed and it was recommended that further areas be established on the Zambezi and Kavango Rivers to maintain an adequate spawner stock of large cichlids.

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Contents

List of acronyms

APE – Average percent error

CPUE – Catch per unit effort

EA – Edge analysis

FPA – Fish protected area

FL – Fork length

GSI – Gonadosomatic index

IRI – Index of relative importance

MFMR – Ministry of Fisheries and Marine Resources

NNF – Namibia Nature Foundation

PC – Probability of capture

SL – Standard length

TL – Total length

WWF – World Wide Fund for Nature

CHAPTER 1

General introduction

1.1 INTRODUCTION

Floodplain rivers such as the Kavango, Kwando and Zambezi Rivers in north-eastern Namibia flow in a well defined channel during periods of low discharge, but as a result of seasonal variations in rainfall in the catchment area breach their banks annually, inundating large fringing plains. Floodplain rivers are amongst the most species rich and productive aquatic environments on earth (Arthington et al., 2004; Bayley, 1988; Junk & Wantzen, 2004; Ward & Tockner, 2001; Ward, Tockner, & Schiemer, 1999; Welcomme, 2001). River-floodplain environments are able to support large fisheries as a result of their high productivity (Welcomme, 1979). In Namibia, the fisheries in the Kavango, Kwando and Zambezi Rivers and their associated floodplains and lakes provide a major source of protein, employment and a source of income for rural communities (Purvis, 2001; Turpie, Smith, Emerton, & Barnes, 1999; Tvedten, 2002).

River-floodplain fisheries are complex, being both multi-species and multi-gear in nature (Welcomme, 1979, 1985). They are generally highly resilient to increased effort and often display an asymptotic relationship between total effort and long-term yield (Arthington et al., 2004; Jul-Larsen, Kolding, Nielsen, Overa, & van Zwieten, 2003). This is because with increasing fishing effort, the larger, slower growing species in the assemblage are fished out and replaced by small, fast-growing species that continue to produce high yields even under high fishing pressure (Arthington et al., 2004; Jul-Larsen et al., 2003; Welcomme, 1999; Welcomme et al., 2010). In the traditional sense, it is not possible to overfish these systems as the yield does not decline with increasing fishing effort (Jul-Larsen et al., 2003). Instead, the first sign of overfishing from an ecosystem perspective is the collapse of certain stocks within the assemblage (Allan et al., 2005; Murawski, 2000). It is neither economically nor ecologically desirable to overfish systems in this manner as the economic return to each fisher decreases with increasing effort, and the larger species in the assemblage become highly threatened (Allan et al., 2005; Arthington et al., 2004).

Most floodplain fisheries are open-access and are managed using various technical measures, as well as through traditional management authorities (Abbott, 2001; Welcomme, 1979, 2001). In Namibia, technical measures include gear restrictions, mesh size regulations, the number and length of gillnets allowed per fisher and the method used to catch fish. Despite these management measures, stocks of the larger, commercially valuable cichlid species are declining, particularly in the Zambezi River (Hay & van der Waal, 2009; Hay et al., 2000). This decline has been attributed to increased fishing effort which is driven by human population growth (Hay & van der Waal, 2009; Jul-Larsen et al., 2003). Fishing effort is likely to increase further as more people turn to fishing as a full-time occupation and commercialisation of the fishery increases as a result of improved road communications and greater demand for fish by a growing population (Abbott, 2001; Tvedten, 2002).

1.2 CICHLIDS OF THE KAVANGO, KWANDO AND ZAMBEZI RIVERS

The cichlid assemblage in the Kavango, Kwando and Upper Zambezi Rivers is made up of nineteen formally described species from seven genera, as well as several other species that are yet to be described (Tweddle et al., 2004). Large cichlids of the genera *Oreochromis*, *Tilapia*, *Serranochromis* and *Sargochromis* are the major target species of the subsistence and commercial gillnet fisheries in the Kavango and Caprivi Regions (van der Waal, 1980, 1990, 1991). By far the most important species in the fisheries are *Oreochromis andersonii* and *Oreochromis macrochir*. These two species contribute up to 60% of the weight of the commercial and subsistence catch in the Kavango and Zambezi Rivers and in Lake Liambezi (van der Waal, 1980, 1990, 1991). *Tilapia rendalli* is less important, but still a significant component of the fisheries, contributing up to 10% of the catch (van der Waal, 1980, 1990, 1991).

Biological information on *O. andersonii*, *O. macrochir* and *T. rendalli* in Namibia is limited. Current management regulations are thus not based upon reliable scientific information. The proper assessment and management of a fishery requires an understanding on the biology, life history and distribution of the target species (King, 1995). Life history traits such as size at maturity and growth rates of cichlids vary between populations that experience different hydro-climatic conditions (James & Bruton, 1992; Weyl & Hecht, 1998). As the timing, magnitude and duration of floods differ significantly between the Kavango, Kwando, Lake Liambezi and Zambezi Rivers, these traits are likely to differ significantly between populations. The variation in life history traits between populations means that separate management regulations may have to be developed for distinct populations in each system.

1.3 THESIS OUTLINE

The primary aim of this thesis is to provide management recommendations for the sustainable use of three large, commercially important cichlid species, *O. andersonii*, *O. macrochir* and *T. rendalli* in the Kavango and Caprivi Regions in north-eastern Namibia. To do this the age, growth, reproduction and relative abundance of the three cichlids was investigated in relation to the biotic and abiotic environments in Lake Liambezi and the Kavango, Kwando and Zambezi Rivers.

The thesis is divided into six chapters. After the general introduction (Chapter 1), Chapter 2 reviews the relevant literature, describing floodplain ecosystem dynamics and their effects on fish biology. Chapter 3 describes the study area and the basic hydrology and water quality in each system, as well as the sampling strategy and general methods used in this study. Chapter 4 examines the fish community composition and discusses the relative abundance of *O. andersonii*, *O. macrochir* and *T. rendalli* in each of the four systems. In Chapter 5, the age, growth, size and age at maturity and the reproductive season of *O. andersonii*, *O. macrochir* and *T. rendalli* are presented and discussed in relation to the abiotic (Chapter 3) and biotic (Chapter 4) environments in the four systems. Chapter 6 discusses the findings of the study and makes management recommendations for the sustainable use of these species.

CHAPTER 2

Literature review of floodplain ecology, ageing techniques and cichlid biology

2.1 INTRODUCTION

Ecological processes in large, unregulated lowland rivers are best described by the flood pulse concept (Junk & Wantzen, 2004; Junk, Bayley, & Sparks, 1989). This concept emphasises lateral linkages between the floodplain and the river channel and postulates that the bulk of productivity in the system is derived from the floodplain and not from downstream transport of organic matter (Junk et al., 1989). A seasonal flood pulse creates high spatio-temporal habitat heterogeneity and is thus the main driving force behind the maintenance of biotic diversity in the system (Junk et al., 1989). In their natural state, river-floodplains are among the most diverse and biologically productive environments on earth, but many are under threat from human activities such as the alteration of habitat and flow regimes (Tockner & Stanford, 2002). Major disturbances such as alteration of the natural flood cycle (Bayley, 1995) or the introduction of highly competitive alien species (Gozlan, 2008) undermines the resilience and productivity of river-floodplain ecosystems.

The Kavango, Kwando and Upper Zambezi Rivers are unregulated and remain in a relatively pristine state. These systems support large fisheries on which the livelihoods of many people depend (Abbott, 2001; Purvis, 2001; Turpie et al., 1999). The fisheries are, however, threatened by increasing fishing effort and require proper management to prevent overfishing which poses serious threats to biodiversity and to the sustainability of fisheries and the livelihoods of those who depend on them (Allan et al., 2005). The biology and ecology of fishes inhabiting floodplain rivers are strongly linked to flooding (Bailly, Agostinho, & Suzuki, 2008; Junk et al., 1989; Welcomme, 1985; Welcomme & Halls, 2001). An understanding of the response of fish populations to changes in the timing, duration and amplitude of flooding is therefore essential for the management of floodplain fisheries (Welcomme, 1985; Welcomme & Halls, 2001). Knowledge of the biology of key species can be used to predict the response of the species to variations in flooding between years in an unregulated system (Welcomme & Halls, 2001). Life history traits such as age, growth, maturity and mortality have to be assessed in order to obtain those parameters essential for modelling fish population dynamics in floodplain-rivers (Halls, Kirkwood, & Payne, 2001).

2.2 AGEING TECHNIQUES

Appropriate structures

Understanding the biology of a species requires accurate and precise age estimation that is essential for the calculation of growth rates, mortality rates, maturity and productivity (Campana, 2001). The formation of periodic growth increments on calcified structures are most commonly used to estimate age in fish (Campana, 2001). Most calcified structures, however, are prone to calcium resorption which may compromise the retention of growth increments (Campana & Thorrold, 2001). Otoliths, on the other hand, are acellular and metabolically inert, and so material deposited on the otolith is not susceptible to resorption (Campana, 1999; Gauldie & Nelson, 1990). Otoliths grow continually throughout the life of the fish, recording their entire lifespan (Campana, 1999). In cichlids, both scales (Dudley, 1974; Hecht, 1980; Kapetsky, 1974; van der Waal, 1985) and otoliths (Booth & Merron, 1996; Booth, Merron, & Buxton, 1995; Chimatiro, 2004; Weyl & Hecht, 1998) have been used to estimate age. Using scales, however, is considered to be somewhat unreliable as it has been shown to underestimate the true age of fishes and hence overestimate growth rates (Booth et al., 1995; Hecht, 1980). Sectioned otoliths are now considered to be the most suitable structures for ageing cichlids (Booth et al., 1995; Hecht, 1980).

Growth zone deposition rate

In otoliths and other hard parts the formation of growth checks occurs as a result of reduced growth rates in response to one or more environmental variables (Gauldie & Nelson, 1990). In floodplain fishes, these variables may include lower temperature, reproduction and the effects associated with the drawdown phase, such as reduced food availability and increased density-dependant competition (Dudley, 1974; Welcomme, 1979). The period of annulus formation may vary from one water body to another depending on the environmental variables which are responsible for annulus formation. Annulus formation in *O. andersonii*, *O. macrochir* and *T. rendalli* from the Kafue floodplain, and in *O. andersonii* and *O. macrochir* from the Okavango Delta occurred during the hotter summer months from October to January while floodwaters were beginning to rise (Booth & Merron, 1996; Booth et al., 1995; Dudley, 1974; Kapetsky, 1974). Similarly, annulus formation in *O. mossambicus* in Mnjoli Dam, Swaziland, occurred during November and December at the onset of summer rains (Booth & Khumalo, 2010). Annulus formation in these cases was asynchronous with flooding and was thought to occur as a result of increased reproductive activity during this time (Booth & Khumalo, 2010; Booth & Merron, 1996; Booth et al., 1995; Dudley, 1974). In Lake Chicamba, annulus formation in *O. mossambicus* and *T. rendalli* occurred in July and August at the end of winter when water temperatures were at their lowest and the lake was in the drawdown phase (Weyl & Hecht, 1998). Annulus formation in *O. mossambicus* from the Shire River floodplain occurred mainly during July and August, coinciding with low temperatures and the drawdown of the floodplain (Chimatiro, 2004).

From the above studies, it can be seen that growth zones were either formed as a result of spawning activity or low winter temperatures. In some cases, two growth zones can form in a single year as a result of both of these factors. The deposition of two growth zones in a year has been observed in several fish populations in southern Africa. Hecht (1980) observed biannual growth zone deposition in *O. mossambicus* in South Africa, with one deposition in winter when temperatures were low and a second during the spawning season. Biannual growth zone deposition has also been observed by Weyl and Booth (1999) and Winker, Weyl, Booth, and Ellender (2010) in the cyprinids *Labeo cylindricus* in Lake Chicamba and *Cyprinus carpio* in Lake Gariep respectively. Dudley (1974) found that older *O. andersonii*, *O. macrochir* and *T. rendalli* from the Kafue floodplain formed annuli later than younger fish. Annulus formation in *O. mossambicus* from the Shire River floodplain occurred from May right through to October (Chimatiro, 2004). The results of Chimatiro (2004) and Dudley (1974) suggest that both low winter temperatures and the early spawning season overlap slightly so that a single, large opaque zone is formed over a longer period in mature fishes, rather than two separate opaque zones such as those observed by Hecht (1980) in a more temperate region. Validation of the periodicity of growth zone deposition is particularly important for understanding the life history of species in different geographical localities because the timing and number of growth zone depositions can vary widely between populations of conspecifics (Winker et al., 2010).

Validation

Although several ageing studies on cichlids have been carried out, few of these studies validated the periodicity of growth zone formation. Those that did validate growth zone formation did so using a technique known as edge analysis. This method is one of the most difficult to carry out properly because of difficulties associated with viewing a partial increment affected by variable light refraction (Campana, 2001). It is commonly used because of its low cost and modest sampling requirements (Campana, 2001). Edge analysis is often used to corroborate the results of more reliable age validation methods such as the mark-recapture of chemically-tagged fish (Campana, 2001; Weyl & Booth, 2008; Winker, Ellender, Weyl, & Booth, 2010; Winker et al., 2010). No studies have validated the formation of the first annulus in young of the year cichlids in southern Africa. This is particularly important in populations where annulus formation is thought to occur as a result of increased reproductive activity as annulus formation in juveniles is unlikely to occur at the same time as adults (Campana, 2001).

2.3 GROWTH RATES

Growth of fish in floodplain environments is seasonal, being fastest during the flood season and slowest during the dry season (Welcomme, 2001). Rapid growth during the flood season has been correlated with periods of increased food availability, high temperatures and reduced density-dependant competition, conditions which are reversed during the dry season (Jobling, 1995; Lowe-McConnell, 1987; Welcomme, 2001). Explanations for the seasonal variation in growth are, however, often inconsistent or contradictory between different species and systems (Welcomme, 1985, 2001). In addition to intra-annual variation, fishes often show inter-annual variation in growth in floodplain systems (Dudley, 1974, 1979; Kapetsky, 1974). Growth rates also vary considerably within and between populations of conspecifics and are usually the result of different environmental conditions experienced by individuals or populations (Bokhutlo, 2011; Booth & Merron, 1996; Booth et al., 1995; Oliveira, Ferreira, & Ferreira, 2002; Shephard & Jackson, 2006; Weyl & Hecht, 1998).

Seasonal variation in condition factor may influence growth rates throughout the year. Chimatiro (2004) found that the condition factor of *O. mossambicus* and *C. gariepinus* in the Lower Shire floodplain was significantly related to the flood regime. The condition of *O. mossambicus* was highest during the receding flood in June, while that of *C. gariepinus* was highest during the low-but-rising flood and early peak flood from October to January. The high condition factor of the detritivorous *O. mossambicus* during the receding flood was linked to the increase in food intake during the flood period. The high condition factor of the predatory *C.*

gariepinus during the drawdown period corresponded to increased prey availability as prey species were forced off the floodplain (Chimatiro, 2004). The condition factor of *O. mossambicus* and *T. rendalli* in Lake Chicamba was also highest in June, during the early drawdown period of Lake Chicamba and was attributed to high food availability during flooding in the previous months (Weyl, 1998).

Dudley (1974) found that growth of *O. andersonii*, *O. macrochir* and *T. rendalli* on the Kafue floodplains varied considerably from year to year, which was correlated significantly to flooding, temperature and fish density. Growth of the three cichlid species investigated by Dudley was fastest during years of high floods, possibly related to increased food availability and decreased density-dependant competition (Dudley, 1974). Similarly, Chimatiro (2004) observed an increase in annulus width of *O. mossambicus* and *C. gariepinus* during years of high floods. Dudley (1974) found that fishes grew slower during years with lower dry season temperatures.

The initial growth rate in cichlids is rapid, with many species reaching asymptotic length between 2 and 3 years of age (Booth & Merron, 1996; Booth et al., 1995; Chimatiro, 2004; Weyl & Hecht, 1998). On the Kafue floodplain, Juvenile *O. andersonii*, *O. macrochir* and *T. rendalli* achieved 75 per cent of the expected first year growth within six weeks of the flood peak (Dudley, 1974, 1979). Juvenile *O. andersonii* reached average standard lengths of 168, 106, and 143 mm after one year in Lake Liambezi, the Kafue floodplain and the Okavango Delta respectively (Booth et al., 1995; Kapetsky, 1974; van der Waal, 1985). Juvenile *T. rendalli* reached average standard lengths of 119, 132 and 72 mm after one year in Lake Liambezi, Lake Chicamba and Lake Kariba respectively (Kolding, Tirasin, & Karenge, 1992; Weyl & Hecht, 1998; van der Waal, 1985). Rapid first year growth is thought to allow juvenile fishes to attain a size large enough to avoid intense predation as they move out of the relatively safe floodplain environment and into permanent water bodies during the drawdown phase, and to ensure rapid attainment of sexual maturity to enable reproduction in unstable environments (Booth & Merron, 1996; Booth et al., 1995; Chimatiro, 2004; Weyl & Hecht, 1998). Once maturity is reached, growth rates decrease markedly. This is thought to reflect a change in resource utilisation from somatic growth to reproduction (Booth & Merron, 1996; Booth et al., 1995; Weyl & Hecht, 1998).

Geographic variation in growth rate of cichlids is evident when the results of several previous studies are compared. Booth et al. (1995) and Booth and Merron (1996) compared the growth of *O. andersonii* and *O. macrochir* respectively in several systems within their natural distributions. *Oreochromis andersonii* grew fastest in Lake Liambezi, reaching an average standard length of 315 mm after 5 years compared to 245 mm on the Kafue floodplain and 221 mm in the Okavango Delta (Booth et al., 1995). The maximum ages observed for *O. andersonii* were 8, 10 and 13 years for Lake Liambezi (van der Waal, 1985), the Kafue floodplain (Dudley, 1974) and the Okavango Delta (Booth et al., 1995) respectively. *Oreochromis macrochir* also grew fastest in Lake Liambezi, reaching an average standard length of 277 mm after 5 years compared to 213 mm on the Kafue floodplain and 197 mm in the Okavango Delta (Booth & Merron, 1996). Maximum ages observed for *O. macrochir* were 8, 7 and 11 years for Lake Liambezi (van der Waal, 1985), the

Kafue floodplain (Dudley, 1974) and the Okavango Delta (Booth & Merron, 1996) respectively. However, fishes from the Kafue floodplain and Lake Liambezi were aged using scales, thus ages of larger fish may have been underestimated and growth rates over-emphasised for these populations (Booth & Merron, 1996; Booth et al., 1995). Weyl and Hecht (1998) compared the results of their study on the growth of *T. rendalli* to several previous studies from other water bodies. *Tilapia rendalli* grew fastest in Lake Liambezi, attaining an average standard length of 216 mm after 5 years compared to 211 mm in Lake Kariba and 184 mm in Lake Chicamba (Weyl & Hecht, 1998). The maximum ages observed for *T. rendalli* were 7 and 16 years for Lake Liambezi (van der Waal, 1985) and Lake Chicamba (Weyl & Hecht, 1998) respectively. Fishes from Lake Liambezi were aged using scales as mentioned above, so age may have been underestimated. Chimatiro (2004) compared the growth rate of *O. mossambicus* in various water bodies in southern Africa using an index of growth performance, phi-prime (ϕ') (Pauly & Munro, 1984). The growth rate of *O. mossambicus* was fastest in Lake Chicamba ($\phi' = 4.55$) while growth was the same in the Lower Shire floodplain ($\phi' = 4.14$) and Lake Sibaya ($\phi' = 4.14$) (Chimatiro, 2004). The variation in growth rates and sizes at maturity of cichlids between populations means that an assessment of locality specific life history parameters is necessary for the proper assessment and management of a fishery (Chimatiro, 2004; Weyl & Hecht, 1998).

2.4 REPRODUCTION AND MATURITY

Reproduction is generally timed so that it coincides with a seasonal abundance of food, shelter from predators and optimal abiotic conditions (Wooton, 1990). The reproductive activity of species exhibiting equilibrium or periodic life history strategies is generally greatest just prior to flooding, whereas that of species exhibiting opportunistic life history strategies is generally greatest during peak flooding (Winemiller & Rose, 1992; Zeug & Winemiller, 2007). Reproduction just prior to or during flooding allows juveniles to seek refuge from predators amongst flooded terrestrial vegetation and take advantage of abundant food resources associated with flooding (Welcomme, 1985; Wooton, 1990; Zeug & Winemiller, 2007, 2008).

Cichlids typically begin spawning shortly before flooding occurs as increasing temperature and day length are thought to be the primary reproductive cues (Booth & Khumalo, 2010; Chimatiro, 2004; Dudley, 1974; Merron, 1991; Weyl & Hecht, 1998; Winemiller, 1991; van der Waal, 1985). Gonad development in *O. andersonii*, *O. macrochir* and *T. rendalli* usually begins as early as July with the first ripe individuals being observed in September and spawning in October (Dudley, 1974; Merron, 1991; van der Waal, 1985). Cichlids have an extended spawning season that lasts throughout the warmer summer months from October to April, during which time multiple broods may be raised (Chimatiro, 2004; Dudley, 1974; Merron, 1991; Weyl & Hecht, 1998; van der Waal, 1985).

Length at maturity in cichlids differs significantly between populations as a result of environmental variability in conditions experienced by each population (James & Bruton, 1992; Merron, 1991). Larger sizes at maturity have been observed under favourable environmental conditions, and smaller sizes at maturity have been found in harsher habitats (James & Bruton, 1992; Merron, 1991). Merron (1991) recorded lengths-at-maturity for *O. andersonii* ranging from 105 mm SL to 155 mm SL in perennially and seasonally flooded areas in the Okavango Delta while 50% maturity in Lake Liambezi was attained at 207 mm SL (van der Waal, 1985). *Tilapia rendalli* reached 50 % maturity at 109 mm (SL) in Lake Liambezi (van der Waal, 1985), compared to 171 mm (males) and 161 mm (females) in Lake Chicamba (Weyl & Hecht, 1998), and 184 (males) and 164 (females) in Lake Kariba (Kolding et al., 1992).

2.5 RECRUITMENT AND MORTALITY

Spawning success and recruitment in floodplain-rivers is highly dependent on the hydrological regime which plays an important role in determining mortality rates (Merron, Bruton, & la Hausse de Lalouviere, 1993; Zeug & Winemiller, 2008). Mortality in exploited fish populations is a combination of fishing and natural mortality (Welcomme, 2001). The major factors influencing mortality rates in floodplain river systems include fishing, predation, stranding, disease and adverse abiotic conditions such as temperature extremes and low dissolved oxygen (Welcomme, 1985, 1989). These conditions vary with the flood cycle. During the high water period when conditions for growth are optimal, mortality is assumed to be low (Welcomme, 2001). Juvenile fishes are able to take refuge on the floodplain where they are less vulnerable to predation, and are able to feed on abundant food sources and grow rapidly before the floodwaters recede (Welcomme, 1979). Adverse conditions intensify during the drawdown phase and with the onset of the low water phase, during which fishes become concentrated in the main river channels and permanent floodplain lagoons (Welcomme, 1985, 1989). During the dry season, fishes become more vulnerable to capture by both fisherman and predators (Welcomme, 2001). Density dependant competition is increased during the dry season and food may become limiting, resulting in reduced growth rates (Ward, Webster, & Hart, 2006). During extreme dry seasons both fishing and natural mortality are likely to be higher as fishes become more densely congregated in smaller water bodies.

CHAPTER 3

Study area and methodology

3.1 STUDY AREA

The study was conducted in the Kavango and Caprivi Regions in north-eastern Namibia. Research was carried out on four major aquatic systems in the region, namely the Kavango, Kwando, Lake Liambezi and Zambezi Rivers (Figure 3.1).

The Kavango and Caprivi Regions

Namibia is one of the most arid countries in Africa with an average annual rainfall of less than 250 mm and a mean annual evaporation as high as 2500 mm in some regions (Mendelsohn, Jarvis, Roberts, & Robertson, 2002) . The rainfall may be characterised as tropical semi-humid in the north-east to hyper-arid in the west (Mendelsohn et al., 2002). The Kavango and Caprivi Regions in north-eastern Namibia have the highest annual rainfall in the country. The region is bordered by Angola in the north, Zambia in the north and east, Zimbabwe in the south-east and Botswana in the south. The region has a very flat topography with elevations ranging from approximately 1300 m in western Kavango to 930 m in eastern Caprivi (Mendelsohn & Roberts, 1997; Mendelsohn & el Obeid, 2003).

Hydrology

The area is home to three large perennial rivers, namely the Kavango, Kwando and Zambezi Rivers (Figure 3.1). Rainfall in the upper catchments of the Kavango and

Kwando Rivers averages 1200 mm and gradually decreases to between 500 and 600 mm at Rundu and Kongola and to 450 mm at Maun on the southern edge of the Okavango Delta (Mendelsohn & el Obeid, 2004). Rainfall in the Zambezi catchment decreases from 1400 mm at the source to 930 mm on the central Barotse floodplains (Kampata, Parida, & Moalafhi, 2008), and 680 mm at Katima Mulilo (Mendelsohn & Roberts, 1997). Rainfall in the catchments is seasonal, with the majority of rain falling in the summer months between November and April (Kampata et al., 2008; Mendelsohn & Roberts, 1997; Mendelsohn & el Obeid, 2003).

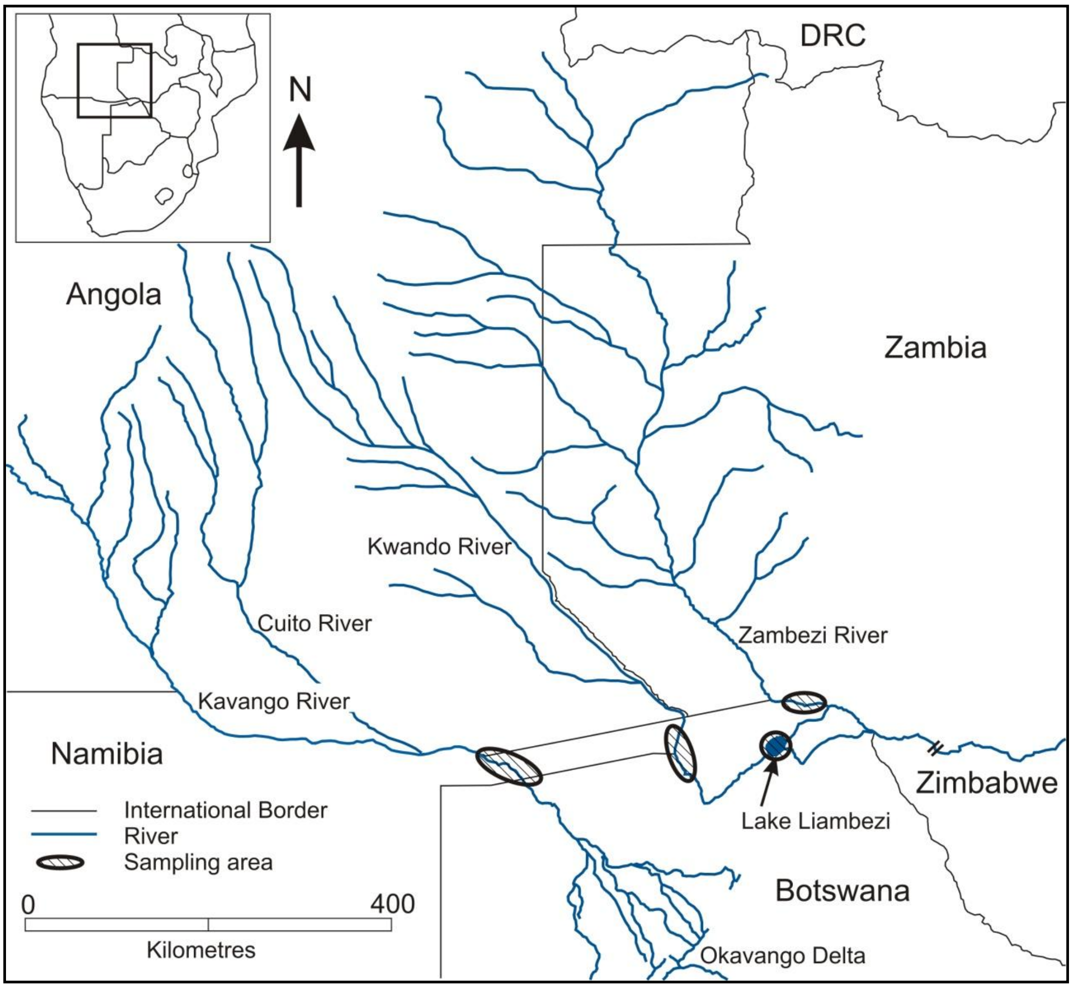

Figure 3.1. A map of the major rivers showing the sampling areas on each in north-eastern Namibia.

The Kavango River

The Kavango River rises on the southern slopes of the Angolan highlands and has a total catchment of approximately 156 000 km^2 before reaching the Okavango Delta (Mendelsohn & el Obeid, 2004). From the Angolan highlands the Kavango flows in a south-easterly direction to the Namibian border where it turns eastward to form the border between the two countries (Figure 3.1). The Cuito River, a major northern tributary, which also rises in the Angolan highlands, joins the Kavango River on the Namibian border before it turns south-east and flows across the Caprivi Strip into Botswana (Figure 3.1). The Cuito River and its tributaries accounts for approximately 40 per cent of the total annual flow into the delta (Mendelsohn & el Obeid, 2004). The seasonal Omatako River is the only noteworthy southern tributary. The Kavango River enters Botswana in the north and meanders along a broad floodplain known as the “panhandle” before branching out into the Okavango Delta (Figure 3.1).

Physical characteristics

Along its course, the Kavango River changes markedly. As it forms the Angola-Namibia border and between Rundu and the Cuito confluence, the river flows along a well defined, but shallow valley. It is characterised by a relatively fast-flowing channel with rocky substrate (Hay et al., 2000; Mendelsohn & el Obeid, 2004). Before reaching Rundu, the river flows over sandy substrates along a wide floodplain valley through which it meanders and forms numerous backwaters and lagoons lined by dense reeds (Mendelsohn & el Obeid, 2004). Broad floodplains form at the Cuito confluence before the river resumes its flows along a well defined valley

(Mendelsohn & el Obeid, 2004). The river flows over a large series of rapids and small waterfalls between Mukwe and Divundu and at Popa Falls, shortly after which it meanders and spreads out to form the panhandle, the uppermost reach of the Okavango Delta (Mendelsohn & el Obeid, 2004).

Figure 3.2. Habitat types in the Kavango River, (a) extensive floodplains at peak flood, (b) a small backwater (c) mainstream during rising water and (d) floodplain channel during drawdown.

The river is lined by dense reeds for much of its length, except where people have cleared marginal vegetation, most notable along the southern bank where population densities are higher in Namibia compared to Angola (Mendelsohn & el Obeid, 2004). Numerous small trees and shrubs line the bank of the river where it flows through well defined valleys. Floodplain vegetation is made up of short terrestrial grasses and occasional trees and shrubs which eventually give way to dense reed beds lining the panhandle (Mendelsohn & el Obeid, 2004).

The Kwando River

The Kwando River rises on the south-eastern slopes of the Angolan highlands and has a catchment area of approximately 57 000 km^2 (Mendelsohn & Roberts, 1997). The river flows in a south-easterly direction and enters the Silowana plains which later form the border between Angola and Zambia. The river enters Namibia where the three countries meet and flows across the Caprivi Strip to form the border between Namibia and Botswana. The River then flows into the Linyanti Swamps on the border between Namibia and Botswana which are drained by the Linyanti Channels which flow eastward into Lake Liambezi (Figure 3.1).

Physical characteristics

The Silowana floodplains have an enormous storage capacity and, hence, have a significant impact on the flow of the Kwando River in Namibia. These floodplains delay the peak flood at the northern border of the Caprivi till July and the Linyanti Swamps further delay the peak floods arrival at Lake Liambezi till September (van der Waal & Skelton, 1984). The Linyanti Channels stopped feeding Lake Liambezi in 1982 because of poor rainfall in the Kwando River catchment and only began flowing again in 2001(Næsje et al., 2004).

The Kwando River has a broad range of habitats including a main channel, small side streams, backwaters, lagoons and extensive floodplains (Figure 3.3). The main channel is slow-flowing and meanders extensively. During high floods broad floodplains form on the Silowana plains, in the Linyanti swamps and along the Linyanti channels. Deep isolated backwaters are common during low water. The substrate of the main channel is mostly sandy with few rocky habitats. Backwaters and lagoons usually have muddy substrates with large quantities of vegetative detritus. Floodplains are mostly sandy with few areas of muddy substrate, and also have large quantities of vegetative detritus.

All channels have plentiful marginal vegetation consisting mainly of reeds and grasses, as well as small trees and shrubs. The slow flow of the main channel makes it possible for plants to fasten themselves to the substrate. Backwaters and lagoons are well vegetated and contain submerged aquatic weeds, lilies, reeds and grasses.

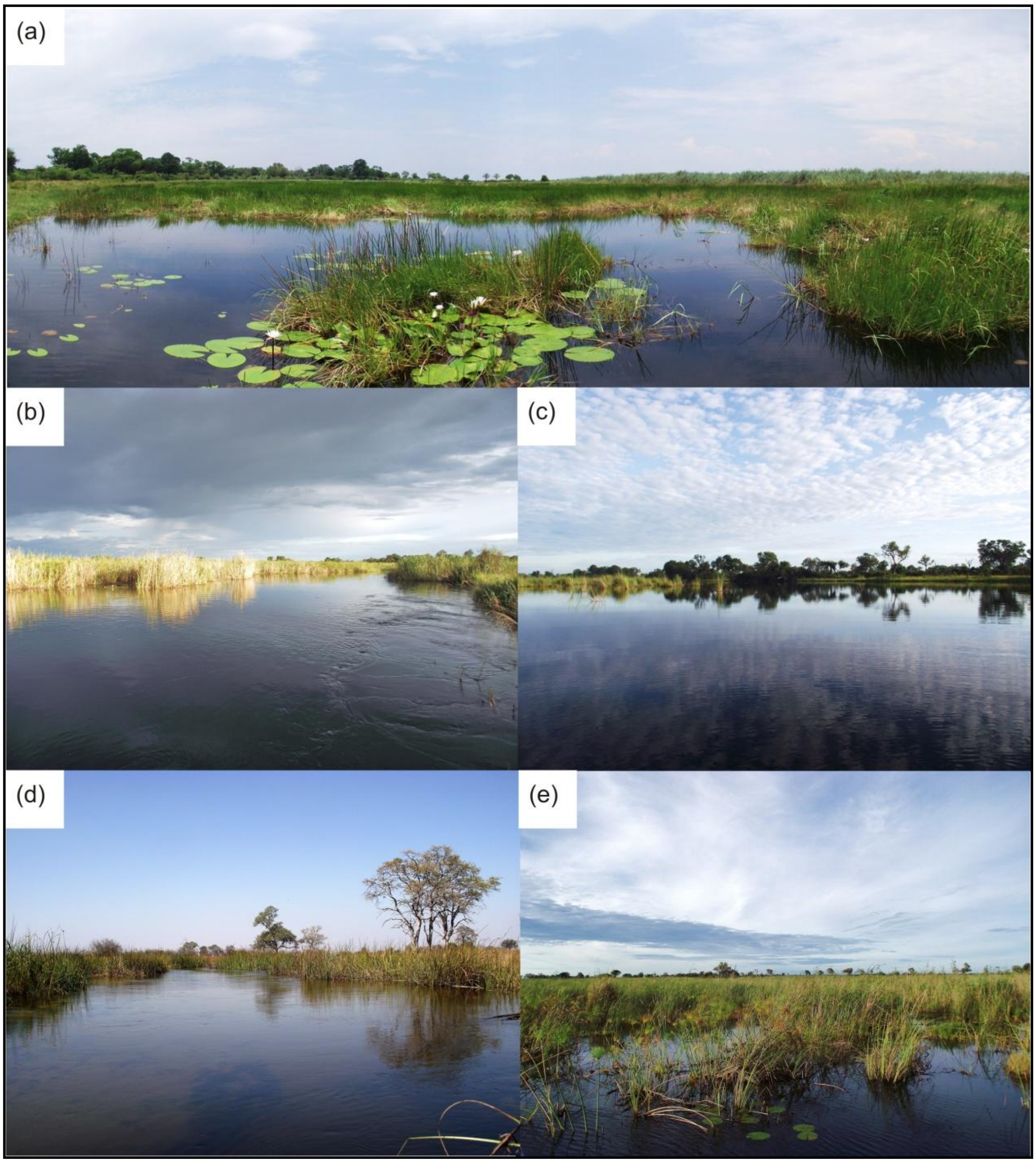

Figure 3.3. Habitat types in the Kwando River, (a) densely vegetated floodplains, (b) mainstream, (c) a large open backwater, (d) side channel and (e) swamp.

The Upper Zambezi and Chobe Rivers

The Zambezi River rises in north-western Zambia and has a total catchment area of approximately 1 200 000 km^2 (Hughes & Hughes, 1992). From its source it flows westward into eastern Angola where it slowly changes course and begins to flow in a south-easterly direction back into Zambia (Figure 3.1). The river forms the border between Zambia and Namibia for approximately 120 km from Katima Mulilo to Impalila Island at the Chobe/Zambezi junction (Hay et al., 2002), after which it forms the border between Zambia and Zimbabwe. The southern limit of the Upper Zambezi drainage is marked by the Victoria Falls.

Physical characteristics

The Zambezi River has a diverse range of habitats including a deep, wide mainstream with many small vegetated islands and sandbanks, small side streams, backwaters, lagoons and floodplains (Figure 3.4). There are several large side channels, the Kalimbeza, Kasai and Bukalo Channels and a perennial lake, Lake Lisikili (Hay et al., 2002). There are two sets of rapids on the length of river bordering Namibia, the first at Katima Mulio and the second, the Mambova Falls at Impalila Island (Hay et al., 2002). The substrate of the main river channel and associated side channels is predominantly sandy. Areas where the water velocity is reduced such as backwaters, lagoons and floodplains usually have muddy substrates with large amounts of vegetative detritus.

The main river channel and large side channel habitats are characterised by abundant marginal vegetation made up of overhanging or fallen trees, shrubs and grasses and reeds. There is little submerged aquatic vegetation in the main channel as it is not possible for plants to anchor themselves on the constantly shifting sandy substrate (Hay et al., 2002). Aquatic vegetation in backwaters and lagoons is abundant and consists of submerged weed beds, floating weeds, lilies, reeds and aquatic grasses.

Floodplain vegetation consists mainly of submerged terrestrial grasses, reeds and occasional trees and shrubs. An extensive swamp-like floodplain is formed near the Zambezi/Chobe junction, and vegetation in this area is comprised mainly of dense impenetrable reeds and papyrus.

The Chobe River extends from Lake Liambezi in the west, along the Botswana border to the Zambezi River at Impalila Island (Figure 3.1). The river consists of a narrow channel near Lake Liambezi, which rapidly becomes an extensive shallow floodplain above the border town of Ngoma. Nearer its confluence with the Zambezi River, the river becomes wider and deeper with extensive swamp-like floodplains on the northern border with Namibia and narrow floodplains in Botswana. The substrate of the river channel is predominantly sandy, with muddy backwaters and floodplains.

The direction of water flow in the Chobe River changes seasonally, depending on floodwater levels in the Zambezi (Hay et al., 2002). Under normal conditions, the Chobe River flows from Lake Liambezi when full, eastwards to the Zambezi River. During high floods in the Zambezi River, usually from February to May, the Zambezi River backs up the Chobe River, occasionally as far as Lake Liambezi, supplying Lake Liambezi with water (Hay et al., 2002). When Lake Liambezi has had little inflow from the Kwando/Linyanti, and the Zambezi River does not back up as far as Lake Liambezi, the Chobe River simply forms a large backwater to the Zambezi River.

Figure 3.4. Habitat types in the Zambezi River, (a) main channel, (b) side channel, (c) backwater, (d) Chobe floodplain and (e) rapids at Impalila Island.

Lake Liambezi

Lake Liambezi is an ephemeral lake situated on the Namibia/Botswana border between the Linyanti Channels in the west and the Chobe River in the east (Figure

3.1). Lake Liambezi formed an important part of the fishery of the eastern Caprivi until it dried up in 1985 (Hay et al., 2002; van der Waal, 1980). The nutrient rich sediments in the lake bed meant it was important for crop and livestock farming when dry. The lake was partially filled each year from 2001 to 2007 and was completely filled in 2008 (C. J. Hay, pers. comm.). Once again, the fishery in Lake Liambezi is very important, with the majority of the catch being transported to and sold on the open market in Katima Mulilo.

In 1975 the lake covered an area of approximately 300 km^2, of which 101 km^2 was open water (Seaman, Scott, Walmsley, van der Waal, & Toerien, 1978). The lake is fed by the Kwando-Linyanti River from the west and by the Zambezi River via the Chobe River and Bukalo Channel from the south-east and east (van der Waal, 1976). The hydrology of the lake is complex, with two distinct flood peaks during years of high floods in the Zambezi and Kwando Rivers. The first flood occurs between March and May as a result of inflow from the Zambezi at its flood peak via the Chobe River and Bukalo Channel (van der Waal, 1976). The second flood occurs between August and September as a result of inflow from the Kwando-Linyanti River whose flood waters are delayed by the reservoir like properties of the Silowana floodplains and by the Linyanti Swamp (van der Waal, 1976; van der Waal & Skelton, 1984). Outflow from the lake via the Chobe River is intermittent and depends on lake level and the direction of flow of the Chobe River (Seaman et al., 1978).

Physical characteristics

The lake has retained many of its physical features from before it dried up in 1985. It is shallow (< 5 m) and the depth fairly constant in open water (Seaman et al., 1978). There is extensive reed growth throughout the lake in areas less than three meters deep, especially in the south-west where vast, dense reed beds border the open water (Seaman et al., 1978). In sheltered areas there are dense beds of submerged macrophytes. The substrate of the lake is characterised by abundant detritus overlaying a thick layer of peat and occasional small patches of open sand close to the shore in the north-east and south-east of the lake.

Figure 3.5. Habitat types in Lake Liambezi, (a) open water with reeds, (b) dense macrophyte beds, (c) flooded marginal grasses and (d) open water.

Flood regimes

Flooding is predictable in the Kavango, Kwando and Zambezi Rivers in that it occurs annually, but the timing, magnitude, duration and number of flood peaks varies between systems and from year to year depending on rainfall in the catchment areas. Flooding in Lake Liambezi is dependent on inflow from the Zambezi River via the Bukalo Channel and Chobe River and from the Kwando River via the Linyanti Channels during years of exceptionally high floods. Available water level data for the Kavango River, Lake Liambezi and the Zambezi River are summarised in Figure 3.6.

Water quality

Temperature and secchi depth readings were taken at each experimental gillnet site on a bi-monthly basis in the four systems between August 2010 and July 2011 (see maps in Figures 3.9, 3.10, 3.11, 3.12, 3.13). The average annual surface water temperatures during the study period for the Kavango, Kwando, Lake Liambezi and Zambezi Rivers were 22.4 °C, 22.8 °C, 23.2 °C and 23.2 °C respectively (Figure 3.7). Temperatures ranged between 16.6 °C and 29.4 °C in the Kavango River, 16.1 °C and 28.2 °C in the Kwando River, 16.7 °C and 28.0 °C in Lake Liambezi and 17.7 °C and 28.3 °C in the Zambezi River (Figure 3.7).

Only secchi depth readings taken in backwaters in the Kwando River were used as transparency in the main channel was always greater than the maximum depth of 6 m. The average secchi depth readings during the study period in the Kavango, Kwando, Lake Liambezi and Zambezi Rivers were 2.0 m, 2.1 m, 1.6 m and 1.8 m respectively. Secchi depth readings ranged between 0.3 m and 3.5 m in the Kavango River, 1.2 m and > 6.0 m in the Kwando River, 0.5 m and 2.3 m in Lake Liambezi and 0.7 and 3.2 m in the Zambezi River.

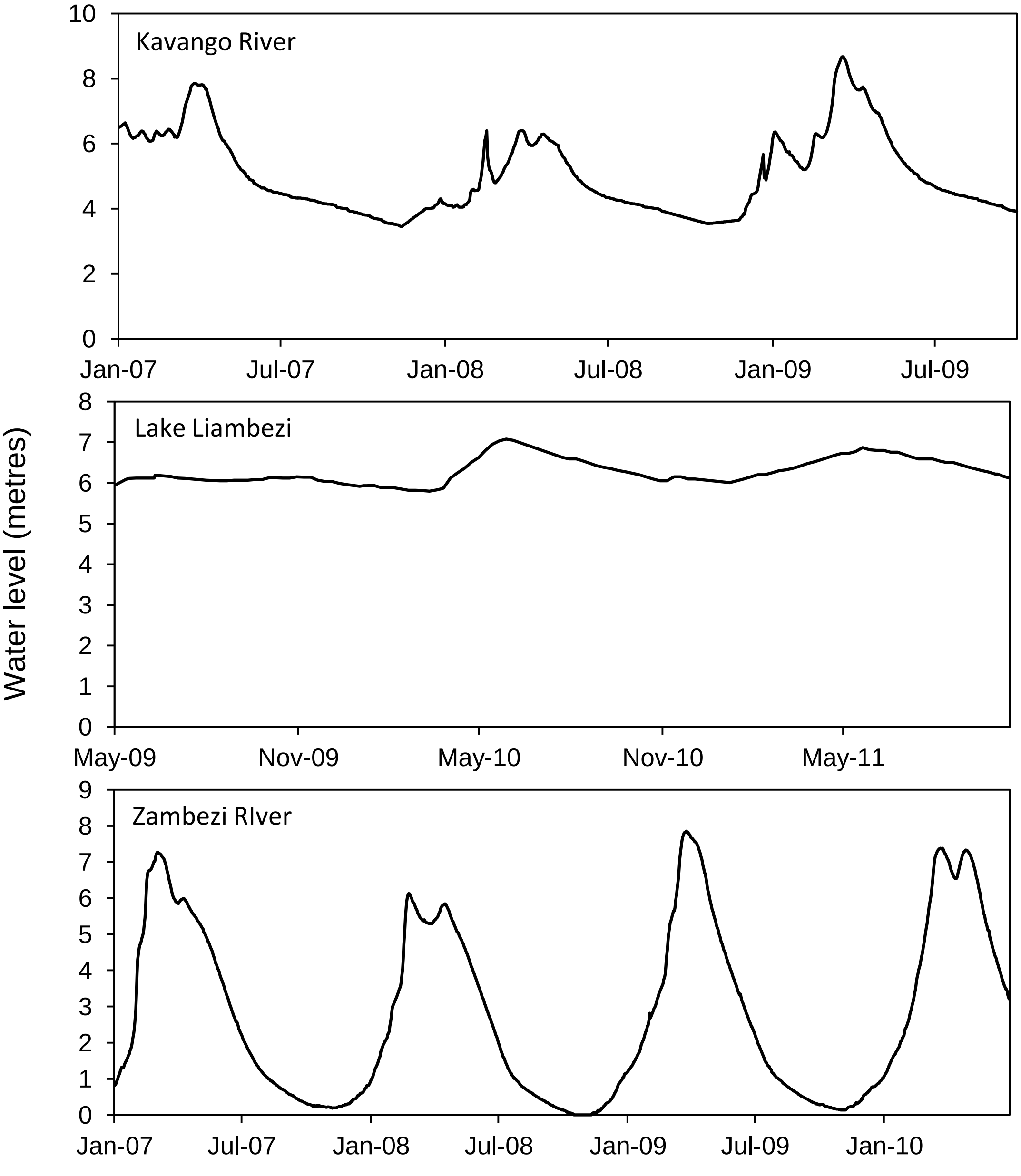

Figure 3.6. Water levels for the Kavango River at Rundu, Lake Liambezi at Muyako and the Zambezi River at Katima Mulilo. River level data were obtained from the Ministry of Agriculture Water and Forestry. Lake Liambezi data were obtained from the Namibia Nature Foundation, Zambezi/Chobe Transboundary Fisheries Resource Management Project. Kwando River level data were not monitored.

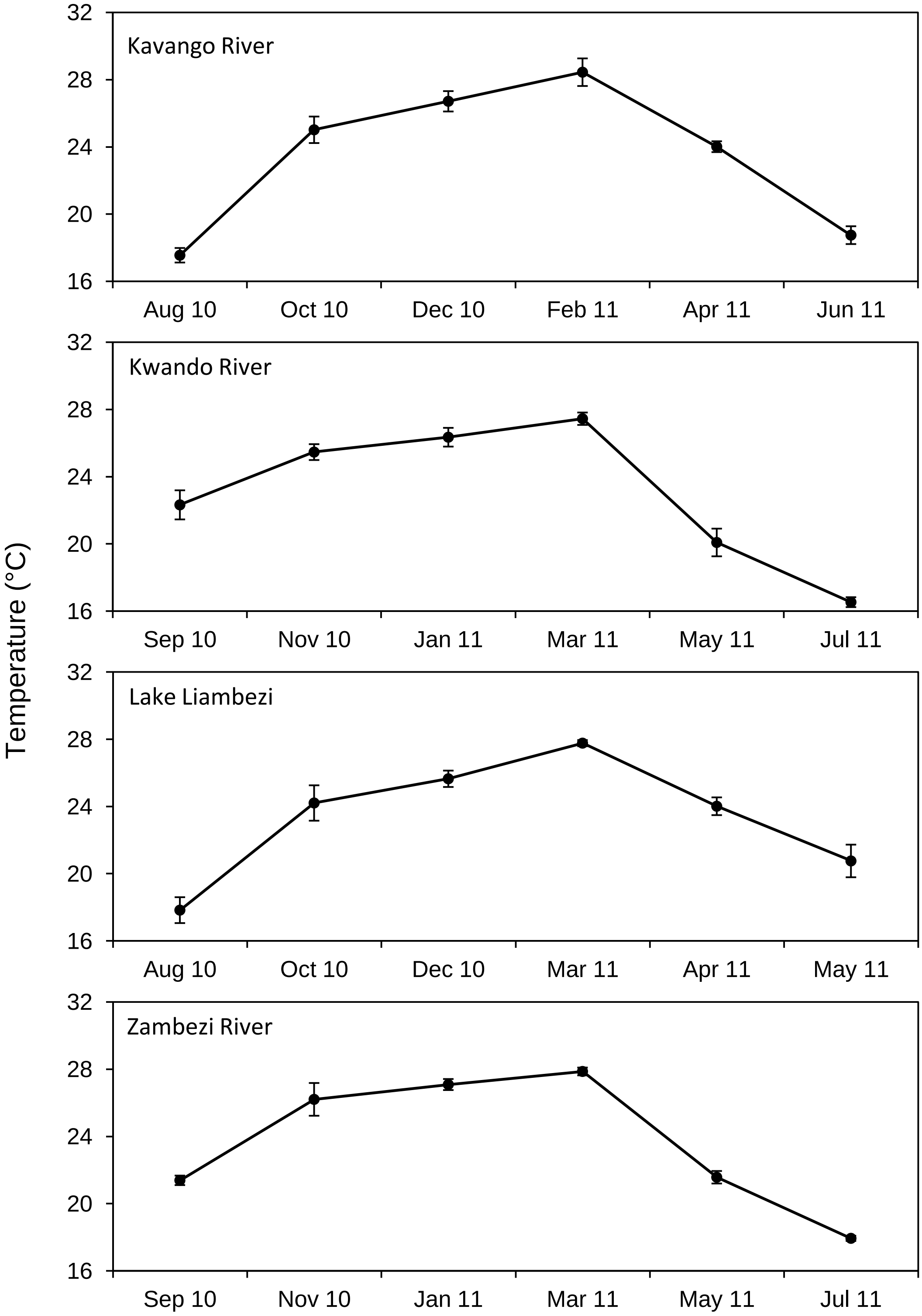

Figure 3.7. Mean (± standard deviation) bi-monthly temperature readings from the Kavango, Kwando, Lake Liambezi and Zambezi Rivers, Namibia.

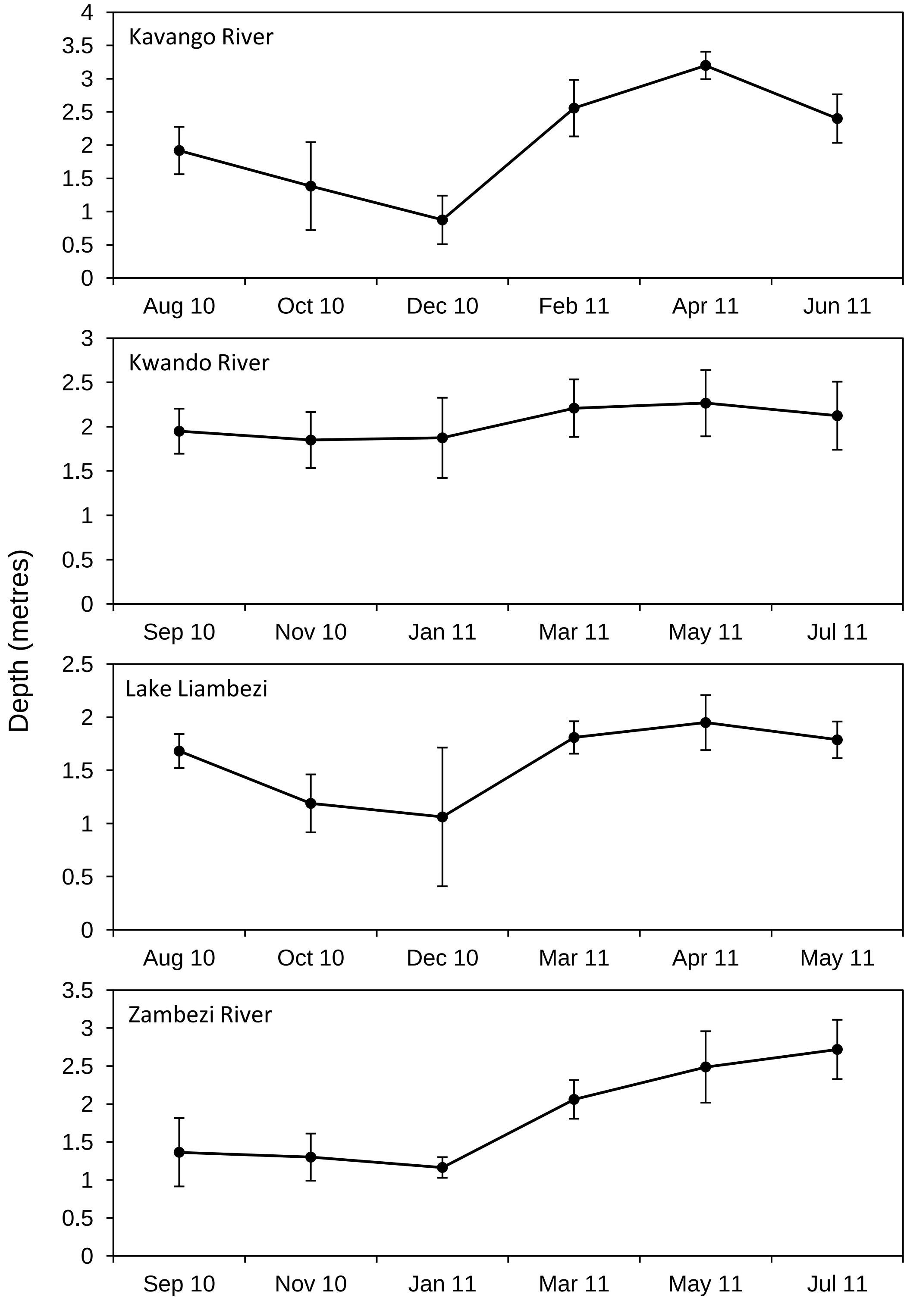

Figure 3.8. Mean (± standard deviation) bi-monthly secchi depth readings from the Kavango, Kwando, Lake Liambezi and Zambezi Rivers. Kwando River backwaters only, main channel secchi depth was > 6 m.

Secchi depth readings varied most in the Kavango and Zambezi Rivers where water level fluctuations were greatest, and varied least in the Kwando River. Depths were greatest in winter after the flood peaks and least in summer at the end of the drawdown period. Mean conductivity was 60 µS.cm^{-1} in the Kavango River, 85 µS.cm^{-1} in the Kwando River, 120 µS.cm^{-1} in Lake Liambezi and 90 µS.cm^{-1} in the Zambezi River.

Sampling stations

The sampling stations chosen fell within the areas sampled annually by the Ministry of Fisheries and Marine Resources (MFMR) during their long-term monitoring programmes in the Kavango and Caprivi Regions. The first survey conducted on the Kavango River in collaboration with the MFMR was extensive, sampling along the entire course of the river in Namibia, from Nkurenkuru in the north-west to Mohembo in the south-east. Because of logistical and time constraints in sampling numerous stations along the course of the river, subsequent sampling trips were restricted to Kwetche. Kwetche (18°13’S, 21°45’E), lies within the Bwabwata National Park, between the Mahango and Buffalo core areas on the border with Botswana. The area is protected and levels of exploitation are very low. The sampling area is illustrated and gillnet sampling sites during high and low water periods are shown in Figure 3.9.

The Kwando River was sampled at two stations, namely Nakatwa and Susuwe. Nakatwa (18°10’S, 23°25’E) is an extensive swamp like system with numerous large open lagoons, fed by a single narrow channel from the main river. Susuwe (17°44’S, 23°21’E) is on the main river and has many backwaters and large floodplain areas. Both areas lie within protected areas where levels of exploitation are very low. Nakatwa lies within Mudumu National Park and Susuwe in the Bwabwata National Park (Susuwe core area). Susuwe did not form part of the MFMR monitoring programme but was included because of its extensive riverine habitat and large floodplains. Nakatwa and Susuwe sampling areas are illustrated in Figures 3.10 and 3.11 and gillnet sampling sites are shown.

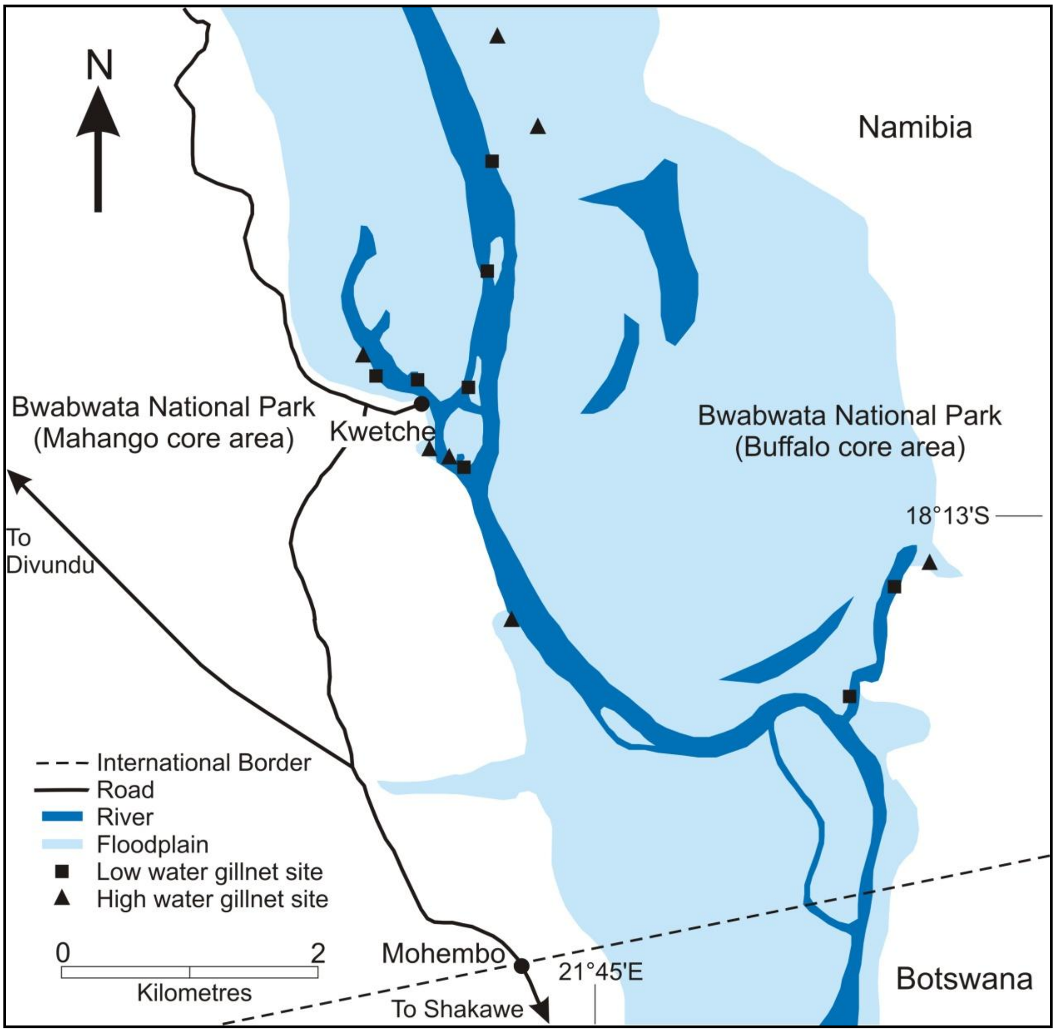

Figure 3.9. A map of Kwetche, the study area on the Kavango River, Namibia, showing gillnet sampling sites.

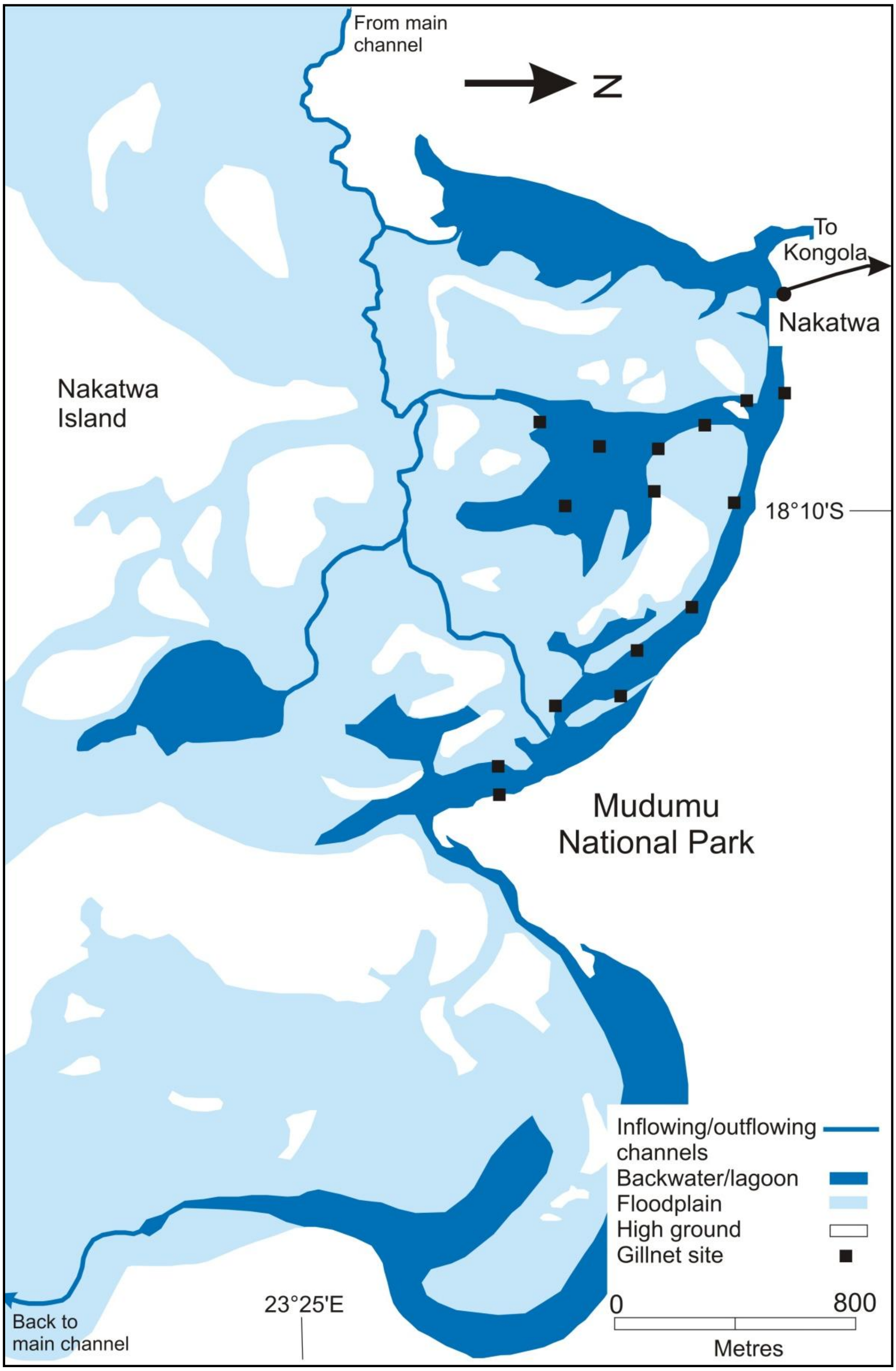

Figure 3.10. A map of Nakatwa on the Kwando River, Namibia, showing gillnet sampling sites.

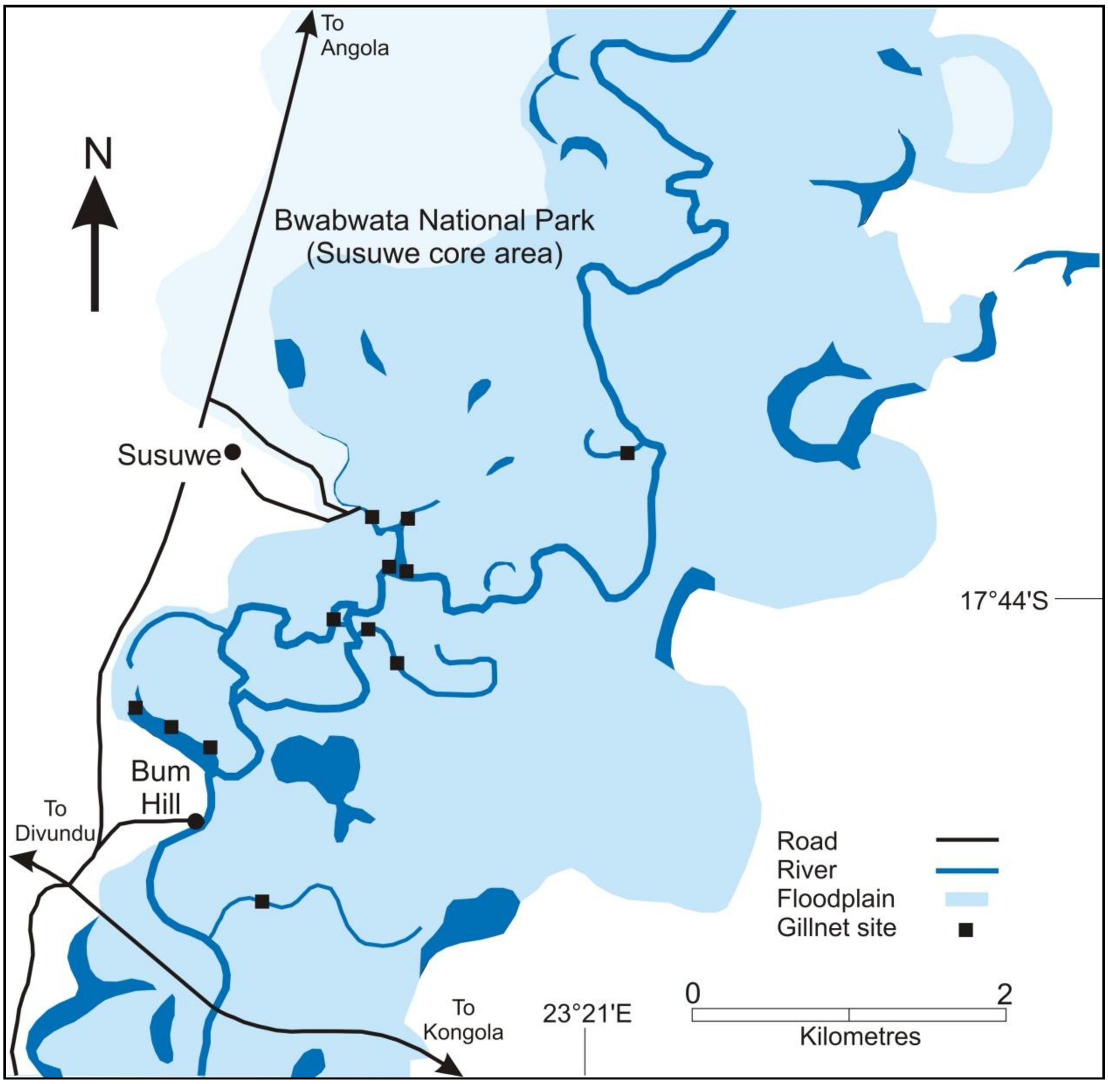

Figure 3.11. A map of Susuwe on the Kwando River, Namibia, showing gillnet sampling sites.

Lake Liambezi (17°53'S, 24°17'E) was sampled from Muyako on the south-east shore of the Lake (Figure 3.12). Muyako is one of the few areas where there is easy access to the lake shore and is also close to the major fish landing site of Shamahuka. Gillnet sampling sites in the lake are shown in Figure 3.12.

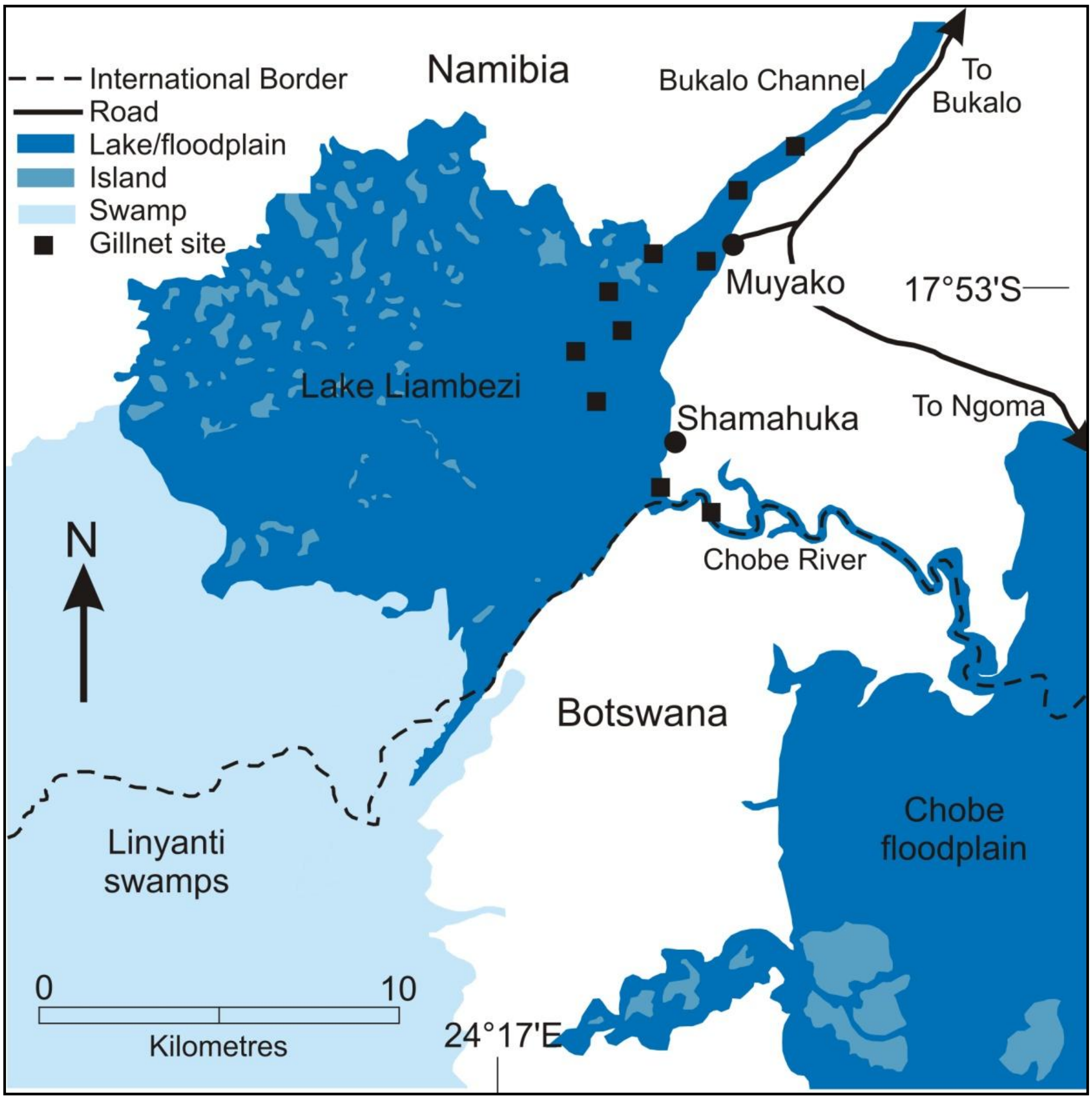

Figure 3.12. A map of Lake Liambezi, Namibia, showing gillnet sampling sites.

The Zambezi was sampled at Kalimbeza. Kalimbeza (17°31’S, 24°32’E) is a large side channel of the Zambezi with numerous large backwaters and extensive floodplain areas (Figure 3.13). A single extensive survey was carried out in collaboration with the MFMR in May/June 2011, sampling areas from Katima Mulio to Kalimbeza and Lake Lisikili on the Zambezi River and from Ngoma to Impalila Island at the Zambezi/Chobe confluence on the Chobe River.

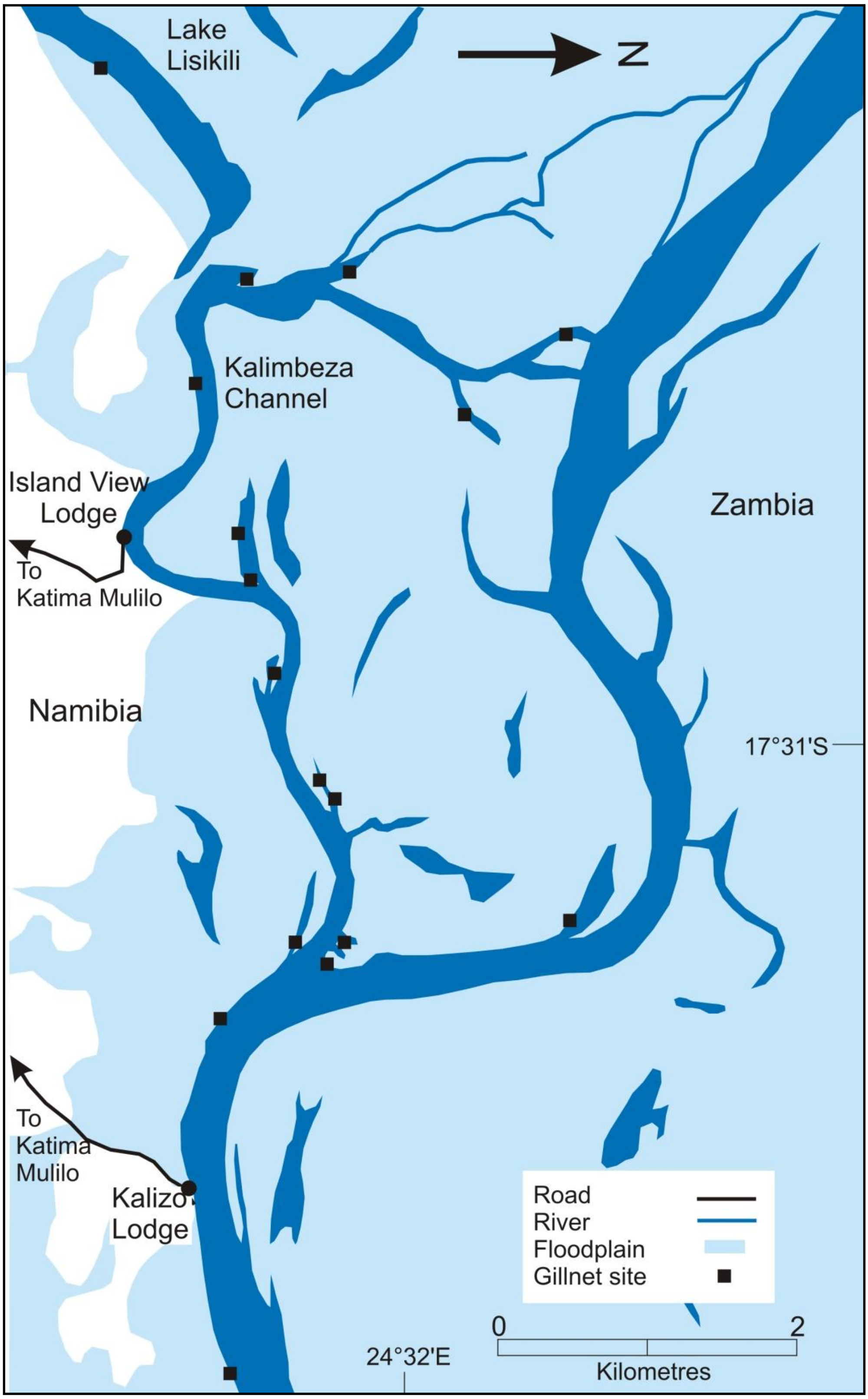

Figure 3.13. A map of Kalimbeza, the study area on the Zambezi River, Namibia, showing gillnet sampling sites.

3.2 SAMPLING METHODS

Fish community data used in this study were obtained by experimental gillnetting and biological data were obtained by experimental gillnetting, monofilament gillnetting, seine netting, purchases from fishermen, at angling competitions and occasional angling during field trips (see Chapter 5).

Experimental gillnetting

Experimental gillnetting was carried out bi-monthly on the Kavango, Kwando, Lake Liambezi and Zambezi Rivers between August 2010 and July 2011. Gillnets were made of six ply, brown multifilament nylon with manufacturer-quoted stretch mesh sizes of 12, 16, 22, 28, 35, 45, 57, 73, 93, 118 and 150 mm. Each fleet was 110 m long by 2.5 m deep and consisted of eleven randomly distributed 10 m mesh panels. Gill nets were surface set between 17:00 and 19:00 in the evening and retrieved between 06:00 and 08:00 the following morning. Nets were set in a variety of habitats to ensure that a representative sample of the fish fauna in the rivers was collected.

All fishes caught were identified to species level, except where identification was in doubt, measured to the nearest millimetre total length (TL) or fork length (FL) depending on the species, and weighted to the nearest gram.

All *O. andersonii*, *O. macrochir* and *T. rendalli* were dissected, sexed and the stage of maturity determined macroscopically according to the criteria outlined in Weyl and Hecht (1998) (Table 5.2, Chapter 5). Ovaries of mature females were removed and weighed to the nearest 0.1 g and the eviscerated mass was measured to the nearest g. Sagittal otoliths were removed and stored in Eppendorf tubes for later age estimation. Specific methods will be addressed where appropriate in the following chapters.

Figure 3.14. Experimental gillnet catches in Lake Liambezi (a and b) and in the Kwando River (c), setting gillnets in the Kwando River (d) gillnet catch in the Kavango River (e) and a typical gillnet setting in a backwater of the Zambezi River (f).

CHAPTER 4

Gillnet catch composition and abundance of *Oreochromis andersonii*, *Oreochromis macrochir* and *Tilapia rendalli* in the Kavango, Kwando, Lake Liambezi and Zambezi Rivers in Namibia

4.1 INTRODUCTION

The Kavango and Caprivi Regions of north-eastern Namibia fall within the Upper Zambezi region of the ‘Zambezian’ ichthyofaunal province (Roberts, 1975). The Upper Zambezi region comprises the Zambezi River upstream from Victoria Falls, the Kavango, Kwando, Kafue and Cunene Rivers (Roberts, 1975). Fish species diversity within the region is high, although many species are shared between the river systems (Tweddle et al., 2004). Harvesting of the diverse fish resources in the Kavango and Caprivi Regions is carried out using a number of traditional and modern gears, but the fishery is dominated by gillnets (van der Waal, 1980, 1990, 1991). Large cichlids of the genera *Oreochromis*, *Tilapia*, *Serranochromis* and *Sargochromis* are the major target species of the gillnet fishery (van der Waal, 1980, 1990, 1991).

Increasing pressure is being placed on the fish resources in the region by growing human populations. In recent years, the fisheries on the Zambezi River and Lake Liambezi have seen increasing commercialisation and the introduction of effective modern fishing gears in the form of monofilament gillnets (Abbott, 2001; Tvedten, 2002; Tweddle, 2009). Fisheries on the Kavango and Kwando Rivers have remained largely subsistence, but differences in the size and abundance of fishes between exploited and unexploited areas of the Kavango River have been reported (Hay et al., 2000).

With increasing fishing pressure, fish populations go through a series of changes in size, species composition and abundance (Allan et al., 2005; Turner, Tweddle, & Makwinja, 1995; Tweddle, Turner, & Seisay, 1995; Welcomme, 2001). This is because multi-species fisheries initially target the few largest or most valuable species in a fish community (Welcomme, 2001). As larger individuals and species are removed there is a decline in the average size of fish in the population (Welcomme, 1999). Fishermen adapt to the decrease in average fish size by reducing their mesh sizes (Jul-Larsen et al., 2003; Karenge & Kolding, 1995a; Welcomme, 1999), which is accompanied by an increase in the number of species caught in a multi-species fishery (Allan et al., 2005; Jul-Larsen et al., 2003; Welcomme, 1999). This process is known as “fishing down the food web” and involves the successive removal of the larger fish from an assemblage and their replacement in catches by smaller species from lower trophic levels (Allan et al., 2005; Pauly, Christensen, Dalsgaard, Froese, & Torres, 1998; Regier & Loftus, 1972). Changes in fish communities may as a consequence alter the biotic interactions between species. For example the removal of predators results in reduced predation and reduced population sizes result in reductions in density dependent competition (Allan et al., 2005; Chapin et al., 2000; Hooper et al., 2005).

Biotic interactions such as predation and competition can affect the growth and life history of a species (Jackson, Peres-Neto, & Olden, 2001; Ward et al., 2006). Prey species tend to congregate in habitats offering better refuge from predators (Jackson et al., 2001). This congregation may lead to increased inter and intraspecific competition for food resources in the restricted area (Jackson et al., 2001; Ward et al., 2006). The result of increased competition may be a reduction in the quality of diets and therefore, reduced growth rates, smaller size at maturity, reduced fecundity and increased mortality (Jackson et al., 2001). To understand differences in growth and life history of *O. andersonii*, *O. macrochir* and *T. rendalli* between systems one needs to understand both the physical environment and biotic environment.

The aim of this chapter is to assess the differences in the biotic environment between the Kavango, Kwando, Lake Liambezi and the Zambezi Rivers by investigating the species composition, diversity and relative abundance of fish communities caught in experimental gillnets, and to provide baseline information on the relative abundance and gillnet selectivity of *O. andersonii*, *O. macrochir* and *T. rendalli*.

4.2 MATERIALS AND METHODS

General sampling

Fishes were sampled using multi-meshed gillnet fleets as described in Chapter 3, and were identified to species level, except where identification was in doubt, measured to the nearest millimetre total length (TL) or fork length (FL) depending on the species and weighed to the nearest gram. Where one species was particularly numerous in a single mesh size, a sub-sample were measured and weighed individually and the remainder counted and weighed collectively. Except for the easily distinguishable *Synodontis nigromaculatus*, members of the *Synodontis* spp. group (6 species) are pooled because of taxonomic uncertainties.

Catch composition

Indices used to quantify biological diversity can be used to monitor changes in fish assemblages and to infer a measure of the health of the systems by comparing results of this study to previous literature and between river systems. The index of relative importance (IRI) has been used to describe the species composition of experimental gillnet catches in previous studies in the area by Hay et al. (2000), Næsje et al. (2004) and Hay et al. (2002) on the Kavango, Kwando and Zambezi Rivers respectively. The IRI was used to determine the most important species in gillnet catches by number, weight and frequency of occurrence, and was calculated as:

$$\mathrm{IRI} = (\%\mathrm{N} + \%\mathrm{W})\mathrm{x}(\%\mathrm{FO})$$

where %N and %W are percentage contribution of each species by number and by weight to the total catch of each system and %FO is the percentage frequency of occurrence of each species in the total number of net settings.

Species diversity

Species diversity can be broken into two components of species richness and species evenness. The Shannon-Wiener index of diversity is a measure of species richness, weighted by their relative abundances or evenness and was calculated as:

$$\mathrm{H}' = -\Sigma\, p_i \ln p_i$$

where p_i is the proportion of individuals found in the ith species. The ratio of observed diversity to maximum diversity was then used to calculate Shannon's evenness index as follows:

$$\mathrm{J}' = \mathrm{H}'/\mathrm{H}_{\max} = \mathrm{H}'/\ln S$$

J' assumes a value between 0 and 1, a value of 1 meaning all species are equally abundant in the area. Both H' and J' assume that all species in the area are accounted for in the sample.

Catch per unit effort

Relative fish abundance was expressed as catch per unit effort (CPUE), and is expressed in numbers and in weight. CPUE is calculated as:

$$CPUE = C_i / E_i$$

where Ci is the catch of species i (in numbers or weight) and Ei is the effort expended to obtain i. CPUE was standardised as kg/net.night^{-1} and fish/net.night^{-1}.

CPUE data of *O. andersonii*, *O. macrochir* and *T. rendalli* were not normally distributed and contained a high proportion of zero observations. This is a common occurrence when sampling rare species or species with low vulnerability to sampling gears (Maunder & Punt, 2004). In such cases, a Delta-X distribution is commonly used to derive more realistic estimates of error around the estimated CPUE (Ellender, Weyl, Winker, & Booth, 2010; Fletcher, MacKenzie, & Villouta, 2005; Lo, Jacobson, & Squire, 1992; Maunder & Punt, 2004; Stefánsson, 1996). Delta is the probability of a non-zero observation occurring and X refers to the distribution of these non-zero observations (Ellender et al., 2010). The non-zero CPUE observations ($CPUE_{pos}$) were log-transformed to normalise the data and the expected $CPUE$ was calculated by scaling $CPUE_{pos}$ by the probability of capture (PC) in any net night. CPUE for any net night i, $CPUE_i$, was calculated using the delta-lognormal model:

$$CPUE_i = PC_i \times \exp(\log CPUE_{pos,i} + \frac{\sigma^2}{2})$$

where PC_i is the probability of capture in any net night i, $\log CPUE_{pos,i}$ are the log-transformed $CPUE_{pos}$ observations and σ^2 is the variance of $\log CPUE_{pos}$.

Gillnet Selectivity

Selectivity of the target species *O. andersonii*, *O. macrochir* and *T. rendalli* was estimated using the regression framework method according to Hovgård and Lassen (2000). It was assumed that the the morphology of the target species did not differ between systems, and thus experimental gillnet catches from all four systems were combined. All fish caught in experimental gillnet fleets were grouped into 10 mm TL size classes *l* for any given mesh size *m*. The selection curves were assumed to be log-normal with Poisson distribute errors ($\beta = 0.5$). The selectivity of a given length class *l by* mesh size m_i was calculated as:

$$S_{lm} = \exp\left(\frac{\left(-0.5\left(\ln\left(\frac{l}{m}\right) - \ln K \right)^2 \right)}{\sigma^2} \right)$$

where *K* is the mode and σ is the spread of the log-normal selection curve. The number of fish *N* encountering the gear per length class *l* was estimated as:

$$qN_l = \left[\frac{\sum_m (C_{lm} S_{lm})^{\beta}}{\sum_m (S_{lm})^{2\beta}} \right]^{\frac{1}{\beta}}$$

where C_{lm} and S_{lm} are the catch and selectivity of a given length class *l* by mesh size *m* respectively. Parameters were estimated by minimising the least squares sum as:

$$Lsq = \sum_m \sum_l \left[(C_{lm}^{\beta} - (S_{lm} qN_l)^{\beta} \right]^2$$

Statistical analyses

A contingency table (4 systems × 10 fish families) was used to test whether the family biomass distribution was system-dependent. Variations in total CPUE between systems were compared using the non-parametric Kruskal-Wallis one-way analysis of variance (ANOVA) on ranks, and a Mann-Whitney U-test was used for pair-wise comparison. The log-normally distributed, Delta-X transformed CPUE data of *O. andersonii*, *O. macrochir* and *T. rendalli* were tested for differences between systems using a one-way ANOVA. A 95% confidence level was used in all tests.

4.3 RESULTS

Catch composition by system

Catch composition and %IRI for each species in each system are summarised in Table 4.1. In the Kavango River, 7 126 fishes representing 9 families and 41 species were sampled in 76 net nights (Table 4.1). The most numerous species was *Schilbe intermedius* (21.1%), while the large predatory characin, *Hydrocynus vittatus* contributed the most weight (20.1%). The five most important species, accounting for 80 %IRI were *S. intermedius* (29%), *H. vittatus* (17.7%), *Brycinus lateralis* (12.7%), *Synodontis nigromaculatus* (9.9%) and *Marcusenius altisambesi* (9.9%).

In the Kwando River, a total of 8 159 fishes representing 9 families and 40 species were sampled in 84 net nights (Table 4.1). The small planktivorous characin, *B. lateralis* was the most numerous species (50.4%) and the predatory *S. intermedius* contributed the most weight (31.8%). The five most important species accounting for 91 %IRI were *S. intermedius* (36.1%), *B. lateralis* (35.4%), *M. altisambesi* (11.4%), *Clarias gariepinus* (4.3%) and *Hepsetus odoe* (4.3%).

In Lake Liambezi a total of 21 194 fishes representing 8 families and 29 species were sampled in 45 net nights (Table 4.1). *Brycinus lateralis* was the most numerous species (67.1%) and *S. intermedius* contributed the most weight (38.9%). The five most important species, accounting for 89 %IRI were *B. lateralis* (52.86%), *S. intermedius* (24.63%), *Rhabdalestes maunensis* (5.95%), *M. altisambesi* (2.90%) and *Petrocephalus catostoma* (2.66%).

In the Zambezi River, a total of 6 237 fishes representing 10 families and 42 species were sampled in 63 net nights (Table 4.1). The small mormyrid, *P. catostoma* was the most numerous species (26.3%) and *C. gariepinus* contributed the most weight (18.7%). The five most important species, accounting for 78 %IRI were *S. intermedius* (24.6%), *B. lateralis* (17.4%), *P. catostoma* (15.5%), *H. vittatus* (14.3%) and *H. odoe* (6.3%).

Figure 4.1. *Brycinus lateralis*, the most important species in experimental gillnet catches in Lake Liambezi.

Table 4.1. Experimental gillnet catch composition in percent number (%N), percent weight (%W) and percent frequency of occurrence (%FO) and the percent index of relative importance (%IRI) of all fish species sampled in the Kavango, Kwando, Lake Liambezi and Zambezi Rivers, Namibia between August 2010 and July 2011.

	Kavango River (n = 7 126)				**Kwando River** (n = 8 159)				**Lake Liambezi** (n = 21 194)				**Zambezi River** (n = 6 237)			
Species	%N	%W	%FO	%IRI	%N	%W	%FO	%IRI	%N	%W	%FO	%IRI	%N	%W	%FO	%IRI
Mormyridae																
Cyphomyrus cubangoensis	0.2	0.1	7.9	0.02	0.1	0.0	9.5	0.01	-	-	-	-	0.6	0.2	20.6	0.14
Marcusenius altisambesi	16.6	5.4	50.0	9.88	9.0	9.5	92.9	11.36	1.8	4.0	84.4	2.90	3.7	2.4	58.7	2.84
Mormyrus lacerda	0	0.1	1.3	0.00	0.1	0.8	13.1	0.08	0.0	0.2	8.9	0.10	0.0	0.3	3.2	0.01
Petrocephalus catostoma	3.3	0.2	43.4	1.34	2.4	0.4	44.0	0.81	3.8	1.5	93.3	2.66	26.3	3.1	66.7	15.52
Pollimyrus castelnaui	0.9	0.0	6.6	0.05	0.3	0.0	20.2	0.05	0.1	0.0	15.6	0.05	1.0	0.1	23.8	0.21
Cyprinidae																
Barbus afrovernayi	0.0	0.0	2.6	0.00	-	-	-	-	-	-	-	-	-	-	-	-
Barbus barnardi	0.1	0.0	3.9	0.00	0.3	0.0	13.1	0.03	0.0	0.0	8.9	0.01	-	-	-	-
Barbus barotseensis	0.1	0.0	2.6	0.00	-	-	-	-	-	-	-	-	-	-	-	-
Barbus bifrenatus	0.0	0.0	3.9	0.00	0.3	0.0	14.3	0.02	0.1	0.0	22.2	0.03	-	-	-	-
Barbus eutaenia	0.3	0.0	13.2	0.04	-	-	-	-	-	-	-	-	0.5	0.0	17.5	0.08
Barbus fasciolatus	0.1	0.0	6.6	0.01	0.2	0.0	11.9	0.01	-	-	-	-	0.0	0.0	1.6	0.00
Barbus multilineatus	-	-	-	-	0.0	0.0	1.2	0.00	-	-	-	-	0.2	0.0	7.9	0.01
Barbus paludinosus	1.9	0.1	13.2	0.23	0.0	0.0	1.2	0.00	0.3	0.1	53.3	0.20	0.1	0.0	6.3	0.00
Barbus poechii	2.6	0.3	34.2	0.89	0.2	0.0	17.9	0.03	0.5	0.2	60.0	0.35	3.6	1.1	71.4	2.65
Barbus radiatus	1.4	0.0	23.7	0.31	0.5	0.0	26.2	0.10	0.8	0.2	77.8	0.48	2.3	0.2	39.7	0.76
Barbus thamalakanensis	-	-	-	-	-	-	-	-	-	-	-	-	0.1	0.0	3.2	0.00
Barbus unitaeniatus	0.1	0.0	9.2	0.01	0.2	0.0	14.3	0.02	0.0	0.0	8.9	0.01	0.3	0.0	17.5	0.04
Labeo cylindricus	0.1	0.0	7.9	0.01	-	-	-	-	0.1	0.1	20.0	0.09	0.1	0.1	4.8	0.01
Labeo lunatus	0.3	1.2	17.1	0.23	-	-	-	-	-	-	-	-	0.3	0.9	25.4	0.25
Opsaridium zambezense	-	-	-	-	-	-	-	-	-	-	-	-	0.0	0.0	1.6	0.0
Characidae																
Brycinus lateralis	18.8	2.6	65.8	12.65	50.4	5.8	95.2	35.36	67.1	38.7	100.0	52.86	19.0	5.2	90.5	17.35
Hydrocynus vittatus	5.3	20.1	77.6	17.71	0.1	3.7	13.1	0.33	-	-	-	-	5.1	17.2	81.0	14.31
Micralestes acutidens	6.8	0.3	65.8	4.16	0.0	0.0	1.2	0.00	0.0	0.0	4.4	0.03	2.9	0.2	58.7	1.42
Rhabdalestes maunensis	0.0	0.0	3.9	0.0	0.1	0.0	6.0	0.00	10.8	1.1	84.4	5.95	0.0	0.0	3.2	0.00
Hepsetidae																
Hepsetus odoe	0.5	2.3	26.3	0.65	1.8	8.0	66.7	4.31	0.1	1.7	26.7	0.90	2.5	16.0	42.9	6.25
Claroteidae																
Parauchenoglanis ngamensis	0.0	0.0	3.9	0.00	0.4	0.6	22.6	0.15	-	-	-	-	0.1	0.3	9.5	0.04

Schilbeidae																
Schilbe intermedius	21.1	17.1	86.8	29.86	22.8	31.8	100.0	36.11	10.4	38.9	100.0	24.63	18.0	15.7	92.1	24.55
Clariidae																
Clarias gariepinus	0.4	12.7	22.4	2.65	0.8	15.9	39.3	4.33	0.1	3.3	28.9	1.67	0.3	18.7	19.0	2.86
Clarias ngamensis	0.4	4.8	23.7	1.10	0.5	4.6	31.0	1.06	0.0	0.8	13.3	0.42	-	-	-	-
Clarias stappersii	-	-	-	-	-	-	-	-	-	-	-	-	0.0	0.0	1.6	0.00
Clarias theodorae	-	-	-	-	0.0	0.1	1.2	0.00	-	-	-	-	-	-	-	-
Mochokidae																
Synodontis nigromaculatus	9.1	9.6	59.2	9.94	1.2	1.5	20.2	0.37	0.0	0.1	8.9	0.07	0.4	0.8	20.6	0.20
Synodontis sp.	5.7	3.2	55.3	4.43	1.6	2.1	41.7	1.02	0.5	1.1	62.2	0.83	5.6	4.3	73.0	5.74
Cichlidae																
Hemichromis elongatus	-	-	-	-	0.1	0.0	7.1	0.01	-	-	-	-	-	-	-	-
Oreochromis andersonii	0.1	0.9	7.9	0.07	0.5	3.5	28.6	0.76	0.1	0.7	28.9	0.42	0.0	0.5	3.2	0.01
Oreochromis macrochir	0.0	0.1	1.3	0.00	0.7	3.2	32.1	0.82	0.1	0.5	20.0	0.26	0.0	0.1	3.2	0.00
Pharyngochromis acuticeps	0.3	0.1	11.8	0.03	1.5	0.4	51.2	0.64	0.6	0.7	77.8	0.65	1.4	0.6	39.7	0.63
Pseudocrenilabrus philander	0.0	0.0	2.6	0.00	0.1	0.0	10.7	0.01	0.4	0.1	62.2	0.25	0.1	0.0	6.3	0.01
Sargochromis carlottae	0.1	0.3	7.9	0.03	0.3	0.6	26.2	0.16	0.0	0.1	6.7	0.04	0.2	0.7	11.1	0.08
Sargochromis codringtonii	0.1	0.3	5.3	0.02	0.6	1.1	34.5	0.40	0.1	0.6	28.9	0.34	0.1	0.3	7.9	0.03
Sargochromis giardi	0.3	1.3	14.5	0.20	0.2	0.8	15.5	0.11	-	-	-	-	0.1	0.1	4.8	0.01
Serranochromis altus	0.8	8.7	21.1	1.80	0.2	1.3	16.7	0.17	-	-	-	-	0.3	2.2	17.5	0.35
Serranochromis angusticeps	0.5	4.2	17.1	0.73	0.3	1.0	23.8	0.20	-	-	-	-	0.5	1.2	22.2	0.30
Serranochromis macrocephalus	0.4	2.2	18.4	0.44	0.3	1.0	23.8	0.20	0.3	2.2	66.7	1.25	0.9	2.7	30.2	0.86
Serranochromis robustus	0.1	0.7	3.9	0.03	0.0	0.3	3.6	0.01	-	-	-	-	0.0	0.1	4.8	0.01
Serranochromis thumbergi	-	-	-	-	0.0	0.1	1.2	0.00	-	-	-	-	-	-	-	-
Tilapia rendalli	0.1	0.8	10.5	0.09	0.2	0.7	13.1	0.07	0.2	0.4	42.2	0.29	0.0	0.1	3.2	0.00
Tilapia sparrmanii	0.9	0.3	34.2	0.39	1.5	0.9	56.0	0.89	1.9	2.6	97.8	2.25	3.2	3.9	44.4	2.49
Anabantidae																
Ctenopoma multispine	-	-	-	-	-	-	-	-	-	-	-	-	0.0	0.0	1.6	0.00

Catch composition by mesh size

The catch composition by mesh size in terms of %IRI for all species in the Kavango, Kwando, Lake Liambezi and Zambezi Rivers are summarised in Tables 4.2, 4.3, 4.4 and 4.5 respectively.

Brycinus lateralis was the most important species in the 22 and 28 mm mesh sizes in the Kavango River (Table 4.2). *Schilbe intermedius*, the most important species overall in the Kavango River, was the most important species in the 35, 45, 57 and 73 mm mesh sizes. *Hydrocynus vittatus* dominated catches in the 93 mm mesh and the largest mesh sizes, 118 and 150 mm, were dominated by the catfish, *C. gariepinus* and the predatory cichlid, *Serranochromis altus* respectively.

Brycinus lateralis was the most important species in the 16, 22 and 28 mm mesh sizes in the Kwando River (Table 4.3). *Schilbe intermedius* was the most important species in the 35, 45 and 57 mm mesh sizes. The 73 mm mesh was dominated by the piscivorous *H. odoe*. *Clarias gariepinus* dominated catches in the 93 and 150 mm mesh whilst *Oreochromis andersonii* was most important in the 118 mm mesh.

Figure 4.2. *Schilbe intermedius*, the most important species in experimental gillnet catches in the Kavango, Kwando and Zambezi Rivers.

Table 4.2. Percent index of relative importance (%IRI) of all fish species for each experimental gillnet mesh size (mm) sampled in the Kavango River, Namibia between August 2010 and July 2011.

	%IRI by mesh size (mm)										
Species	12	16	22	28	35	45	57	73	93	118	150
Mormyridae											
Cyphomyrus cubangoensis	-	-	-	0.02	0.02	-	0.01	-	-	-	-
Marcusenius altisambesi	-	0.01	2.39	13.91	32.91	5.62	0.39	-	-	-	-
Mormyrus lacerda	-	-	-	-	-	-	-	-	0.07	-	-
Petrocephalus catostoma	-	0.67	7.13	0.16	0.01	-	-	-	-	-	-
Pollimyrus castelnaui	0.16	0.80	-	-	-	-	-	-	-	-	-
Cyprinidae											
Barbus afrovernayi	0.05	-	-	-	-	-	-	-	-	-	-
Barbus barnardi	0.62	-	-	-	-	-	-	-	-	-	-
Barbus barotseensis	0.76	-	-	-	-	-	-	-	-	-	-
Barbus bifrenatus	0.37	-	-	-	-	-	-	-	-	-	-
Barbus eutaenia	2.49	0.21	-	-	-	-	-	-	-	-	-
Barbus fasciolatus	1.64	-	-	-	-	-	-	-	-	-	-
Barbus paludinosus	3.31	2.43	0.01	-	-	-	-	-	-	-	-
Barbus poechii	0.04	1.84	2.38	0.97	0.04	-	-	-	-	-	-
Barbus radiatus	49.93	0.49	0.01	-	-	-	-	-	-	-	-
Barbus unitaeniatus	2.10	-	-	-	-	-	-	-	-	-	-
Labeo cylindricus	-	-	-	0.08	-	-	-	-	-	-	-
Labeo lunatus	-	-	-	-	0.02	0.02	0.36	0.74	0.82	-	-
Characidae											
Brycinus lateralis	4.99	23.07	40.55	38.51	0.68	-	-	-	-	-	
Hydrocynus vittatus	-	0.92	0.64	3.49	13.78	11.55	16.94	28.84	58.74	22.11	6.35
Micralestes acutidens	6.26	59.16	0.48	-	-	-	-	-	-	-	-
Rhabdalestes maunensis	0.37	-	-	-	-	-	-	-	-	-	-
Hepsetidae											
Hepsetus odoe	-	-	-	-	0.01	0.05	0.70	10.49	0.72	-	-
Claroteidae											
Parauchenoglanis ngamensis	-	-	-	0.01	-	-	-	-	-	-	-
Schilbeidae											
Schilbe intermedius	23.43	9.74	39.58	30.56	38.07	45.15	45.96	45.08	0.40	0.09	-
Clariidae											
Clarias gariepinus	-	-	-	-	-	0.08	-	0.88	8.24	35.66	16.42
Clarias ngamensis	0.04	-	-	-	-	0.08	0.02	4.16	6.13	2.13	0.59
Mochokidae											
Synodontis nigromaculatus	2.34	0.60	3.53	6.48	9.57	28.69	28.97	2.81	0.22	1.45	0.22
Synodontis sp.	1.03	0.02	2.61	5.58	4.84	8.68	6.50	0.51	0.04	0.09	-
Cichlidae											
Oreochromis andersonii	-	-	-	-	-	-	-	-	-	2.38	1.37
Oreochromis macrochir	-	-	-	-	-	-	-	-	-	0.13	-
Pharyngochromis acuticeps	-	-	0.02	0.02	0.01	0.04	-	-	-	-	-
Pseudocrenilabrus philander	0.04	-	-	-	-	-	-	-	-	-	-
Sargochromis carlottae	-	-	-	-	-	-	0.01	0.93	0.06	-	-
Sargochromis codringtonii	-	-	-	-	-	-	-	0.04	-	0.78	-
Sargochromis giardi	-	-	-	-	-	-	0.01	0.15	1.35	6.78	-
Serranochromis altus	-	-	-	-	-	-	0.03	0.50	11.94	14.03	64.38
Serranochromis angusticeps	-	-	-	-	0.02	-	0.02	0.79	4.56	9.34	7.49
Serranochromis macrocephalus	-	-	-	0.01	-	-	-	2.54	6.58	3.93	-
Serranochromis robustus	-	-	-	-	-	-	-	-	0.06	1.07	-
Tilapia rendalli	-	-	-	-	-	-	0.01	0.44	0.06	-	3.17
Tilapia sparrmanii	0.05	0.01	0.66	0.19	0.01	0.03	0.07	1.10	-	-	-

Table 4.3. Percent index of relative importance (%IRI) of all fish species for each experimental gillnet mesh size (mm) sampled in the Kwando River, Namibia between August 2010 and July 2011.

	%IRI by mesh size (mm)										
Species	12	16	22	28	35	45	57	73	93	118	150
Mormyridae											
Cyphomyrus cubangoensis	-	-	-	0.01	0.03	-	-	-	-	-	-
Marcusenius altisambesi	-	-	0.01	0.95	6.59	26.30	24.77	1.24	-	-	-
Mormyrus lacerda	-	-	-	-	-	-	-	0.47	1.90	-	-
Petrocephalus catostoma	-	-	0.04	8.30	0.42	-	-	-	-	-	-
Pollimyrus castelnaui	-	0.01	0.13	-	-	-	-	-	-	-	-
Cyprinidae											
Barbus barnardi	31.07	-	-	-	-	-	-	-	-	-	-
Barbus bifrenatus	25.31	0.01	-	-	-	-	-	-	-	-	-
Barbus fasciolatus	9.94	0.06	-	-	-	-	-	-	-	-	-
Barbus multilineatus	0.11	-	-	-	-	-	-	-	-	-	-
Barbus paludinosus	-	0.01	-	-	-	-	-	-	-	-	-
Barbus poechii	-	-	-	0.21	0.03	-	-	-	-	-	-
Barbus radiatus	-	1.87	0.10	-	-	-	-	-	-	-	-
Barbus unitaeniatus	0.11	0.17	0.02	0.01	-	-	-	-	-	-	-
Characidae											
Brycinus lateralis	2.77	91.82	91.67	64.42	0.01	-	-	-	-	-	-
Hydrocynus vittatus	-	-	-	-	-	-	0.08	0.05	1.87	0.98	12.11
Micralestes acutidens	-	0.01	-	-	-	-	-	-	-	-	-
Rhabdalestes maunensis	2.89	-	-	-	-	-	-	-	-	-	-
Hepsetidae											
Hepsetus odoe	-	0.09	0.01	0.13	0.39	1.10	2.86	35.51	1.36	-	-
Claroteidae											
Parauchenoglanis ngamensis	-	-	-	0.07	0.20	0.10	0.11	0.01	-	-	-
Schilbeidae											
Schilbe intermedius	27.68	5.84	7.92	24.81	90.30	69.41	67.31	32.61	1.01	-	-
Clariidae											
Clarias gariepinus	-	-	-	-	-	-	0.09	4.57	43.34	28.37	69.37
Clarias ngamensis	-	-	-	0.02	-	-	0.10	7.33	9.37	0.21	-
Clarias theodorae	-	-	-	-	-	-	-	0.02	-	-	-
Mochokidae											
Synodontis nigromaculatus	-	-	0.01	0.01	0.06	0.33	1.06	0.14	0.04	-	-
Synodontis sp.	-	-	-	-	0.22	1.26	1.60	1.49	-	-	-
Cichlidae											
Hemichromis elongatus	0.11	-	-	-	0.01	-	-	-	-	-	-
Oreochromis andersonii	-	-	-	-	-	-	-	0.04	10.27	32.70	18.53
Oreochromis macrochir	-	-	-	-	-	-	0.01	0.77	16.31	30.72	-
Pharyngochromis acuticeps	-	0.10	0.07	1.00	1.29	0.55	0.01	-	-	-	-
Pseudocrenilabrus philander	-	0.03	0.01	0.01	-	-	-	-	-	-	-
Sargochromis carlottae	-	-	-	-	-	-	0.04	2.85	0.28	-	-
Sargochromis codringtonii	-	-	-	-	-	-	0.12	8.07	1.36	-	-
Sargochromis giardi	-	-	-	-	-	-	-	0.53	2.06	0.53	-
Serranochromis altus	-	-	-	-	-	-	-	0.35	0.50	5.79	-
Serranochromis angusticeps	-	-	-	-	-	-	0.01	1.26	4.44	-	-
Serranochromis macrocephalus	-	-	-	-	-	-	0.01	2.27	3.43	-	-
Serranochromis robustus	-	-	-	-	-	-	-	-	0.06	0.58	-
Serranochromis thumbergi	-	-	-	-	-	-	-	0.02	-		-
Tilapia rendalli	-	-	-	-	-	-	-	0.14	2.39	0.13	-
Tilapia sparrmanii	-	-	-	0.03	0.45	0.94	1.83	0.26	-	-	-

In Lake Liambezi, catches in the smallest mesh size, 12 mm, were dominated by the small characin, *R. maunensis* (Table 4.4). *Brycinus lateralis*, the most important species overall in Lake Liambezi (Table 4.1), was most abundant in the 16, 22 and 28 mm mesh sizes. The 35, 45 and 57 mm mesh sizes were dominated by *S. intermedius*. The small predatory cichlid, *Serranochromis macrocephalus* was most important in the 73 mm mesh, accounting for 46.6% of the catch by IRI. *Clarias gariepinus* dominated catches in the 93 mm mesh and was the only species caught in the 118 mm mesh. No fish were caught in the 150 mm mesh in Lake Liambezi.

Petrocephalus catostoma, the most numerous species overall in the Zambezi River, was the most important species in the 22 mm mesh, accounting for 49.6% of the catch by IRI (Table 4.5). *Brycinus lateralis* was the most important species in the 16 and 28 mm mesh sizes. *Schilbe intermedius* dominated catches in the 35 and 45 mm mesh sizes and *H. odoe* was most important in the 57 and 73 mm mesh sizes. The 93, 118 and 150 mm mesh sizes were all dominated by *C. gariepinus*.

Figure 4.3. *Serranochromis macrocephalus*, the most abundant cichlid in experimental gillnet catches in Lake Liambezi and the Zambezi River.

Table 4.4. Percent index of relative importance (%IRI) of all fish species for each experimental gillnet mesh size (mm) sampled in Lake Liambezi, Namibia between August 2010 and July 2011.

	%IRI by mesh size (mm)									
Species	12	16	22	28	35	45	57	73	93	118
Mormyridae										
Marcusenius altisambesi	-	-	-	0.51	8.21	4.77	5.70	0.22	-	-
Mormyrus lacerda	-	-	-	-	-	0.01	0.04	-	-	-
Petrocephalus catostoma	-	0.02	2.34	6.92	-	-	-	-	-	-
Pollimyrus castelnaui	-	-	-	0.02	-	-	-	-	-	-
Cyprinidae										
Barbus barnardi	0.01	-	-	-	-	-	-	-	-	-
Barbus bifrenatus	0.13	-	-	-	-	-	-	-	-	-
Barbus paludinosus	0.44	1.18	0.01	-	-	-	-	-	-	-
Barbus poechii	-	0.14	0.21	0.15	0.01	-	-	-	-	-
Barbus radiatus	0.56	0.94	0.19	0.07	-	-	-	-	-	-
Barbus unitaeniatus	0.02	-	-	-	-	-	-	-	-	-
Labeo cyclindricus	-	-	-	0.01	0.05	-	-	-	-	-
Characidae										
Brycinus lateralis	0.18	87.76	93.13	81.37	24.41	-	-	-	-	-
Micralestes acutidens	-	0.03	-	-	-	-	-	-	-	-
Rhabdalestes maunensis	96.57	0.48	-	-	-	-	-	-	-	-
Hepsetidae										
Hepsetus odoe	-	-	-	-	-	0.24	0.28	5.09	2.51	-
Schilbeidae										
Schilbe intermedius	2.10	9.26	3.85	9.56	58.47	86.62	84.79	13.74	1.14	-
Clariidae										
Clarias gariepinus	-	-	-	-	-	-	0.03	13.36	10.52	100
Clarias ngamensis	-	-	-	-	-	-	-	6.87	-	-
Mochokidae										
Synodontis nigromaculatus	-	-	-	-	-	0.01	0.01	0.11	-	-
Synodontis sp.	-	0.01	0.01	0.05	0.74	2.25	0.38	-	-	-
Cichlidae										
Oreochromis andersonii	-	-	-	-	-	0.08	0.23	0.87	35.27	-
Oreochromis macrochir	-	-	-	-	-	-	0.02	0.90	13.93	-
Pharyngochromis acuticeps	-	-	0.03	0.26	1.34	1.00	0.03	-	-	-
Pseudocrenilabrus philander	-	0.12	0.18	0.14	-	-	-	-	-	-
Sargochromis carlottae	-	-	-	-	-	0.01	0.01	-	-	-
Sargochromis codringtonii	-	-	-	-	-	-	0.24	9.48	-	-
Serranochromis macrocephalus	-	-	-	-	0.01	0.28	0.90	46.62	36.62	-
Tilapia rendalli	-	-	-	-	0.07	0.28	0.04	2.64	-	-
Tilapia sparrmanii	-	00.06	0.06	0.95	6.68	4.43	7.30	0.10	-	-

Table 4.5. Percent index of relative importance (%IRI) of all fish species for each experimental gillnet mesh size (mm) sampled in the Zambezi River, Namibia between August 2010 and July 2011.

	%IRI by mesh size (mm)										
Species	12	16	22	28	35	45	57	73	93	118	150
Mormyridae											
Cyphomyrus cubangoensis	-	0.01	0.09	0.39	0.04	0.01	-	-	-	-	-
Marcusenius altisambesi	-	-	1.40	2.80	2.36	4.24	0.42	0.28	0.59	-	-
Mormyrus lacerda	-	-	-	-	-	-	-	-	0.99	-	-
Petrocephalus catostoma	0.18	28.11	49.55	1.02	-	-	-	-	-	-	-
Pollimyrus castelnaui	0.50	0.83	0.25	-	-	-	-	-	-	-	-
Cyprinidae											
Barbus eutaenia	4.96	0.05	0.01	-	-	-	-	-	-	-	-
Barbus fasciolatus	0.03	-	-	-	-	-	-	-	-	-	-
Barbus multilineatus	0.41	0.09	-	-	-	-	-	-	-	-	-
Barbus paludinosus	0.14	0.02	-	-	-	-	-	-	-	-	-
Barbus poechii	0.04	2.20	3.56	2.91	1.22	-	-	-	-	-	-
Barbus radiatus	34.36	4.12	0.16	-	-	-	-	-	-	-	-
Barbus thamalakanensis	-	0.03	-	-	-	-	-	-	-	-	-
Barbus unitaeniatus	0.44	0.23	0.02	-	-	-	-	-	-	-	-
Labeo cylindricus	-	-	-	-	0.02	-	-	-	-	-	-
Labeo lunatus	-	-	-	-	0.18	0.41	0.39	0.23	-	-	-
Opsaridium zambezense	0.04	-	-	-	-	-	-	-	-	-	-
Characidae											
Brycinus lateralis	9.79	41.45	29.75	43.97	1.85	-	-	-	-	-	-
Hydrocynus vittatus	-	-	0.07	1.61	29.47	24.18	9.20	17.42	10.69		3.36
Micralestes acutidens	33.79	14.99	0.04	-	-	-	-	-	-	-	-
Rhabdalestes maunensis	0.18	-	-	-	-	-	-	-	-	-	-
Hepsetidae											
Hepsetus odoe	-	-	-	-	2.22	3.63	48.69	47.82	-	-	-
Claroteidae											
Parauchenoglanis ngamensis	-	-	0.05	-	-	0.16	-	-	-	-	-
Schilbeidae											
Schilbe intermedius	14.72	7.53	13.89	38.29	51.10	46.78	9.34	0.83	0.60	-	-
Clariidae											
Clarias gariepinus	-	-	-	-	-	-	-	0.81	60.94	95.95	87.27
Clarias ngamensis	-	-	-	-	-	-	-	0.48	-	-	-
Clarias stappersii	-	-	-	-	0.004	-	-	-	-	-	-
Mochokidae											
Synodontis nigromaculatus	-	0.25	0.04	0.01	0.11	0.37	0.32	-	-	-	-
Synodontis sp.	0.30	0.07	1.10	7.64	9.66	8.02	4.52	0.62	0.55	-	-
Cichlidae											
Oreochromis andersonii	-	-	-	-	-	-	-	0.18	-	-	1.76
Oreochromis macrochir	-	-	-	-	-	-	-	-	2.46	-	-
Pharyngochromis acuticeps	-	0.02	0.02	1.09	0.91	0.60	0.08	-	-	-	-
Pseudocrenilabrus philander	0.14	-	-	-	-	-	-	-	-	-	-
Sargochromis carlottae	-	-	-	-	-	0.01	-	6.75	2.74	-	-
Sargochromis codringtonii	-	-	-	-	-	0.01	0.02	1.70	-	-	-
Sargochromis giardi	-	-	-	-	-	0.03	-	0.17	-	-	-
Serranochromis altus	-	-	-	-	0.02	0.05	0.62	2.20	0.91	-	7.61
Serranochromis angusticeps	-	-	-	-	0.01	0.99	0.33	5.45	-	4.05	-
Serranochromis macrocephalus	-	-	-	0.01	0.10	1.15	3.75	11.69	19.52	-	-
Serranochromis robustus	-	-	-	-	-	-	0.19	-	-	-	-
Tilapia rendalli	-	-	-	-	-	-	-	0.16	-	-	-
Tilapia sparrmanii	-	-	0.01	0.25	0.72	9.35	22.12	3.20	-	-	-
Anabantidae											
Ctenopoma multispine	-	0.003	-	-	-	-	-	-	-	-	-

Species richness and diversity

Species richness was similar between the Kavango, Kwando and Zambezi Rivers, the Zambezi River being the most species rich (42 species), followed by the Kavango (41 species) and the Kwando Rivers (40 species). Species richness was considerably lower in Lake Liambezi with only 29 species. Species richness by family in the four systems is illustrated in Figure 4.4**.** The most species rich family in every system was the Cichlidae with 15 species recorded in the Kwando River, 13 in the Kavango and Zambezi Rivers and 9 in Lake Liambezi. Cyprinidae was the second most species rich family in each system with 12 species recorded in the Kavango River, 11 in the Zambezi River, 8 in the Kwando River and 7 in Lake Liambezi.

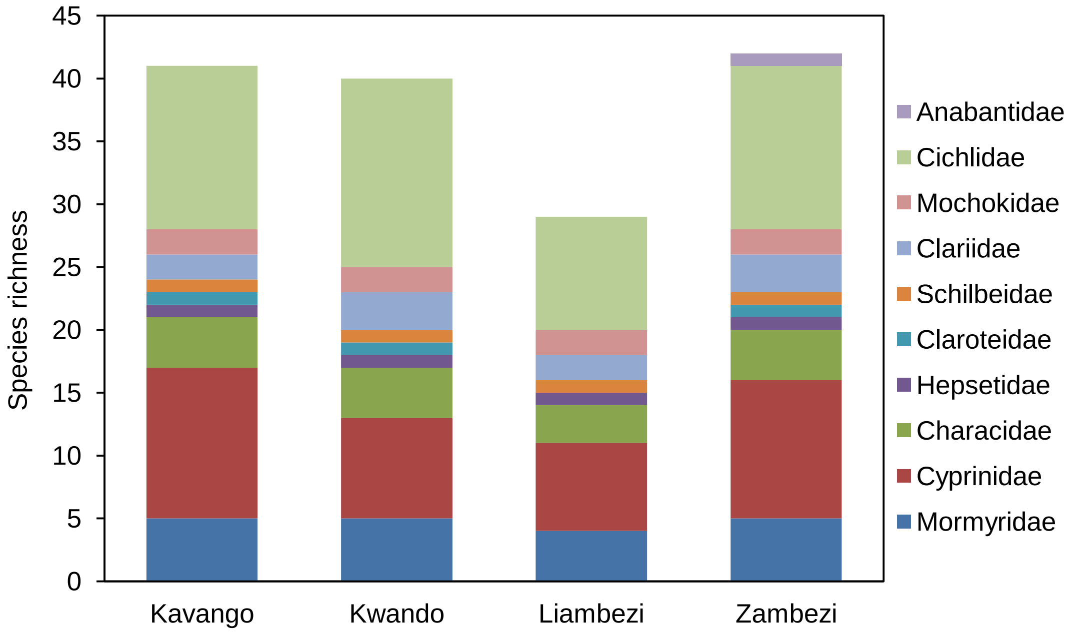

Figure 4.4. Species richness by family in experimental gillnet catches in the Kavango, Kwando, Lake Liambezi and Zambezi River systems, Namibia sampled between August 2010 and July 2011.

Species diversity was highest in the Kavango River with a Shannon-Wiener diversity index of 2.41 and lowest in Lake Liambezi with an index of 1.26 (Table 4.6). Similarly, the evenness index was highest in the Kavango (0.65) and lowest in Lake Liambezi (0.37) (Table 4.6). The Shannon-Wiener diversity and evenness indices summarised in Table 4.6 indicate high diversity and evenness in the Kavango and Zambezi Rivers compared with moderate and low diversity and evenness in the Kwando and Lake Liambezi respectively.

Table 4.6. Shannon-Wiener diversity (H') and evenness (J') indices for experimental gillnet catches in the Kavango, Kwando, Lake Liambezi and Zambezi Rivers between August 2010 and July 2011.

Indices	Kavango	Kwando	Liambezi	Zambezi
H'	2.41	1.74	1.26	2.23
J'	0.65	0.47	0.37	0.60

Biomass

The relative biomass of each family in experimental gillnet catches for the four systems is summarised in Figure 4.5. The family biomass distribution was significantly dependent on system (4 × 10 contingency table: $\chi^2 = 89.2$, df = 9, $p < 0.001$). The Characidae was the most important family in the Kavango and Zambezi Rivers and in Lake Liambezi. The Characidae contributed 23%, 22.6% and 39.8% to the total biomass in the Kavango and Zambezi Rivers and in Lake Liambezi respectively. The Kwando River had the lowest relative biomass of characins with 9.5%. Schilbeidae was the most important family in the Kwando River, contributing 31.8%, and was the second most important family in Lake Liambezi, contributing

38.9%. Clariids contributed 20.6% and 19.1% biomass in the Kwando and Zambezi Rivers respectively. Cichlids were most abundant in the Kwando River, contributing 20% and least abundant in Lake Liambezi, where they contributed 4.1%.

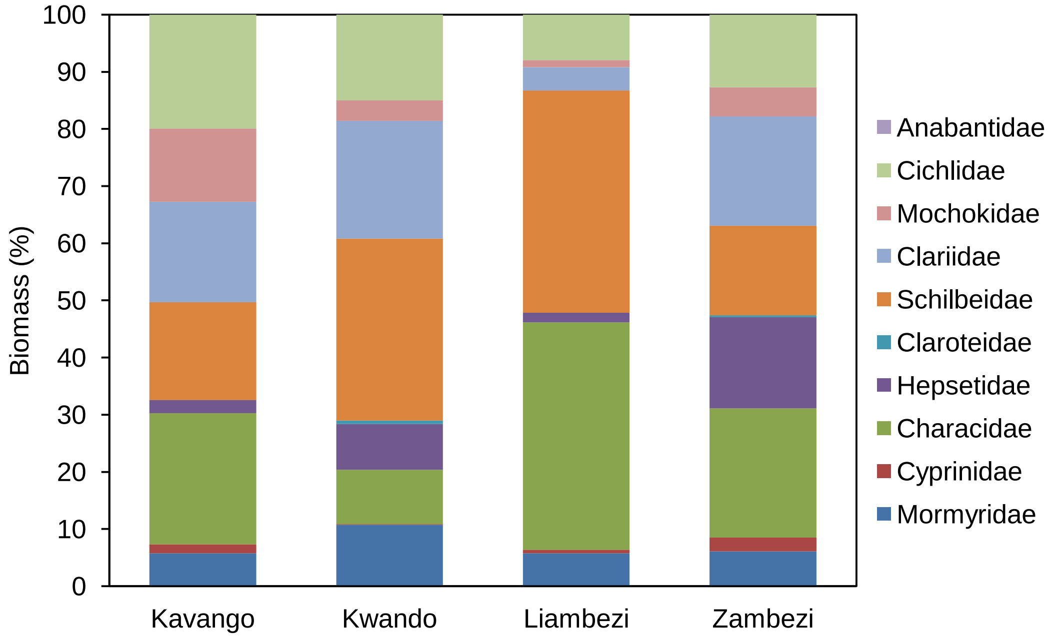

Figure 4.5. Percent biomass contribution by family to experimental gillnet catches in the Kavango, Kwando, Lake Liambezi and Zambezi Rivers, Namibia sampled between August 2010 and July 2011.

Catch per unit effort

CPUE by number in the four systems is illustrated in Figure 4.6. CPUE differed significantly between systems (Kruskal-Wallis ANOVA; $p < 0.05$). CPUE was significantly higher in Lake Liambezi (588.7 ± 274.1 fish/net.night^{-1}) compared to in the Kwando River (116.9 ± 53.1 fish/net.night^{-1}) which was in turn significantly higher than in the Zambezi River (118.7 ± 131 fish/net.night^{-1}) and in the Kavango River (106.4 ± 135.6 fish/net.night^{-1}).

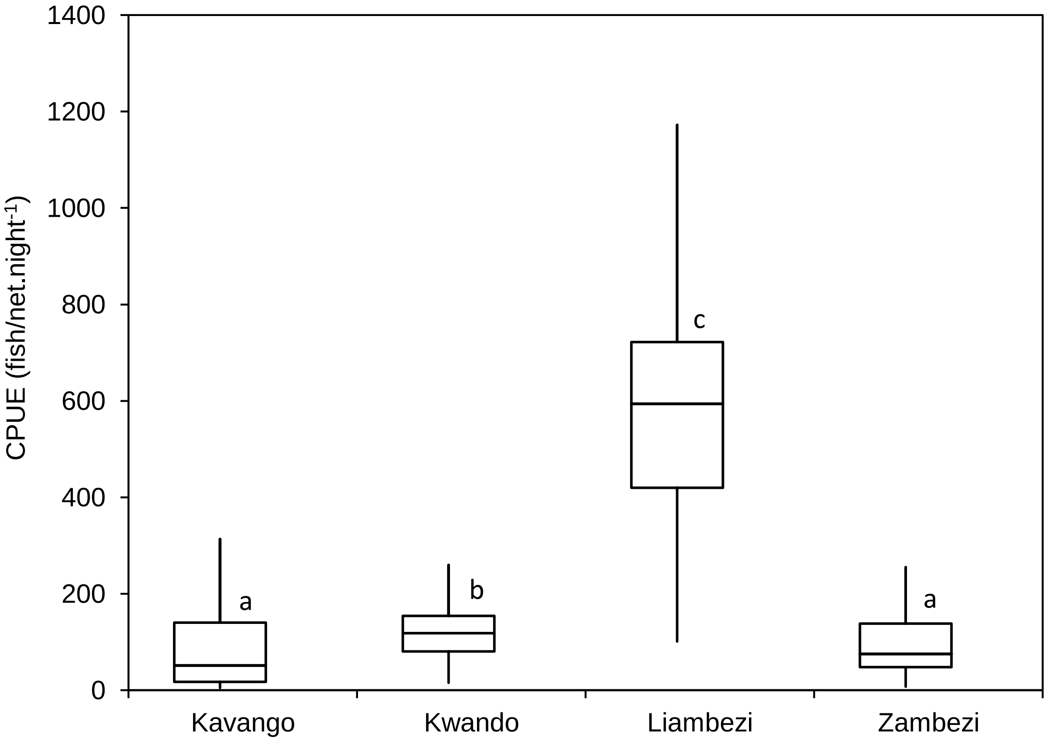

Figure 4.6. Box and whisker plots of experimental gillnet CPUE by number for all species in the Kavango, Kwando, Lake Liambezi and Zambezi Rivers in Namibia, sampled between August 2010 and July 2011. Boxes represent the median and upper and lower quartiles and whiskers represent the minimum and maximum. Different letters denote significant differences (Kruskal-Wallis one-way ANOVA on ranks; Mann-Whitney U-test comparison, $p \leq 0.05$).

CPUE by weight in the four systems is illustrated in Figure 4.7. CPUE differed significantly between systems (Kruskal-Wallis ANOVA; $p < 0.05$). CPUE in Lake Liambezi (10.3 ± 5.6 kg/net.night^{-1}) and in the Kwando River (8.5 ± 4.6 kg/net. night^{-1}) was significantly higher than that in the Kavango River (8.9 ± 9.9 kg/net.night^{-1}), which in turn was significantly higher than that in the Zambezi River (4.3 ± 3.4 kg/net.night^{-1}).

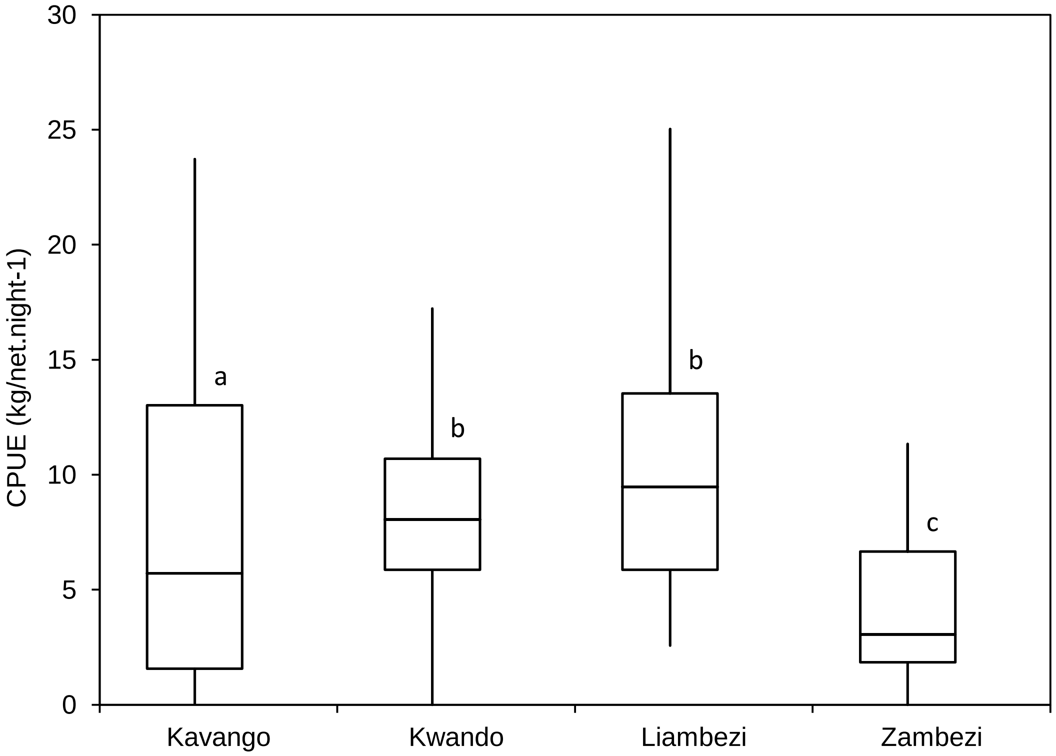

Figure 4.7. Box and whisker plots of experimental gillnet CPUE by weight for all species in the Kavango, Kwando, Lake Liambezi and Zambezi Rivers in Namibia, sampled between August 2010 and July 2011. Boxes represent the median and upper and lower quartiles and whiskers represent the minimum and maximum. Different letters denote significant differences (Kruskal-Wallis one-way ANOVA on ranks; Mann-Whitney U-test comparison, $p \leq 0.05$).

CPUE by weight in each mesh size in the four systems is illustrated in Figure 4.8. In the Kavango River, CPUE was highest in the 118 mm mesh size. CPUE by weight in the Kwando and Zambezi Rivers was highest in the 57 mm mesh size. In Lake Liambezi, CPUE was highest in the 22 mm mesh size. CPUE by weight in mesh sizes >73 mm was considerably higher in the Kavango and Kwando Rivers compared to that in lake Liambezi and the Zambezi River.

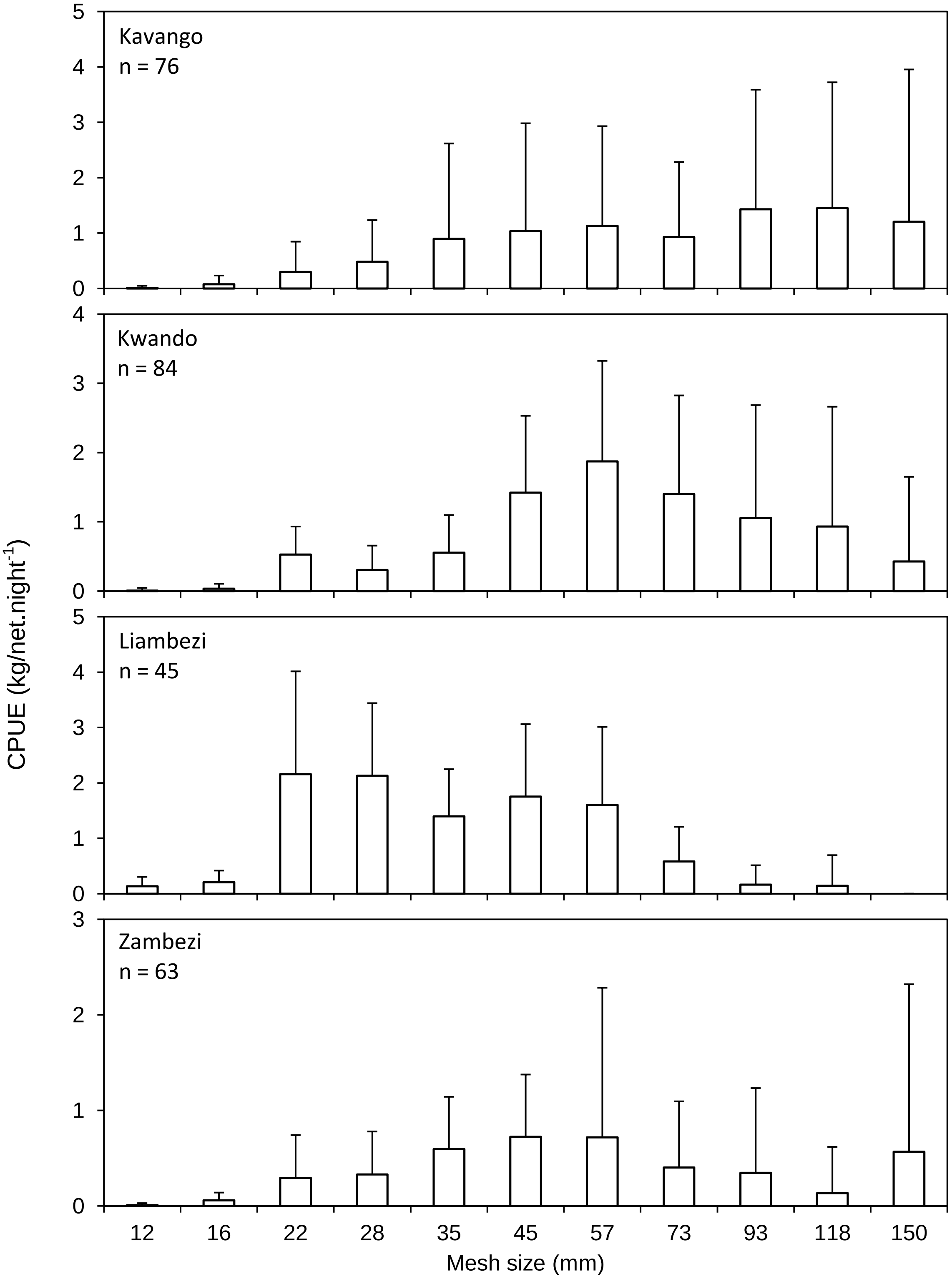

Figure 4.8. Catch per unit effort by weight for all species in each mesh size in the Kavango, Kwando, Lake Liambezi and Zambezi Rivers in Namibia, sampled between August 2010 and July 2011.

Cichlid probability of capture and catch per unit effort

The PC and CPUE of the target species, *O. andersonii*, *O. macrochir* and *T. rendalli* in experimental gillnets is summarised in Table 4.7. The PC of *O. andersonii* in Lake Liambezi and the Kwando River was relatively high (0.29 and 0.27 respectively) compared to that in the Kavango and Zambezi Rivers (0.08 and 0.03). The PC of *O. macrochir* was highest in the Kwando River (0.30), followed by Lake Liambezi (0.20), and was considerably lower in the Kavango and Zambezi Rivers (0.01 and 0.02 respectively). The PC of *O. macrochir* in the Kavango and Zambezi Rivers was extremely low as only a single specimen was captured in each system in 76 and 63 net nights respectively. The PC of *T. rendalli* was highest in Lake Liambezi (0.42), was similar in the Kavango and Kwando Rivers (0.11 and 0.13 respectively), and was considerably lower in the Zambezi River (0.02). Only a single *T. rendalli* was captured in the Zambezi River in 63 net nights.

CPUE of *O. andersonii* differed significantly between systems (ANOVA; $p < 0.05$) and ranged from 0.27 ± 0.08 kg/net.night^{-1} to 0.03 ± 0.02 kg/net.night^{-1}. CPUE of *O. andersonii* was highest in the Kwando River, followed by Lake Liambezi and the Kavango River and was lowest in the Zambezi River. CPUE of *O. macrochir* was very low in the Kavango and Zambezi Rivers as only a single specimen was captured in each system. CPUE of *O. macrochir* was significantly higher in the Kwando River (0.25 ± 0.13 kg/net.night^{-1}) compared to that in Lake Liambezi (0.10 ± 0.05 kg/net.night^{-1}) (ANOVA; $p < 0.05$). CPUE of *T. rendalli* in Lake Liambezi (0.14 ± 0.07 kg/net.night^{-1}) was significantly higher than that in the Kwando River (0.09 ± 0.02 kg/net.night^{-1}), while that in the Kavango River did not differ significantly from either (ANOVA; $p<0.05$). Only one *T. rendalli* was caught in the Zambezi River and so the CPUE was very low.

Table 4.7. $CPUE_{pos}$ (CPUE excluding zero catches) and *CPUE* (Delta-X transformed $CPUE_{pos}$) (kg/net.night^{-1}) (± standard deviation) and the probability of capture (PC) of *Oreochromis andersonii*, *Oreochromis macrochir* and *Tilapia rendalli* from experimental gillnet catches in the Kavango, Kwando, Lake Liambezi and the Zambezi Rivers in Namibia, sampled between August 2010 and July 2011. Different letters denote significant differences (ANOVA, $p \leq 0.05$).

	$CPUE_{pos}$ (kg/net.night^{-1})	*CPUE* (kg/net.night^{-1})	PC	n (net nights)	n (with fish)
O. andersonii					
Kavango	0.99 (0.36)	0.08 (0.01)^{a}	0.079	76	6
Kwando	1.07 (0.72)	0.27 (0.08)^{b}	0.274	84	23
Liambezi	0.25 (0.25)	0.15 (0.07)^{c}	0.289	45	13
Zambezi	0.76 (0.78)	0.03 (0.02)^{d}	0.032	63	2
O. macrochir					
Kavango	0.72	0.01	0.013	76	1
Kwando	0.90 (1.14)	0.254 (0.13)^{a}	0.298	84	25
Liambezi	0.24 (0.30)	0.096 (0.05)^{b}	0.200	45	9
Zambezi	0.33	0.01	0.016	63	1
T. rendalli					
Kavango	0.72 (0.45)	0.10 (0.05)^{ab}	0.105	76	8
Kwando	0.45 (0.27)	0.09 (0.02)^{a}	0.131	84	11
Liambezi	0.10 (0.11)	0.14 (0.07)^{b}	0.422	45	19
Zambezi	0.15	0.01	0.016	63	1

Gillnet selectivity

As the abundance of *O. andersonii*, *O. macrochir* and *T. rendalli* in experimental gillnet catches was low (Table 4.7), selectivity could not be estimated for all mesh sizes (Figures 4.9 and 4.10). Parameter estimates for the log-normal selection model are summarised in Table 4.8.

Table 4.8. Summary of parameters (standard deviation, σ and selection factor, K) estimated using the log-normal regression framework method (Hovgård & Lassen, 2000) for *Oreochromis andersonii*, *Oreochromis macrochir* and *Tilapia rendalli*.

	Parameters		
Species	K	σ	β (Poisson distributed errors)
O. andersonii	2.78	0.059	0.5
O. macrochir	2.58	0.068	0.5
T. rendalli	2.72	0.063	0.5

Observed and model predicted gillnet catches, illustrated in Figure 4.9, show that the model fitted the data relatively well despite small sample sizes. Relative selectivity curves estimated for *O. andersonii, O. macrochir* and *T. rendalli* are illustrated in Figure 4.10 and peak relative selectivities for each mesh size are summarised in Table 4.9.

Table 4.9. Predicted length class at maximum selectivity for different gillnet selectivity curves for *Oreochromis andersonii*, *Oreochromis macrochir* and *Tilapia rendalli*.

	Mesh size					
Species	45 mm	57 mm	73 mm	93 mm	118 mm	150 mm
O. andersonii	-	160	200	260	330	420
O. macrochir	-	-	190	240	300	-
T. rendalli	120	160	200	250	-	-

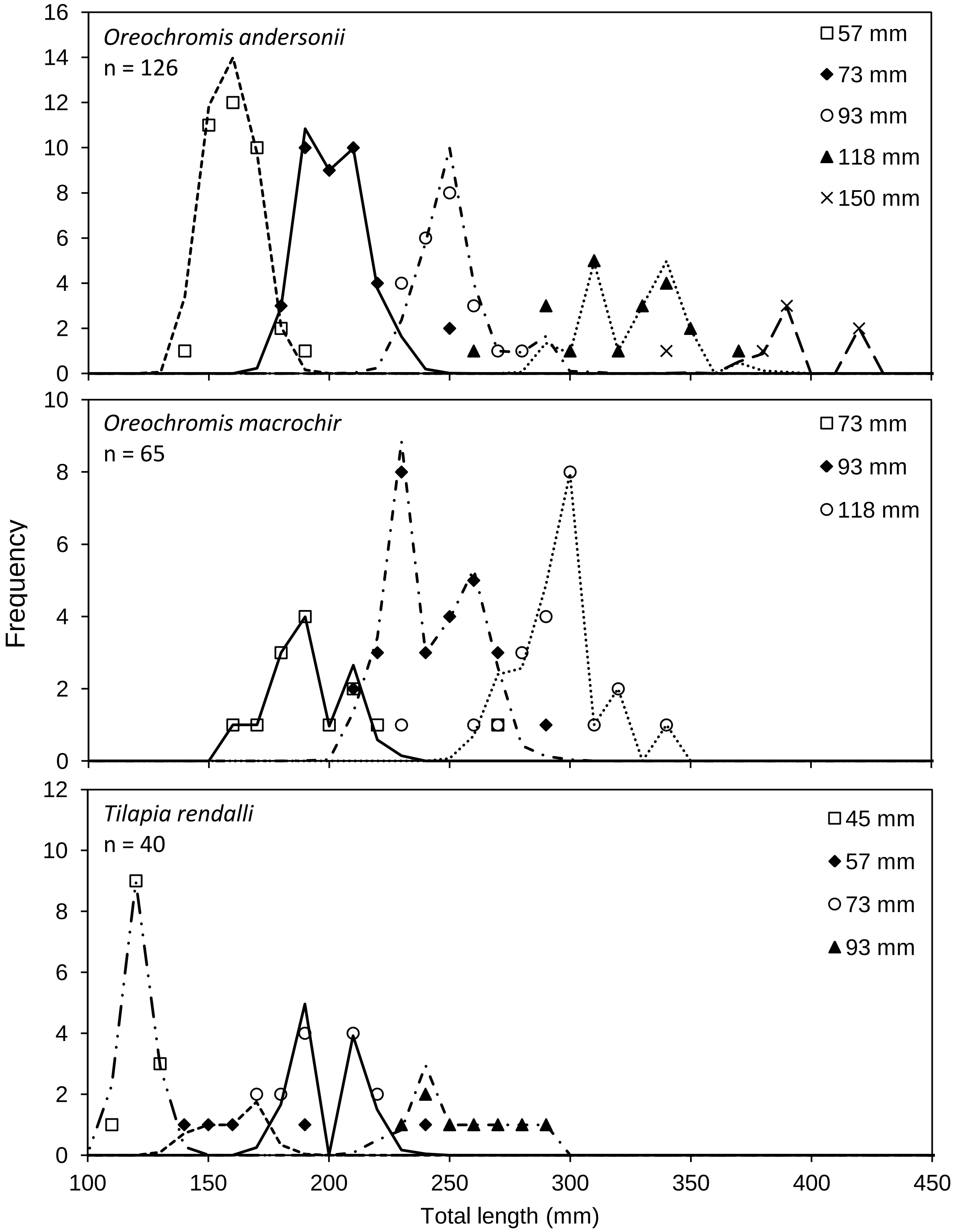

Figure 4.9. Observed (markers) and model predicted (lines) gillnet catches of *Oreochromis andersonii, Oreochromis macrochir* and *Tilapia rendalli* using the regression framework method (Hovgård & Lassen, 2000).

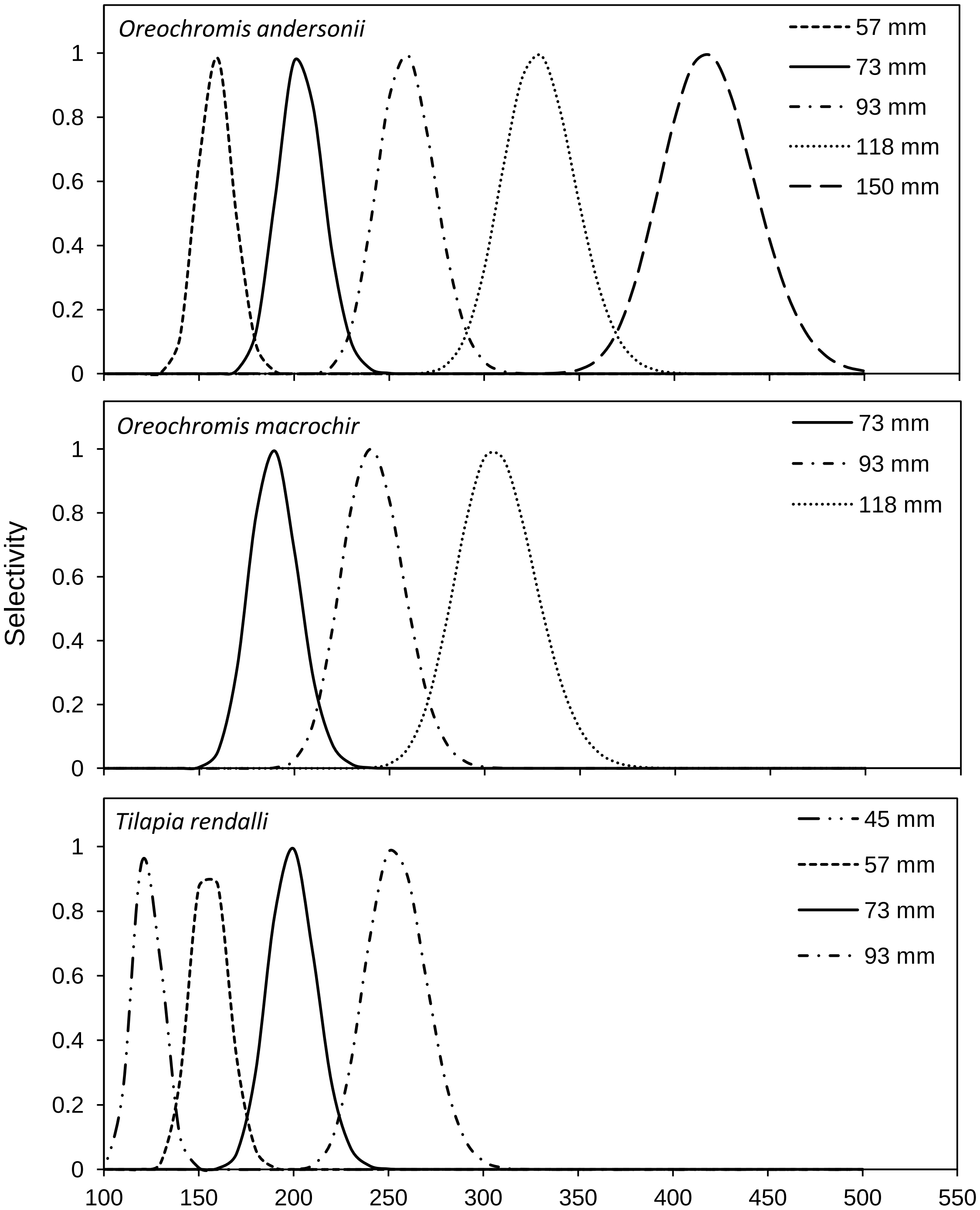

Figure 4.10. Relative gillnet selectivity curves estimated for *Oreochromis andersonii*, *Oreochromis macrochir* and *Tilapia rendalli* using the regression framework method (Hovgård & Lassen, 2000).

4.4 DISCUSSION

Species richness and diversity

Fish diversity in freshwater environments has been demonstrated to be significantly correlated to habitat structural complexity (Arrington & Winemiller, 2006; Willis, Winemiller, & Lopez-Fernandez, 2005). Higher species diversity in the river systems compared to Lake Liambezi may be attributed to the more diverse and more structurally complex habitats available to fishes in them. The absence of riverine habitat in Lake Liambezi may exclude some riverine fish species such as *Labeo cylindricus*, as they might be unable to establish successful breeding populations (Weyl & Booth, 1999). Other riverine species such as *Micralestes acutidens* were captured in the lake but in very low numbers. These species may not be able to successfully breed in the lake, but are present because of migration from the Zambezi and Chobe Rivers during flooding.

Studies carried out by Hay et al. (2000, 2002) and Næsje et al. (2004) recorded 40 species in experimental gillnets from the Zambezi River, 41 species in the Kavango River and only 31 species in the Kwando River. The gillnets used in these studies lacked the two smallest mesh sizes (12 and 16 mm) used in the present study. A comparison excluding those species caught only in 12 and 16 mm mesh in this study means 34 species were recorded in the Zambezi, 31 in the Kavango and 33 in the Kwando. The studies carried out by Hay et al. (2000, 2002) on the Kavango and Zambezi Rivers were extensive, sampling the entire courses of the rivers in Namibia, in a wider range of habitats, and over a longer period of time than was sampled in this study and the study by Næsje et al. (2004). This may explain why fewer species were recorded in the same mesh sizes in this study compared to Hay et al. (2000, 2002). Species recorded by Hay et al. (2000) in the Kavango that were not recorded in this study include *Hippopotamyrus ansorgii, Barbus kerstenii, Clarias theodorae, Clarias stappersii, Serranochromis thumbergi, Tilapia ruweti* and *Ctenopoma multispine*. In the Zambezi, Hay et al. (2002) recorded four species that were not recorded in this study: *Hemichromis elongatus, Serranochromis longimanus, Tilapia ruweti,* and *Clarias theodorae*. Two species were recorded by Næsje et al. (2004) in the Kwando River that were not recorded in this study: *Hippopotamyrus ansorgii* and *Tilapia ruweti*.

The Cichlidae was the most speciose family in every system in this study with 15 species recorded in the Kwando, 13 in the Kavango and Zambezi and 9 in Lake Liambezi. Hay et al. (2000, 2002) and Næsje et al. (2004) found the same in gillnet catches, with 15 species of Cichlidae in the Zambezi and 14 species in the Kavango and Kwando Rivers. The small mouth brooding cichlid *Pseudocrenilabrus philander* was only caught in 12 mm mesh in the Kavango and Zambezi Rivers, reducing the species count for comparison to 12 for these two systems.

The Cyprinidae was the second most speciose family in each system in this study with 12 species recorded in the Kavango, 11 in the Zambezi, 8 in the Kwando and 7 in Lake Liambezi. Hay et al. (2000, 2002) and Næsje et al. (2004) recorded 8 Cyprinid species from the Zambezi and Kavango Rivers and only 3 species from the Kwando River. Several small *Barbus* species were recorded only in 12 and 16 mm mesh during this study, reducing counts for comparison to 5 species in the Kavango, 6 in the Zambezi and 3 in the Kwando.

Species richness in this study was similar to that observed by Næsje et al. (2004) but lower than that observed by Hay et al. (2000, 2002). These differences are, however, not large and it is unlikely that the species richness in these systems has changed since the previous studies were carried out. Species diversity is, unfortunately, not directly comparable between this and previous studies. Catches in gears other than gill nets, such as seine nets and D-nets, were included in diversity indices calculated by Hay et al. (2000, 2002) and Næsje et al. (2004), resulting in considerably higher values than were found in the present study.

Catch composition

Catch composition in the three river systems was similar, with a single species, *Schilbe intermedius* dominating in all three systems. The dominance of this species was also noted by Hay et al. (2000) in the Kavango River, and by Bokhutlo (2011) in the Okavango Delta. Hay et al. (2002) and Næsje et al. (2004) found that *Brycinus lateralis* and *Marcusenius altisambesi* dominated catches in the Zambezi and Kwando Rivers respectively. *Brycinus lateralis* was the second most important species in the Zambezi and Kwando Rivers and third in the Kavango River. *Marcusenius altisambesi* was the third and fifth most important species in the Kwando and Kavango Rivers respectively. *Hydrocynus vittatus* was the second and fourth most important species in the Kavango and Zambezi Rivers respectively but was uncommon in the Kwando River and absent from catches in Lake Liambezi.

This agrees with van der Waal (1980) who found a very low abundance of *H. vittatus* in Lake Liambezi, but in contrast to Næsje et al. (2004) who found that *H. vittatus* was the second most important species in gillnet catches in the Kwando River. Kwando River levels were considerably lower between 1997 and 1999, the period during which Næsje et al. (2004) conducted their research, compared to the present study. During high water, fishes become much more highly dispersed and prey species are able to take refuge amongst flooded vegetation (Welcomme, 1979, 2001), but at low water, fish densities increase and predator-prey interactions are more intense (Rodríguez & Lewis, Jr, 1994; Winemiller, 1990). Low fish densities and abundant refugia during the higher water period over the present study may have resulted in unfavourable feeding conditions for *H. vittatus*, which could possibly account for their low abundance compared to that observed by Næsje et al. (2004). *Schilbe intermedius* was considerably more important in catches in this study compared to that observed by Næsje et al. (2004). This suggests that *S. intermedius*, under lower predation pressure from *H. vitattus*, may have occupied the vacant predatory niche left by *H. vitattus*. *Schilbe intermedius* may be better suited to foraging in floodplain habitats than *H. vitattus*.

In Lake Liambezi two species, the planktivore *B. lateralis* and the predatory *S. intermedius* were overwhelmingly dominant. Combined these two species accounted for over two thirds of the total catch by IRI. Before the lake dried up in 1985, *S. intermedius* dominated experimental gillnet catches and *P. catostoma* was the most abundant species in the 25 mm mesh net. *Brycinus lateralis*, dominant in the smaller mesh sizes in this study, was only a minor component of the catch in similar mesh sizes before the lake dried (van der Waal, 1980). The third most important species, *Rhabdalestes maunensis*, was recorded in all three river systems but was rare (%FO ≤ 6.0). Although an important component of the catch in this study, this species was not recorded in gillnet catches by van der Waal (1976) as the smallest gillnet mesh size he used was 25 mm and in this study *R. maunensis* was only caught in the 12 and 16 mm mesh. The fish fauna in Lake Liambezi has undergone significant changes since it began to receive water in 2001 (Hay & van der Waal, 2009), but the differences in species composition and abundance between those recorded by van der Waal (1980) and this study suggest that the fish fauna in the lake may still be developing.

Relative abundance

Catch per unit effort by number was significantly higher in Lake Liambezi compared to the three river systems, because two small characins, *B. lateralis* and *R. maunensis* were very abundant in the lake. Mean CPUE by number was similar in the rivers, but varied considerably more in the Kavango and Zambezi Rivers than in the Kwando River, resulting in a significant difference in the median CPUE between the Kwando River and the Kavango and Zambezi Rivers (Figure 4.6). Differences in variation of CPUE can be accounted for by differences in the magnitude of flooding between the Kwando River and the Kavango and Zambezi Rivers. The Kwando River level rarely changes by more than 2 meters between flooding and dry seasons, while the Kavango and Zambezi Rivers may vary by as much as 5 and 8 meters respectively between seasons (see Chapter 3). During peak floods in the Kavango and Zambezi Rivers catches are dramatically reduced as a result of dilution of the fishes whereas in the Kwando River the smaller variation in water level has a lesser impact on catches. CPUE in the rivers was similar despite the Zambezi being heavily fished, while the areas sampled on the Kavango and Kwando Rivers were unfished. With the continuous removal of larger fishes through exploitation in the Zambezi River, small prey species may proliferate under reduced levels of predation (Layman, 2004). The elevated abundance of small fishes in the Zambezi River appears to account for the even CPUE by number between systems. Næsje et al. (2004) found that the CPUE by number in the Kwando River was lower than the Zambezi and Kavango Rivers (Hay et al., 2000, 2002), but catches in the Zambezi River, especially in larger mesh sizes, have decreased from 1997 to 2007 as a result of increased fishing pressure (Hay & van der Waal, 2009).

Catch per unit effort by weight was highest in Lake Liambezi despite catches being dominated by the small *B. lateralis*. Mean CPUE in the Kwando and Kavango Rivers was similar. High variability in CPUE in the Kavango River, however, resulted in the median CPUE being significantly lower than that in the Kwando River (Figure 4.7). CPUE was significantly lower in the Zambezi River compared to the other three systems. The fact that CPUE by number between the river systems is even and the CPUE by weight differs indicates that fishing in the Zambezi River has reduced the abundance of larger fish. CPUE by weight for the larger mesh sizes was higher in the Kavango and Kwando Rivers compared to that in Lake Liambezi and the Zambezi River (Figure 4.8). Hay et al. (2002) recorded the highest CPUE by weight in the Zambezi River in a 28 mm mesh, and attributed this to a high abundance of *B. lateralis* and *P. catostoma* sampled in Lake Lisikili. Similarly, in Lake Liambezi, the overwhelming dominance of *B. lateralis* resulted in CPUE being highest for the small mesh sizes. Catches for larger mesh sizes in Lake Liambezi were exceptionally low with no fish being caught by the largest mesh size (150 mm). This, like the Zambezi River, may have been a result of heavy fishing pressure in the areas of the lake that were sampled. Alternatively, cichlids may not have grown to sizes large enough to be caught by the 150 mm mesh size in this young lake.

Cichlid relative abundance

Large, commercially valuable cichlids form the basis of the subsistence and commercial gillnet fisheries in the Caprivi and Kavango Regions (van der Waal, 1980, 1990, 1991). Cichlids were the most diverse family in every system (Figure 4.4) but did not contribute more than 20% to the total weight of the catch in any system (Figure 4.5). Cichlid abundance was surprisingly low despite their importance in the fisheries. Cichlids contributed most to the experimental catch in the Kavango River, largely a result of the contribution of the large piscivorous *Serranochromis altus* in the large mesh sizes (Table 4.2). Outside of the protected area in the Kavango River, the CPUE of large cichlids was significantly lower (Hay et al., 2000; This study). The most important large cichlid in experimental catches in the Kavango River between 1992 an 1997 was *Sargochromis carlottae* (Hay et al., 2000). In the Kwando River, cichlids were the third most important family by weight, after the Schilbeidae and Clariidae. The tilapiines, *O. andersonii* and *O. macrochir* contributed significantly to experimental catches in the Kwando River in this study (Table 4.3). Næsje et al. (2004) also recorded cichlids as the third most important family after the Characidae and Clariidae. *Sargochromis giardi* was the single most important cichlid species recorded by Næsje et al. (2004) in the Kwando River. In the Zambezi River cichlids were only the fifth most important family. *Serranochromis macrocephalus* was the most abundant large cichlid in experimental catches in the Zambezi River in this study as well as in previous studies in the Caprivi (Hay et al., 2002) and the Upper Zambezi in Zambia (Winemiller, 1991). Historically, cichlids contributed more to experimental catches in the Zambezi (Hay et al., 2002), but have declined in abundance as a result of increased exploitation in recent years (Hay & van der Waal, 2009). In Lake Liambezi, where a major fishery has developed for tilapiine cichlids after its refilling, cichlids contributed less than 8% of the experimental catch by weight. The most important cichlid in experimental catches was *S. macrocephalus,* which was also the most abundant large cichlid in experimental catches before the lake dried in 1985 (van der Waal, 1980).

The tilapiines *O. andersonii*, *O. macrochir* and *T. rendalli* made up three-quarters of the commercial gillnet fishery catch in Lake Liambezi prior to it drying up, half of which was *O. andersonii* (van der Waal, 1980). The current commercial catch composition is similar, with *O. andersonii* perhaps playing an even more important role (Ministry of Fisheries and Marine Resources, unpublished data). In the Zambezi and Kavango Rivers, the tilapiines were less important than in Lake Liambezi, but were still a major component of the fisheries (van der Waal, 1990, 1991). *Oreochromis andersonii* accounted for one third of catches in the eastern Caprivi (van der Waal, 1990) and one quarter of catches in the Kavango River (van der Waal, 1991). Despite their importance in commercial and subsistence fisheries, the probability of capture and CPUE of the tilapiines in experimental gillnets was low in all systems. Low probabilities of capture are normally obtained when sampling rare species or species with low vulnerability to sampling gears (Maunder & Punt, 2004). As tilapiine cichlids are a major component of the fisheries in the region, it can be assumed that the species are not rare, especially in unfished areas such as those sampled on the Kavango and Kwando Rivers. *Tilapia rendalli* are suspected to evade capture in stationary gillnets (Karenge & Kolding, 1995a; Kenmuir, 1984). The low probability of capture of *T. rendalli*, as well as *O. andersonii* and *O. macrochir*, can potentially be partly explained by their low vulnerability to experimental gillnets.

The probability of capture (PC) of *O. andersonii* was highest in Lake Liambezi and in the Kwando River. This indicates that population densities of *O. andersonii* in Lake Liambezi and the Kwando River were significantly higher than in the Kavango and Zambezi Rivers. Similarly, the PC of *O. macrochir* was highest in the Kwando River and in Lake Liambezi. The PC of *T. rendalli* was significantly higher in Lake Liambezi compared to the other systems and was lowest in the Zambezi River. The CPUE of *O. andersonii* and *O. macrochir* was highest in the Kwando River and second highest in Lake Liambezi. The average size of *O. andersonii* caught in the Kwando River was greater than in Lake Liambezi as indicated by the greater CPUE in the Kwando River. CPUE of *O. macrochir* was very low in the Kavango River, despite the sampling area in the Kavango being in an unfished area. PC and CPUE of all three tilapiines were very low in the Zambezi River, possibly as a result of heavy exploitation by subsistence and commercial gillnet fisherman.

CPUE and therefore the PC is density dependent in river-floodplain environments (Bokhutlo, 2011; Welcomme, 1979; de Merona, 1990). The PC and CPUE of the tilapiines in the Kavango and Zambezi Rivers was lower than in the Kwando River and Lake Liambezi as a result of greater variations in fish densities associated with flooding. Although Lake Liambezi is heavily exploited like the Zambezi River, the PC and CPUE of the tilapiines in Lake Liambezi was relatively high when compared to the Zambezi River. Tilapiine cichlids prefer still waters such as backwater and lagoon habitats (Winemiller & Kelso-Winemiller, 2003). The area of suitable habitat available to the tilapiines relative to other habitats is much greater in Lake Liambezi compared to the river systems. The high productivity of the recently flooded lake environment coupled with large areas of suitable breeding and feeding habitat may account for the high PC and CPUE of the tilapiines in Lake Liambezi.

Selectivity

Currently, the minimum legal gillnet mesh size under the regulations for the Inland Fisheries Resources Act in Namibia is 3” (76mm). This corresponds to peak selectivity modes of roughly 190 mm for *O. macrochir* and 200 mm for *O. andersonii* and *T. rendalli* (Table 4.9). *Oreochromis macrochir* is a relatively shorter and deeper bodied fish than *O. andersonii* and *T. rendalli*, resulting in a smaller length at maximum selectivity. Gillnet selectivity is discussed in relation to the biology of *O. andersonii*, *O. macrochir* and *T. rendalli* (Chapter 5) in Chapter 6.

Conclusion

The first sign of overfishing in complex, multi-species fisheries is often the collapse of specific stocks, while the fish assemblage as a whole continues to produce at a high level (Allan et al., 2005; Murawski, 2000; Welcomme, 1999). Species richness and diversity in the Kavango, Kwando and Zambezi River systems was very similar, while species composition differed slightly. Diversity between fished and unfished areas in the different systems was similar, possibly because increased fishing effort in the Zambezi River is relatively recent and the fishery still targets the largest, most valuable cichlid species in the assemblage. This indicates that “fishing down” may not have occurred yet and that overfishing, from an ecosystem perspective (Murawski, 2000), may not yet be taking place. Species richness and diversity were lower in Lake Liambezi because of the rarity of riverine specialists. Catches in the lake were dominated by a few small species. The fish fauna in the lake have undergone significant changes since it began to refill in 2001, and are still different from the community in the lake before it dried in 1985. This suggests that the fish community may still be stabilising after the recent filling of the lake.

High overall CPUE in Lake Liambezi may reflect the high productivity of the recently flooded lake environment. CPUE in the Zambezi River was the lowest of the four systems, most likely as a result of higher levels of exploitation and a reduced biomass of large species. Cichlid abundance in experimental catches was low despite their importance in the fisheries. Cichlids contributed most to experimental catches in the Kwando and Kavango Rivers. CPUE of the tilapiines was highest in the Kwando River and Lake Liambezi and was lowest in the Zambezi River. The current legal minimum mesh size of 3” (76 mm) selects for *O. andersonii, O. macrochir* and *T. rendalli* at a relatively small size. To understand the possible impacts of this requires an understanding of the biology of these species. This is the focus of the next chapter.

CHAPTER 5

Age, growth and reproduction of *Oreochromis andersonii*, *Oreochromis macrochir* and *Tilapia rendalli* in the Kavango, Kwando, Lake Liambezi and Zambezi Rivers in Namibia

5.1 INTRODUCTION

The threespot tilapia, *Oreochromis andersonii,* the greenhead tilapia, *Oreochromis macrochir*, and the redbreast tilapia*, Tilapia rendalli* are three common small-mouthed cichlid species indigenous to the Upper Zambezi and Kavango River systems (Trewavas, 1983). Of the three species, *O. andersonii* has the narrowest natural distribution, occurring in the Kunene, Kavango, Upper Zambezi and Kafue Rivers. In addition to occurring in these systems, *O. macrochir* and *T. rendalli* occur in the Zambian Congo and southern and eastern tributaries of the Congo River respectively. *Tilapia rendalli* is also found in east flowing coastal rivers south to the Phongolo River and in Lakes Malawi and Tanganyika. *Oreochromis andersonii* is the largest of the three species, attaining over 500 mm total length while *O. macrochir* and *T. rendalli* are medium sized, attaining 400 mm total length (Trewavas, 1983).

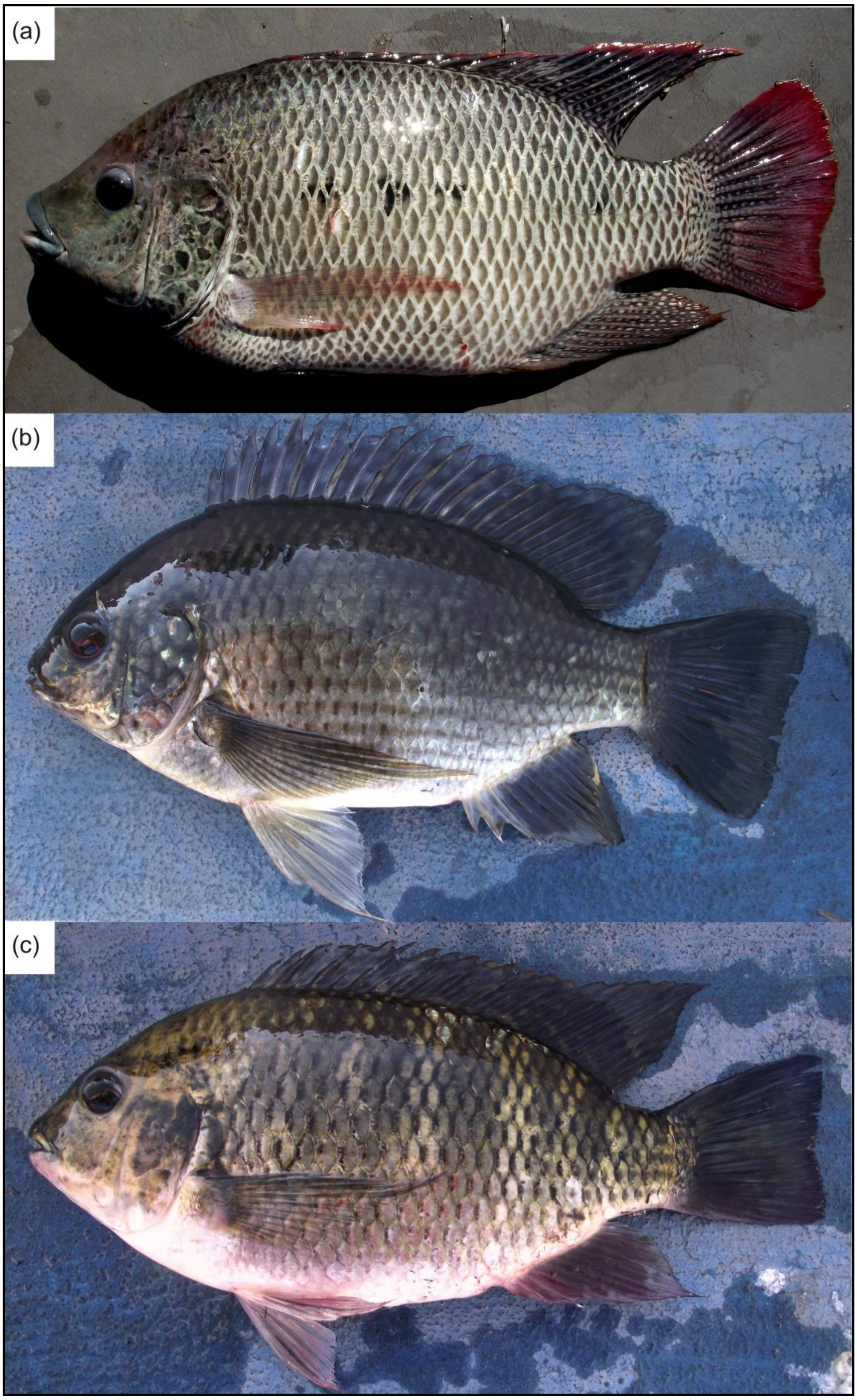

Figure 5.1. The target species, (a) *Oreochromis andersonii*, (b) *Oreochromis macrochir* and (c) *Tilapia rendalli*.

Reproduction is generally in summer, and all three species have extended spawning seasons which last throughout the warmer months, usually from October to April, during which multiple broods may be raised (Merron, 1991; Weyl & Hecht, 1998; van der Waal, 1985). *Oreochromis andersonii* and *O. macrochir* are female mouthbrooders, whilst *T. rendalli* is categorised as a guarder (Balon, 1975). Male *O. andersonii* and *O. macrochir* build saucer-shaped nests on sandy substrates in shallow water, often grouped together in arenas, which they then defend (Merron, 1991; van der Waal, 1985). Spawning takes place in the nest with successive receptive females which then mouthbrood the eggs and fry for approximately one month before releasing them into shallow floodplain margins (Merron, 1991). Breeding pairs of *T. rendalli* clear vegetation and excavate nests with tunnel like brood chambers in shallow water (Weyl & Hecht, 1998; van der Waal, 1985). Eggs are deposited into the brood chambers where they are fertilised and the eggs and larvae are guarded and fanned by both parents (Bruton & Kok, 1980; van der Waal, 1985).

Winemiller and Kelso-Winemiller (2003) reported a high degree of habitat overlap for these three species in the Upper Zambezi River. Larger individuals of all three species are habitat generalists, but prefer still waters such as backwaters and floodplain lagoons while juveniles remain inshore, seeking refuge from predators among marginal vegetation (Winemiller & Kelso-Winemiller, 2003). All three species are omnivorous: *O. andersonii* and *O. macrochir* feed predominantly on vegetative detritus while *T. rendalli* feed mainly on aquatic macrophytes (Merron, 1991; Winemiller & Kelso-Winemiller, 2003).

Life history traits including growth rate and length and age at maturity have been shown to differ between populations of conspecific cichlids (Booth & Merron, 1996; Booth et al., 1995; Dudley, 1974; James & Bruton, 1992; Kapetsky, 1974; Weyl & Hecht, 1998; van der Waal, 1985). Growth rates and size at maturity, differ between populations as a result of environmental variability experienced by each population (James & Bruton, 1992; Merron, 1991). Human-induced changes in life history may also occur as a result of intensive harvesting (Enberg et al., 2011; Ernande, Dieckmann, & Heino, 2004). As the biotic and abiotic environment and the harvest intensity differ markedly between systems, it was necessary to investigate the locality specific biology of *O. andersonii*, *O. macrochir* and *T. rendalli* in the Kavango, Kwando, Lake Liambezi and Zambezi Rivers.

The aim of this chapter was to test whether growth rates, length-at-maturity and age-at-maturity differed between populations of *O. andersonii*, *O. macrochir* and *T. rendalli* in the Kavango, Kwando, Lake Liambezi and Zambezi Rivers in Namibia.

5.2 MATERIALS AND METHODS

General sampling

Samples of *O. andersonii*, *O. macrochir* and *T. rendalli* were taken during bi-monthly experimental gillnetting surveys as described in Chapter 4. Because of the low abundance of the target species in experimental gillnets (see Chapter 4), samples were supplemented in several ways. On the Zambezi River and in Lake Liambezi, where commercial fisheries exist, samples were purchased from local fishermen at major landing sites during routine field trips. On the Kavango and Kwando Rivers, where the areas sampled were protected and hence no commercial fisheries exist, additional samples were caught using 3½ and 4 inch monofilament gillnets as used by many commercial fishermen in the region. Samples were also obtained at angling competitions on the Zambezi River and Lake Liambezi, and by angling during routine field trips. Samples of smaller specimens were supplemented using a 10 m long x 2 m deep seine net with a 5 mm mesh size. The number of specimens taken by sampling type are summarised in Table 5.1.

Table 5.1. Number of specimens of *Oreochromis andersonii*, *Oreochromis macrochir* and *Tilapia rendalli* by sampling type in the Kavango, Kwando, Lake Liambezi and Zambezi Rivers, Namibia.

Sampling type	Kavango	Kwando	Liambezi	Zambezi
Experimental gillnet				
O. andersonii	6	43	25	2
O. macrochir	2	55	11	2
T. rendalli	10	14	34	2
Monofilament gillnet				
O. andersonii	78	87	40	-
O. macrochir	35	178	12	-
T. rendalli	39	176	22	-
Seine net				
O. andersonii	-	10	-	-
O. macrochir	10	4	8	6
T. rendalli	5	-	-	11
Purchased from fishermen				
O. andersonii	-	-	292	141
O. macrochir	-	-	220	71
T. rendalli	-	-	172	102
Angling competitions				
O. andersonii	-	-	16	44
O. macrochir	-	-	-	-
T. rendalli	-	-	39	3
Angling				
O. andersonii	18	16	-	-
O. macrochir	1	2	-	-
T. rendalli	8	46	5	-

Specimens were measured to the nearest millimetre total length (TL) and standard length (SL) and weighted to the nearest gram. Fishes were dissected, sexed and the stage of maturity determined macroscopically according to the criteria outlined in Weyl and Hecht (1998) (Table 5.2). Ovaries were removed from all females larger than the length-at-50% maturity and weighed to the nearest 0.1 gram, and the eviscerated mass of each female fish was measured to the nearest gram. Sagittal otoliths were removed, dried and stored in Eppendorf tubes for later age estimation.

Age and growth

Otolith preparation and interpretation

Otolith preparation and interpretation followed techniques used in previous studies on the target species (Booth & Merron, 1996; Booth et al., 1995; Weyl & Hecht, 1998). In previous studies otoliths were burnt over a low intensity ethanol flame to enhance the visibility of growth zones on the otolith. A sample of 30 pairs of otoliths from fish sampled from Lake Liambezi (15 *O. andersonii*, 5 *O. macrochir* and 10 *T. rendalli*) were randomly selected and prepared to determine whether burning the otoliths was necessary. One otolith from each pair was burnt until it turned pale brown, taking care not to char the otolith and obscure the internal structure and margins (Booth & Merron, 1996) and the second was left unburnt.

Otoliths were then mounted medial side down in clear polyester casting resin and sectioned transversely through the nucleus using a double-bladed diamond-edged saw at a thickness of 0.3-0.4 mm. Sections were mounted on microscope slides using DPX mountant and viewed using a compound light microscope under transmitted light at 10-40 × magnification. Examination of the sectioned pairs of otoliths indicated that growth zones were more clearly visible in unburnt otoliths, and it was decided that burning was unnecessary and all fishes were aged without burning the otoliths.

Growth zones were visible as alternating translucent and opaque zones. The number of growth zones was determined by counting the numbers of opaque zones from the nucleus to the margin of the otolith (Figure 5.2). All otoliths were read twice by two independent readers without knowledge of the date of capture or the length of the fish. If the two readings were the same, the count was accepted. If the readings differed a third was taken and if two readings were the same the count was accepted. If the three counts differed at most by two growth zones (e.g. 1, 2, 3), the median estimate was accepted. If a count could not be assigned to an otolith this otolith was rejected as unreadable.

Accuracy and precision

Edge analysis was used to indirectly estimate the periodicity of growth zone formation in sagittal otoliths. The outer edge of sectioned otoliths from fishes caught during bi-monthly surveys of each system was assessed and recorded as either optically opaque (1) or translucent (0). The number of opaque and translucent edges was then expressed as a percentage of the monthly sample and plotted against time.

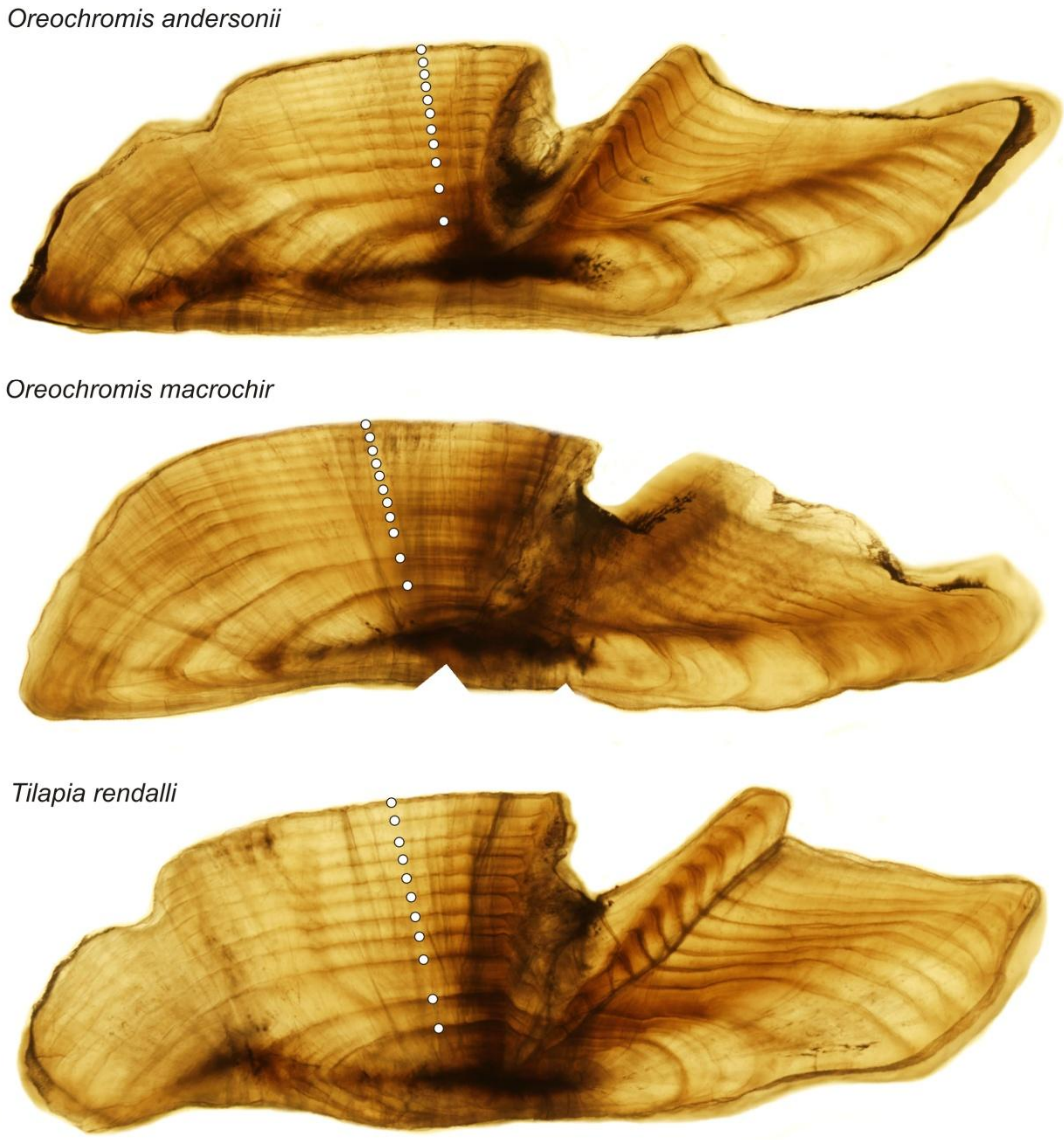

Figure 5.2. Photomicrographs using transmitted light showing sagittal otoliths from a 415 mm TL, 11 year old *Oreochromis andersonii*, a 260 mm TL, 11 year old *Oreochromis macrochir* and a 333 mm TL, 11 year old *Tilapia rendalli* sampled from the Kwando River, Namibia. Note the opaque margin on each otolith.

The precision of growth zone counts was assessed using the average percent error (APE) method (Beamish & Fournier, 1981) and by estimating the coefficient of variation (CV) and index of precision (D) (Chang, 1982). APE is calculated as:

$$\mathrm{APE}_j = 100 \times \frac{1}{R} \sum_{i=1}^{R} \frac{(X_{ij} - X_j)}{X_j}$$

where R is the number of times fish j has been aged, Xij is the ith age determination of the jth fish and Xj is the mean age estimate of the jth fish. APE was averaged across all fish to give an index of average percent error. The CV between age estimates was calculated as:

$$\mathrm{CV}_j = 100 \times \frac{\sqrt{\sum_{i=1}^{R} \frac{(X_{ij} - X_j)^2}{R-1}}}{X_j}$$

where CV_j is the age precision estimate for the jth fish. The CV was averaged across all fish to produce a mean CV. D was then calculated as:

$$\mathrm{D}j = \frac{\mathrm{CV}_j}{\sqrt{R}}$$

Modelling growth

Length-at-age data was described by fitting the three-parameter von-Bertalanffy growth function of the form:

$$L_t = L_\infty (1 - \exp(-K(t - t_0)))$$

where L_∞ is the predicted asymptotic length, K is the Brody co-efficient (Ricker, 1975) and t_0 is the theoretical age at zero length.

Parameters were estimated by minimising the negative log likelihood of the form:

$$-LL = n\ln(\hat{\sigma})$$

where $\hat{\sigma}$ is the maximum likelihood estimate of the model standard deviation, described as:

$$\hat{\sigma} = \sqrt{\frac{\sum_i (L_i - \hat{L}_i)^2}{n}}$$

where L_i is the observed length at age, $\hat{L}_i$ is the predicted length-at-age and n is the total number of observations. Standard deviations of the model parameters were estimated using parametric bootstap resampling (Efron, 1982) with 1000 iterations. Likelihood ratio tests were used to test the null hypothesis that growth was equal between sexes and between populations at a significance level of $p \leq 0.05$. A one-way ANOVA was used to test for differences in observed mean lengths-at-age between systems up to age 4+.

The relationship between weight and total length was described by the power relationship as:

$$W = aL^b$$

where W is the weight (g) and L is the total length (mm) and a and b are the model parameters.

Phi-prime (ϕ') (Pauly and Munro, 1984) was used to compare the growth performance of each population of *O. andersonii*, *O. macrochir* and *T. rendalli*. Phi-prime is described by the equation of the form:

$$\phi' = 2\log L_{\infty} + \log K$$

where L_{∞} is the predicted asymptotic length and K the Brody growth co-efficient from the von Bertalanffy growth model. Phi-prime takes into account the interaction and dependence between the von Bertalanffy growth parameters, L_{∞} and K.

Reproductive biology

Length and age at maturity

Reproductive biology was assessed using techniques outlined in Weyl and Hecht (1998). Samples of *O. andersonii, O. macrochir* and *T. rendalli* were collected during the peak spawning season from October to January to determine the mean length-at-50% maturity (Lm_{50}). Male and female length and age at maturity data were combined as samples sizes were too small to accurately estimate length and age at 50% maturity separately for each sex. Fish were considered mature if they were assigned a gonadal development stage from 3–5 (developing, ripe or spent) according to the criteria summarised in Table 5.2. Length at maturity was expressed as the proportion of mature fish in each 10 mm size class (L) and Lm_{50} was estimated by fitting these data to a two-parameter logistic model of the form:

$$\psi_L = \frac{1}{1 + \exp^{-(L - Lm_{50})/\delta}}$$

where ψ_L is the predicted proportion of mature fish at length L and δ the width of the logistic ogive. Age at maturity was described using age estimates from sectioned otoliths from fish sampled during the peak spawning season and was expressed as the proportion of mature fish per age class. Age-at-50% maturity (tm_{50}) was estimated by fitting the same logistic model used to estimate Lm_{50}. Maximum likelihood estimates of the parameters were obtained by minimising the negative log-likelihood of the form:

$$-LL = -\sum_i \left[m_i \ln(\hat{P}_i) + (n_i - m_i) \ln(1 - \hat{P}_i) \right]$$

where $\hat{P}_i$ is the predicted proportion of mature fish in length class i, n_i is the number of individuals and m_i is the number of these individuals that are mature. Likelihood ratio tests were used to test the null hypothesis that Lm_{50} and tm_{50} were equal between populations at a significance level of $p \leq 0.05$.

Spawning periodicity

Temporal patterns in reproductive activity were assessed using the five-stage gonadal development scale (Table 5.2) by plotting the proportion of maturity stages per sampling month and by calculating the gonadosomatic index (GSI) for females > Lm_{50}. Data from each system were combined as sample sizes were too low to accurately describe reproductive seasonality separately for each system. GSI was used to determine spawning season and was calculated as:

$$GSI = \left[\frac{Gonad\ mass\ (g)}{Eviscerated\ mass\ (g)}\right] \mathrm{x}\,100$$

The eviscerated mass of female fishes was used to minimise bias from variable gut fullness. The sex ratio of adult fishes was determined and compared to a 1:1 ratio using χ^2 contingency tables at a significance level of $p \leq 0.05$.

Table 5.2. Macroscopic criteria used to determine gonadal development stages in *Oreochromis andersonii*, *Oreochromis macrochir* and *Tilapia rendalli* (after Weyl & Hecht, 1998) from the Kavango, Kwando, Lake Liambezi and Zambezi Rivers, Namibia.

Stages	**Gonad appearance**
1 - Juvenile	Gonads present as a thin translucent strip. Unable to determine sex macroscopically.
2 - Resting	Sex distinguishable. Ovaries white or yellowish. Oocytes macroscopically distinguishable. Testes appear as thin white bands.
3 - Developing	Ovaries enlarged, oocytes readily visible and yellow. Testes broadened, distended and cream in colour.
4 - Ripe	Oocytes of maximum size, dull yellow in colour in *O. andersonii* and dark olive green in *T. rendalli*. Testes white and swollen to maximum size.
5 - Spent	Ovaries flaccid with irregular oocyte size. Testes reduced in size and dirty grey in colour.

5.3 RESULTS

Length-frequency

Oreochromis andersonii

Length-frequency distributions by sex are illustrated for each system in Figure 5.3. Sampled fish ranged from 116 to 530 mm TL in the Kavango River, 86 to 415 mm

TL in the Kwando River, 112 to 380 mm TL in Lake Liambezi and 114 to 505 mm TL in the Zambezi River.

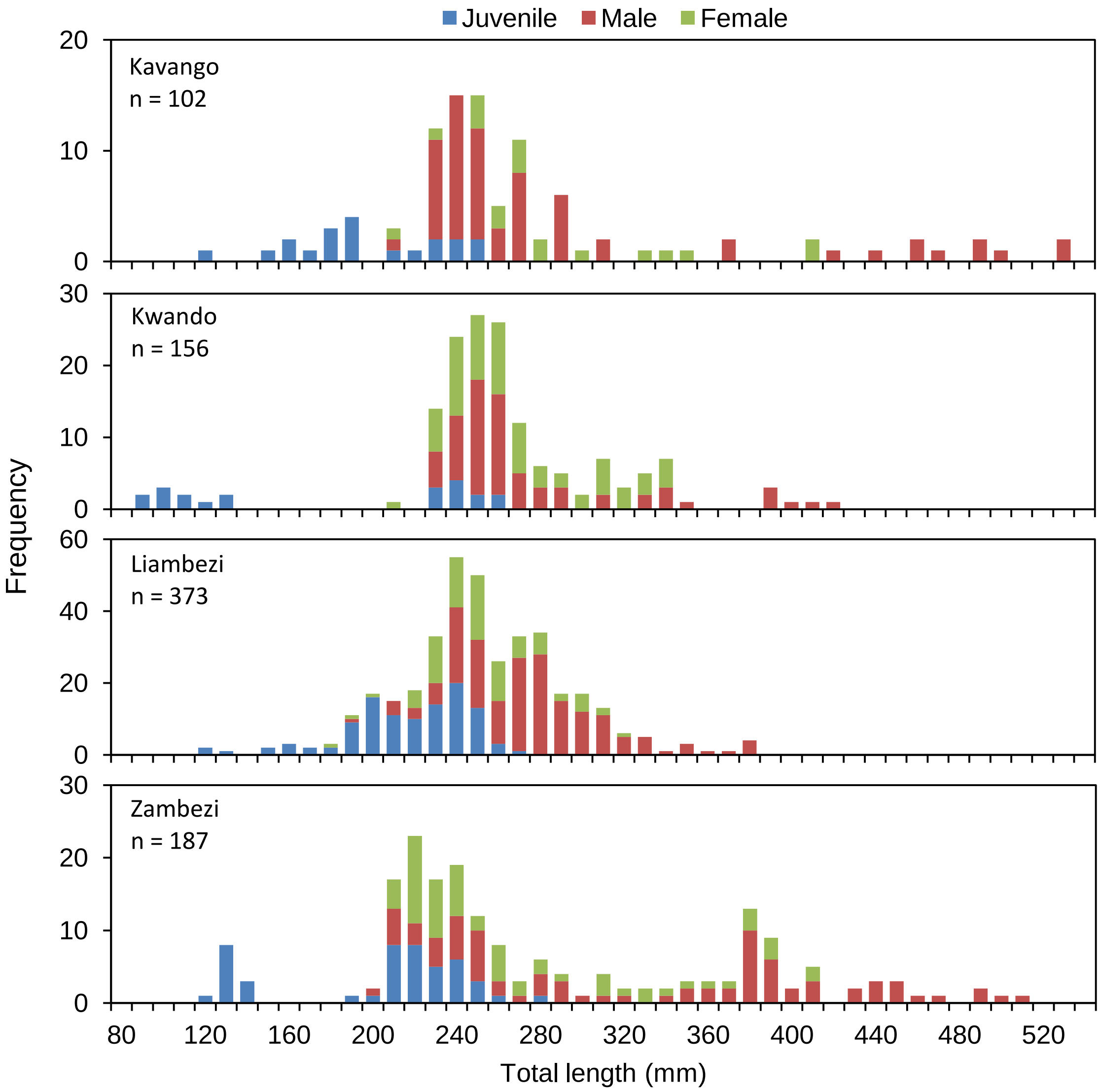

Figure 5.3. Length-frequency distributions of *Oreochromis andersonii* sampled in the Kavango, Kwando, Lake Liambezi and Zambezi Rivers, Namibia between April 2010 and September 2011.

Oreochromis macrochir

Length-frequency distributions by sex are illustrated for each system in Figure 5.4. Sampled fish ranged from 45 to 356 mm TL in the Kavango River, 83 to 331 mm TL in the Kwando River, 92 to 295 mm TL in Lake Liambezi, and 65 to 438 mm TL in the Zambezi River.

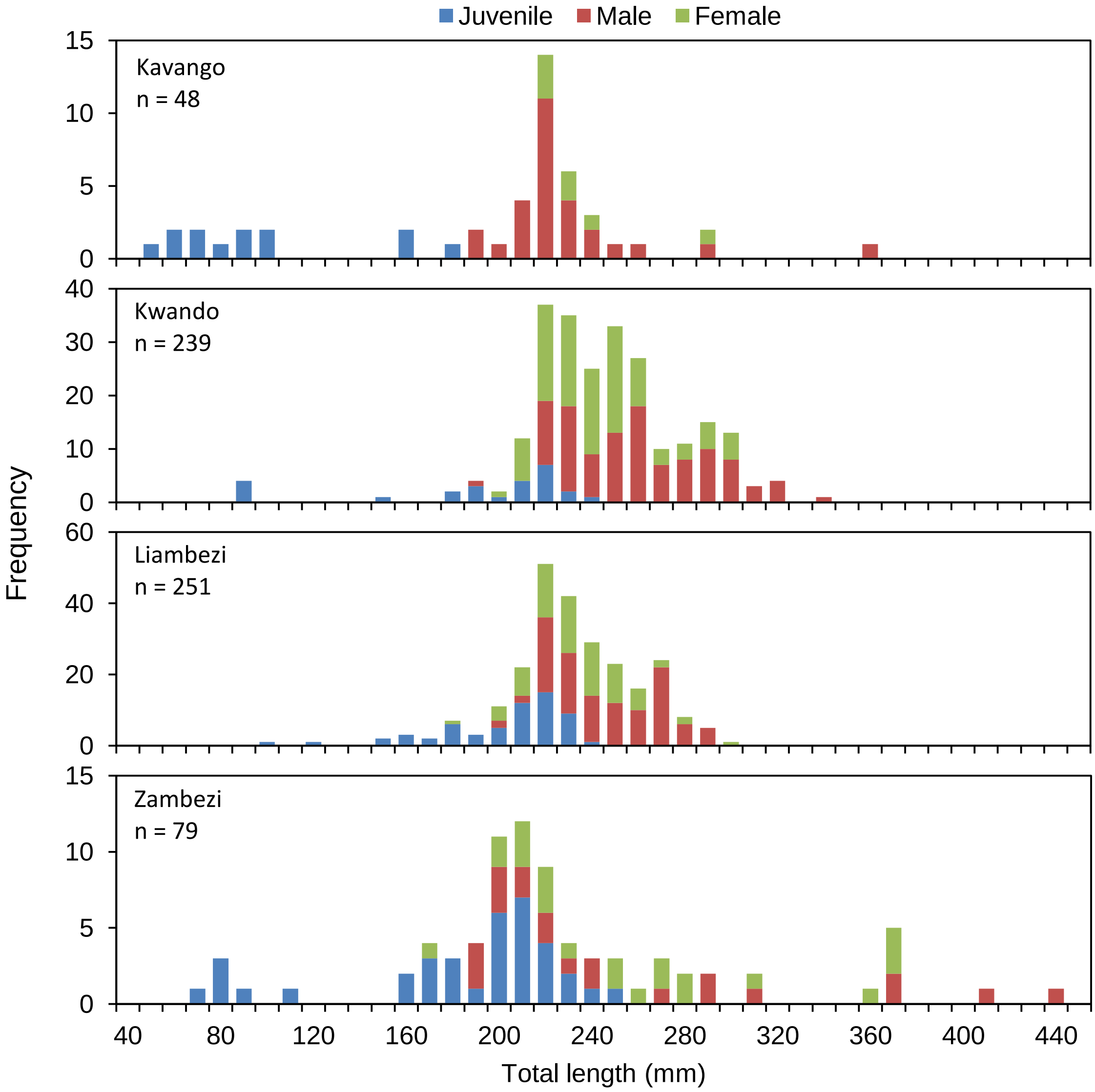

Figure 5.4. Length-frequency distributions of *Oreochromis macrochir* sampled in the Kavango, Kwando, Lake Liambezi and Zambezi Rivers, Namibia between April 2010 and September 2011.

Tilapia rendalli

Length-frequency distributions by sex are illustrated for each system in Figure 5.5. Sampled fish ranged from 105 to 367 mm TL in the Kavango River, 57 to 367 mm TL in the Kwando River, 124 to 322 mm TL in Lake Liambezi, and 46 to 379 mm TL in the Zambezi River.

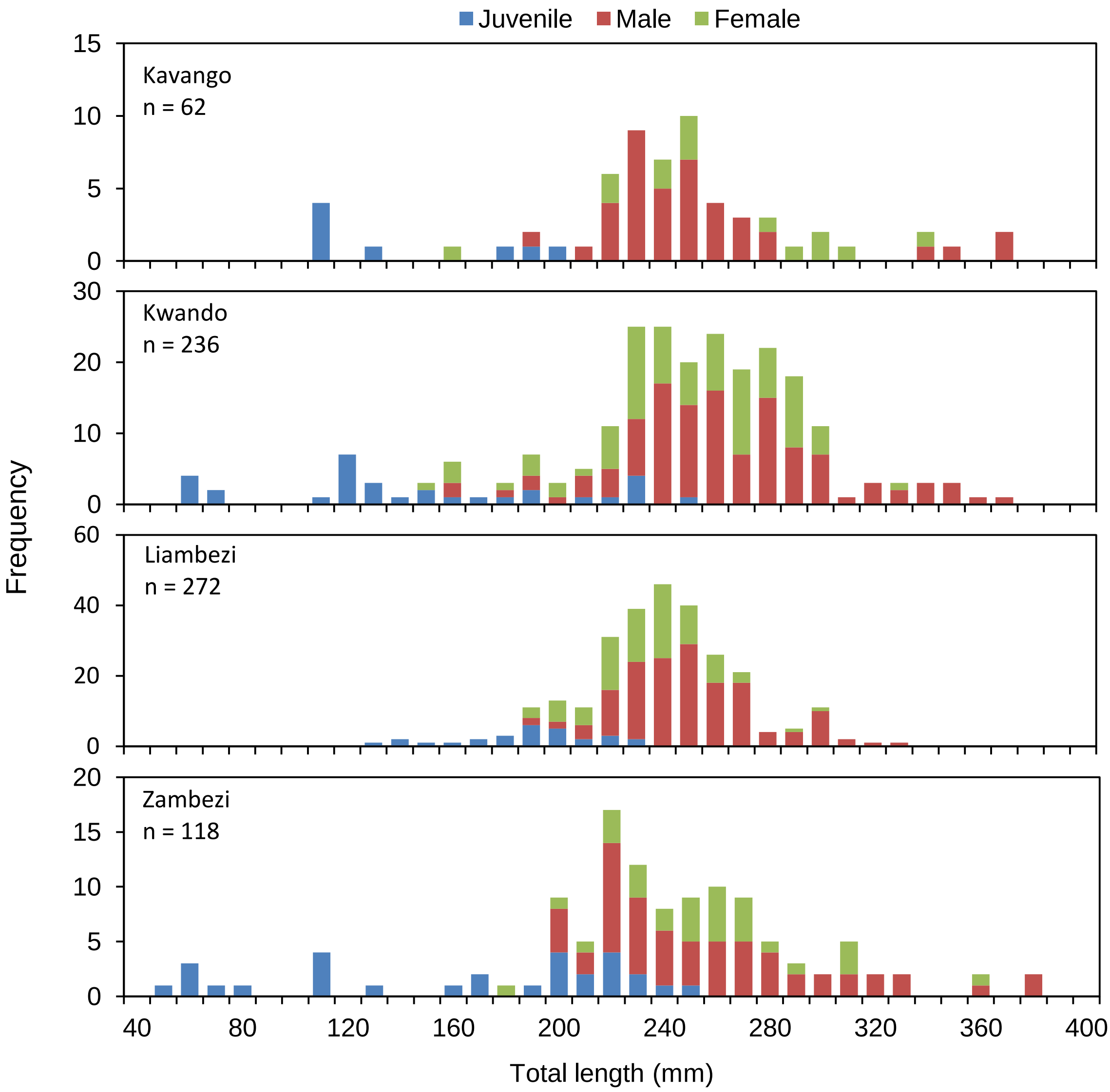

Figure 5.5. Length-frequency distributions of *Tilapia rendalli* sampled in the Kavango, Kwando, Lake Liambezi and Zambezi Rivers, Namibia between April 2010 and September 2011.

Morphometric relationships

Morphometric relationships between total length and weight and total length and standard length are summarised in Table 5.3.

Table 5.3. Morphometric relationships of *Oreochromis andersonii*, *Oreochromis macrochir* and *Tilapia rendalli* sampled in the Kavango, Kwando, Lake Liambezi and Zambezi Rivers, Namibia. Wt = weight, TL = total length, SL = standard length.

		Relationship	r^2	n
O. andersonii				
Kavango	Wt (g)	= 0.00002 TL (mm)$^{3.024}$	0.99	102
	SL (mm)	= -4.855 + 0.822 TL (mm)	0.99	102
Kwando	Wt (g)	= 0.000006 TL (mm)$^{3.211}$	0.97	156
	SL (mm)	= - 9.089 + 0.852 TL (mm)	0.99	156
Liambezi	Wt (g)	= 0.00003 TL (mm)$^{2.946}$	0.98	373
	SL (mm)	= -2.131 + 0.823 TL (mm)	0.98	373
Zambezi	Wt (g)	= 0.000008 TL (mm)$^{3.158}$	0.99	186
	SL (mm)	= -0.346 + 0.815 TL (mm)	0.99	186
O. macrochir				
Kavango	Wt (g)	= 0.00001 TL (mm)$^{3.091}$	0.96	39
	SL (mm)	= -14.54 + 0.856 TL (mm)	0.99	39
Kwando	Wt (g)	= 0.00001 TL (mm)$^{3.088}$	0.98	240
	SL (mm)	= -8.272 + 0.851 TL (mm)	0.98	240
Liambezi	Wt (g)	= 0.00002 TL (mm)$^{3.041}$	0.97	257
	SL (mm)	= 0.335 + 0.804 TL(mm)	0.96	257
Zambezi	Wt (g)	= 0.000008 TL (mm)$^{3.1842}$	0.99	74
	SL (mm)	= -9.320 + 0.855 TL (mm)	0.99	74
T. rendalli				
Kavango	Wt (g)	= 0.000004 TL (mm)$^{3.328}$	0.98	62
	SL (mm)	= -6.414 + 0.828 TL (mm)	0.99	62
Kwando	Wt (g)	= 0.00002 TL (mm)$^{3.021}$	0.99	236
	SL (mm)	= -5.761 +0.852 TL (mm)	0.99	236
Liambezi	Wt (g)	= 0.00002 TL (mm)$^{3.039}$	0.97	272
	SL (mm)	= -0.508 + 0.819 TL (mm)	0.97	272
Zambezi	Wt (g)	= 0.000003 TL (mm)$^{3.36}$	0.99	118
	SL (mm)	= -5.447 + 0.847 TL(mm)	0.99	118

Age and growth

Age Validation

The frequency distribution of opaque and hyaline zones on the edge of the otoliths of *O. andersonii*, *O. macrochir* and *T. rendalli* was unimodal (Figure 5.6). Therefore, one opaque and one hyaline zone were deposited annually in the otoliths of each species and pairs of opaque and hyaline zones were considered as annuli and were used to estimate the age of fish. No difference in the timing of the opaque zone deposition was found between systems for each species so data from the four systems were combined. Peak opaque zone deposition was in December for all three species. In *O. andersonii*, opaque margins on otoliths were recorded in summer between October and January. Opaque margins were recorded over a longer period in *O. macrochir* from September till March, and in *T. rendalli* opaque margins were recorded between September and January.

Ageing precision

Precision estimates between otolith readings are summarised in Table 5.4. Precision between readings was high for all species in the Kavango and Kwando Rivers and for *O. andersonii* in the Zambezi River (APE = 2.1-7.0; CV = 3.4-11.9). Precision was low for all species in Lake Liambezi and for *O. macrochir* and *T. rendalli* in the Zambezi River (APE > 10.8; CV > 12.9). No otoliths were rejected.

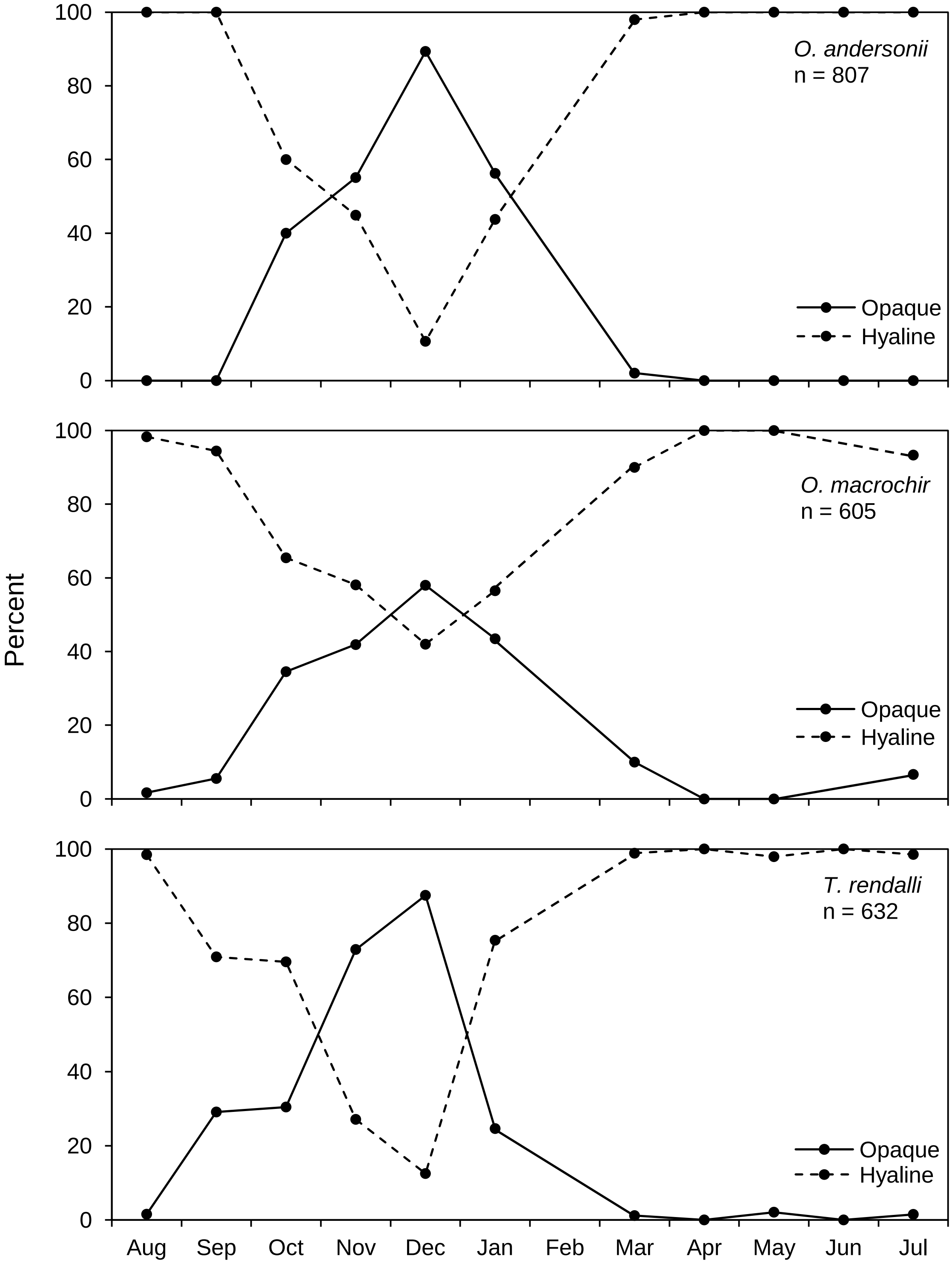

Figure 5.6. Monthly percentage occurrence of opaque and hyaline margins on otoliths of *Oreochromis andersonii, Oreochromis macrochir* and *Tilapia rendalli* sampled between August 2010 and July 2011 in the Kavango, Kwando, Lake Liambezi and Zambezi Rivers, Namibia.

Table 5.4. Average percent error (APE), coefficient of variation (CV) and index of precision (D) between otolith readings, and mean ages of *Oreochromis andersonii*, *Oreochromis macrochir* and *Tilapia rendalli* sampled in the Kavango, Kwando, Lake Liambezi and Zambezi Rivers, Namibia between April 2010 and September 2011.

	APE	CV	D	n	Mean Age
O. andersonii					
Kavango	2.08	3.43	1.98	102	2.44
Kwando	3.72	8.20	4.73	146	4.00
Liambezi	17.02	18.63	10.76	335	1.37
Zambezi	6.15	9.75	5.63	187	2.17
O. macrochir					
Kavango	5.06	8.17	4.71	38	1.91
Kwando	4.24	10.56	6.10	239	4.29
Liambezi	10.77	13.63	7.87	251	1.38
Zambezi	10.45	12.85	7.42	74	1.88
T. rendalli					
Kavango	6.98	11.92	6.88	57	2.05
Kwando	3.99	6.96	4.02	236	4.52
Liambezi	16.51	21.12	12.19	231	1.11
Zambezi	13.50	18.64	10.76	108	2.28

Precision between readings by age class (Table 5.5) were compared because of the high variation in total precision between systems (Table 5.4). Precision varied considerably in younger year classes (0 and 1) as a result of differences in sample sizes and was generally low, but comparable between systems and species. Precision in older year classes (2, 3 and 4+) was higher and comparable between systems and species.

Table 5.5. Average percent error (APE) between otolith readings by age class (0 - 4+) of *Oreochromis andersonii, Oreochromis macrochir* and *Tilapia rendalli* sampled in the Kavango, Kwando, Lake Liambezi and Zambezi Rivers, Namibia between April 2010 and September 2011.

	APE by age class									
	0	n	1	n	2	n	3	n	4+	n
O. andersonii										
Kavango	0.00	1	4.17	24	1.87	57	0.00	8	0.51	12
Kwando	-	-	33.33	1	7.62	26	2.96	71	2.12	48
Liambezi	79.63	36	12.14	151	6.97	138	3.75	8	5.13	2
Zambezi	0.00	2	10.95	67	5.06	64	3.33	18	0.96	36
O. macrochir										
Kavango	-	-	19.05	7	1.90	28	0.00	1	2.89	2
Kwando	0.00	4	4.76	7	9.22	28	4.63	59	3.18	141
Liambezi	42.42	22	7.86	168	7.34	59	8.33	2	-	-
Zambezi	80.00	5	10.56	24	2.99	28	0.00	2	2.42	15
T. rendalli										
Kavango	0.00	2	11.90	14	5.89	36	0.00	1	4.64	4
Kwando	33.33	8	22.22	9	5.29	18	1.45	78	2.15	123
Liambezi	63.77	23	16.57	101	6.42	103	4.44	3	0.00	1
Zambezi	88.89	6	8.69	46	12.89	34	3.81	7	0.04	15

Growth

Oreochromis andersonii

Oreochromis andersonii reached maximum ages of 12, 12, 4 and 6 years in the Kavango, Kwando, Lake Liambezi and Zambezi Rivers respectively. The von Bertalanffy growth model parameter estimates are presented in Table 5.6. For combined sexes and males in Lake Liambezi and combined sexes and females in the Zambezi River the model failed to determine asymptotic lengths for the available data. The best model fit therefore approximated linear growth. Asymptotic lengths predicted for females and males from Lake Liambezi and the Zambezi River respectively were also unrealistically high, indicating that there were insufficient old fish in the sample that had attained asymptotic length.

Fitted von Bertalanffy growth curves for male and female *O. andersonii* are presented in Figure 5.7. Initial growth rates were rapid, whereafter growth rates in fish older than 3 and 4 years declined in the Kwando and Kavango Rivers respectively. No decline in growth rate was observed in Lake Liambezi or the Zambezi River at maximum ages of 4 and 6 years respectively (Figure 5.7). Likelihood ratio tests showed that growth differed significantly between males and females in the Kwando River, Lake Liambezi and the Zambezi River ($p < 0.05$), with males attaining a larger maximum size than females. Growth for combined sexes differed significantly between all systems (likelihood ratio tests, $p < 0.05$). Growth performance of combined sexes was best in the Zambezi River ($\phi' = 5.76$), followed by Lake Liambezi ($\phi' = 5.65$), the Kavango River ($\phi' = 4.78$) and the Kwando River ($\phi' = 4.59$) (Table 5.6).

Observed mean lengths-at-age are summarised in Table 5.7. Observed mean length-at-age 1+ and 2+ was significantly larger in Lake Liambezi compared to the Kavango, Kwando and Zambezi Rivers. At age 3+ mean length was significantly larger in the Zambezi River. Mean length in the Kavango River and Lake Liambezi differed by only a few millimetres, and the Kwando River was significantly smaller. At age 4+ mean length was significantly larger in the Zambezi River and Lake Liambezi compared to the Kwando River.

Table 5.6. Parameter estimates and standard deviations (SD) of combined sex, male and female length-at-age data fitted using the von Bertalanffy growth model for *Oreochromis andersonii* sampled in the Kavango, Kwando, Lake Liambezi and Zambezi Rivers, Namibia between April 2010 and September 2011.

Parameters	L_∞ (±SD)	K (±SD)	t_0 (±SD)	ϕ'
Kavango				
Combined sexes	606.3 (37.4)	0.163 (0.026)	-1.01 (0.27)	4.78
Males	607.2 (36.0)	0.164 (0.026)	-0.94 (0.26)	4.78
Females	513.4 (76.1)	0.229 (0.074)	-0.64 (0.33)	4.78
Kwando				
Combined sexes	343.8 (12.6)	0.329 (0.038)	-0.49 (0.16)	4.59
Males	410.6 (12.2)	0.244 (0.020)	-0.56 (0.14)	4.61
Females	331.2 (6.0)	0.343 (0.022)	-0.38 (0.10)	4.58
Liambezi				
Combined sexes	10000 (1.6)	0.005 (0.0)	-3.65 (0.27)	5.65
Males	10000 (3.5)	0.005 (0.0)	-3.09 (0.26)	5.65
Females	1798 (9496)	0.023 (0.139)	-4.25 (2.41)	4.87
Zambezi				
Combined sexes	10000 (2.9)	0.006 (0.0)	-2.20 (0.16)	5.76
Males	904.5 (248.7)	0.104 (0.046)	-0.97 (0.35)	4.93
Females	10000 (1.2)	0.005 (0.0)	-2.55 (0.28)	5.70

Table 5.7. Observed mean lengths-at age (± standard deviation) for combined sex *Oreochromis andersonii* from the Kavango, Kwando, Lake Liambezi and Zambezi Rivers, Namibia. Different letters denote significant differences in mean lengths-at-age between systems up to age 4+ (ANOVA, $p \leq 0.05$).

Age (years)	Kavango	Kwando	Liambezi	Zambezi
1+	216 (49.9)^{a}		238.8 (23.4)^{b}	208.9 (38.1)^{a}
2+	248 (20.5)^{a}	242.4 (15.6)^{a}	272.2 (28.2)^{b}	256.5 (43.1)^{a}
3+	316 (51.8)^{a}	245.6 (12.2)^{b}	313.1 (40.1)^{a}	359.3 (44.8)^{c}
4+	403	279.0 (30.5)^{a}	371.0 (14.3)^{b}	387.2 (39.3)^{b}
5+		282.2 (21.0)		443.7 (34.4)
6+	438 (42.4)	316.6 (20.2)		495.7 (8.1)
7+	463 (29.9)	318.8 (14.9)		
8+				
9+		385		
10+	530	325 (17.3)		
11+		366.9 (39.5)		
12+	525	393		

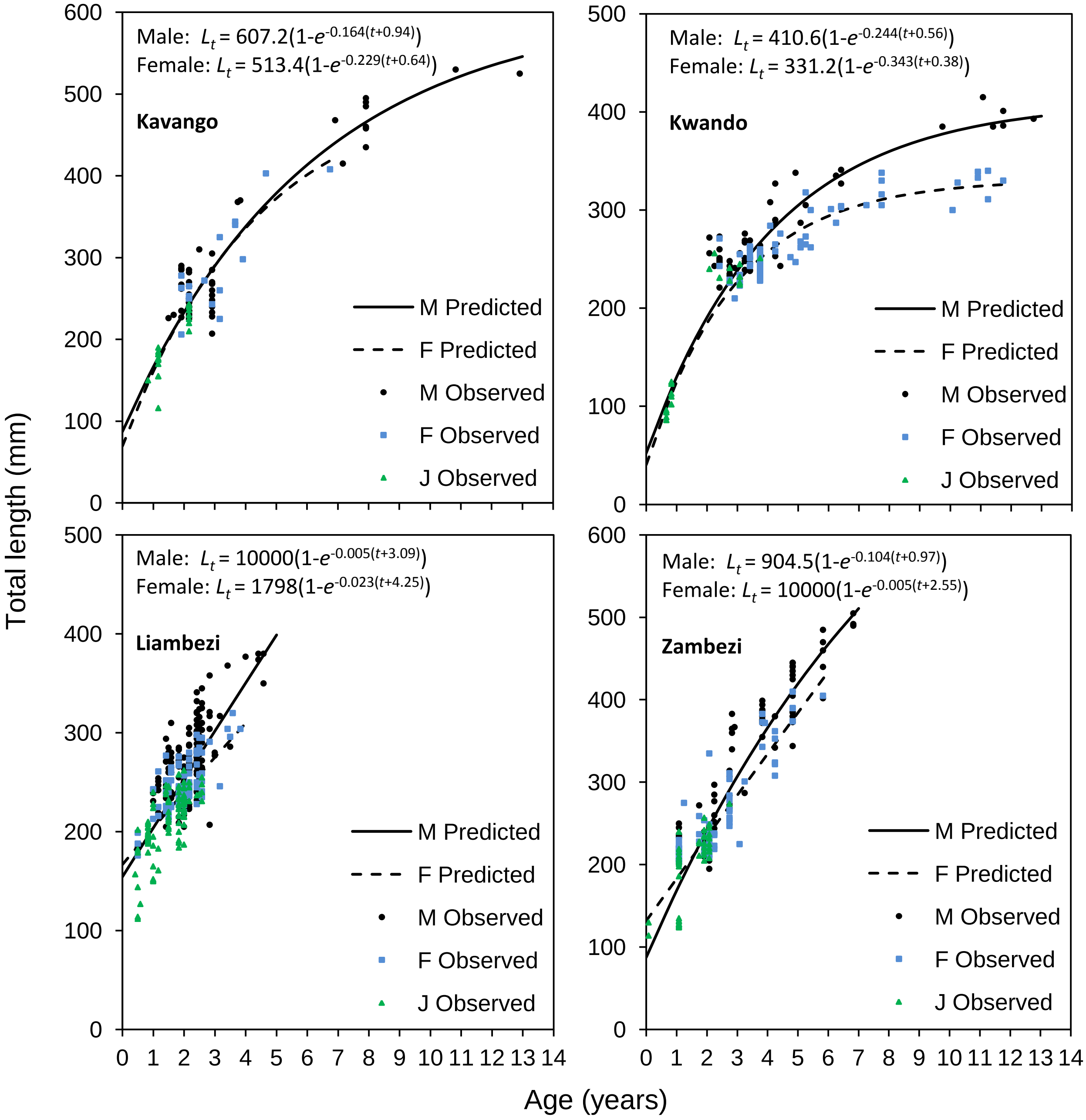

Figure 5.7. Length-at-age data for male and female *Oreochromis andersonii* using sectioned otoliths sampled in the Kavango River, the Kwando River, Lake Liambezi and the Zambezi River, Namibia between April 2010 and September 2011. The growth curves were fitted to the data using the von Bertalanffy growth model.

Oreochromis macrochir

Oreochromis macrochir reached maximum ages of 8, 13, 3 and 11 years in the Kavango, Kwando, Lake Liambezi and Zambezi Rivers respectively. The von Bertalanffy growth model parameter estimates are presented in Table 5.8. Male and Female *O. macrochir* length-at-age data was adequately described using the von Bertalanffy growth model.

Fitted von Bertalanffy growth curves for male and female *O. macrochir* are presented in Figure 5.8. Growth followed a similar pattern in the Kavango, Kwando and Lake Liambezi. Initial growth was rapid, especially in Lake Liambezi and the Kavango River with asymptotic length being reached relatively early in life. Males and females reached asymptotic lengths after 2 years in Lake Liambezi and after 3 years in the Kwando River. In the Kavango River, females reached asymptotic length after 2 years and males after 3 years. In the Zambezi River, initial growth was slower with asymptotic length only being reached after 6 years. Growth differed significantly between males and females in the Kwando River and Lake Liambezi (likelihood ratio tests, $p < 0.05$), with males attaining a larger asymptotic length. Growth for combined sexes differed significantly between all systems (likelihood ratio test, $p < 0.05$). Growth performance of combined sexes was best in Lake Liambezi ($\phi' = 4.81$), followed by the Kavango River ($\phi' = 4.71$), the Zambezi River ($\phi' = 4.59$) and the Kwando River ($\phi' = 4.45$).

Table 5.8. Parameter estimates and standard deviations (SD) of combined sex, male and female length-at-age data fitted using the von Bertalanffy growth model for *Oreochromis macrochir* sampled in the Kavango, Kwando, Lake Liambezi and Zambezi Rivers, Namibia between April 2010 and September 2011.

Parameters	L_∞ (±SD)	K (±SD)	t_0 (±SD)	ϕ'
Kavango				
Combined sexes	286.1 (19.8)	0.630 (0.112)	-0.08 (0.11)	4.71
Males	307.8 (23.4)	0.502 (0.102)	-0.16 (0.13)	4.68
Females	267.9 (15.1)	0.892 (0.174)	0.09 (0.06)	4.81
Kwando				
Combined sexes	280.7 (5.2)	0.355 (0.037)	-1.42 (0.27)	4.45
Males	288.5 (5.9)	0.378 (0.039)	-1.08 (0.23)	4.50
Females	264.2 (4.4)	0.436 (0.042)	-0.98 (0.20)	4.48
Liambezi				
Combined sexes	263.0 (8.8)	0.942 (0.153)	-0.48 (0.18)	4.81
Males	268.5 (16.4)	0.904 (0.195)	-0.48 (0.22)	4.81
Females	256.0 (10.0)	0.846 (0.172)	-0.66 (0.22)	4.74
Zambezi				
Combined sexes	486.2 (54.1)	0.164 (0.034)	-1.55 (0.35)	4.59
Males	507.3 (54.8)	0.167 (0.037)	-1.30 (0.29)	4.63
Females	405.6 (50.0)	0.236 (0.058)	-1.22 (0.34)	4.59

Observed mean lengths-at-age are summarised in Table 5.9. Observed mean lengths-at-age 1+ and 2+ were significantly higher in Lake Liambezi compared to the Kavango, Kwando and Zambezi Rivers. At age 2+ mean length in the Zambezi River was significantly higher than in the Kavango River. At age 3+ mean length was significantly higher in Lake Liambezi compared to the Kwando River while the Zambezi River did not differ significantly from either. At age 4+ mean length was significantly larger in the Zambezi River compared to the Kwando River.

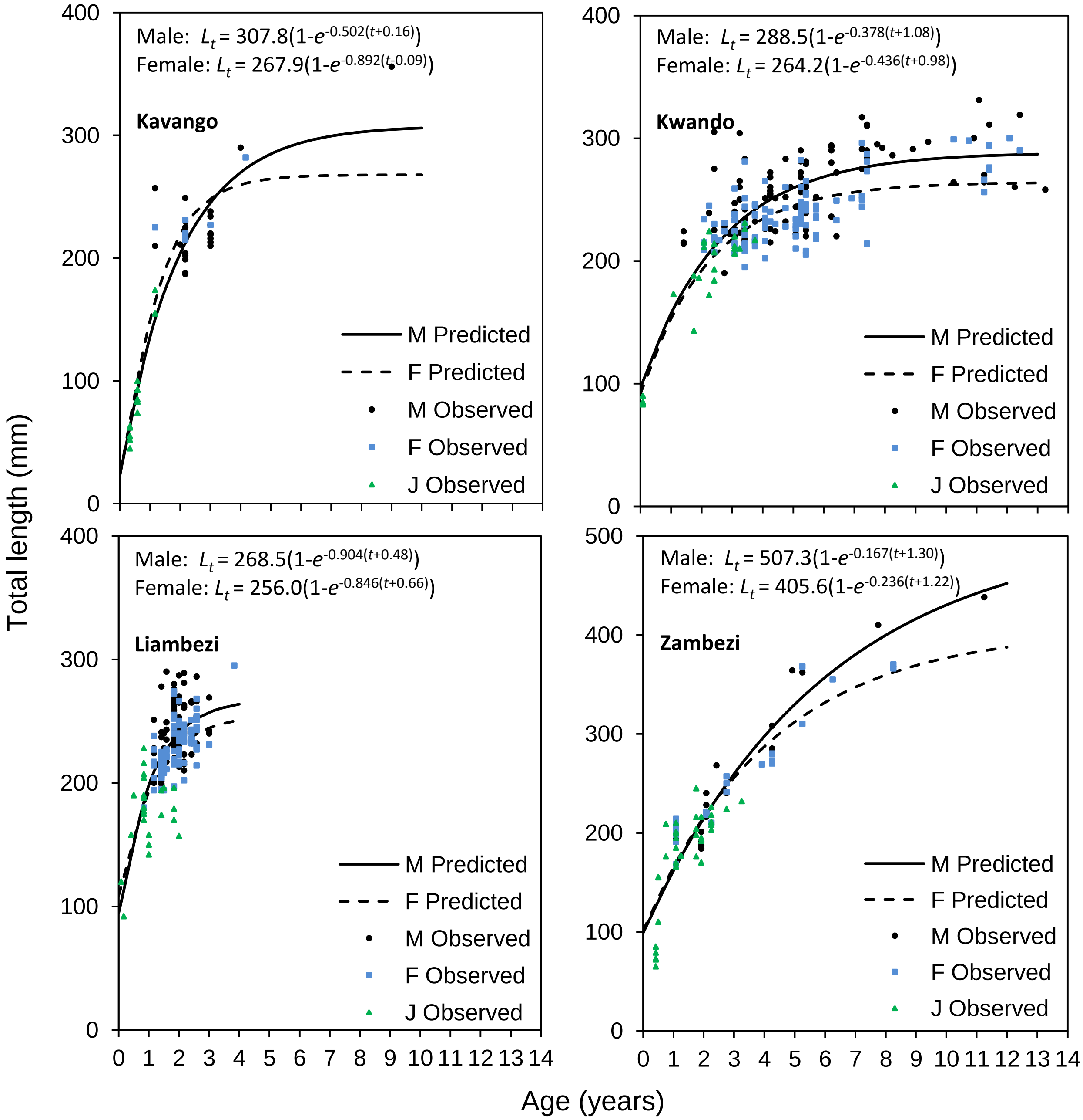

Figure 5.8. Length-at-age data for male and female *Oreochromis macrochir* using sectioned otoliths sampled in the Kavango River, the Kwando River, Lake Liambezi and the Zambezi River, Namibia between April 2010 and September 2011. The growth curves were fitted to the data using the von Bertalanffy growth model.

Table 5.9. Observed mean lengths-at age (± standard deviation) for combined sex *Oreochromis macrochir* from the Kavango, Kwando, Lake Liambezi and Zambezi Rivers, Namibia. Different letters denote significant differences in mean lengths-at-age between systems up to age 4+ (ANOVA, $p \leq 0.05$).

Age (years)	Kavango	Kwando	Liambezi	Zambezi
1+	198 (38.3)^{a}	191 (28.4)^{a}	227 (23.7)^{b}	196 (16.4)^{a}
2+	218 (13.6)^{a}	221 (25.6)^{ac}	243 (18.9)^{b}	227 (17.6)^{c}
3+	290	229 (20.4)^{a}	284 (15.6)^{b}	251 (26.2)^{ab}
4+	282	242 (18.6)^{a}		295 (32.8)^{b}
5+		245 (18.6)		347 (31.9)
6+		262 (27.4)		355
7+		280 (25.3)		410
8+	356	289 (3.5)		368 (2.8)
9+		297		
10+		290 (17.5)		
11+		282 (24.7)		438
12+		292 (24.6)		
13+		258		

Tilapia rendalli

Tilapia rendalli reached maximum ages of 7, 13, 4 and 7 years in the Kavango, Kwando, Lake Liambezi and Zambezi Rivers respectively. The von Bertalanffy growth model parameter estimates are presented in Table 5.10. Male and female *T. rendalli* length-at-age was adequately described using the von Bertalanffy growth model.

Fitted von Bertalanffy growth curves for male and female *T. rendalli* are presented in Figure 5.9. Growth was fastest in Lake Liambezi and the Zambezi River up to 2 years of age after which asymptotic lengths were reached by males and females in Lake Liambezi and by females in the Zambezi River. Males reached asymptotic length after 3 years in the Zambezi River. Growth was rapid in the Kavango River with asymptotic lengths only being reached after 6 years. Growth was slowest in the Kwando River with females reaching asymptotic lengths after 4 years and males after 5 years. Growth differed significantly between males and females in the Kwando River and Lake Liambezi (likelihood ratio test, $p < 0.05$), with males reaching a larger asymptotic length in the Kwando River and females reaching a larger asymptotic length in Lake Liambezi. Growth for combined sexes differed significantly between all systems except for the Kavango and Zambezi Rivers (likelihood ratio test, $p < 0.05$). Growth performance of combined sexes was best in Lake Liambezi ($\phi' = 4.83$), followed by the Zambezi River ($\phi' = 4.78$), the Kavango River ($\phi' = 4.64$) and the Kwando River ($\phi' = 4.51$).

Table 5.10. Parameter estimates and standard deviations (SD) of combined sex, male and female length-at-age data fitted using the von Bertalanffy growth model for *Tilapia rendalli* sampled in the Kavango, Kwando, Lake Liambezi and Zambezi Rivers, Namibia between April 2010 and September 2011.

Parameters	L_∞ (±SD)	K (±SD)	t_0 (±SD)	ϕ'
Kavango				
Combined sexes	403.2 (61.9)	0.267 (0.105)	-0.85 (0.50)	4.64
Males	399.4 (63.8)	0.268 (0.113)	-0.87 (0.55)	4.63
Females	364.7 (261.6)	0.385 (0.684)	-0.23 (1.04)	4.71
Kwando				
Combined sexes	308.3 (6.7)	0.337 (0.026)	-0.54 (0.12)	4.51
Males	351.9 (11.6)	0.262 (0.024)	-0.65 (0.13)	4.51
Females	296.7 (6.3)	0.312 (0.023)	-0.63 (0.11)	4.44
Liambezi				
Combined sexes	264.7 (9.8)	0.966 (0.257)	-0.45 (0.27)	4.83
Males	257.1 (5.8)	1.464 (0.308)	-0.06 (0.15)	4.99
Females	278.8 (17.1)	0.627 (0.174)	-0.84 (0.31)	4.69
Zambezi				
Combined sexes	322.8 (17.7)	0.584 (0.092)	-0.19 (0.09)	4.78
Males	353.3 (15.9)	0.486 (0.058)	-0.21 (0.09)	4.78
Females	285.1 (12.6)	0.756 (0.109)	-0.09 (0.07)	4.79

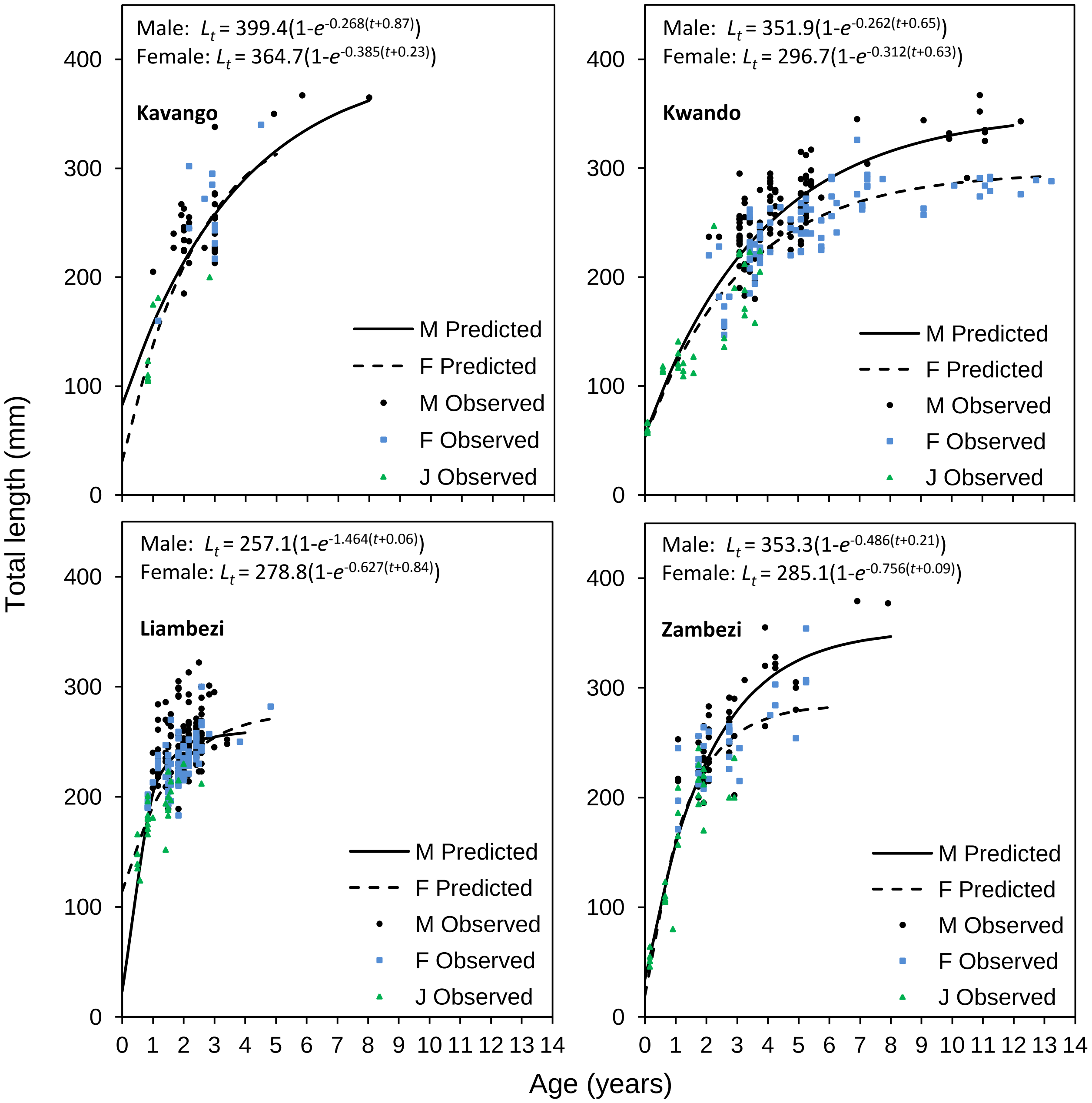

Figure 5.9. Length-at-age data for male and female *Tilapia rendalli* using sectioned otoliths sampled in the Kavango River, the Kwando River, Lake Liambezi and the Zambezi River, Namibia between April 2010 and September 2011. The growth curves were fitted to the data using the von Bertalanffy growth model.

Observed mean lengths-at-age are summarised in Table 5.11. Mean length at age 1+ was significantly higher in Lake Liambezi compared to the Zambezi River, which, together with the Kavango River was significantly higher than Kwando River. At age 2+ and 3+ mean length in the Kwando was significantly lower than the other systems. At age 4+ mean length in the Kavango River was significantly higher than in the Zambezi River which was in turn significantly higher than in the Kwando River.

Table 5.11. Observed mean lengths-at age (± standard deviation) for combined sex *Tilapia rendalli* from the Kavango, Kwando, Lake Liambezi and Zambezi Rivers, Namibia. Different letters denote significant differences in mean lengths-at-age between systems up to age 4+ (ANOVA, $p \leq 0.05$).

Age (years)	Kavango	Kwando	Liambezi	Zambezi
1+	228 (31.7)^{ac}	121 (10.0)^{b}	231 (25.7)^{a}	219 (24.9)^{c}
2+	246 (29.9)^{a}	182 (37.2)^{b}	252 (21.6)^{a}	247 (25.9)^{a}
3+		228 (25.7)^{a}	250 (2.0)^{b}	279 (49.7)^{b}
4+	345 (7.1)^{a}	256 (21.9)^{b}	282	297 (23.4)^{c}
5+	367	264 (22.9)		322 (27.7)
6+		285 (32.1)		379
7+	365	282 (14.6)		377
8+				
9+		305 (41.2)		
10+		310 (39.2)		
11+		305 (24.5)		
12+		303 (35.5)		
13+		288		

Reproductive biology

Sex ratio

The sex ratios of *O. andersonii*, *O. macrochir* and *T. rendalli* are summarised in Table 5.12. The sex ratios of *O. andersonii* were significantly skewed towards males in the Kavango and Kwando Rivers. The sex ratio of *O. macrochir* was significantly skewed towards males in the Kavango River, and the sex ratios of *T. rendalli* were significantly skewed towards males in all four systems.

Table 5.12. Sex ratios and χ^2 test statistics (df = 1) of mature *Oreochromis andersonii*, *Oreochromis macrochir* and *Tilapia rendalli* sampled in the Kavango, Kwando, Lake Liambezi and Zambezi Rivers, Namibia.

	n	Sex ratio (female:male)	χ^2	p
O. andersonii				
Kavango	72	1:3.2	20.05	< 0.001
Kwando	139	1:1.1	0.18	> 0.05
Liambezi	239	1:2.0	27.45	< 0.0001
Zambezi	99	1:1.2	0.82	> 0.05
O. macrochir				
Kavango	36	1:4.1	13.44	< 0.001
Kwando	211	1:1.1	0.38	> 0.05
Liambezi	194	1:1.3	3.48	> 0.05
Zambezi	49	1:1.1	2.06	>0.05
T. rendalli				
Kavango	49	1:3.5	14.87	< 0.001
Kwando	207	1:1.4	5.91	< 0.05
Liambezi	217	1:1.8	16.04	<0.001
Zambezi	88	1:1.2	10.23	<0.001

Length-at-maturity

Oreochromis andersonii

The combined length-at-50% maturity for male and female *O. andersonii* was smallest in the Kavango River at 238 mm TL (δ_L = 27.3 mm^{-1} TL), followed by the Zambezi River at 240 mm TL (δ_L = 16.2 mm^{-1} TL) and the Kwando River at 247 mm TL (δ_L = 27.9 mm^{-1} TL), and was highest in Lake Liambezi at 254 mm TL (δ_L = 22.9 mm^{-1} TL) (Figure 5.10). Likelihood ratio tests showed there was no significant difference in the Lm_{50} between populations in the four systems (p > 0.05).

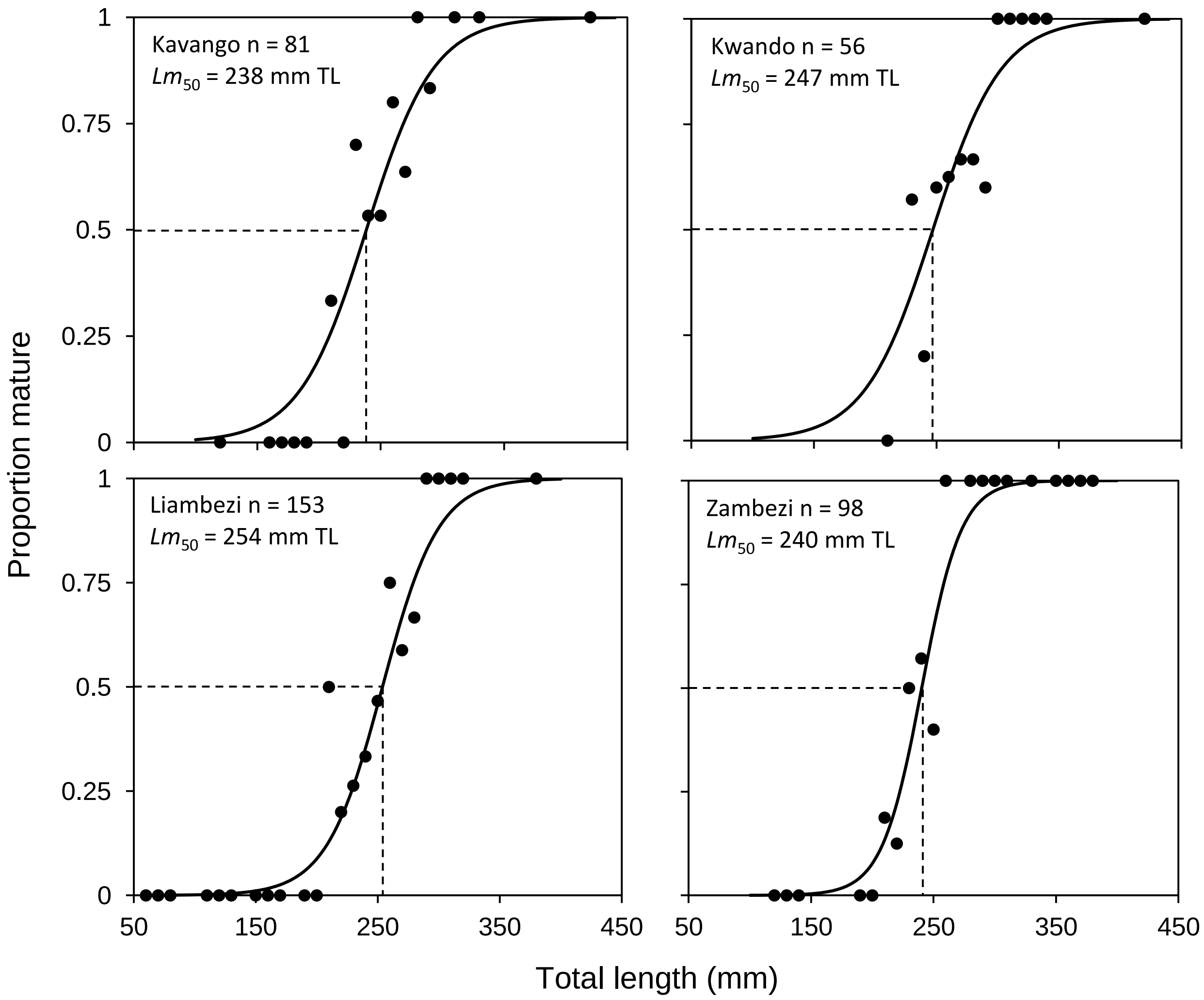

Figure 5.10. Logistic ogives fitted to the proportion of reproductively active *Oreochromis andersonii* (sexes combined) from the Kavango River, the Kwando River, Lake Liambezi and the Zambezi River, Namibia. Length-at-50% maturity = Lm_{50}.

Oreochromis macrochir

The combined length-at-50% maturity for male and female *O. macrochir* was smallest in the Kavango River at 184 mm TL (δ_L = 36.1 mm^{-1} TL), followed by the Kwando River at 215 mm TL (δ_L = 55.6 mm^{-1} TL) and Lake Liambezi at 221 mm TL (δ_L = 21.9 mm^{-1} TL), and was greatest in the Zambezi River at 254 mm TL (δ_L = 16.5 mm^{-1} TL) (Figure 5.11). Likelihood ratio tests showed that Lm_{50} in the Zambezi

River was significantly higher than the other systems and that Lm_{50} in Lake Liambezi was significantly higher than in the Kavango River ($p < 0.05$).

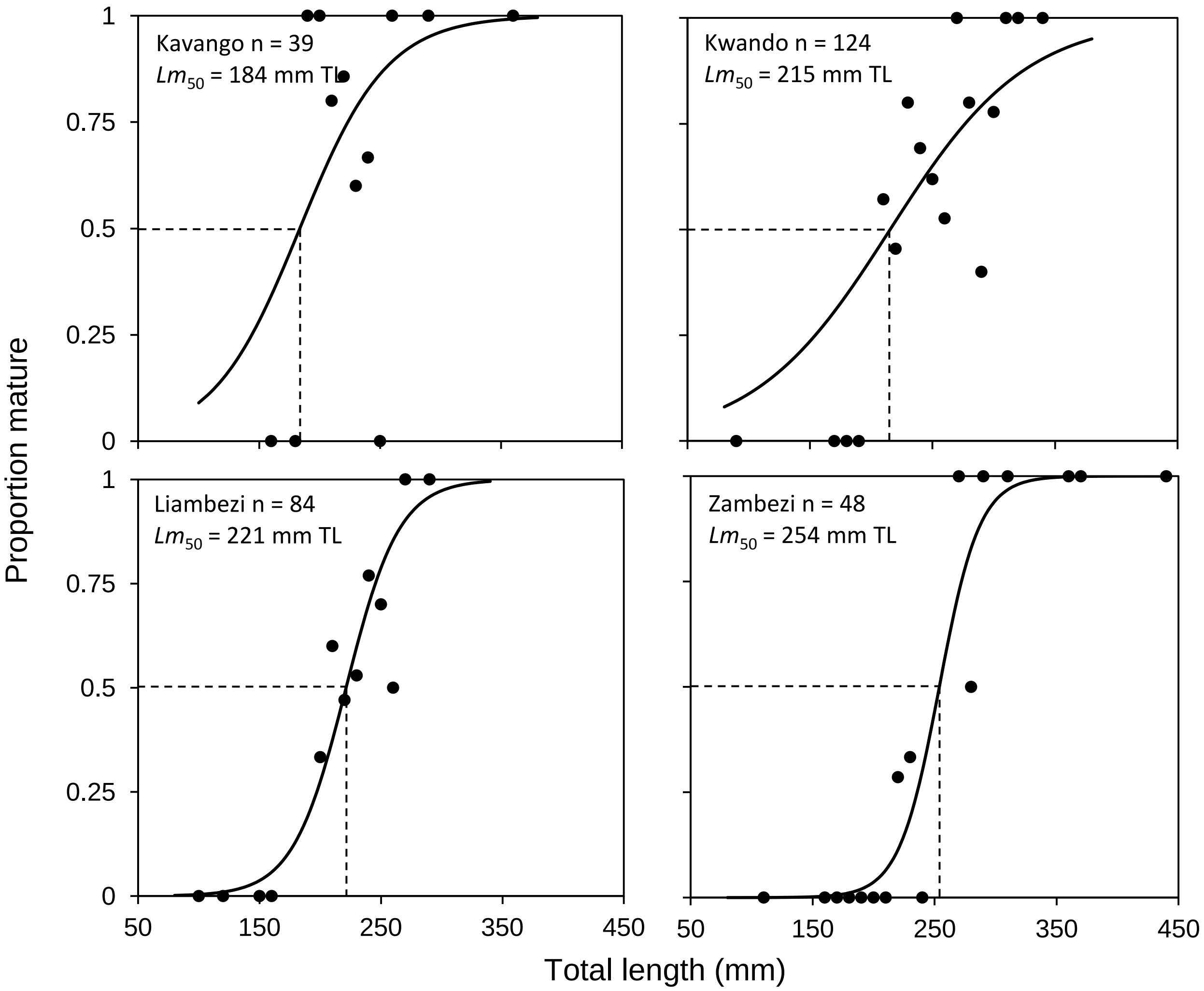

Figure 5.11. Logistic ogives fitted to the proportion of reproductively active *Oreochromis macrochir* (sexes combined) from the Kavango River, the Kwando River, Lake Liambezi and the Zambezi River, Namibia. Length-at-50% maturity = Lm_{50}.

Tilapia rendalli

The combined length-at-50% maturity for male and female *T. rendalli* was smallest in the Kavango River at 195 mm TL (δ_L = 28.1 mm^{-1} TL), followed by the Kwando

River at 203 mm TL (δ_L = 27.7 mm^{-1} TL) and Lake Liambezi at 212 mm TL (δ_L = 18.2 mm^{-1} TL), and was largest in the Zambezi River at 214 mm TL (δ_L = 16.2 mm^{-1} TL) (Figure 5.12). Likelihood ratio tests showed there was no significant difference in the Lm_{50} between populations in the four systems ($p > 0.05$).

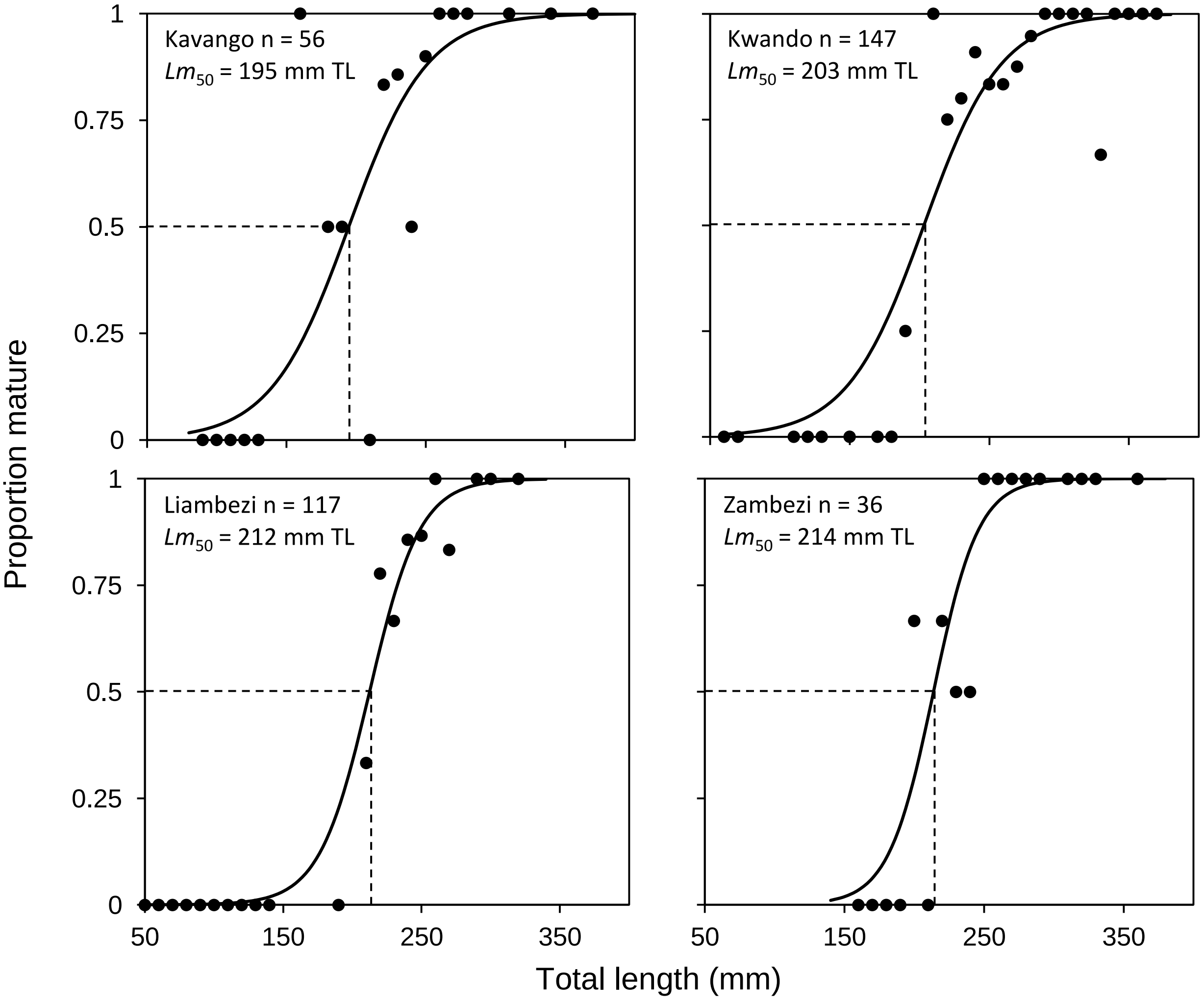

Figure 5.12. Logistic ogives fitted to the proportion of reproductively active *Tilapia rendalli* (sexes combined) from the Kavango River, the Kwando River, Lake Liambezi and the Zambezi River, Namibia. Length-at-50% maturity = Lm_{50}.

Age-at-maturity

Oreochromis andersonii

Parameter estimates from logistic models fitted to age-at-maturity data are summarised in Table 5.13. Age-at-50% maturity (tm_{50}) ranged from 1.5 years in the Kavango River to 2.9 years in the Kwando River. Likelihood ratio tests showed that tm_{50} was significantly higher in the Kwando River compared to the Kavango River and Lake Liambezi, and the Zambezi was significantly higher than Lake Liambezi ($p < 0.05$). There was no significant difference in the rate of maturation (δ_t) between populations (likelihood ratio test, $p > 0.05$). The predicted proportion of mature fish per age class for each system are summarised in Table 5.14.

Table 5.13. Parameter estimates of the logistic curves describing age-at-maturity of *Oreochromis andersonii* from the Kavango, Kwando, Lake Liambezi and Zambezi Rivers, Namibia. Different letters denote significant differences (likelihood ratio test, $p \leq 0.05$).

Parameter	tm_{50}	δ_t
Kavango	1.49^{ac}	1.44^{a}
Kwando	2.90^{b}	0.81^{a}
Liambezi	1.58^{c}	0.72^{a}
Zambezi	2.01^{ab}	0.57^{a}

Table 5.14. Predicted proportion of mature *Oreochromis andersonii* per age class from the Kavango, Kwando, Lake Liambezi and Zambezi Rivers, Namibia.

Age (years)	1	2	3	4	5	6	7	8	9	10
Kavango	0.41	0.58	0.74	0.85	0.91	0.95	0.97	0.99	0.99	0.99
Kwando	0.09	0.25	0.53	0.79	0.93	0.98	0.99	1.0	1.0	1.0
Liambezi	0.31	0.64	0.88	0.97						
Zambezi	0.15	0.49	0.85	0.97	0.99	1.0				

Oreochromis macrochir

Parameter estimates from logistic models fitted to age-at-maturity data are summarised in Table 5.15. Age-at-50% maturity (tm_{50}) ranged from 1 year in Lake Liambezi to 3 years in the Zambezi River. Likelihood ratio tests showed that tm_{50} was significantly higher in the Zambezi River compared to the Kavango River and Lake Liambezi ($p < 0.05$). The rate of maturation (δ_t) was significantly faster in Lake Liambezi and the Zambezi River compared to the Kwando River (likelihood ratio test ($p < 0.05$). The predicted proportion of mature fish per age class for each system are summarised in Table 5.16.

Table 5.15. Parameter estimates of the logistic curves describing age-at-maturity of *Oreochromis macrochir* from the Kavango, Kwando, Lake Liambezi and Zambezi Rivers, Namibia. Different letters denote significant differences (likelihood ratio test, $p \leq 0.05$).

Parameter	tm_{50}	δ_t
Kavango	1.27^{a}	0.75^{ab}
Kwando	2.54^{ab}	2.93^{b}
Liambezi	1.01^{a}	0.59^{a}
Zambezi	2.99^{b}	0.56^{a}

Table 5.16. Predicted proportion of mature *Oreochromis macrochir* per age class from the Kavango, Kwando, Lake Liambezi and Zambezi Rivers, Namibia.

Age (years)	1	2	3	4	5	6	7	8	9	10
Kavango	0.18	0.49	0.81	0.95	0.99	0.99	1.0	1.0		
Kwando	0.37	0.45	0.54	0.62	0.70	0.77	0.82	0.87	0.90	0.93
Liambezi	0.48	0.78	0.94	0.98						
Zambezi	0.18	0.49	0.81	0.95	0.99	0.99	0.99	1.0	1.0	1.0

Tilapia rendalli

Parameter estimates from logistic models fitted to age-at-maturity data are summarised in Table 5.17. Age-at-50% maturity (tm_{50}) ranged from 1.1 years in the Kavango River and Lake Liambezi to 2.5 years in the Kwando River. Likelihood ratio tests showed that tm_{50} was significantly higher in the Kwando River compared to the three other systems ($p < 0.05$). The rate of maturation (δ_t) in Lake Liambezi was significantly faster than in the Kwando River (likelihood ratio test, $p < 0.05$). The predicted proportion of mature fish per age class for each system are summarised in Table 5.18.

Table 5.17. Parameter estimates of the logistic curves describing age-at-maturity of *Tilapia rendalli* from the Kavango, Kwando, Lake Liambezi and Zambezi Rivers, Namibia. Different letters denote significant differences (likelihood ratio test, $p \leq 0.05$).

Parameter	tm_{50}	δ_t
Kavango	1.09^{a}	0.46^{ab}
Kwando	2.53^{b}	0.85^{b}
Liambezi	1.06^{a}	0.39^{a}
Zambezi	1.38^{a}	0.49^{ab}

Table 5.18. Predicted proportion of mature *Tilapia rendalli* per age class from the Kavango, Kwando, Lake Liambezi and Zambezi Rivers, Namibia.

Age (years)	1	2	3	4	5	6	7	8	9	10
Kavango	0.45	0.87	0.98	0.99	0.99	0.99	0.99			
Kwando	0.14	0.34	0.63	0.84	0.94	0.98	0.99	0.99	0.99	0.99
Liambezi	0.47	0.91	0.99	0.99						
Zambezi	0.32	0.78	0.96	0.99	0.99	0.99	0.99			

Reproductive seasonality

<u>*Oreochromis andersonii*</u>

Gonadal recrudescence in *O. andersonii* followed a seasonal pattern. The proportions of reproductively active adults indicate that reproductive activity extended throughout summer from September to April (Figure 5.13).

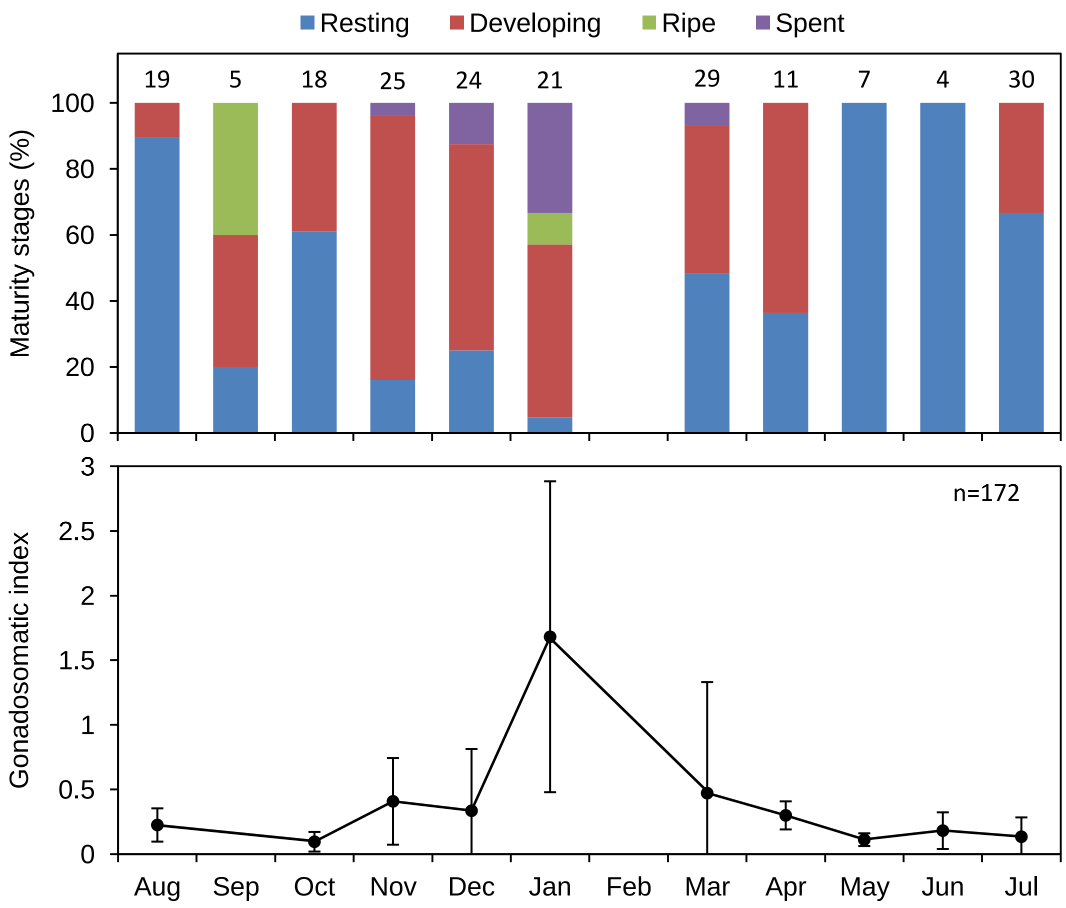

Figure 5.13. Female monthly maturity stages and gonadosomatic indices (GSI) (± standard deviation) for *Oreochromis andersonii* from the Kavango, Kwando, Lake Liambezi and Zambezi Rivers in Namibia sampled between August 2010 and July 2011.

All fish were in a resting stage during the winter months of May and June. Developing individuals were first sampled in July and by September 40% of fish were developing and 40% were in a ripe condition. In November 80% of fish were developing; spent individuals were sampled from November till March with the highest proportion (33%) sampled in January. Few ripe individuals were sampled during the spawning season from September till April. Gonadosomatic indices were low (< 0.5%) throughout most of the year with a distinctive peak in January at 1.7% (Figure 5.13).

Oreochromis macrochir

Gonadal recrudescence in *O. macrochir* followed a seasonal pattern. The proportions of reproductively active adults and the gonadosomatic indices indicate that reproductive activity occurred from the end of winter to the end of summer (July to March) (Figure 5.14). Few individuals were active during the colder winter months from April to June. Sample sizes during this period were however very low. In July, 85% of gonads were categorised as resting, 11% as developing and one individual was categorised as spent. The proportion of developing gonads increased to 50% in August and to 63% in September. The first ripe gonads were sampled in October, making up 24% whilst 53% were still developing. In November and January, all fish sampled were active. In November, 54% of gonads were categorised as spent and 46% were developing. In December and January over 68% of gonads were in a developing state with the remainder being either resting or spent in December and ripe and spent in January. In March, 90% of gonads were still active with 60%

developing and 30% spent. Gonadosomatic indices were low throughout the year but showed a distinct seasonal pattern with peaks in October, November and December above 0.5% (Figure 5.14).

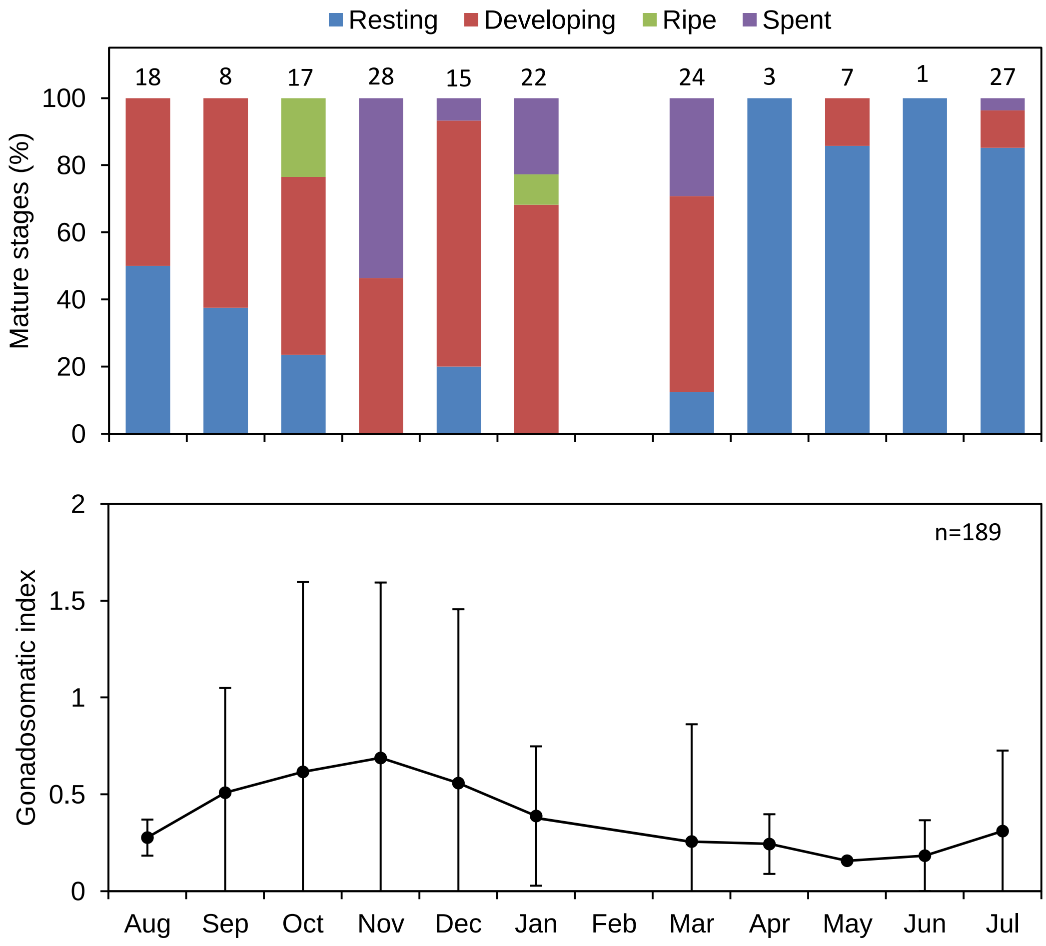

Figure 5.14. Female monthly maturity stages and gonadosomatic indices (GSI) (± standard deviation) for *Oreochromis macrochir* from the Kavango, Kwando, Lake Liambezi and Zambezi Rivers in Namibia sampled between August 2010 and July 2011.

Tilapia rendalli

Gonadal recrudescence followed a seasonal pattern in *T. rendalli*. The proportion of reproductively active adults indicated that gonad activity occurred almost throughout the year with the least activity in the cooler months from April to July (Figure 5.15).

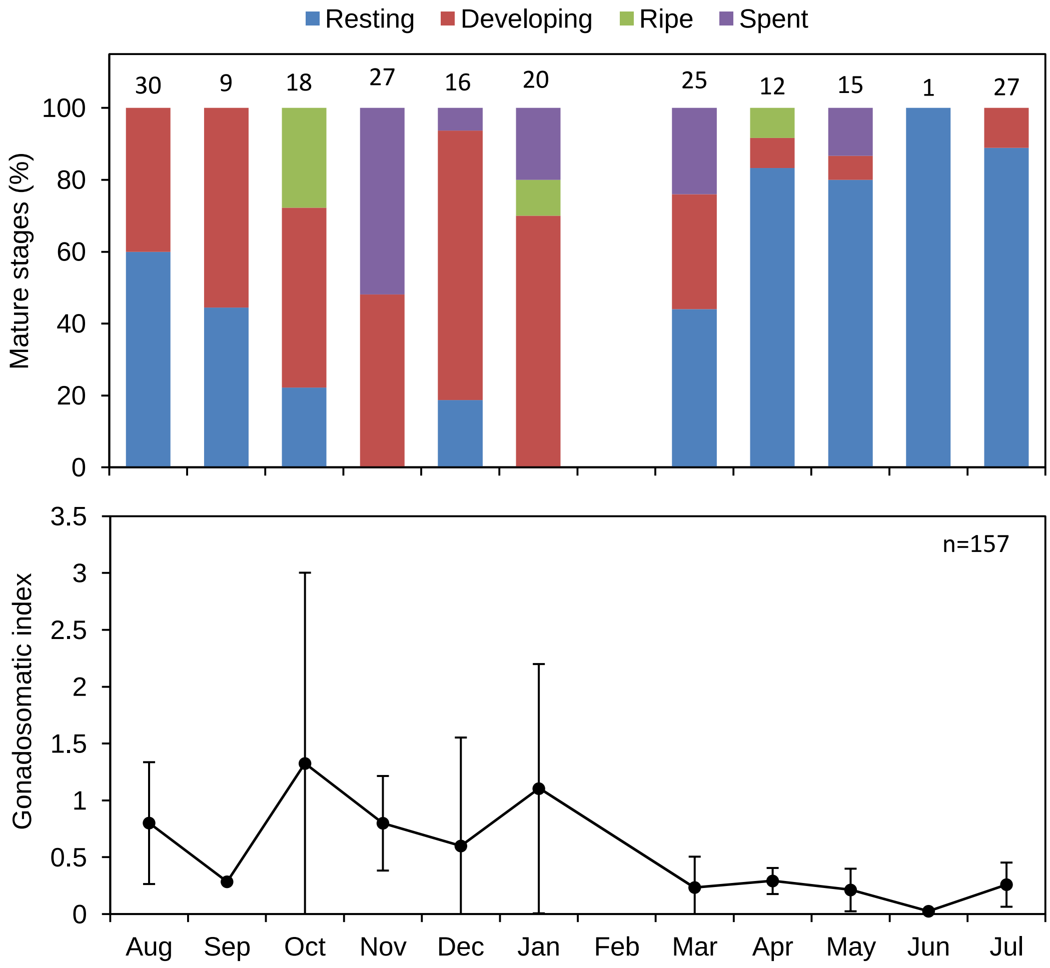

Figure 5.15. Female monthly maturity stages and gonadosomatic indices (GSI) (± standard deviation) for *Tilapia rendalli* from the Kavango, Kwando, Lake Liambezi and Zambezi Rivers in Namibia sampled between August 2010 and July 2011.

From April to July over 80% of gonads were categorised as resting. In August 40% of gonads were developing and by September this had increased to 56%. In October

80% of gonads were active and the first ripe individuals were sampled (28%). In November and January, all fish sampled were active. In November 52% of gonads were spent and the remainder were developing. In December and January over 70% of gonads were developing with the remainder being either resting or spent in December, and ripe and spent in January. The majority of fish (44%) had regressed to a resting state by March and in April and May less than 20% of gonads were active. Gonadosomatic indices were highest in the hot summer months with two distinct peaks in October and January (Figure 5.15).

5.4 DISCUSSION

Ageing

Burning otoliths to enhance growth zone visibility is commonplace in ageing studies of cichlids (Booth & Merron, 1996; Booth et al., 1995; Chimatiro, 2004; Kanyerere, Weyl, & Booth, 2005; Weyl & Hecht, 1998). In this study, however, growth zones were more clearly visible in unburnt otoliths. It is therefore recommended that in any ageing study of cichlids a comparison be carried out to determine whether burning improves the readability of otoliths.

Oreochromis andersonii, *O. macrochir* and *T. rendalli* were aged using both scales and otoliths in several previous studies (Booth & Merron, 1996; Booth et al., 1995; Dudley, 1974; Kapetsky, 1974; Weyl & Hecht, 1998; van der Waal, 1985), but no estimates of ageing precision have previously been carried out. In the present study estimates of precision from sectioned otoliths were compared between four populations of *O. andersonii*, *O. macrochir* and *T. rendalli* in Namibia. Campana

(2001) reviewed 131 ageing studies and found that the median CV was 7.6%, corresponding to an APE of 5.5%. Precision estimates for all three species from the Kavango and Kwando Rivers and for *O. andersonii* from the Zambezi River were similar to values determined by Campana (2001) (Table 5.19). Estimates for all three species from Lake Liambezi and for *O. macrochir* and *T. rendalli* from the Zambezi River were, however, less precise. When compared by age class, however, precision estimates were comparable between systems and species. Precision estimates for younger fish were low in all cases because of difficulties in interpreting the first annulus. The first annulus was considerably easier to distinguish in fishes older than 2 years. Differences in estimates of total precision between systems are likely to be a result of differences in population age structure, with fewer older fish in Liambezi and Zambezi populations, rather than to differences in otolith readability.

Precision estimates from this study are compared to other cichlids and freshwater species from southern Africa in Table 5.19. Only two cichlid ageing papers reported precision values for comparison with this study. One study (Kapute, Kaunda, Banda, & Morioka, 2008) used opercular bones and so may not be directly comparable to estimates obtained from sectioned otoliths in this study. Estimates for *O. andersonii*, *O. macrochir* and *T. rendalli* from the Kavango and Kwando Rivers in this study are amongst the most precise estimates for any species. Precision estimates for *O. macrochir* from Lake Liambezi and the Zambezi, although somewhat low for this study, are comparable to estimates for other cichlids from Lakes Malombe and Malawi aged using sectioned otoliths and opercular bones.

Table 5.19. Age precision estimates (APE = average percent error, CV = coefficient of variation and D = Index of precision) obtained using calcified structures of freshwater fish species in southern African water bodies.

Species	Locality	Ageing method	APE	CV	D
Cichlids					
O. andersonii[1]	Kavango River	Sectioned otoliths	2.08	3.43	1.98
O. andersonii[1]	Kwando River	Sectioned otoliths	3.72	8.20	4.73
O. andersonii[1]	Lake Liambezi	Sectioned otoliths	17.02	18.63	10.76
O. andersonii[1]	Zambezi River	Sectioned otoliths	6.15	9.75	5.63
O. macrochir[1]	Kavango River	Sectioned otoliths	5.06	8.17	4.71
O. macrochir[1]	Kwando River	Sectioned otoliths	4.24	10.56	6.10
O. macrochir[1]	Lake Liambezi	Sectioned otoliths	10.77	13.63	7.87
O. macrochir[1]	Zambezi River	Sectioned otoliths	10.45	12.85	7.42
T. rendalli[1]	Kavango River	Sectioned otoliths	6.98	11.92	6.88
T. rendalli[1]	Kwando River	Sectioned otoliths	3.99	6.96	4.02
T. rendalli[1]	Lake Liambezi	Sectioned otoliths	16.51	21.12	12.19
T. rendalli[1]	Zambezi River	Sectioned otoliths	13.50	18.64	10.76
O. karongae[2]	Lake Malawi	Opercular bones	11.3	8.0	5.7
O. karongae[2]	Lake Malombe	Opercular bones	10.8	7.7	5.4
D. limnothrissa[3]	Lake Malawi	Sectioned otoliths	10.5	7.4	5.3
Other freshwater fish species					
H. vittatus[4]	Okavango Delta	Sectioned otoliths	5.81	7.62	
C. gariepinus[5]	Okavango Delta	Sectioned otoliths	6.0	8.5	6.0
C. gariepinus[6]	Xonxa Dam	Sectioned otoliths	8.5		
L. aeneus[6]	Xonxa Dam	Whole otoliths	11.4		
L. aeneus[7]	Lake Gariep	Whole otoliths	6.3	3.1	1.8
L. kimberlyensis[7]	Lake Gariep	Whole otoliths	4.5	0.9	0.02
L. capensis[8]	Lake Gariep	Whole otoliths	4.94	6.95	
C. carpio[8]	Lake Gariep	Whole otoliths	5.54	7.03	

[1] Present study – Kavango, Kwando, Lake Liambezi and Zambezi Rivers, Namibia
[2] Kapute et al. 2008 – Lake Malawi and Lake Malombe, Malawi
[3] Kanyerere et al. 2005 – Lake Malawi, Malawi
[4] Gerber, Smit, Pieterse, and Durholtz 2009 – Okavango Delta, Botswana
[5] Bokhutlo 2011 – Okavango Delta, Botswana
[6] Richardson, Booth, and Weyl 2009 – Xonxa Dam, South Africa
[7] Ellender 2008 – Lake Gariep, South Africa
[8] Winker 2010 – Lake Gariep, South Africa

Precision estimates for *O. andersonii* from Lake Liambezi and *T. rendalli* from Lake Liambezi and the Zambezi River are lower than any other precision estimates from freshwater fish species in southern Africa. As already noted, this was because there were few older fishes in the sample and not because of poor readability of the otoliths.

Growth zone periodicity

Edge analysis indicated that a single opaque zone was laid down in the otoliths of *O. andersonii*, *O. macrochir* and *T. rendalli* in summer from October to January with peak deposition occurring in December (Figure 5.6). Annulus formation in *O. andersonii*, *O. macrochir* and *T. rendalli* from the Kafue floodplain (Dudley, 1974; Kapetsky, 1974) and *O. andersonii* and *O. macrochir* from the Okavango Delta (Booth & Merron, 1996; Booth et al., 1995) occurred during the same period, while annulus formation in *T. rendalli* from Lake Chicamba, Mozambique occurred at the end of winter in July and August (Weyl & Hecht, 1998). Annulus formation in cichlids has been linked to temporal variations in feeding intensity (Bruton & Allanson, 1974), reproductive periodicity (Booth & Merron, 1996; Booth et al., 1995; Bruton & Allanson, 1974; Dudley, 1974; Hecht, 1980; Kapetsky, 1974; Kapute et al., 2008) and temperature variation (Hecht, 1980; Weyl & Hecht, 1998). Annulus formation during summer corresponded to the reproductive season of *O. andersonii*, *O. macrochir* and *T. rendalli* in the study area (Figures 5.13, 5.14 and 5.15), and to low water levels. High reproductive investment prior to the spawning season and a reduction in feeding intensity and increased energy demand during the spawning season could cause sufficient physiological stress to account for annulus formation in *O. andersonii*, *O. macrochir* and *T. rendalli* from October to January in the Kavango, Kwando, Lake Liambezi and the Zambezi Rivers.

Growth

Length-at-age data of *O. andersonii* from Lake Liambezi and the Zambezi River could not be adequately described by the von Bertalanffy growth model. The best model fits approximated linear growth because of a lack of older fish in the samples. Lake Liambezi has only recently been filled and *O. andersonii* in the lake have not yet lived long enough to reach asymptotic lengths. In other systems *O. andersonii* attained asymptotic lengths at ages between 6 and 8 years. Lake Liambezi and the Zambezi River are also subject to heavy exploitation by commercial and subsistence gillnet fisheries, of which *O. andersonii* is a major target (van der Waal, 1980, 1990). Fisheries tend to remove the larger, older fish from the population (Welcomme, 2001) and there may be few older fishes left in the river that have attained asymptotic lengths as a result. In Lake Liambezi fishes may be harvested before they reach ages at which they attain asymptotic lengths.

Male and female growth differed in most cases with males growing faster and attaining a greater asymptotic length later in life than females (Figures 5.7, 5.8 and 5.9). A notable exception to this was *T. rendalli* from Lake Liambezi where females attained a greater asymptotic length than males (Figure 5.9). Male *T. rendalli* were, however, observed to attain a greater size than females in Lake Liambezi (Figure 5.5). Where male and female growth did not differ, sample sizes were often small and did not include all age and size classes of each sex. This resulted in large error around the fitted von Bertalanffy growth curves and a lack of statistical difference in growth rates.

Growth rates of *O. andersonii*, *O. macrochir* and *T. rendalli* varied considerably between systems (Figures 5.7, 5.8 and 5.9). Initial growth rates of each species were fastest in Lake Liambezi. *Oreochromis andersonii* attained more than 50% and *O. macrochir* and *T. rendalli* attained more than 60% of their maximum observed lengths after 1 year in the lake. Several biotic factors may have contributed to the extremely rapid first year growth in Lake Liambezi. Harvesting of the tilapiines by the commercial gillnet fishery may reduce fish densities and therefore reduce density dependent competition, while the rarity of large predators such as *H. vittatus* means that juveniles are not restricted to habitats in which they can take refuge from predation, resulting in a further reduction in density dependent competition, increased quality of diets and increased growth rates (Jackson et al., 2001). *Oreochromis andersonii* and *O. macrochir* went on to attain a larger size-at-age in the Zambezi River and *T. rendalli* in the Kavango River. Like Lake Liambezi, density dependent competition is likely to be low as a result of harvesting in the Zambezi River. The growth rate of each species was slowest in the Kwando River, possibly because the system is relatively unexploited and fish densities are higher here than in the other systems (see Chapter 4). Higher densities can result in increased inter-and intraspecific competition for food resources. This may lead to a reduction in the quality of diets and reduced growth rates (Jackson et al., 2001). *Oreochromis andersonii* attained asymptotic lengths relatively late in life after 6 years in the Kwando River and 8 years in the Kavango River, while no reduction in growth rate was observed in Lake Liambezi and the Zambezi River, at maximum observed ages of 4 and 6 years respectively. *Oreochromis macrochir* from the Kavango and Kwando Rivers and Lake Liambezi attained asymptotic lengths early in life after 3, 2 and 4 years respectively and later in the Zambezi River after 7 years. *Tilapia rendalli* from Lake Liambezi and the Zambezi River attained asymptotic lengths earlier (after 2 and 3 years respectively), than those from the Kavango and Kwando Rivers (after 6 and 5 years respectively). Cichlids typically display rapid initial growth rates and then reach asymptotic length shortly after maturation occurs (Booth & Merron, 1996; Booth et al., 1995; Chimatiro, 2004; Hecht, 1980; Weyl & Hecht, 1998; van der Waal, 1985). A reduction in growth rate after reaching sexual maturity reflects a shift from somatic growth to reproductive energy requirements (Booth & Merron, 1996; Weyl & Hecht, 1998). Although all of the populations in this study reached maturity before 3 years of age (Tables 5.13, 5.15 and 5.17), all *O. andersonii* populations, *O. macrochir* from the Zambezi River and *T. rendalli* from the Kavango River continued to grow rapidly for several years after reaching maturity. This suggests that food is not limiting in these systems and these fishes are able to invest energy in both somatic growth and reproduction.

The length-at-age and growth performance of *O. andersonii*, *O. macrochir* and *T. rendalli* from this study are compared to other populations in Table 5.20. The growth rate of *O. andersonii* in the Kavango River was faster than in the Kafue River (Kapetsky, 1974) and further down the same river in the Okavango Delta (Booth et al., 1995). Faster growth in the Kavango River compared to the Okavango Delta can be attributed to the difference in nutrient levels between the two areas. Transparency is generally higher and nutrient levels lower in the Okavango Delta compared to the river as nutrients are filtered out by large beds of papyrus (*Cyperus papyrus*) and other aquatic plants as the water enters the delta (Cronberg, Gieske, Martins, Prince Nengu, & Stenstrom, 1995). Generally growth rates in the Kavango River were slightly slower than in Lake Liambezi (van der Waal, 1985), although the ϕ' values were identical as fish attain a larger size in the Kavango River. Growth in the Kwando River was similar to both the Kafue River (Kapetsky, 1974) and the Okavango Delta (Booth et al., 1995). The Kwando River and the Okavango Delta are both nutrient-poor environments with high transparencies and low conductivity (Cronberg et al., 1995), hence the similar slow growth rates. The growth of *O. andersonii* in Lake Liambezi in this study was very similar to that observed by van der Waal (1985) prior to the lake drying up in 1985. The growth performance of *O. andersonii* was, however, higher for this study than in van der Waal's study (1985), although this may possibly be biased by the unrealistically high asymptotic length predicted in this study. A slight difference in growth performance may be linked to a decline in productivity in the lake over time.

When van der Waal (1985) worked on the lake it had contained water for approximately 25 years as compared to being full for only 2 years prior to the initiation of this study. A decrease in lake productivity over time is common, especially in man-made lakes where fish yields are initially high and then decline several years after impoundment (Bailey, 1996; Karenge & Kolding, 1995b). Freshly-inundated terrestrial vegetation decomposes and releases nutrients into the water, similar to the annual flooding cycle in floodplain rivers (Bayley, 1995; Junk et al., 1989), except that flooding does not occur to the same extent after filling for the first time, and the aquatic-terrestrial interactions in lakes tend to be less intensive than in rivers (Wantzen, Junk, & Rothhaupt, 2008). The growth rate of *O. andersonii* in the Zambezi River was faster than all the other populations that have been studied. The Zambezi River is larger than, and has relatively nutrient-rich waters compared to the Kavango, Kwando and Kafue Rivers (Cronberg et al., 1995). The area studied is also subject to heavy fishing pressure, similar to Lake Liambezi, whereas the areas studied on the Kavango and Kwando Rivers were unfished. A combination of higher productivity and potentially less competition for food resources due to fishing may account for the faster growth of *O. andersonii* in the Zambezi River.

The growth rate of *O. macrochir* in the Kavango River was slower than in Lake Liambezi (van der Waal, 1985), similar to the Kafue River (Dudley, 1974) and faster than in the Okavango Delta (Booth & Merron, 1996) (Table 5.20). As with *O. andersonii*, the growth rates of *O. macrochir* in the Kwando River and the Okavango Delta (Booth & Merron, 1996) were almost identical, demonstrating the similarity in environmental conditions in the two systems. Growth in Lake Liambezi (this study) was initially very rapid, but growth became asymptotic early in life and other populations went on to attain a larger size. Fast initial growth of the Lake Liambezi population can be attributed to the high productivity of the recently flooded lake environment (Junk et al., 1989; Wantzen et al., 2008) and the small asymptotic length because of the lack of older and larger individuals in the population. *Oreochromis macrochir* previously attained 8 years of age and a much larger size in Lake Liambezi (van der Waal, 1985). Despite the small asymptotic length, this population had the highest growth performance. Growth in the Zambezi River and Lake Liambezi (van der Waal, 1985) were similar. Nutrient levels in Lake Liambezi at the time (Seaman et al., 1978) were higher than in the Zambezi River. High nutrient levels and primary productivity may account for the fast growth in the lake, while the seasonal inundation of the extensive Caprivi floodplains and the subsequent high seasonal abundance of food may account for the fast growth observed in the Zambezi River.

The growth rate of *T. rendalli* in the Kavango River was faster than that in Lake Liambezi (van der Waal, 1985), Lake Kariba (Kolding et al., 1992) and Lake Chicamba (Weyl & Hecht, 1998) (Table 5.20). Lakes Liambezi, Kariba and Chicamba do not undergo seasonal flooding to the same extent as the Kavango River. Favourable feeding conditions during the seasonal floods in the Kavango River may account for the faster growth in this system. The growth rate in the Kwando River was very similar to that in Lake Liambezi, Lake Kariba and Lake Chicamba. Initial growth rate is fastest in Lake Chicamba but becomes asymptotic after 3 years, sooner than in the other systems. Growth performance in these four systems was almost identical. Initial growth rates in Lake Liambezi were slower prior to the lake drying up (van der Waal, 1985) than they were in this study. The faster growth of *T. rendalli* in this study and its similar maximum size to that observed by van der Waal (1985) reflects a decline in productivity in the lake over time, as pointed out for *O. andersonii*.

Table 5.20. Calculated length-at-age, von Bertalanny growth parameters and calculated phi-prime (ϕ') (Pauly & Munro, 1984) for combined sex *Oreochromis andersonii*, *Oreochromis macrochir* and *Tilapia rendalli* in southern African water bodies based on published data. All data has been standardised to standard length (SL). von Bertalanffy growth parameters for *O. andersonii* and *O macrochir* from the Kafue River[2,5] and Lake Liambezi[3] were obtained from Booth et al. (1995) and Booth and Merron (1996) and parameters for *T. rendalli* from Lake Liambezi[3] were calculated from observed lengths at age from van der Waal (1985).

	Length (mm SL)-at-age (years)					Growth performance		
Species/Locality	1	2	3	4	5	L_∞	*K*	ϕ'
O. andersonii								
Kavango River[1]	136	187	232	270	303	493	0.163	4.60
Kwando River[1]	104	155	191	217	236	284	0.329	4.42
Lake Liambezi[1]	168	205	241	277	312	8223	0.005	5.53
Zambezi River[1]	149	195	241	287	332	8145	0.006	5.60
Kafue River[2]	108	152	188	218	243	366	0.186	4.40
Lake Liambezi[3]	171	221	259	287	308	370	0.291	4.60
Okavango Delta[4]	146	172	193	209	222	267	0.247	4.25
O. macrochir								
Kavango River[1]	106	164	192	212	220	230	0.630	4.52
Kwando River[1]	130	160	181	196	206	231	0.355	4.28
Lake Liambezi[1]	159	191	204	209	211	212	0.942	4.63
Zambezi River[1]	133	174	210	239	265	406	0.164	4.43
Kafue River[5]	88	142	177	199	214	240	0.440	4.40
Lake Liambezi[3]	139	183	219	249	274	393	0.190	4.47
Okavango Delta[6]	122	156	178	193	203	221	0.420	4.31
T. rendalli								
Kavango River[1]	124	171	208	236	258	327	0.267	4.46
Kwando River[1]	101	145	177	200	216	257	0.337	4.35
Lake Liambezi[1]	163	196	209	213	215	217	0.966	4.66
Zambezi River[1]	131	192	225	244	255	268	0.584	4.62
Lake Liambezi[3]	119	157	183	201	214	240	0.380	4.34
Lake Kariba[7]	72	114	151	183	211	387	0.145	4.34
Lake Chicamba[8]	132	158	172	180	184	188	0.636	4.35

[1] Present study – Kavango, Kwando, Lake Liambezi and Zambezi Rivers, Namibia
[2] Kapetsky 1974 – Kafue floodplain, Zambia
[3] van der Waal 1985 – Lake Liambezi, Namibia
[4] Booth et al. 1995 – Okavango Delta, Botswana
[5] Dudley 1974 – Kafue Floodplain, Zambia
[6] Booth and Merron 1996 – Okavango Delta, Botswana
[7] Kolding et al. 1992 – Lake Kariba, Zimbabwe
[8] Weyl and Hecht 1998 – Lake Chicamba, Mozambique

The growth rate of *T. rendalli* in the Zambezi River was initially slower than in Lake Liambezi (this study) but larger sizes were attained in the Zambezi River. The resulting growth performances are very similar, as they were for *O. andersonii* in Lake Liambezi and the Zambezi River.

Maturity

James and Bruton (1992) and Weyl and Hecht, (1998) showed the variation in length-at-maturity of *O. mossambicus* and *T. rendalli* between different populations. For male *O. mossambicus* it ranged from 110 mm SL to 265 mm SL in small reservoirs in the Eastern Cape Province of South Africa (James & Bruton, 1992). *Tilapia rendalli* reached 50% maturity at 109 mm SL in Lake Liambezi (van der Waal, 1985), considerably smaller than in Lake Chicamba (Weyl & Hecht, 1998) and Lake Kariba (Kolding et al., 1992). Merron (1991) recorded lengths-at-maturity for *O. andersonii* ranging from 105 mm SL to 155 mm SL in perennially and seasonally flooded areas in the Okavango Delta, while 50% maturity in Lake Liambezi occurred at 207 mm SL (van der Waal, 1985). These variations in length-at-maturity have been attributed to the different environmental conditions experienced by each population (James & Bruton, 1992; Merron, 1991). Greater lengths-at-maturity have been observed under favourable environmental conditions and smaller lengths-at-maturity have been found in less favourable habitats (James & Bruton, 1992). *Oreochromis andersonii* from the more stable perennially-flooded habitats in the Okavango Delta had a significantly larger length-at-maturity than those from seasonally flooded areas (Merron, 1991).

In contrast to the large degree of variability in length-at-maturity in the above examples, length-at-50% maturity of *O. andersonii* and *T. rendalli* did not differ significantly from each other in the four sampling areas. For *O. macrochir* it did, however, differ between systems. The length-at-50% maturity was significantly larger in the Zambezi River compared to that in the Kwando River. These estimates were, however, based on small sample sizes. As lengths-at-50% maturity of *O. andersonii* and *T. rendalli* did not differ between systems, it can be assumed that the differences for *O. macrochir* are an artefact of the data, although larger sample sizes for these systems are required to substantiate this hypothesis. The similarities in length-at-maturity between populations observed in this study indicate that the environmental variables influencing length-at-maturity are similar in each system, despite the fact that growth varies considerably.

Lengths-at-maturity of *O. andersonii* in this study were similar to that observed by van der Waal (1985) in Lake Liambezi, and large compared to those observed by Merron (1991) in the Okavango Delta. Lengths-at-maturity of *O. macrochir* in the Kwando River and Lake Liambezi were similar to that observed by van der Waal (1985) in the lake prior to it drying out while estimates from the Zambezi River were larger and estimates from the Kavango River were smaller. *Tilapia rendalli* in this study matured at similar sizes to those in Lake Kariba (Kolding et al., 1992) and Lake Chicamba (Weyl & Hecht, 1998) and larger sizes than in Lake Liambezi (van der Waal, 1985).

Age-at-50% maturity, unlike length-at-50% maturity, differed markedly between populations, a result of variation in growth rates between populations, where length-at-50% maturity did not differ. Age-at-50% maturity was lowest in Lake Liambezi where the initial growth rate was fastest, and highest in the Kwando River where growth was slowest (Tables 5.13, 5.15 and 5.17).

Cichlids usually begin to spawn shortly before flooding occurs: increasing day length and temperature are thought to be the primary cues (Chimatiro, 2004; Dudley, 1974; Merron, 1991; Weyl & Hecht, 1998; Winemiller, 1991; van der Waal, 1985). *Oreochromis andersonii*, *O. macrochir* and *T. rendalli* have an extended spawning season which usually lasts throughout summer, during which multiple broods may be raised (Dudley, 1974; Merron, 1991; Weyl & Hecht, 1998; van der Waal, 1985). The reproductive season of *O. andersonii*, *O. macrochir* and *T. rendalli* did not differ between the Kavango, Kwando, Lake Liambezi and Zambezi Rivers. Reproduction in all three species took place between September and April, which was consistent with what was previously known about the breeding seasonality of these species.

Conclusion

This chapter presents the first otolith-based age estimates of *O. andersonii*, *O. macrochir* and *T. rendalli* in the Kavango, Kwando, Lake Liambezi and Zambezi Rivers in Namibia. Precision estimates between otolith readings of the study species were comparable to other cichlids and to other freshwater fish species in southern Africa. Edge analysis revealed that a single opaque zone was formed annually in each species between October and January, with a peak in December, which coincided with reproduction and low water levels.

Addressing the hypotheses

The null hypothesis that growth rates did not differ between systems was rejected as combined sex growth rates differed significantly between populations for all three species. Initial growth rates for each species were fastest in Lake Liambezi, but *O. andersonii* and *O. macrochir* attained larger sizes in the Zambezi River. *Tilapia rendalli* attained larger sizes in the Kavango River. The growth performance of each species was highest in Lake Liambezi and lowest in the Kwando River.

The null hypothesis that length at maturity did not differ between systems was accepted for *O. andersonii* and *T. rendalli* as length-at-maturity did not differ significantly between populations of these two species. Differences in length-at-maturity of *O. macrochir* between systems were tentatively ascribed to the small sample sizes in the Kavango and Zambezi Rivers.

Age at maturity of each species differed significantly between populations as a result of differences in growth rates. The null hypothesis that age-at-maturity did not differ between populations was therefore rejected.

The life history traits of *O. andersonii*, *O. macrochir* and *T. rendalli* are affected by a suite of environmental and biotic variables. Determining which variable or which combination of variables affects the growth rates and size-at-maturity of the different populations of these species was beyond the scope of this study and requires future research. However, this study does set the baseline for making some management recommendations for the fishery. These are discussed in Chapter 6.

CHAPTER 6

General discussion and management recommendations for the cichlid fisheries in the Kavango and Caprivi Regions, Namibia

Riparian communities in the Kavango and Caprivi Regions in north-eastern Namibia rely heavily on the fish resources of the Kavango, Kwando and Zambezi Rivers and their associated floodplains and lakes for food, income and employment (Purvis, 2001; Turpie et al., 1999; Tvedten, 2002). Increasing fishing effort, driven by human population growth, threatens to overexploit the fish resources in the region (Hay & van der Waal, 2009). Overfishing may result in the loss of biodiversity and ecosystem goods and services on which riparian communities rely (Allan et al., 2005; Arthington et al., 2004). Effective management is urgently required to prevent the overfishing of large cichlids and the onset of the “fishing down” process, particularly in the Zambezi River where effort is increasing fastest.

The first indication of overfishing in a system is often the disappearance of certain stocks or species (Allan et al., 2005; Welcomme, 1999). Analyses of experimental gillnet catches showed that species richness and diversity were similar between the three river systems (Chapter 4). The similarity between fished areas in the Zambezi River and unfished areas in the Kavango and Kwando Rivers indicated that fishing has not significantly altered the fish assemblage in the Zambezi River. The similarity between systems was likely because of increased fishing effort in the Zambezi River being recent and that the fishery still targets the largest, most valuable cichlids in the assemblage. Species richness and diversity were lower in Lake Liambezi because of the absence of some riverine specialists such as *H. vittatus* and rarity of others such as *M. acutidens* (see Chapter 4). The fish fauna in Lake Liambezi has undergone significant changes since the lake began to fill in 2001, with small pioneering barb species being replaced by small characins, and the numbers of large catfish have decreased while large cichlids have increased. The fish fauna in the lake is likely to develop further until the lake reaches a stable state similar to that observed by van der Waal in 1976. Cichlids were the most diverse family in every system but contributed little to experimental gillnet catches (Chapter 4). Catch per unit effort of the tilapiines was highest in the Kwando River and Lake Liambezi, and was significantly lower in the Zambezi River (Chapter 4). The lower abundance of cichlids in the Zambezi River was most likely a result of higher levels of exploitation.

The proper assessment and management of a fishery requires an understanding of the biology, life history and distribution of the target species (King, 1995). As a first step towards the development of scientifically based management strategies for the multispecies fisheries in the Kavango and Caprivi Regions, the life history traits of three key cichlid species were assessed. As life history traits of cichlids vary from one water body to another (James & Bruton, 1992; Weyl & Hecht, 1998), it was necessary to investigate the locality specific biology of *O. andersonii*, *O. macrochir* and *T. rendalli* in the Kavango, Kwando, Lake Liambezi and the Zambezi Rivers (Chapter 5).

The present study provided the first otolith-based age estimates of *O. andersonii, O. macrochir* and *T. rendalli* in the four study areas in Namibia. The deposition of a single growth zone annually on the otoliths of these species was validated indirectly by edge analysis. The growth rates of the three species differed significantly between the four populations, most likely as a result of differences in productivity and food availability in each system, as well as competition and predation. Initial growth rates of each species were fastest in the highly productive, recently-flooded Lake Liambezi and were slowest in the Kwando River where productivity was lowest.

The length-at-maturity of *O. andersonii*, and *T. rendalli* did not differ significantly between systems. It did, however, differ for *O. macrochir*, but these differences were most likely a result of sample size limitations in the Kavango and Zambezi Rivers. This differs from populations of *O. mossambicus* in the Eastern Cape, South Africa, in which the length-at-maturity varied considerably between populations (James & Bruton, 1992). This suggests that the variables influencing the length-at-maturity of these species were similar between the four systems. Age-at-maturity differed significantly between populations as a result of variations in growth rates.

Biology and harvest patterns

Rapid first year growth (see Chapter 5) is thought to allow juvenile cichlids to attain a size large enough to avoid intense predation from species such as *H. vittatus* as they move off the floodplains and into permanent water bodies during the drawdown phase (Booth & Merron, 1996; Booth et al., 1995; Chimatiro, 2004; Weyl & Hecht, 1998). After floodwaters recede and fishes migrate back into permanent water bodies, most juvenile tilapiines are large enough to avoid predation but need protection from the fishery. The legal minimum mesh size of 3” (76 mm) selects for juvenile *O. andersonii* and *O. macrochir,* but is optimal for *T. rendalli,* selecting for fish at or near their length-at-maturity (Chapters 4 and 5). The consequence of targeting juvenile fish can be extremely detrimental to the fishery and has resulted in the collapse of cichlid fisheries or disappearance of certain species from the fisheries in Lakes Malawi and Malombe in Malawi (Turner et al., 1995; Weyl, Ribbink, & Tweddle, 2010; van Zwieten, Njaya, & Weyl, 2003).

In Lake Malombe, heavy fishing pressure on adult and juvenile size classes of *Oreochromis karongae* and *Oroechromis squamipinnus* by a multi-species fishery using seine nets for small species and gillnets for large species lead to a collapse of the fishery (Tweddle et al., 1995; van Zwieten et al., 2003). Similarly, in Lake Malawi the Chambo (*Oreochromis* spp.) fishery collapsed as a result of the introduction of purse seines called “kauni” nets that targeted juvenile fish in an already fully exploited fishery (D. Tweddle, pers. comm.; Tweddle & Magasa, 1989; Weyl et al., 2010). An increase in minimum mesh size which would select for the tilapiines after the size at 50% maturity would ensure that juveniles are protected from the fishery and would give fish the chance to breed before entering the fishery.

Management recommendations

In southern Africa most river-floodplain fisheries are open-access and are managed by means of regulating fishing effort through the use of various technical measures (Welcomme, 1979, 2001). One of the most commonly used and easily applied technical measures is mesh size restrictions (Jul-Larsen et al., 2003). Problems arise in multispecies fisheries when trying to decide on the correct mesh size (Welcomme, 1985, 1999). In the fisheries in the Kavango and Caprivi Regions *O. andersonii* is one of the most commonly caught and highly sought after species (van der Waal, 1980, 1990, 1991). It therefore makes sense to select a minimum mesh size that manages the fishery optimally for this species.

The lack of significant differences in the lengths-at-50% maturity of *O. andersonii* between systems means that a single minimum mesh size can be set for all four systems. Targeting *O. andersonii* before they have reached maturity, as the current minimum legal mesh size of 3” (76 mm) does, could result in “growth overfishing” — where fish are harvested before they are given a chance to grow to the size at which the maximum yield would be obtained for each recruit—that results in a reduced yield. Furthermore, regulations do not consider the maintenance of an adequate spawner biomass. Excessive effort, as a result of human population growth and the open-access nature of the fishery could reduce the spawner biomass to very low levels, resulting in “recruitment overfishing” —where the spawner stock is reduced to levels at which recruitment is negatively affected. It is therefore recommended that the minimum legal mesh size be increased to 3.5” (89 mm), as the Lake Liambezi fishing community have already done (D. Tweddle, pers. comm.).

This would ensure that *O. andersonii* enter the fishery at or near to the length-at-50% maturity, avoiding growth overfishing and allowing some fish to breed before they are large enough to be caught. An increase in the minimum legal mesh size to 3.5” (89 mm) will also ensure the sustainability of the *O. macrochir* and *T. rendalli* stocks as these fish will only enter the fishery after reaching maturity.

This management strategy relies heavily on the enforcement of the minimum mesh size regulations. In the absence of strict enforcement, there is a tendency for fishers to reduce their mesh sizes to compensate for the smaller average size of fish in the assemblage as a result of harvesting (Jul-Larsen et al., 2003; Welcomme, 1985, 1999). If this occurs, smaller, lower value species such as *S. intermedius* and *M. altisambesi* and juveniles of the large cichlid species will become the main target of the fisheries. This may result in the collapse of large cichlid stocks as happened in Lakes Malawi and Malombe.

The maintenance of an adequate spawner stock of *O. andersonii* under heavy fishing pressure is essential to ensure the sustainability of the fishery. One way to achieve this is to establish protected areas. With the assistance of the MFMR/NNF/WWF Zambezi/Chobe fisheries project, two Fish Protection Areas (FPA’s) have been established by conservancies along the course of the Zambezi River in Namibia. These areas will act as refuges for mature fish during the drawdown and low water phases when they are most vulnerable to capture. The aim of the FPA’s is to enhance the fishery in areas adjacent to them through improved recruitment and the outward migration of large fishes from the protected areas. FPA’s may also reduce conflict between recreational anglers and subsistence and commercial fisherman. Anglers may pay the fishing communities, responsible for the management of these areas, to practice catch and release angling within them.

If the FPA’s on the Zambezi River prove to be successful, the same principle may also help manage the fish resources of the Kavango River. Much of the Kwando River already lies within protected areas and there is thus little need for the establishment of community managed protection areas to maintain an adequate spawner stock. But conservancies may want to establish FPA’s anyway to earn revenue from angling tourists. Lake Liambezi is an unpredictable ephemeral lake and harvesting should be maximised when the lake contains water. There is no need to establish FPA’s in the lake, but management should rather focus on maximising economic benefits through harvesting of the large tilapiine species.

Recommendations for future research

The assessment of the life history traits of important target species presented in this thesis should form the basis of management strategies for the river-floodplain fisheries in the Caprivi and Kavango Regions. Assessment of the life histories of other large and important cichlid species such as *Serranochromis robustus* and *Sargochromis giardi* and keystone predators such as *H. vitattus* needs to be carried out to ensure these stocks are being fished sustainably. The effects of the flood pulse on the growth, recruitment and mortality of important species should be studied and those parameters necessary for describing fish population dynamics estimated.

This information can be incorporated into predictive river-floodplain fisheries models (Halls et al., 2001) to determine which harvest strategies maximise potential yields of the large cichlid species under different hydrological regimes. Management recommendations for the complex multispecies fisheries can be made based on the predictions of these models.

The current study showed that the fish assemblage in the Zambezi River has not been significantly altered by fishing pressure based on its similarity to protected areas in the Kwando and Kavango Rivers. Once established, the recovery of fish assemblages in FPA's needs to be monitored and their contribution to the fisheries in the adjacent areas quantified in comparison to areas further away. Further research examining the differences in fish communities between protected and unprotected areas in the Kavango River needs to be undertaken to assess the impact of fishing on the fish assemblages in that river. Research should be carried out at the most suitable locations for Fish Protection Areas in the Kavango River so that this management strategy may be implemented to protect the spawning stocks of large cichlids.

The development of the fish stocks in Lake Liambezi should continue to be monitored. This will provide managers with information for adaptive management decisions as the fish stocks continue to develop, and will be invaluable in formulating management strategies for Lake Liambezi in the future. Traditional stock assessment models, although not applicable to the river fisheries, may be useful in managing the important tilapiine cichlid stocks in Lake Liambezi.

Long term experimental gillnet monitoring data collected by the MFMR are available for the Kavango, Kwando and Zambezi Rivers. Analyses of these data need to be carried out in order to examine changes in fish populations over time in response to flooding and fishing pressure. Monitoring data can provide crucial information to fisheries managers about changes in the fish assemblages so that they may make adaptive management decisions.

Selective harvesting of the larger fish species in a diverse assemblage such as those in river-floodplain environments can have significant and unpredictable effects on food web dynamics and fish community structure (Winemiller, 2004). The assessment of food web dynamics using traditional gut content and stable isotope analysis should be carried out to determine the trophic relationships between species. Seasonal variation in production and consumption dynamics and species interactions can be examined in relation to the different flood regimes in each system. Food web dynamics between fished and unfished areas in each system should be examined to help us better understand how fishing impacts on the ecosystem. This will allow for the determination of harvesting regimes that allow us to maximise yield without disturbing the food web to the extent that biodiversity and biological productivity are lost.

Concluding remarks

The results presented in this thesis will hopefully contribute to the sustainable management of the fisheries in the Kavango and Caprivi Regions in Namibia. Assessment of the growth and maturity patterns of three cichlid species from the

Kavango, Kwando, Lake Liambezi and Zambezi Rivers revealed significant variations in growth rates and a lack of differences in the length-at-maturity between the four populations. This has important implications for the potential productivity of each system and the sustainable management of these species and the fisheries as a whole.

Two management recommendations were made. The first was to increase the legal minimum mesh size from 3” (76 mm) to 3.5” (89 mm) to ensure that *O. andersonii* are selected for at or near their size-at-maturity to prevent growth overfishing. The second was to endorse the establishment of community-run Fish Protection Areas in the Zambezi River and to recommend the establishment of further areas in the Zambezi and Kavango Rivers to maintain an adequate spawner stock of large cichlids.

Finally, a significant amount of research still needs to be carried out before we can begin to properly understand and effectively manage the complex floodplain fisheries in the Kavango and Caprivi Regions.

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