COMPARATIVE FISH ECOLOGY IN THREE PERIODICALLY CONNECTED RIVERS IN THE UPPER ZAMBEZI AND OKAVANGO ECOREGIONS

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GERALDINE CLAIRE TAYLOR

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ABSTRACT

The Upper Zambezi, Kavango and Kwando rivers are three periodically interlinked floodplain rivers which share the same Upper Zambezian floodplain ichthyofauna. The aim of this thesis was to compare the biology and ecology of the fish communities in these three rivers. The objective was to test the hypothesis that fish community composition and assemblage structure, fish diets, food web structure and trophic dynamics, fish growth rates and total mortality are influenced by the differing flood magnitudes of the three rivers, in support of the flood pulse concept. To understand the abiotic characteristics of each river, water temperature, flood regime, total dissolved inorganic nitrogen concentrations and water quality parameters were measured and compared between rivers. Water temperatures varied seasonally, and seven day moving averages peaked above 30 °C in January, and fell to between 16 and 19 °C in June. The Zambezi River had the largest flood (6.14 m), followed by the Kavango River (3.80 m), while the Kwando River had the smallest flood (0.65 m). Total dissolved inorganic nitrogen concentrations were low in the Kavango and Zambezi Rivers (0.2 – 0.6 mg/l), and slightly higher in the Kwando River (<1 mg/l). Conductivity, total dissolved solids and total dissolved inorganic nitrogen concentrations decreased with the flood (dilution effect).

Using biomass catch per unit effort data from experimental gillnets, fish community composition and assemblage structure was described, and differed between rivers in all hydrological seasons. In the Zambezi and Kavango rivers, fish assemblages varied with hydrological season as a result of the homogenising influence of the flood pulse, while in the Kwando River fish assemblages did not differ seasonally as flood pulses were small and often irregular. Differences in community composition were attributed to the abundance of *Hydrocynus vittatus*, a large bodied open water predator, in the Zambezi and Kavango rivers, and its relative absence in the Kwando River.

Based on the results of the community composition, six focus species were chosen that were abundant and representative of the various feeding modes and life history strategies of the fish community. These were the striped robber *Brycinus lateralis*, sharptooth catfish *Clarias gariepinus*, blunttooth catfish *Clarias ngamensis*, African pike *Hepsetus cuvieri*, silver catfish *Schilbe intermedius* and purpleface largemouth *Serranochromis macrocephalus.* Stomach contents analysis was then used to compare the feeding ecology of the six example species between rivers. *Clarias gariepinus*, *C. ngamensis* and *S. intermedius* were piscivorous in the Zambezi and Kavango rivers, and preyed upon more invertebrates in the Kwando River, while *Hepsetus cuvieri* and *S. macrocephalus* were piscivorous in all three rivers. Differences in diets were attributed to seasonal prey abundance, with prey fishes abundant during falling and low water when the Zambezi and

Kavango rivers were sampled, while invertebrates were abundant during rising and high water when the Kwando River was sampled. Prey mastication by *B. lateralis* made prey identification difficult. For other predators, the usefulness of stomach contents analysis for dietary descriptions was restricted by the high proportion of empty stomachs. As a result, whole ecosystem stable isotope analysis was used to gain a holistic understanding of the food web structure and fish feeding ecology of the three rivers. The Zambezi and Kavango river food webs were supported by ^{13}C enriched resources such as C_4 and C_3 riparian vegetation from the floodplain, while the Kwando River food web was based on ^{13}C depleted resources such as filamentous algae and aquatic macrophytes. The Zambezi River food web had a restricted nitrogen range, with reduced food chain length and the predators in this river did not occupy such elevated trophic positions compared to in the Kavango and Kwando river food webs. This was attributed to the overfishing of the primary and tertiary consumers in the Zambezi River, a phenomenon known to reduce food chain length.

Focussing on predator communities, in the Zambezi and Kavango rivers, *H. vittatus* isotopic niche width was large and overlapped significantly with most other predators, while in the Kwando River predator niches were more distinct. This supported previously proposed hypotheses by describing *H. vittatus* as a dominant predator which excludes all other fishes by predation or competition. Despite the dominance of *H. vittatus*, *C. gariepinus* occupied the position of top predator in all three rivers, and information on the habitat use, feeding habits and trophic niches of the serranochromine cichlids added understanding of their ecology.

Lastly, age was determined using sectioned sagittal otoliths for *C. gariepinus*, *C. ngamensis*, *S. intermedius* and *S. macrocephalus* and using whole asteriscus otoliths for *B. lateralis* and *H. cuvieri*, and growth was modelled using the von Bertalanffy growth equation. Growth performance was high in the Zambezi and Kavango rivers, and lower in the Kwando River, most likely in response to the varying flood magnitudes. Total mortality rates, estimated using Hoenig's maximum-age based equation, were high in the Zambezi River as a result of the high fishing pressure on this river.

Overall floodplain fish ecology in the Zambezi, Kavango and Kwando rivers was influenced by the flood pulse, as was predicted by the flood pulse concept. Periodic and equilibrium life history strategists were found to adapt either to the pulsing environments of the Zambezi and Kavango rivers, or to the more stable environment of the Kwando River, and large bodied, long lived periodic strategists such as *C. gariepinus* tended to be highly plastic and able to thrive in most conditions. Data also suggested that Zambezi River food web structure and fish mortality rates have been impacted by overfishing, for which more information is needed to conserve and manage this system.

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CONTENTS

CHAPTER 1: General Introduction

Introduction

Riverine flood plains, or areas of land subject to inundation by lateral overflow of rivers, are considered some of the Earths most distinct ecosystems (Tockner and Stanford 2002). They are highly productive, contain a diverse and complex array of organisms (Bayley 1988; Ward et al. 1999; Tockner and Stanford 2002), and support a large proportion of the world's aquatic biodiversity (Arthington et al. 2004). As a result of their wealth in natural resources and fertile soils, floodplain ecosystems have historically been important for human livelihoods (Tockner and Stanford 2002), and floodplain fisheries in particular support multitudes of people (Arthington et al. 2004). Understanding ecological processes in these systems is crucial for their conservation and management.

The Flood Pulse Concept

The driving force behind the functioning of floodplain ecosystems is the flood pulse, and the flood pulse concept (FPC) was developed as an explanation of the relationships between the biota and the environment of unmodified, large river floodplain systems (Junk et al. 1989). The FPC states that the rising of river waters onto the floodplain creates a "moving littoral" over the aquatic terrestrial transition zone which is responsible for the adaptations of most of the biota, and drives the productivity and diversity of the system (Junk et al. 1989; Bayley 1995). Periodic inundation of the flood plains releases nutrients mineralised in the sediment and there is an influx of organic matter and detritus from the decomposition of plants, so boosting productivity (Bayley 1995; Roach et al. 2014). Biodiversity is driven by the heterogeneity of the floodplain environments, which are a mosaic of complex habitats of differing physical and chemical conditions, changing annually with the magnitude and duration of the flood (Junk et al. 1989; Bayley 1995; Ward et al. 1999). As a result, the floodplain acts as an ideal spawning and feeding environment for adult fishes, a nursery area for juvenile fishes, and provides near optimal conditions for invertebrates (Jackson 1986; Junk et al. 1989; Bayley 1995; Hocutt and Johnson 2001). The extent to which inundation occurs and the timing of this inundation would therefore directly influence ecological and biological processes such as fish assemblage structure, food web dynamics, reproduction and fish growth rates within floodplain systems.

The occurrence of annual flood pulses is known to influence patterns of species abundance and assemblage structure in tropical floodplain rivers (Winemiller 1996a; Arrington and Winemiller 2004). Flooding has a homogenising effect on fish assemblage structures (Tejerina-Garro et al. 1998; Thomaz et al. 2007; Gomes et al. 2012), and creates heterogeneous habitats for the reorganisation of assemblages. An explanation for the processes involved in structuring assemblages is offered by a number of metacommunity models, including the *patch dynamics* model (Townsend 1989), which describes a trade-off between colonisation and competition abilities as the driver of community structure. The *species sorting* model (Whittaker 1962; Holt 1985) describes a heterogeneous environment where assemblage structure is driven by the filtering of species by environmental conditions and habitat selection. The *mass effect* model proposed by Shmida and Wilson (1985) states that dispersal of species along a source-sink gradient determines assemblage structure whereby competitively inferior species move to habitats that are less biotically and abiotically favourable. The *neutral* model (Hubbell 2001) provides a null model against which predictions from the other models can be compared (Leibold et al. 2004; Holyoak et al. 2005; Jackson et al. 2013). Jackson et al. (2013), for example, found that the patch dynamics, species sorting and mass effect models in combination, were best used to describe the patterns in assemblage structure of floodplain whedos of the Ouémé River, Benin.

Vellend (2010) offered an alternative explanation, suggesting that all patterns structuring assemblages could be explained by selection (i.e. filtering species by hypoxia and/or predation Jackson et al. 2013), drift (random changes in species abundance), speciation (the creation of new species) and dispersal (i.e. colonisation of floodplain habitats by fishes during the flood Jackson et al. (2013)). Winemiller (1996a) attributed patterns in assemblage structure to a combination of stochastic and deterministic processes acting over the broad array of spatial and temporal scales within floodplain systems. There are therefore many patterns and processes potentially driving fish assemblage structure in floodplain systems, and the most likely scenarios involve initial homogenous dispersal into the floodplain, or as stated by Arrington and Winemiller (2004) "dispersal is most important in structuring assemblages in newly formed patches", followed by selection, with drift as a constantly impacting process.

Fish feeding patterns and food web structure are also influenced by the flood pulse (Balcombe et al. 2005; Zeug and Winemiller 2008; Roach et al. 2009). In tropical floodplain rivers, as temperatures do not change considerably throughout the year, flooding generally drives ecological dynamics and stimulates primary and secondary productivity (Junk et al. 1989). Primary productivity, which supports consumer populations, varies spatiotemporally within most systems (Winemiller 2005a), and in floodplain systems the main producers include both terrestrial and aquatic sources in the form of phytoplankton, algae, aquatic macrophytes or seasonally flooded terrestrial plants (Bayley 1988; Thorp and Delong 1994; Thorp et al. 1998; Lewis et al. 2001; Thorp and Delong 2002; Wantzen et al. 2002; Lindholm et al. 2007; Zeug and Winemiller 2008). Basal carbon production, reflected in the diets of higher consumers of floodplain river food webs, may change seasonally in relation to the high and low water phases (Winemiller 1990; Zeug and Winemiller 2008). For example, during flooding, the contribution of detrital C_3 riparian macrophytes and C_4 grasses could outweigh autochthonous production, while at low water levels algae and phytoplankton could dominate (Winemiller 1990; Wantzen et al. 2002; Winemiller 2005a). Consequently, detritivores may have access to unlimited detritus during the descending and low water phases, as was noted on the Zambezi River (Winemiller 1990), while fishes specialising on invertebrates would have access to an abundant source of food in newly flooded tropical habitats (Winemiller 1989a; Wantzen et al. 2002). The abundance of terrestrial and aquatic vegetation on the floodplain may enhance the diets of specialist feeders such as a number of siluriform catfishes which eat fruits and seeds in the Amazon (Araújo-Lima et al. 1995; de Mérona and Rankin-de-Mérona 2004), while fewer attachment surfaces are available for algae and benthic fauna during the low water season, reducing available food sources for herbivorous fishes (Winemiller 1996a). During the descending and low water periods, prey fishes congregate in the main channel, increasing the feeding opportunities for piscivorous fishes (Winemiller 1989a; Winemiller 1990; Wantzen et al. 2002; Winemiller 2005a). As a consequence of these fluctuations in resources, many fishes change their diets seasonally and thus directly influence food web structure (Merron and Mann 1995; de Almeida et al. 1997; Wantzen et al. 2002; Eggleton and Schramm 2004). Dispersal (e.g. migration) and reproduction are two other biological and ecological processes directly influenced by the annual flood, which in turn could affect food webs (Winemiller and Jepsen 1998; Winemiller 2005a).

As seasonal flood pulses influence the fluctuation of resources in river floodplain environments, it is not surprising that flood magnitude has been positively correlated to fish growth rates (Dudley 1974; de Graaf 2003). Larger floods are thought to promote greater primary and secondary production on the floodplains, consequently increasing fish growth rates (Junk et al. 1989). Seasonal growth rates have been correlated to the rising flood waters by Pérez and Fabré (2009) for a piracatinga catfish in the Amazon and by de Graaf (2003) for a number of fishes in the River Brahmaputra, Bangladesh.

Gutreuter et al. (1999) found that species dependent on the littoral zone grew faster with larger floods in the Upper Mississippi River system, while those not dependant did not show significant difference in growth rates. In the Central Amazon River, Bayley (1988) found that juvenile omnivores exhibited faster growth during rising water while juvenile detritivores did not as the areas of greatest detritus build up were also hypoxic. It is therefore evident that annual flood pulses influence the biology and ecology of floodplain ecosystems.

The Zambezi, Kavango and Kwando rivers

Situated within southern Africa, the Zambezi, Kavango and Kwando rivers are three large, interconnected floodplain rivers. They all flow through Namibia in the previously named Caprivi Strip, now the Zambezi and East Kavango regions in the north-eastern most corner of the country (Figure 1.1). In this thin peninsular of Namibia, there are four towns (Katima Mulilo, Kongola, Divundu and Rundu) and five National Parks (Mamili, Mudumu, and Kwando, Buffalo and Mahango Core Ares of Bwabwata), with tourism in the region contributing significantly to the country's economy (Turpie et al. 1999). According to the 2001 census, the Zambezi Region was home to 39 077 people, projected to be 47 514 people in 2015, while the Kavango Region was home to 96 513 people (154 323 people in 2015) (Angula 2006). In 1999, the population estimate for the Caprivi floodplains was 20 846 (Turpie et al. 1999), implying that less than half of the Zambezi Region's population resides in Katima Mulilo and Kongola, and most of the region's population is rural. The main livelihood activity for people in the Caprivi floodplain is agriculture (Turpie et al. 1999); however this is a multipurpose economy and fishing is part of the livelihoods strategy contributing to income and to household dietary nutrition (Tvedten 2002; Tweddle 2010).

In recent years the growing demand for fresh and dried fish, in both neighbouring Zambia and the Democratic Republic of Congo (DRC) sourced from the Caprivi floodplain and the ephemeral floodplain Lake Liambezi has increased pressure on the Zambezi Regions fisheries (Abbott et al. 2015; Tweddle et al. 2015). Exploitation has been aided by improved transportation and communications in Namibia, Zambia and the DRC, which allows fresh fish on ice to move across the Sasheke border to Zambian towns such as Livingstone, and dried fish to be transported to the DRC (Abbott et al. 2015). This demand for fish has driven illegal fishing and harvesting methods (Tweddle 2010; Abbott et al. 2015; Peel et al. 2015; Tweddle et al. 2015). Illegal Zambian fishers have been arrested and deported from Lake Liambezi, and are often caught fishing on the Namibian side of the Caprivi floodplain (Abbott et al. 2015). Illegal and environmentally destructive fishing methods and gears, such as drag netting with small meshed gillnets, bashing the water to chase fishes into nets, and drifting gillnets down the river (Figure 1.2), are now in use as fishers try to maintain catch rates by diversifying fishing techniques and targeting smaller, previously non-target species (Tweddle 2010; Abbott et al. 2015; Tweddle et al. 2015). As a result of this now organised, semi-commercial trade, the livelihoods and food security of subsistence fishers and local traders are endangered (Abbott et al. 2015; Tweddle et al. 2015).

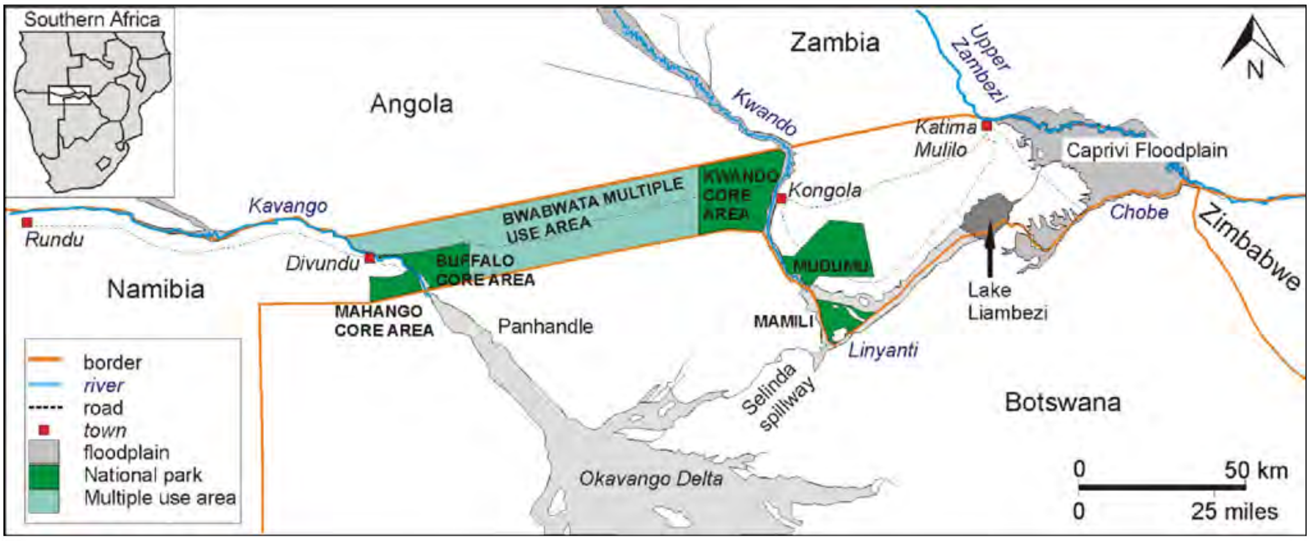

Figure 1.1: Map of the Zambezi and East Kavango Regions of Namibia, illustrating the study rivers, towns and national parks.

In the Kavango Region, fishing is also used to subsidise incomes and provide necessary protein (van der Waal 1991; Hocutt et al. 1994); fishing pressures are also increasing (Hocutt and Johnson 2001), however to a lesser extent compared to that in the Zambezi Region. It is hypothesised that with increasing fishing pressure on the Zambezi River system, fishers will move westwards to the smaller Kwando River. In addition, increased pressure on the Kavango River by the growing Rundu population may also displace fishers towards the Kwando River.

Figure 1.2: Illegal gears and fishing techniques employed by fishers on the Upper Zambezi River, A: drag netting using a monofilament gillnet, B: fishers bashing vegetation to drive fishes into their nets (Photo by Richard Peel), C: a fine meshed seine net, D: the use of small meshed monofilament gillnets targeting immature tigerfish (Photo by Richard Peel).

Review of literature on the Upper Zambezi, Kavango and Kwando river fishes

These floodplain rivers are very important, both ecologically, and for local people, and information on the biology and ecology of the fishes that inhabit them is limiting. A few studies on the biology and ecology of the fishes of the Barotse floodplain, a large floodplain 200 km north of Katima Mulilo on the Upper Zambezi River, were undertaken in the 1960s (Kelley 1968; Duerre 1969; Weiss 1970) and again in the 1990s (Winemiller 1991a; Winemiller and Kelso-Winemiller 1994; Winemiller and Kelso-Winemiller 1996). In the 1960s, the research was undertaken by the Food and Agriculture Organisation of the United Nations (FAO), and aimed to advise the Government of

Zambia on the characterisation, management and development of the fishery. Some ecological information was collected by Kelley (1968) and Duerre (1969), who described the seasonal habitat utilisation, movement, reproduction, growth, and diets of a number of abundant fish species. In the 1990s, comprehensive ecological studies on the seasonal habitat utilisation, feeding behaviour, reproduction, growth and population structure of catfishes (Winemiller and Kelso-Winemiller 1996), serranochromine cichlids (Winemiller 1991a; Winemiller and Kelso-Winemiller 1991), *Hydrocynus vittatus* and *Hepsetus cuvieri* (Winemiller and Kelso-Winemiller 1994) were undertaken. In addition, the diets of a number of herbivorous/detritivorous cichlids (Winemiller and Kelso-Winemiller 2003) and invertivorous mormyrid species (Winemiller and Adite 1997) were described. Using stomach contents analysis, food web structure was examined by Winemiller (1996a), and ecological niches were investigated by Winemiller (1991b) and Winemiller et al. (1995).

More recently there have been a number of studies quantifying the fishery and investigating the fish biology and ecology of the Caprivi Floodplains, Upper Zambezi River, Namibia. The movement and habitat utilisation of *Serranochromis robustus* (Thorstad et al. 2005), *Oreochromis andersonii* (Økland et al. 2007), *Oreochromis macrochir* (Thorstad et al. 2007), *Hydrocynus vittatus* (Økland et al. 2005), and *Oreochromis andersonii*, *Sargochromis giardi*, and *Serranochromis altus* (Thorstad et al. 2001), and the effects of catch and release angling on *S. robustus* and *O. andersonii* (Thorstad et al. 2004), have been investigated. In addition, the movement and migration of a number of species in response to flooding has been documented by van der Waal (1996). Within the Caprivi and Chobe Floodplains, information is available on the subsistence and recreational fisheries (Næsje et al. 2003); the state of the fish resources and the commercial fishery (Hay et al. 2002; van der Waal et al. 2010); the buying and selling of fish resources (Purvis 2002a; Abbott et al. 2007a; Abbott et al. 2015); the management of the fish resources (Purvis 2002b; Tvedten 2002; Purvis et al. 2003; Abbott et al. 2007b), and the value of the natural resources of the system (Turpie et al. 1999). Peel (2012) undertook a comprehensive study on the comparative biology and ecology of the commercially important large cichlids *O. andersonii*, *O. macrochir* and *Coptodon rendalli*, investigating their abundance, distribution, age, growth, reproduction and recommending management strategies for the Upper Zambezi River, the Kavango River, the Kwando River and Lake Liambezi, Namibia.

On the Kavango River in Namibia, besides the study by Peel (2012), Bethune and Roberts (1991) published a checklist of fish species from the Kavango River and the Caprivi Floodplains, and van der Waal (1991) surveyed the fisheries of the Kavango River and described fishers' catches and gear use. Hocutt et al. (1994) described the seasonal abundance and distribution of the ichthyofauna along the rivers course in Namibia for the development of an index of biotic integrity. Hay (1995) described the seasonal fish community composition and abundance for the same index of biotic integrity, and investigated the growth, mortality, reproduction, diet and habitat preference for *Schilbe intermedius*, *Marcusenius altisambesi*, *Brycinus lateralis*, *H. vittatus* and *Synodontis nigromaculatus*. Hay et al. (2000) surveyed the fishery and, using experimental gear, assessed fish biodiversity, abundance and length at maturity to develop management recommendations for the fishery. Hocutt and Johnson (2001) assessed the response of the fish communities to the annual flood pulse by documenting seasonal fluctuations in the abundance of fishes with varying life history strategies.

In the Kwando River, besides the work by Peel (2012), a sole report was published by Næsje et al. (2004), which aimed to inform management recommendations. This report described the fish diversity, abundance and distribution of 18 common fish species including *B. lateralis*, *S. intermedius*, *Clarias gariepinus*, *H. cuvieri* and the large tilapiine and serranochromine cichlids.

There is a therefore a lack of information on the biology and ecology of the Kwando River fishes, as emphasised by Næsje et al. (2004). In addition, the ecological information available on the Upper Zambezi and Kavango river fishes has been generated using scales, pectoral spines or vertebrae for age determination, the use of stomach contents analysis for dietary descriptions and food web analysis, and general descriptions of assemblages based on abundances of individual species. New techniques, such as the use of metabolically inert otoliths for age determination (Campana and Neilson 1985; Campana and Thorrold 2001), a combination of stable isotope and stomach contents analyses for dietary descriptions and the construction and comparison of food webs (e.g. Harrigan et al. 1989; Renones et al. 2002; Kadye and Booth 2011; Pedreschi et al. 2015), and the use of multivariate techniques for the analysis of assemblage structure and community composition (e.g. Clarke 1993; Anderson and Underwood 1997; Clarke and Warwick 2001; Zeug et al. 2005), have been developed that can provide more robust information than past techniques.

In addition, with exception of the seasonal changes in species abundance described by Hocutt and Johnson (2001), an understanding of the response of fish communities to hydrological regimes and other physicochemical characteristics is lacking. Hocutt and Johnson (2001) and Merron (1991) called for more research on the influence of the annual flood pulse on fish communities and their life history strategies in the Kavango River and Okavango Delta respectively. Lastly, comparisons of fish ecology and biology across these periodically interconnected systems are not available, although Næsje et al. (2004) and Peel (2012) touched on the potential differences in fish community composition, abundance and biology in the Kwando River compared to in the Upper Zambezi and Kavango rivers.

From this brief review of the literature, it is clear that research should focus on: investigating fish biology and ecology in the Kwando River, revisiting the biology and ecology of the fishes of the Upper Zambezi and Kavango rivers using new techniques, comparing the biology and ecology of the fishes in these three rivers, and relating any differences to variations in hydrological regime and other physicochemical parameters.

Thesis Overview

This thesis aims to contribute to the understanding of the ecology of African floodplain systems by comparing fish communities between the Upper Zambezi, Kavango and Kwando rivers using contemporary techniques, to test the overall hypothesis that differences in the ecology of fishes can be attributed to differences in the annual flood regime of these rivers. From this aim, the following alternative hypotheses were posed:

H_a1: The flood regimes of the three rivers differ. This consequently influences the fish assemblage structure and community composition.

H_a2: The ecology of the fishes in the three rivers are influenced by the differing flood regimes with respect to 1) fish feeding behaviour and diet, 2) food web structure and isotopic niche, and 3) fish growth and mortality rates.

In order to test the above hypotheses, the following steps were taken.

After a general introduction and review of the literature from the region (Chapter 1), Chapter 2 identifies and describes the sampling sites, quantifies and compares a number of physicochemical parameters of each river, and describes the fish community composition and assemblage structure of each river by hydrological season. With the overall aim to compare fish ecology between rivers, it is imperative to quantify and compare the biotic and abiotic factors that may influence fish communities in each river system. Hence, water temperatures, flood regimes, total dissolved inorganic nitrogen concentrations and water quality were measured and compared between rivers, as literature on the water quality, nutrients and flood regimes of these three rivers was limited

(Cronberg et al. 1995; Mazvimavi and Wolski 2006; West et al. 2015). Fish community composition and assemblage structure were described using biomass catch per unit effort data generated from experimental gillnet sets, and compared between rivers and hydrological seasons.

Arthington et al. (2004) emphasised the need for knowledge on ecological processes at the species, assemblage, and ecosystem levels of heterogeneous systems for their effective management. Consequently, from the suite of more than 100 species which make up the Upper Zambezian ichthyofauna inhabiting the three rivers (Tweddle 2010), which is illustrated in Appendix 1, six abundant fish species characteristic of various feeding modes, occupying a variety of habitats, and representative of the three life history strategies, were chosen as example species for fish ecology comparisons. These species were the striped robber *Brycinus lateralis*, the African sharptooth catfish *Clarias gariepinus*, blunttooth catfish *Clarias ngamensis*, African pike *Hepsetus cuvieri*, silver barbel *Schilbe intermedius* and the purpleface largemouth *Serranochromis macrocephalus* (Box 1). The commercially important cichlid species, threespot tilapia *Oreochromis andersonii*, greenhead tilapia *Oreochromis macrochir* and redbreast tilapia *Coptodon rendalli*, were not studied because there is extensive, up to date information available on these species in the study systems already. For example, Peel (2012) compared their abundance, distribution, age, growth and reproduction in the three rivers. Their biology has been investigated in Lake Liambezi, Namibia (van der Waal 1985), the Okavango Delta, Botswana (Merron 1991), and the Barotse Floodplains, Zambia (Kelley 1968; Duerre 1969). Growth rates of these cichlids have been investigated using otoliths in the Okavango Delta (Booth et al. 1995; Booth and Merron 1996) and their diets have been described in the Barotse Floodplain, Zambia (Winemiller et al. 1995; Winemiller and Kelso-Winemiller 2003) and the Okavango Delta (Mosepele et al. 2012). Their movement behaviour (Thorstad et al. 2001; Thorstad et al. 2007; Økland et al. 2007) and response to recreational angling has been studied in the Upper Zambezi River, Namibia (Thorstad et al. 2004).

For an understanding of fish ecology, the investigation of feeding behaviour and diet is critical as they directly influence fish growth, mortality and reproduction, and essentially define the functional role of fishes in the ecosystem (Wootton 1990; Pedreschi et al. 2015). Previous research has described the diets of *B. lateralis, S. intermedius* from the Kavango River, Namibia (Hay 1995), *C. gariepinus*, *C. ngamensis, H. cuvieri, S. intermedius* and *S. macrocephalus* from the Barotse Floodplain, Upper Zambezi River, Zambia (Duerre 1969; Winemiller 1991a; Winemiller and Kelso-Winemiller 1994; Winemiller and Kelso-Winemiller 1996), and all six species from the Okavango

Delta, Botswana (Merron 1993; Merron and Mann 1995; Booth and McKinlay 2001; Mosepele et al. 2012). However, there is no information on the diets of fishes from the Kwando River, or the Caprivi Floodplains in the Upper Zambezi River, Namibia. The diets of the six example species were therefore described and compared between rivers, using stomach contents analysis (Chapter 3).

Although stomach contents analysis has a high taxonomic resolution (Pinnegar and Polunin 2000; Jepsen and Winemiller 2002; Kadye and Booth 2011; Layman et al. 2012), the use of this method for dietary descriptions is constrained by a number of factors. Firstly stomach contents analysis only gives a "snapshot" of an organisms diet (Pinnegar and Polunin 2000). Secondly, digestion makes prey identification difficult so hard bodied prey are over-represented while soft bodied prey are often overlooked (Hyslop 1980; Stapp 2002), and thirdly, the high energy content of the prey consumed by piscivores means feeding is infrequent and as a consequence many stomachs are empty (Arrington et al. 2002; Kadye and Booth 2011). As a result, the more contemporary technique of stable isotope analysis has been developed to aid in the description of fish diets and the unpacking of the trophodynamics of food webs (Harrigan et al. 1989; Pinnegar and Polunin 2000; Renones et al. 2002; Cocheret de la Morinière et al. 2003; Kadye and Booth 2011; Pedreschi et al. 2015). This analysis uses a combination of carbon and nitrogen stable isotopes to quantify the assimilated food intake of an organism over time, and can be used to better understand food web structure (DeNiro and Epstein 1978; DeNiro and Epstein 1981; Fry and Sherr 1984; Peterson and Fry 1987; Post 2002; Layman et al. 2012), and estimate trophic niches (Bearhop et al. 2004; Newsome et al. 2007; Layman et al. 2007; Layman et al. 2012). Using stable isotope samples collected from all fish species sampled, and a collection of invertebrates, molluscs, crustaceans, aquatic and terrestrial plants, detritus and particulate organic matter (POM), Zambezi, Kavango and Kwando river community food webs were compared. In addition, stable isotope analysis was used in conjunction with stomach contents analysis to describe and compare the isotopic niches and trophic positions of a number of predatory species between rivers systems (Chapter 4). The use of stable isotope analysis for food web and isotopic niche comparisons added another dimension to the understanding and comparison of fish ecology (Abrantes et al. 2014).

Growth is an important aspect of the ecology and life history of fishes, and fish growth rates are directly influenced by diet and food web structure (Summerfelt and Hall 1987; Weatherley and Gill 1987). Chapter 5 aimed to assess the variations in growth, relative condition and total mortality rates between populations in the three rivers, to test the hypotheses that i) trends in fish growth rates would be positively correlated to the magnitude of the flood pulse of the three rivers, and ii) in the Zambezi River, fish growth and mortality rates would be influenced by heavy fishing pressure. Age was determined using whole asteriscus or sectioned sagittal otoliths from the three populations of the six example species, and the accuracy and precision of age estimates were quantified. Growth was then modelled using the von Bertalanffy growth equation, and an index of growth performance was used to compare river populations. Length weight relationships of the study species were used to compare the relative condition of each species by river system, and total mortality was estimated using maximum age and Hoenig's (1983) empirical equation.

Finally, Chapter 6 provided an overall synthesis and discussion of the research findings, and related any differences in fish biology and ecology between rivers to adaptations in life history strategy in response to variations in hydrological regime. The implications of these finding for resource management and conservation were outlined in light of future climate change scenarios, and the threats imposed by increased water demand for human consumption, hydroelectricity and irrigation. Recommendations for future research were highlighted.

Box 1: Biological synopsis of the focus species used for the comparison of fish biology and ecology between the Upper Zambezi, Kavango and Kwando rivers, Namibia

Striped Robber *Brycinus lateralis* (Boulanger, 1900)

Brycinus lateralis is distributed within the Zambezi, Okavango, Cunene, Buzi and Luapula river systems, and the St Lucia catchment (Skelton 2001). *Brycinus lateralis* is a small species (Figure 1.3A) that grows to a maximum of 140 mm total length (Kolding et al. 1992), and lives to four years (Hay 1995). This species is an opportunistic strategist, maturing at 60 mm TL (Hay 1995; Booth and McKinlay 2001), spawning over a protracted period during the summer months (van der Waal 1985; Hay 1995; Booth and McKinlay 2001), with a maximum fecundity of over 5000 eggs (Hay 1995). *Brycinus lateralis* has been categorised as an opportunistic micro-carnivore and an omnivore, and feeds on zooplankton, terrestrial and aquatic insects, and seeds (Hay 1995; Booth and McKinlay 2001; Mosepele et al. 2012). *Brycinus lateralis* is abundant in a range of habitats encompassing both fast and slow flowing water (Booth and McKinlay 2001), however it is most often recorded in slow flowing water with vegetation (Merron and Bruton 1988; Hay 1995), and is utilised by subsistence fishers (Booth and McKinlay 2001).

Blunttooth catfish *Clarias ngamensis* Castelnau, 1861

Claris ngamensis is found within the Zambezi, Cunene, Okavango, Kafue, lower Shire, Save, Limpopo and Phongolo river systems, and within the Zambian Congo and Cuanza river systems (Skelton 2001). *Clarias ngamensis* grows to a large size (Figure 1.3B) of 740 mm TL (Kelley 1968; Duerre 1969) at a maximum age of 6 years (van der Waal 1985). This species is a periodic strategist, maturing at about two years and 300 mm TL, spawning over a short period cued by seasonal rainfall of the annual flood, and with a fecundity of over 50000 eggs (Willoughby and Tweddle 1978; van der Waal 1985). *Clarias ngamensis* has been described as a predator, an omnivore, a molluscivore and a herbivore (Willoughby and Tweddle 1978; van der Waal 1985), and eats fish, molluscs, invertebrates, zooplankton and detritus (Willoughby and Tweddle 1978; van der Waal 1985; Merron 1993; Winemiller and Kelso-Winemiller 1996; Mosepele et al. 2012). This species favours river channel and marginal floodplain habitats, and has been recorded in the catches of commercial and subsistent fishers (Winemiller and Kelso-Winemiller 1996).

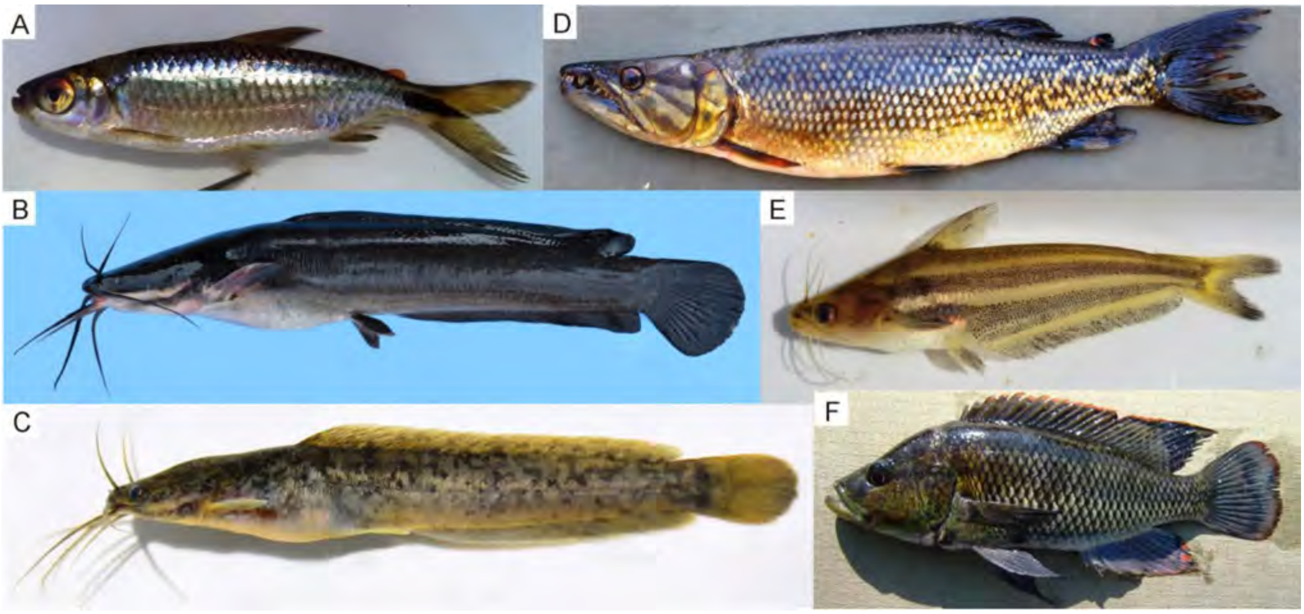

Figure 1.3: Photographs of the six study species A: *Brycinus lateralis*, B: *Clarias ngamensis* (Photo by Denis Tweddle), C: *Clarias gariepinus* (Photo by Denis Tweddle), D: *Hepsetus cuvieri*, E: *Schilbe intermedius*, F: *Serranochromis macrocephalus*.

Sharptooth Catfish *Clarias gariepinus* (Burchell, 1822)

Clarias gariepinus (Figure 1.3C) has a wide natural distribution, from the Orange and Umtamvuna river systems in the south, to the Nile River, Israel, Lebanon and Turkey in the north (Skelton 2001), and is invasive with an extensive non-native range within Africa and globally (Vitule et al. 2006;

Radhakrishnan et al. 2011; Ellender et al. 2014). *Clarias gariepinus* is a fast growing species reaching a maximum length of 2000 mm TL (Bruton 1976), and a maximum age of 25 years (Wartenberg et al. 2013). It is a periodic strategist, which matures around 300 mm TL at 2 years of age (Willoughby and Tweddle 1978; Bruton 1979a; van der Waal 1985; Merron 1991; Potts et al. 2008; Richardson et al. 2009), spawns over a discrete period in response to flooding (van der Waal 1974; Bruton 1979a), with a maximum fecundity of more than 160 000 eggs (Willoughby and Tweddle 1978; Bruton 1979a). This species is an opportunistic feeder, capable of feeding on a range of prey items from fish prey, to crustaceans, molluscs, invertebrates, zooplankton, macrophytes and detritus (Willoughby and Tweddle 1978; Bruton 1979b; van der Waal 1985; Dorgeloh 1994; Winemiller and Kelso-Winemiller 1996; Dadebo 2009; Kadye and Booth 2011; Mosepele et al. 2012; Dadebo et al. 2014). In possession of an accessory air breathing organ, *C. gariepinus* is capable of surviving desiccation (van der Waal 1998), and has been recorded in a variety of habitats (Winemiller and Kelso-Winemiller 1996). This large species is important in both commercial and subsistence catches in the Upper Zambezi River (Duerre 1969; Winemiller and Kelso-Winemiller 1996), the Okavango Delta (Bokhutlo et al. 2015), and the Shire Valley (Willoughby and Tweddle 1978).

African Pike *Hepsetus cuvieri* Castelnau, 1861

Hepsetus cuvieri, illustrated in Figure 1.3D, is distributed within the Cuanza, Cunene, Upper Zambezi, Okavango, Kafue river systems and the middle and upper Congo Basins (Zengeya et al. 2011). This species was recently separated from *Hepsetus odoe,* which is widely distributed up the west coast of Africa (Zengeya et al. 2011). *Hepsetus cuvieri* grows to maximum size and age of 470 mm and five years, respectively (van der Waal 1985). This species is an equilibrium strategist which matures at 150 – 200 mm at the age of 1+ years (van der Waal 1985; Merron et al. 1990), is a nest guarder which spawns 1000 to 2500 eggs per spawn over an extended period during warm temperatures (van der Waal 1985; Merron et al. 1990). Since this species spawns in multiple batches, it has an average fecundity of more than 6000 eggs per spawning season (Merron et al. 1990). *Hepsetus cuvieri* prefers quiet backwater habitats with aquatic vegetation (Duerre 1969; Merron et al. 1990; Winemiller and Kelso-Winemiller 1994), and is a piscivorous ambush predator (Duerre 1969; van der Waal 1985; Merron et al. 1990; Winemiller and Kelso-Winemiller 1994; Mosepele et al. 2012). This species is targeted both as a recreational angling species (Merron et al. 1990) and as an important component of subsistence fisheries (Merron et al. 1990; Winemiller and Kelso-Winemiller 1994).

Silver Catfish *Schilbe intermedius* Rüppell, 1832

Schilbe intermedius is found throughout the Zambezi, Okavango, Cunene, Phongolo river systems, and throughout Africa to the Nile in the north and Senegal in the west (Skelton 2001), however there is evidence of more than one species (van der Bank et al. 1998). *Schilbe intermedius* grows to a maximum length and age of 340 mm (Kolding et al. 1992) and eight years (Booth and Khumalo 2009), respectively. In Lake Liambezi, van der Waal (1985) described it as a species with a short life span and slow growth (Figure 1.3E). It is a periodic strategist, maturing at 110 – 190 mm (Hecht 1980a; van der Waal 1985; Hay 1995; Merron and Mann 1995; Booth and Khumalo 2009) and at two years of age (Hecht 1980a; Booth and Khumalo 2009), a broadcast monocyclic spawner cued by rains or floods (Hecht 1980a; van der Waal 1985; Merron and Mann 1995), with a fecundity of up to 100000 eggs (van der Waal 1985; Hay 1995; Merron and Mann 1995). *Schilbe intermedius* is an opportunistic crepuscular predator or omnivore which feeds on fish, crustaceans, and aquatic and terrestrial insects (van der Waal 1985; Hay 1995; Merron and Mann 1995; Winemiller and Kelso-Winemiller 1996; Mosepele et al. 2012), in slow flowing backwaters, lagoons or floodplains (Hay 1995; Winemiller and Kelso-Winemiller 1996). It is an abundant species underutilised by subsistence fishers (Hay 1995; Merron and Mann 1995; Winemiller and Kelso-Winemiller 1996).

Purpleface Largemouth *Serranochromis macrocephalus* (Boulanger, 1899)

Serranochromis macrocephalus is found within the Cunene, Okavango, Upper Zambezi and Kafue river systems, Lake Kariba and southern tributaries of the Congo system (Skelton 2001). This largemouth bream species (Figure 1.3F) is medium bodied, growing to 430 mm TL (Kelley 1968), and to a maximum age of about 8 years (van der Waal 1985). This is an equilibrium strategist, which matures at 150 – 200 mm at approximately two years (van der Waal 1985; Winemiller 1991a), is a mouth brooder with an extended spawning season over the summer months (Kelley 1968; Duerre 1969; van der Waal 1985; Winemiller 1991a), with a total fecundity of more than 1500 eggs (van der Waal 1985). Inhabiting slow flowing backwaters and floodplains (Winemiller 1991a), *S. macrocephalus* is a crepuscular ambush predator which eats fish and occasionally insect prey (Duerre 1969; van der Waal 1985; Winemiller 1991a; Zengeya and Marshall 2010). This species is mainly harvested in the commercial fishery, but is not uncommon in the subsistence fishery (Duerre 1969; Winemiller 1991a).

CHAPTER 2: A comparison of the physicochemical properties and the fish assemblage structures of the Zambezi, Kavango and Kwando rivers

Introduction

This chapter aims to firstly, describe the rivers and study sites, and secondly, quantify the physiochemical differences between the rivers by comparing surface water temperatures, flood regimes, total dissolved inorganic nitrogen concentrations and water quality parameters. Thirdly, although all three rivers are home to the same general suite of fish species, community composition and assemblage structures will be compared to quantify any differences between rivers.

Geomorphological history

After the breakup of Gondwana, high lands were formed by continental doming over major mantle plumes, creating headwaters for a new drainage system in Africa (Tweddle 2010). In the early Cretaceous period (about 120 Ma), the Palaeo-Limpopo River system was formed, comprised of three major south-east flowing headwater tributaries, the upper Zambezi, the Okavango and the Kwando rivers, which were linked to the Limpopo via the Shashe River (Moore et al. 2007). This historical connection between systems explains the common Upper Zambezian floodplain ichthyofauna, and the suite of species shared between the Zambezi and Limpopo rivers (Moore et al. 2007; Tweddle 2010). In the early Cretaceous, uplift along the Okavango-Kalahari-Zimbabwe (OKZ) Axis severed the Limpopo link of the Palaeo-Limpopo River, creating an endorheic system where the Zambezi, Okavango, Kwando and Kafue rivers culminated in the Kalahari Basin in Lake Palaeo-Makgadigkadi (Moore et al. 2007). Here, an adaptive radiation of Haplochromine cichlids produced the diverse suite of species present throughout southern Africa today (Joyce et al. 2005).

In the early Tertiary, movement along this OKZ Axis rejuvenated the lower Zambezi, and headwater erosion capture events linked the Palaeo-Luangwa, and the lower and middle Zambezi sections through Cahorra Bassa Gorge (Moore et al. 2007). Continued erosion lowered the middle Zambezi, eventually capturing the Upper Zambezi, Kwando and Kafue rivers, and diverting their flow south-east in the lower Pleistocene (Moore et al. 2007). At this time there was a reorganisation in the area where Zimbabwe, Namibia, Botswana and Zambia meet, and uplift of the Chobe and Linyanti faults created the Chobe/Kwando/Zambezi floodplain complex (Moore et al. 2007).

Physical characteristics of the rivers

In the present day, the Zambezi, Okavango and Kwando rivers can be found within 360 km of each other, in the flat and tropical semi-humid Zambezi and East Kavango regions of north eastern Namibia (Mendelsohn et al. 2003). The Okavango and Kwando rivers culminate in inland delta/swamp complexes, and the Okavango Delta is linked to the Kwando-Linyanti system through the Selinda spillway at high water periods, while the Kwando-Linyanti system is linked to the Zambezi via Lake Liambezi and the Chobe River (Figure 2.1).

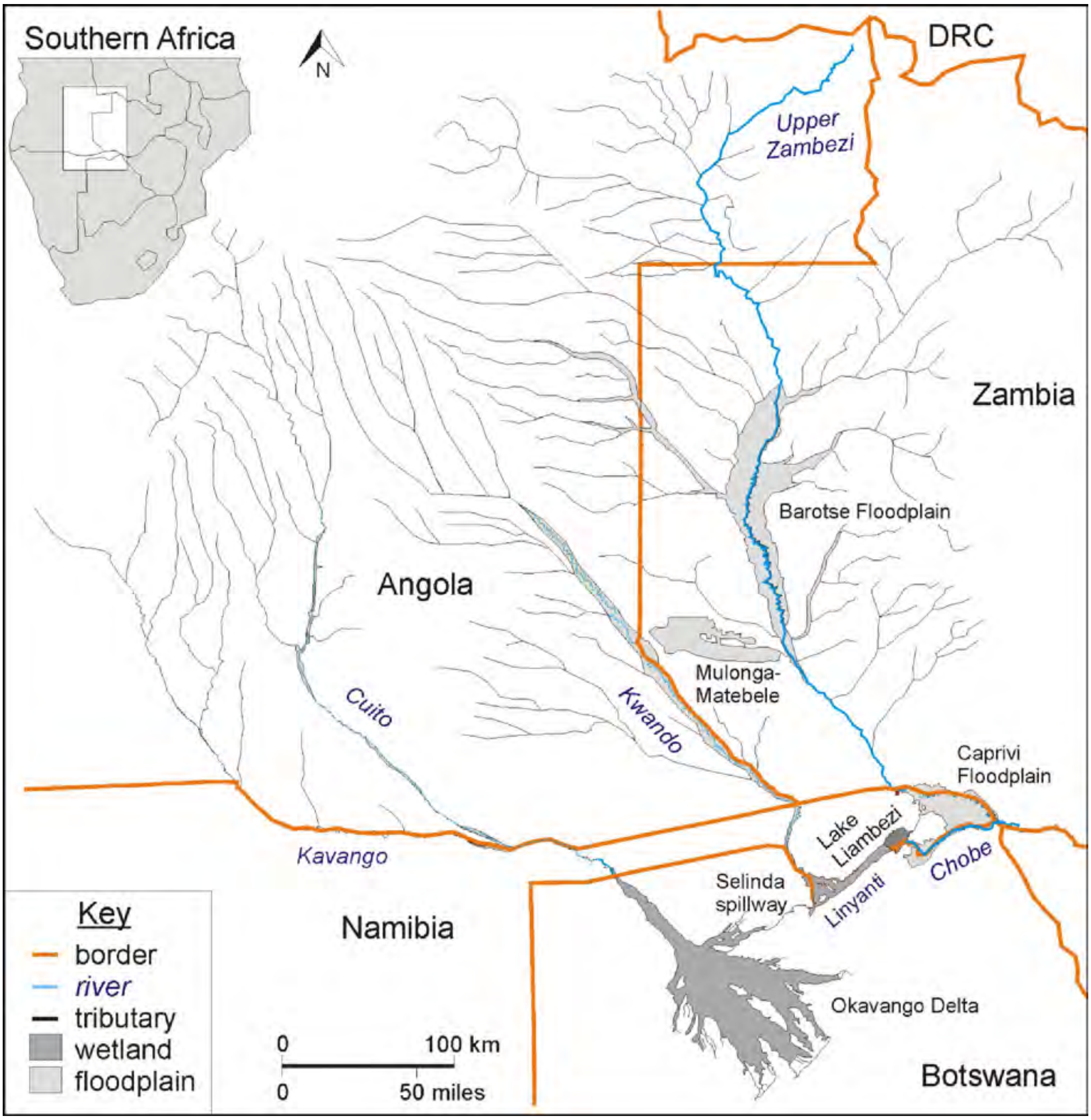

Figure 2.1: The Upper Zambezi, Kavango and Kwando rivers and their catchments in southern Africa.

The Zambezi River rises in north western Zambia and eastern Angola on the Central African Plateau, has an estimated total catchment area of 1.32 million km^2 (Moore et al. 2007), and an annual average flow rate of 1050 m^3/s (Mazvimavi and Wolski 2006). Its northern tributaries in Zambia are mainly forested and they receive water throughout the year from the Kalahari Sand formation which makes up the main regional aquifer (Tweddle 2010). Its other main tributaries drain the Angolan highlands that receive 1300 mm of rainfall annually (Moore et al. 2007) and are responsible for the annual flood (Tweddle 2010). Tributaries that feed the Upper Zambezi River in the Barotse floodplain area originate in dambos: sponge like shallow grassy valleys characterised by a permanently high water table (Moore et al. 2007).

The Okavango River (locally known as the Kavango River in Namibia) rises in the central Angolan highlands that receive 1200 mm of rainfall annually, contributing 95% of the rivers flow (Scudder et al. 1993). As the river enters Namibia, its gradient levels off producing large sandy floodplains with rocky outcrops. The river flows 460 km within Namibia at an average flow rate of 296 m^3/s (Mazvimavi and Wolski 2006) before entering Botswana, where it is lost to evaporation in the inland Okavango Delta (Hay et al. 2000). Its total catchment is 430 000 km^2, of which 15 000 km^2 constitute the Okavango Delta itself (Scudder et al. 1993).

The Kwando (or Cuando) River is a major tributary of the Upper Zambezi River, which follows a south-easterly course to the Botswana – Namibia border, where it turns north-eastwards to join the Zambezi via the Linyanti-Chobe floodplain (Moore et al. 2007). The mid-section of the Kwando is a floodplain, which links to the Barotse floodplain by the Mulonga-Matebele Plain, an alluvium subject to flooding in the wet season, and lined with dambos which feed local tributaries (Moore et al. 2007). The Kwando River originates in eastern Angola and has a catchment area of 57000 km^2 (Næsje et al. 2004) and an annual average flow rate of 38 m^3/s (*sensu* Schlettwein et al. 1991).

The location of these three rivers, their periodic connectivity, and the presence of similar fish fauna, provides an opportunity to compare ecological processes between them, which is the aim of this thesis.

Study site

The Zambezi and East Kavango regions of Namibia are biodiversity hotspots because they receive high rainfall, and are interspersed by a variety of wetland, woodland and forest habitats not common to the rest of the country (Mendelsohn et al. 2003). Mahango Core Area and an area west of Ngoma, for example, are home to the highest diversity of birds (>400 species) within Namibia (Schlettwein et al. 1991; Mendelsohn et al. 2003). Large herbivores and carnivores are also abundant (Mendelsohn et al. 2003); for example more than 5000 elephants *Loxodonta africana*, 2500 buffalo *Syncerus caffer*, and 500 hippopotami *Hippopotamus amphibius* were counted in the protected areas during an aerial census in 1994 (Rodwell et al. 1995). Acting as ecosystem engineers, hippopotami and elephants are responsible for the creation of channels and the maintenance of pools within the Kwando and Kavango rivers (Figure 2.2), habitats which are utilised by fishes (Mosepele et al. 2009). The concentrations of large herbivores recycle vegetation into a usable form of nutrients by producing dung (McLachlan 1971; Mosepele et al. 2009), which promotes fish production, and the constant movement of hippopotami reduces the likelihood of anoxia at low water (Wolanski and Gereta 1999). This biodiversity is protected by the five National Parks (Figure 1.1), and managed within numerous conservancies in the region (Rodwell et al. 1995; Mendelsohn et al. 2003). With minimal protection for wildlife on the Upper Zambezi River and the Caprivi Floodplains, the suite of large herbivores native to this area has been replaced by cattle (Schlettwein et al. 1991; Rodwell et al. 1995). This is likely to have an impact on the fish communities of this river.

On the Zambezi River, the study area was the Kalimbeza (or Sikunga) Channel (Figure 2.3). This is a sandy bottomed side channel to the main Zambezi River of 10 km in length, with an average width of 140 m, and with numerous backwater and main channel habitats lined with hippo grass (*Vossia cuspidata*) and *Phragmites mauritianus* (Figure 2.4). In response to intensive fishing pressure by Namibian and Zambian fishers, this channel (excluding backwaters) has been managed as a fish protection area since 2012 by the Sikunga Conservancy in conjunction with the Namibian Nature Foundation-European Union Community Conservation Fisheries in Kavango, Zambezi Transfrontier Conservation Area (KAZA) Project.

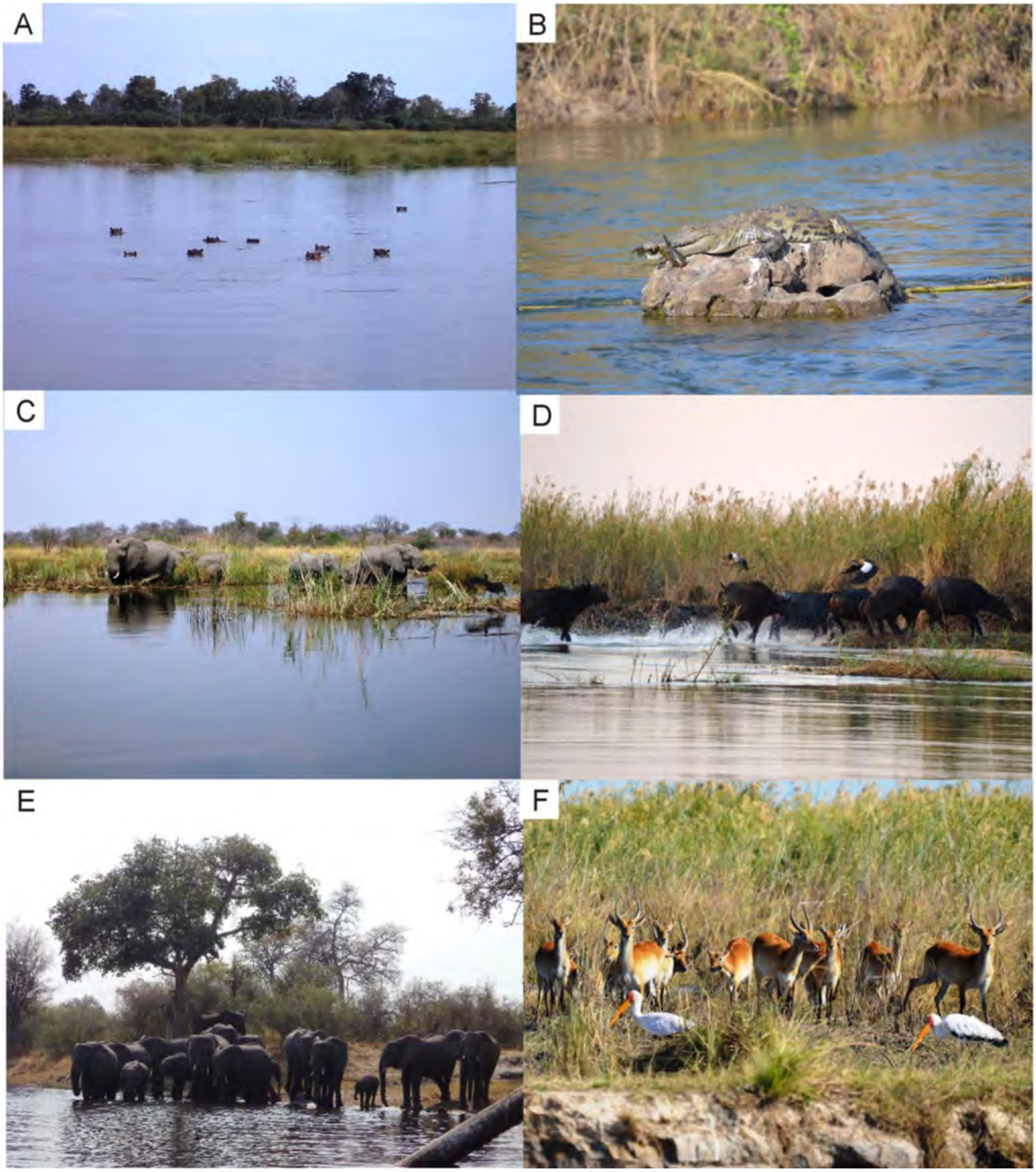

Figure 2.2: Photographs illustrating wildlife encountered on the Kavango and Kwando rivers, A: hippopotami *Hippopotamus amphibius*, Kwando River, B: a crocodile *Crocodylus niloticus* with a synodontid in its mouth, Kavango River (Photo by Richard Peel), C: elephants *Loxodonta africana* feeding on *Phragmites mauritianus* in the Kwando River, D: buffalo *Syncerus caffer* on the Kavango River floodplain (Photo by Richard Peel), E: elephants *Loxodonta africana* drinking at Nakatwa on the Kwando River, F: red letchwe *Kobus leche leche* on the Kavango River floodplain.

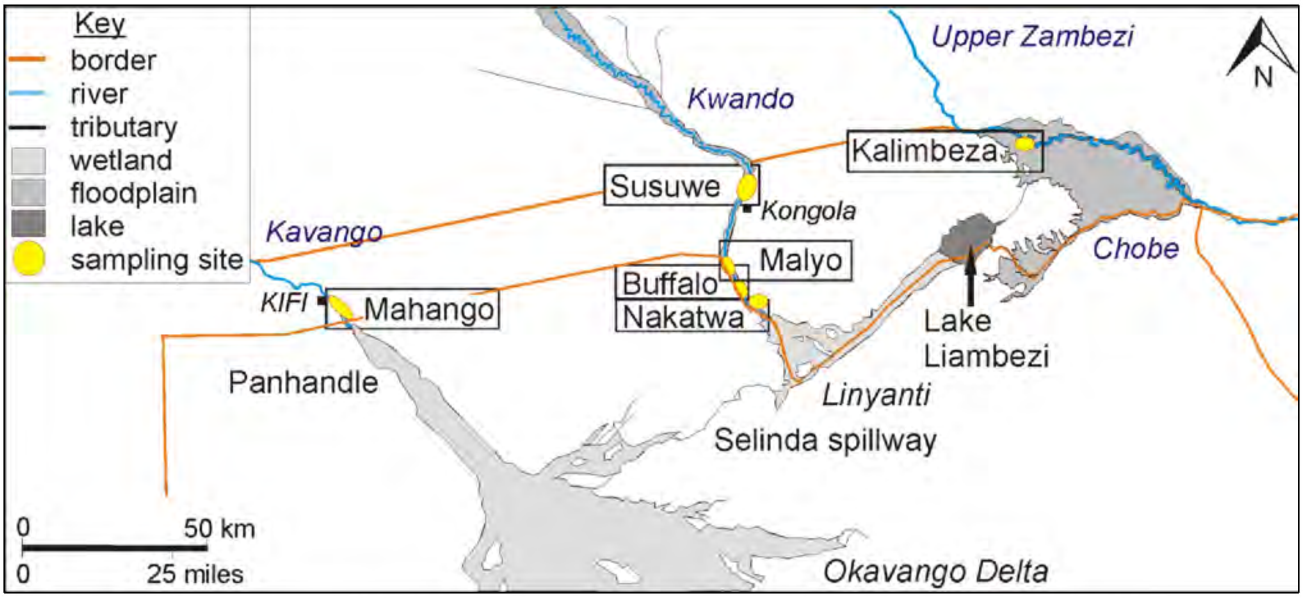

Figure 2.3: The location of the study area in the north-eastern Zambezi and Kavango Regions of Namibia, illustrating the study sites sampled on the Zambezi, Kavango and Kwando rivers.

On the Kavango River, the study site was within the Mahango and Buffalo Core Areas of Bwabwata National Park between the Kamutjonga Inland Fisheries Institute (KIFI) and the Botswanan border (Figure 2.3). This is a 17 km long protected stretch of sandy bottomed river approximately 180 m wide (Figure 2.5), with main channel and muddy bottomed backwater habitats dominated by submerged aquatic vegetation, *Cyperus papyrus* and *P. mauritianus*.

On the Kwando River, four study sites were used: Susuwe, Malyo, Buffalo and Nakatwa (Figure 2.3). Susuwe is a 10 km stretch of river north of the Kongola Bridge, within the Kwando Core Area of Bwabwata National Park on the west side, and unprotected on the east side. Malyo is a 10 km stretch of river on either side of the Malyo Wilderness Camp, protected on the Botswanan side within the Kwando Concession (private wildlife reserve), unprotected on the Namibian side although within a conservancy. Buffalo is an 8 km stretch of river from Lianshulu Lodge to the channel entering the Nakatwa backwaters, protected on the Botswanan side within the Kwando Concession and on the Namibian side within the Mudumu National Park (Figure 2.6). All three sites are fast flowing main channel (± 40 m wide) surrounded by complex lentic backwater sites, interconnected by hippopotami channels through floating *P. mauritianus* and *C. papyrus* mats. The Nakatwa site is a series of large backwaters covering an area of approximately 16 km^2 (open water interspersed with islands) within Mudumu National Park to the east of the main channel, fed by a small meandering side channel, and drained by a series of channels. This site is comprised of lentic water bodies interconnected by slowly flowing channels. The backwaters of the Kwando River are bedded with benthic detritus from surrounding *C. papyrus* and *P. mauritianus* stands and submerged aquatic vegetation. Although some sites were unprotected on one side of the river, the protection from the other side of the river, and abundant hippopotami and elephants, ensured fishing pressure was light and generally subsistence based.

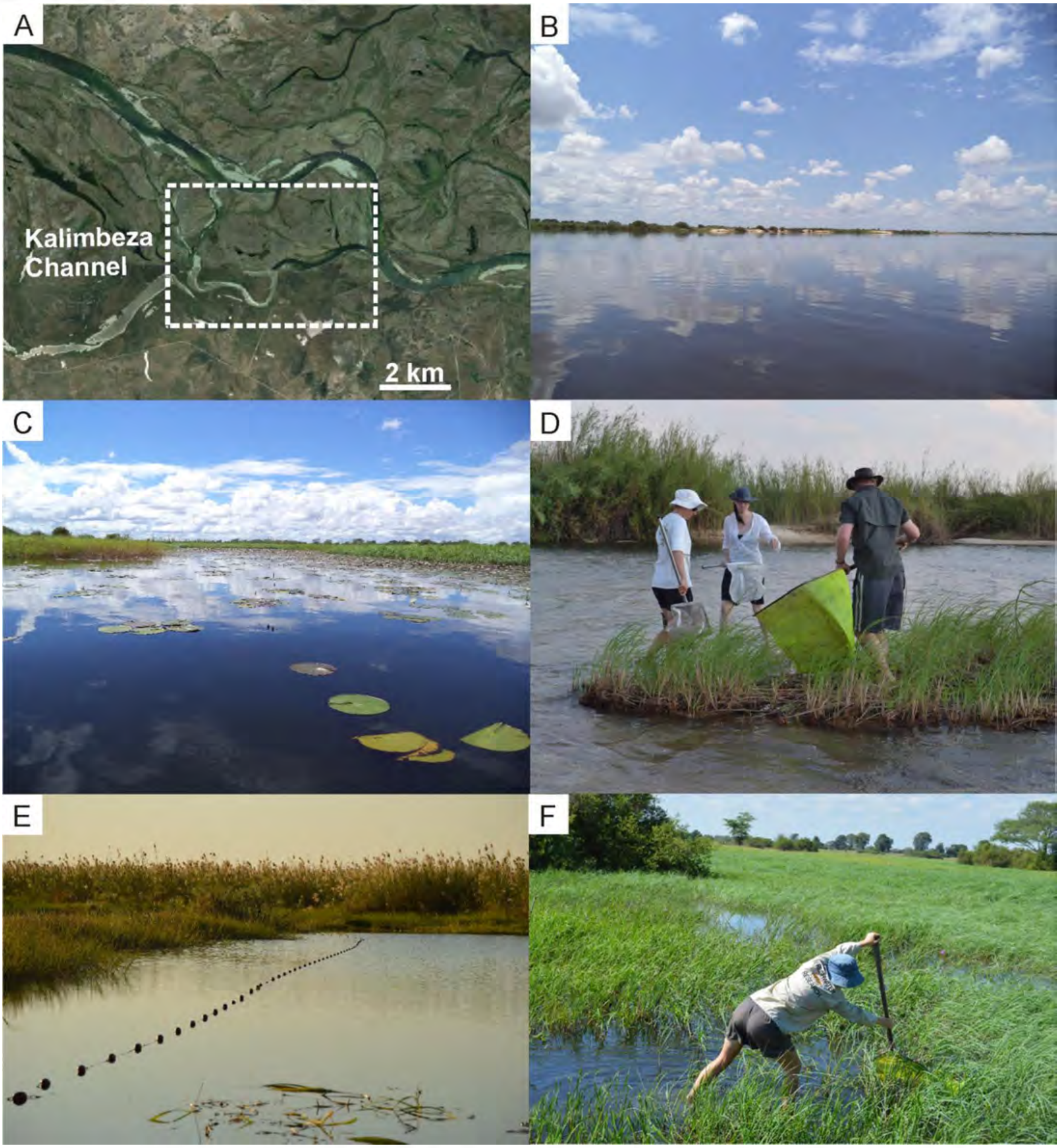

Figure 2.4: Photographs illustrating A: the Kalimbeza Channel, B: the Zambezi main channel at the entrance to the Kalimbeza Channel, C: a typical backwater in the Kalimbeza Channel, D: D-netting and SASS netting for stable isotope samples at the exit of the Kalimbeza Channel, E: an experimental gillnet set in a backwater, F: D-netting in *Vossia cuspidata* on the Caprivi Floodplain.

Figure 2.5: Photographs illustrating A: Kavango River, with the Mahango Core Area on the west bank and the Buffalo Core Area on the east bank, B: the Kavango River, C: Kwetche backwater and a good catch of *Clarias gariepinus* from the longlines, D: angling on the Kavango River, E: a large backwater near the Botswana border with extensive mats of *Vossia cuspidata*, F: removing an *Oreochromis macrochir* from the experimental gillnet set in a backwater lined with *Cyperus papyrus*.

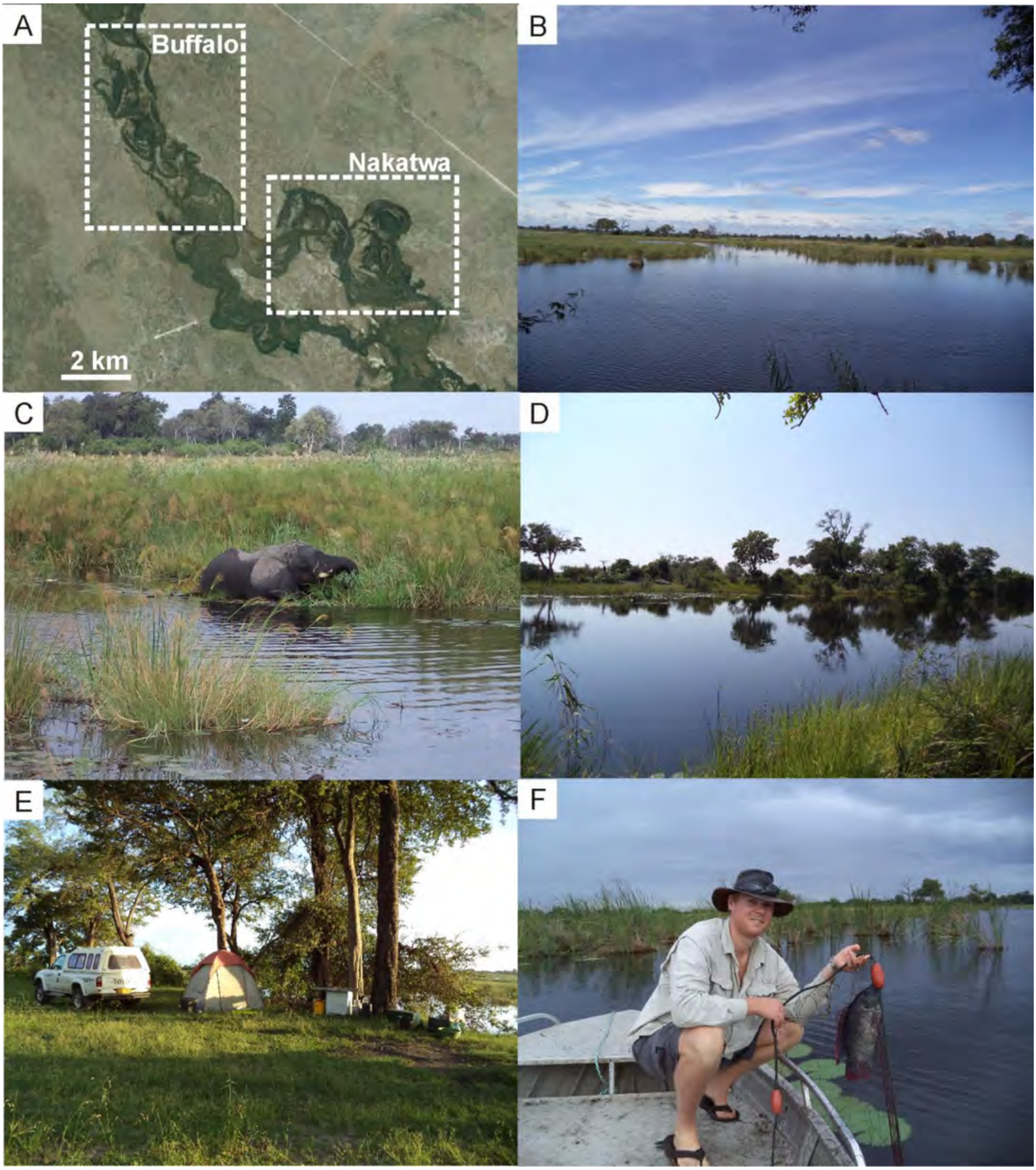

Figure 2.6: Photographs illustrating A: the Buffalo and Nakatwa sampling sites in the Mudumu National Park on the Kwando River, B: a large backwater in Nakatwa, C: an elephant eating *Cyperus papyrus* in the Kwando River, D: the main channel of the Kwando River, E: our campsite and field laboratory in the Mudumu National Park at Nakatwa, F: Richard Peel with an *Oreochromis andersonii* caught in an experimental gillnet.

Methods

For the purpose of this thesis, hydrological seasons have been used instead of austral seasons, as the proximity to the equator (17 to 18° S) diminishes the effects of spring and autumn, essentially creating a wet (summer) and dry (winter) season. In addition, these floodplain river environments are mainly influenced by water level. The hydrological cycle is characterised by four distinct seasons: low water: September – November (hot and dry, rains start), rising water: December – February (hot and wet), high water: March – May (cool and wet, rains stop), falling water: June – August (cool and dry), based on the flood pulse of the Zambezi and Kavango rivers.

Temperature

Surface water temperatures were recorded every six hours using HOBO temperature loggers (2 HOBO Pendant® temperature/light data loggers, 1 HOBO water temperature Pro v2 data logger, Onset®, Bourne, MA, USA) from September 2013 to September 2014 in the Zambezi River at Katima Mulilo (17°29’28.55”S 24°18’57.79”E), from August 2013 to August 2014 in the Kavango River at KIFI (18°09’07.64”S 21°41’25.31”E), and from August 2013 to September 2014 in the Kwando River at Camp Kwando (18°02’32.36”S 23°19’16.85”E). Temperature data were summarised to daily minimum, maximum and mean values. Four indices were then used to compare temperature regimes between rivers: the annual maximum of a seven-day running average of mean daily temperature (MWAT), the annual minimum of a seven-day running average of mean daily temperature (MiWAT), the annual maximum of a seven-day running average of maximum daily temperature (MWMT), and the annual minimum of a seven-day running average of minimum daily temperature (MiWMiT).

Flood regime

Water level data were supplied by the Hydrology division at the Ministry of Agriculture, Water and Forestry, Namibia. Readings were taken for the Zambezi River at Katima Mulilo (17°29’22.40”S 24°16’30.75”E), for the Kavango River at Rundu (17°54’37.08”S 19°45’39.21”E) and for the Kwando River at Kongola (17°47’27.50”S 23°20’37.38”E). The measuring gauges on each river do not represent the baseline water level, or residual water remaining in the river at lowest flow, hence flood magnitude is calculated from the lowest discharge to the level at peak flood. Water levels were plotted according to a hydrological year (from the lowest water level month).

Dissolved inorganic nitrogen concentrations

Concentrations of nitrate (NO_3-N) and ammonium (NH_4-N) were taken at high water on the Zambezi and Kavango rivers and low water on the Kwando River (May 2015), and at low water on the Zambezi and Kavango rivers and high water on the Kwando River (August 2015) using Vernier Ion Specific Electrodes interfaced to a WavePro2 hand held recording unit.

Five water samples were taken per river on two consecutive days (sites) per trip, and added to give five total dissolved inorganic nitrogen values per site. Sites were chosen from the main channel and from the backwaters in Kalimbeza on the Zambezi River, channel and backwater in Mahango on the Kavango River, and main channel at Malyo and backwater at Nakatwa on the Kwando River. Nitrate, ammonium and total dissolved inorganic nitrogen values were compared between sites and between rivers at high and low water periods using Students *t*-tests, to provide temporal comparisons of nitrogen concentrations between sites and rivers.

During the low water period in August 2015, five water samples were taken at a number of additional sites, encompassing backwaters, main channels and side channels in the same sampling areas of all three rivers (Kalimbeza, Mahango, Malyo and Nakatwa). Mean nitrate, ammonium and total dissolved inorganic nitrogen values were displayed using pie charts of total area proportional to total dissolved inorganic nitrogen values (ammonium + nitrate) per site on maps of the study areas to visually illustrate spatial variation.

Water quality parameters

Conductivity (µs/cm), total dissolved solids (ppm) and pH were measured using a Hanna HI98129 Combo pH and Electrical Conductivity meter; turbidity (NTU) was measured using an AquaLytic AL250T-IR Turbidity meter daily during surveys to each river (Kalimbeza, Mahango, Malyo, Buffalo and Nakatwa sites). Mean (± SE) values per river were compared by hydrological season.

Community composition and relative abundance

Data from gillnet nights set during bimonthly sampling events in 2010 and 2011 from Kalimbeza on the Zambezi River, Susuwe, Buffalo and Nakatwa on the Kwando River and Mahango on the Kavango River were used for analyses. Data were collected as part of a long term joint project by the Namibian Nature Foundation in collaboration with the Ministry of Fisheries and Marine Resources and the University of Namibia. Two consecutive years of data were necessary to cover the varying water level seasons. Multifilament gillnets comprised of randomised 10 m panels of 12, 16, 22, 28, 35, 45, 57, 73, 93, 118 and 150 mm stretched diamond mesh approximately 2.5 m deep were set overnight (6 pm to 6 am). Data from gillnets not of the standard 10 m mesh lengths were standardised to 10 m prior to analysis. Gillnets do not provide an unbiased estimate of species-relative density; for example mobile species of a fusiform body shape may be overestimated due to their higher encounter rates and increased catchability respectively, however standardised sampling between rivers may be compared as they are subject to the same biases at each site (Hoeinghaus et al. 2003). These data were used to test the hypothesis that assemblage structure differed by water level season between rivers.

Relative fish abundance was expressed as catch per unit effort (CPUE) in numbers and weight. CPUE is calculated as: $CPUE = \frac{C_i}{E_i}$,where C_i is the catch of species i (in numbers or weight) and E_i is the effort expended to obtain i. CPUE was standardised as number.net night^{-1} and kg.net night^{-1} (Kolding 1998). Tables of CPUE by number and by weight per species per river are presented in Appendix 2.

The following indices of species richness and evenness were calculated from relative abundance data: Pielous index of species evenness (J'), Shannon-Weiner index of species diversity (H'), and Simpsons index of diversity. Log transformed CPUE values and indices of species richness and evenness were then tested for homogeneity of variance using permutational analysis of multivariate dispersions (PERMDISP), based on the mean distance to centroid and was performed using 9999 permutations. Comparisons among rivers were made using univariate permutational analysis of variance (PERMANOVA) tests on matrices based on Euclidean distance using the Plymouth Routines in Multivariate Ecological Research (PRIMER) package, version 6 with PERMANOVA add on software (PRIMER-E Ltd, Plymouth United Kingdom; Clarke and Gorley 2006; Anderson et al. 2008).

Assemblage structure

Relative biomass per species per net (kg.net night^{-1} CPUE data) were used for assemblage structure analyses as sizes of species ranged from less than a gram, to tens of kilograms, and it was reasoned that more importance should be placed on those of a higher mass than their relative abundance would depict. Those species occurring in less than 5% of the samples were classified as rare species and removed from the analyses (see Duffy-Anderson et al. 2006) and none of these rare species were of the largest size range (more than 1 kg). The removal of rare species is recommended as they are unlikely to contribute to patterns under investigation and may disrupt any potential clustering (Duffy-Anderson et al. 2006). The data were then fourth root transformed to reduce the influence of the most abundant species (Clarke and Warwick 2001). The Bray-Curtis dissimilarity matrices were then used for hierarchical clustering, as this resolves inter-species associations (Duffy-Anderson et al. 2006).

A permutational analysis of variance (PERMANOVA) was performed on all the biomass data from all rivers and seasons, to test if assemblages varied across seasons and rivers, after the use of PERMDISP for testing of homogeneity of variance. With differences detected between both factors, data were first split into rivers to test for differences between seasons, and then split into seasons to test for differences between rivers. Unconstrained ordinations were done using principal coordinate ordination (PCO) on the Bray-Curtis dissimilarity matrix to visualise the data, and ultimately canonical analysis of principal coordinates (CAP) were used to emphasise differences between seasons within rivers, and within seasons between rivers. CAP is a useful constrained ordination procedure which uses any distance or dissimilarity measure, while also taking into account correlation structure among variables, and can be used to uncover patterns in multivariate data with reference to hypotheses (Anderson and Willis 2003). Species were correlated with the canonical axes of the CAP to identify the species driving the differences between rivers, using Pearson correlations of fourth root transformed species biomass with canonical axes (Anderson and Willis 2003). A correlation of $|r| = 0.5$ was used as a cut off to display potential relationships between individual species and the canonical axes. All analyses were performed using PRIMER v6 with PERMANOVA add on (PRIMER-E Ltd, Plymouth United Kingdom; Clarke and Gorley 2006; Anderson et al. 2008).

Results

Temperature

Annual average surface water temperatures in the three rivers followed a very similar pattern, rising from August to a peak in the summer month of February, and falling from March to a minimum in the winter month of July (Figure 2.7). Maximum temperatures for all three rivers were very similar, with MWAT values all over 30 °C within half a degree, and MWMT within a degree of each other (Table 2.1). Annual minimum temperatures were less similar, with the Kwando River showing the lowest MiWAT and MiWMiT values, followed by the Kavango River that was slightly warmer, and the Zambezi River that was warmer still during the winter months.

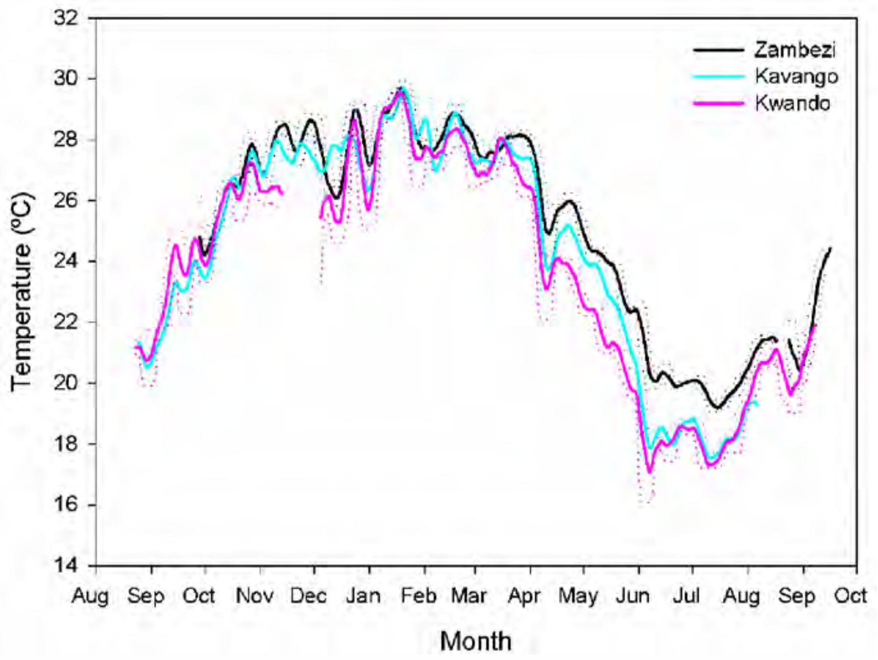

Figure 2.7: Seven day running averages of mean daily surface water temperatures (± 95% CI) taken between August 2013 and September 2014 in the Zambezi, Kavango and Kwando rivers.

Table 2.1: Metrics (± 95% CI) describing the annual surface water temperatures (°C) in the Zambezi, Kavango and Kwando rivers: the annual maximum of a seven-day running average of mean daily temperature (MWAT), the annual minimum of a seven-day running average of mean daily temperature (MiWAT), the annual maximum of a seven-day running average of maximum daily temperature (MWMT), and the annual minimum of a seven-day running average of minimum daily temperature (MiWMiT).

	Zambezi	Kavango	Kwando
MWAT	29.57 (29.43, 29.69)	29.71 (29.42, 30.15)	29.56 (29.37, 29.72)
MiWAT	19.25 (19.19, 19.34)	17.53 (17.43, 17.68)	17.08 (16.09, 17.75)
MWMT	30.07 (29.87, 30.26)	30.46 (29.91, 31.18)	30.30 (30.15, 30.46)
MiWMiT	19.02 (18.81, 19.17)	17.00 (16.82, 17.17)	16.41 (15.33, 17.08)

Flood regime

The Zambezi River started rising in December, peaking in April, and was at its lowest levels in November (Figure 2.8). From 2000 to 2013, the average magnitude of the flood (measured from the annual minimum water discharge) was 6.14 m, with the smallest flood of 3.31 m recorded in 2005, and the largest flood of 7.71 m recorded in 2009. The Kavango River was at its lowest in November, rising in December to an initial small peak in January - February, followed by the maximum flood peak in March - April. The flood magnitude was smaller than the Zambezi River with an average of 3.80 m (data from 2000-2013), a minimum flood of 2.60 m in 2006 and a maximum of 5.02 m in 2010. The Kwando River differed from the other two rivers in the magnitude and timing of the flood.

A small rise in water level was recorded during the rainy season (February – March); however the main floodwaters only reached the Namibian Kwando River around July (Figure 2.8). The flood was smaller than the other rivers, averaging 0.65 m (data from 1980 – 2002), with a minimum flood of 0.20 m recorded in 1998 and a maximum flood of 1.39 m recorded in 2001.

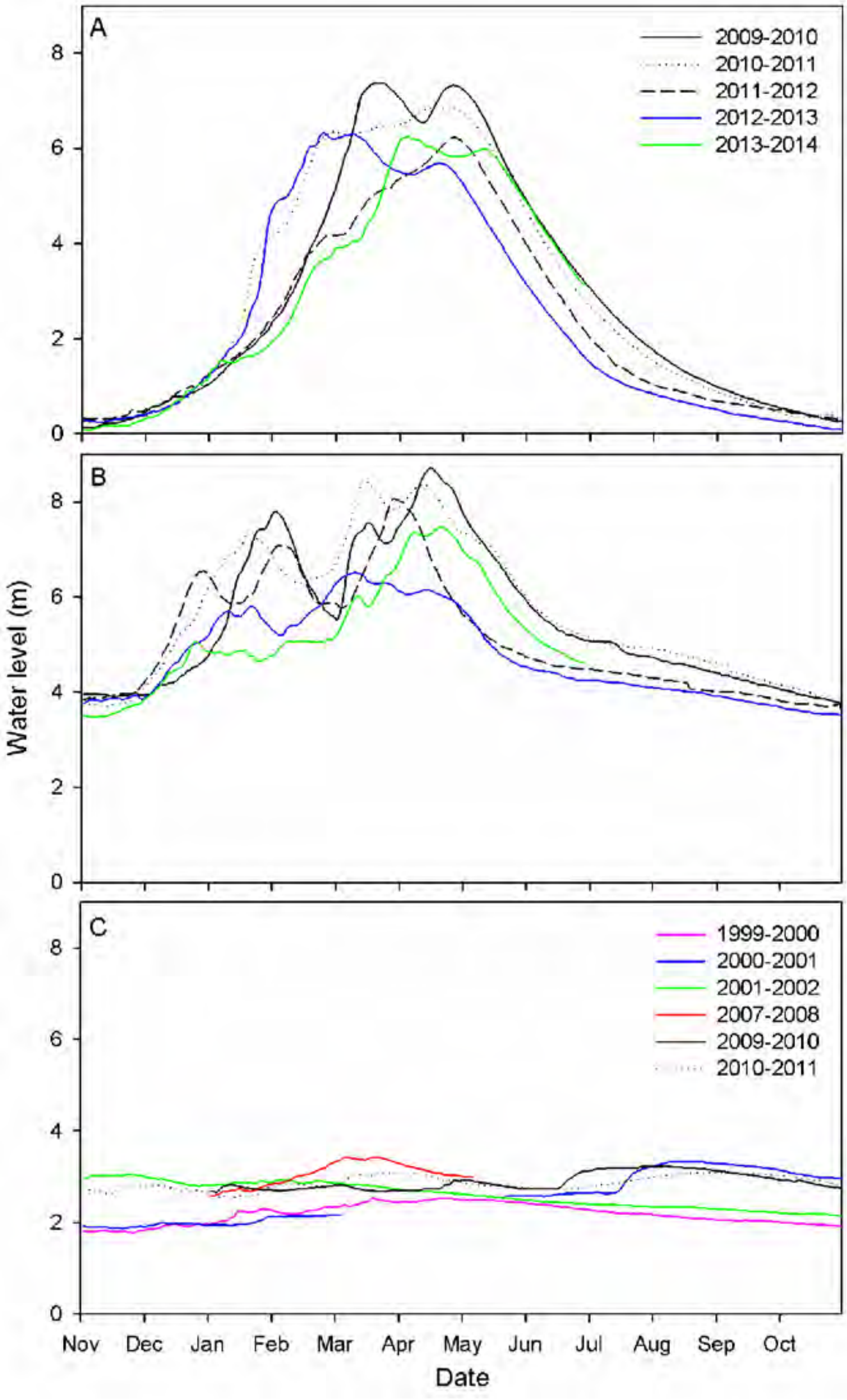

Figure 2.8: The annual flood regimes illustrated by daily water level data recorded at hydrological measuring stations at, A: the Zambezi River at Katima Mulilo; B: the Kavango River at Rundu; and C: the Kwando River at Kongola, Namibia. Baseline measurements did not represent the residual water in the river, and flood magnitude was measured from the minimum water discharge level.

Dissolved inorganic nitrogen concentrations

Temporal changes

Nitrate concentrations decreased between high and low water periods in the Zambezi River, increased in the Kwando River in both the main channels and the backwaters, and showed no change in the Kavango River (Table 2.2). Ammonium concentrations increased between high and low water periods for all habitats in the Zambezi and Kwando rivers. Total dissolved inorganic nitrogen decreased in the Zambezi River between high and low water periods, but increased in the Kavango and Kwando rivers. Overall total dissolved inorganic nitrogen concentrations were highest in the Kwando River, followed by in the Zambezi, and in the Kavango River total dissolved inorganic nitrogen concentrations were the lowest.

Table 2.2: The average nitrogen concentrations ± SE (mg/l) measured in main channel and backwater sites (+ combined sites) during high and low water periods, on the Zambezi, Kavango and Kwando rivers. Significant differences (Students *t*-test) between high and low water periods within rivers and habitats, for NO_3, NH_4 and total N, are denoted using letter superscripts (i.e. Zambezi Channel NO_3 at high water is significantly different to Zambezi Channel NO_3 at low water). Significantly different values are highlighted in grey.

River	Habitat	High water (May)			Low water (August)		
		NO_3	NH_4	Total N	NO_3	NH_4	Total N
Zambezi	Channel	0.53 ± 0.02^{a}	0.02 ± 0.01^{a}	0.55 ± 0.02^{a}	0.32 ± 0.00^{b}	0.12 ± 0.00^{b}	0.44 ± 0.00^{b}
Zambezi	Backwater	0.28 ± 0.02^{a}	0.02 ± 0.01^{a}	0.30 ± 0.03^{a}	0.20 ± 0.00^{b}	0.10 ± 0.00^{b}	0.30 ± 0.00^{a}
Zambezi	Total	0.41 ± 0.04^{a}	0.02 ± 0.01^{a}	0.43 ± 0.04^{a}	0.26 ± 0.00^{b}	0.11 ± 0.00^{b}	0.37 ± 0.01^{b}
Kavango	Channel	0.11 ± 0.01^{a}	0.10 ± 0.00^{a}	0.21 ± 0.01^{a}	0.10 ± 0.00^{a}	0.26 ± 0.00^{b}	0.36 ± 0.00^{b}
Kavango	Backwater	0.12 ± 0.01^{a}	0.12 ± 0.02^{a}	0.24 ± 0.03^{a}	0.10 ± 0.00^{a}	0.10 ± 0.00^{a}	0.20 ± 0.00^{a}
Kavango	Total	0.12 ± 0.01^{a}	0.11 ± 0.01^{a}	0.23 ± 0.02^{a}	0.10 ± 0.00^{a}	0.18 ± 0.01^{a}	0.28 ± 0.01^{a}
Kwando	Channel	0.30 ± 0.00^{a}	0.26 ± 0.05^{a}	0.56 ± 0.05^{a}	0.40 ± 0.00^{b}	0.30 ± 0.00^{a}	0.70 ± 0.00^{b}
Kwando	Backwater	0.39 ± 0.01^{a}	0.13 ± 0.03^{a}	0.52 ± 0.02^{a}	0.52 ± 0.00^{b}	0.30 ± 0.00^{b}	0.82 ± 0.00^{b}
Kwando	Total	0.35 ± 0.02^{a}	0.20 ± 0.03^{a}	0.54 ± 0.03^{a}	0.46 ± 0.00^{b}	0.30 ± 0.00^{b}	0.76 ± 0.00^{b}

Spatial variation

On the Zambezi River during low water levels, total dissolved inorganic nitrogen concentrations were highest in the main and Kalimbeza channels, and lower in the backwaters (Figure 2.9). In the Kavango River at that time, concentrations of total dissolved inorganic nitrogen were very low and increased downstream (particularly ammonium levels). In the Kwando River total dissolved inorganic nitrogen concentrations were higher than in the Zambezi and Kavango rivers, and were highest in the entrance to the Nakatwa backwaters.

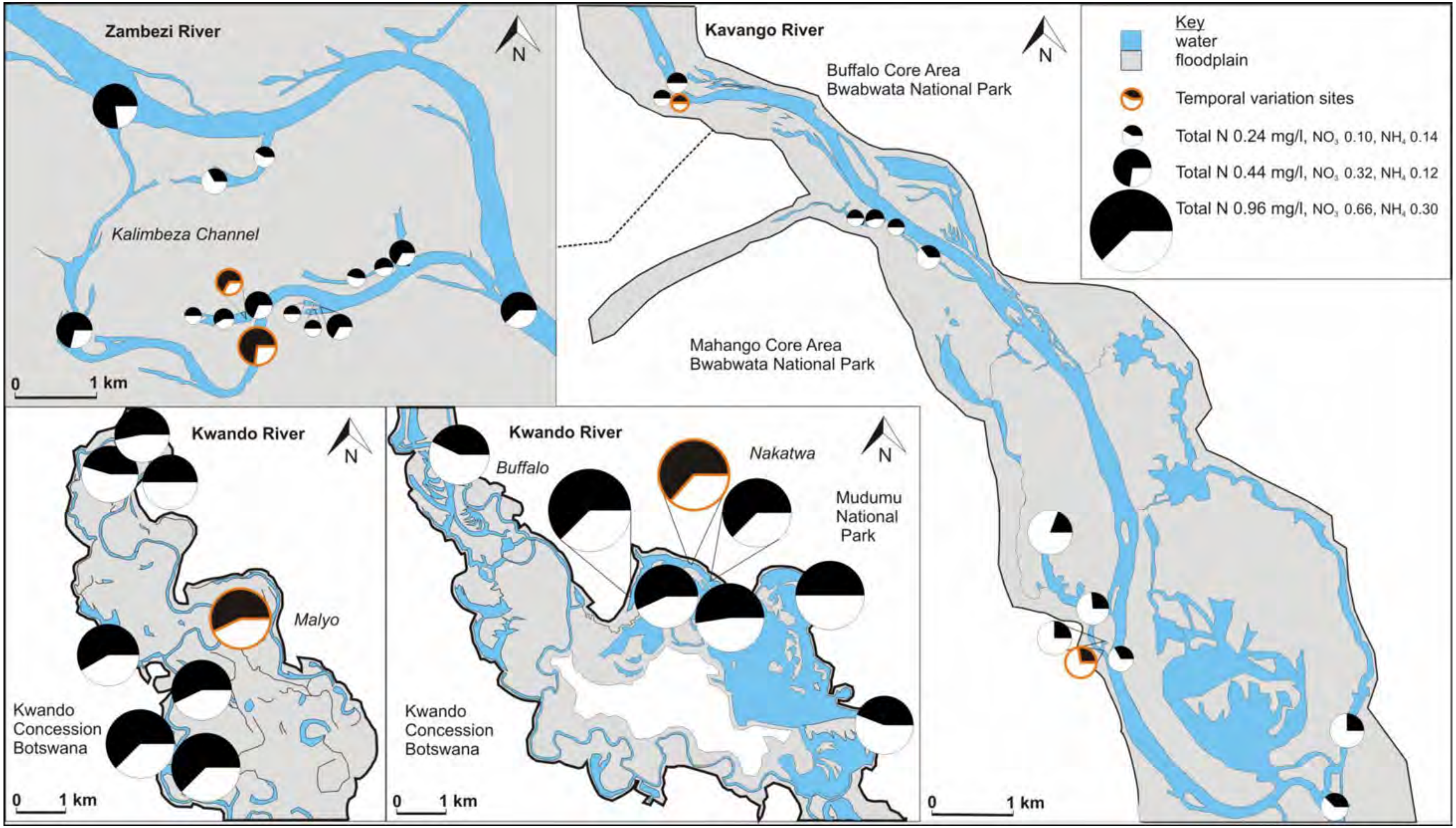

Figure 2.9: Spatial variation of total dissolved inorganic nitrogen concentrations illustrated using proportional pie charts of total dissolved inorganic nitrogen (pie total area), nitrate (NO_3 - black segment) and ammonium (NH_4 - white segment) collected in August 2015 from the Zambezi, Kavango and Kwando rivers.

Water quality parameters

Overall, the conductivity and total dissolved solids were lower in the Kavango River compared to the Zambezi and Kwando rivers. The conductivity and total dissolved solids for the Zambezi and Kavango rivers were also generally lower than those in the Kwando River in high and falling water periods (Table 2.3). During low water on the Zambezi and Kavango rivers, conductivity and total dissolved solids increased to levels similar to those in the Kwando River. With respect to pH, the Kwando River was generally neutral in rising, high and falling water levels, while the Zambezi and Kavango rivers were slightly more acidic. In low water the Zambezi River had a more alkaline pH compared to the rest of the year. Turbidity, although generally clear, was highest in high water in the Kwando River, followed by falling water in the Kavango River. The Kavango and Zambezi rivers were very clear in high water, while the Kwando River was very clear in falling water.

Table 2.3: Water quality parameters per water level season sampled in the Zambezi, Kavango and Kwando rivers. Differing samples sizes (N) for turbidity are given in parentheses.

Season	River	N	Conductivity (µs)	TDS (ppm)	pH	Turbidity (NTU)
Low	Zambezi	5	83.4 ± 0.60	41.4 ± 0.4	8.39 ± 0.07	4.57 ± 0.46
Rising	Kwando	9	86.4 ± 1.25	42.8 ± 0.43	7.55 ± 0.04	4.39 ± 0.42
High	Zambezi	10	34.2 ± 0.25	16.8 ± 0.13	6.88 ± 0.07	1.62 ± 0.06
High	Kavango	10	24.3 ± 0.30	11.8 ± 0.13	6.68 ± 0.09	1.67 ± 0.14
High	Kwando	10	78.7 ± 0.62	39.4 ± 0.22	7.32 ± 0.05	6.93 ± 0.09
Falling	Zambezi	10	52.6 ± 1.16	26.3 ± 1.49	7.35 ± 0.13	3.22 ± 0.31
Falling	Kavango	8	23.6 ± 1.02	11.5 ± 0.42	7.26 ± 0.27	4.83 ± 0.59 (7)
Falling	Kwando	3	85.7 ± 5.67	43.7 ± 3.67	7.56 ± 0.03	1.98 (1)

Community composition and relative abundance

The CPUE by species in number and weight per river is illustrated in Appendix 2. The Kavango River had significantly higher total CPUE in weight, followed by the Kwando River and finally the Zambezi River, while total CPUE by number did not differ significantly between rivers (Table 2.4). While the Kwando River had the highest species richness per net, the Kavango and Zambezi rivers had significantly higher evenness and diversity indices (Pielous, Shannon-Weiner and Simpsons indices) compared to the Kwando River. However, significant differences found among CPUE by weight as well as differences between species richness and the Simpsons diversity index may be a result of the heterogeneity of variance uncovered by the PERMDISP analyses.

Table 2.4: The CPUE in number and biomass, and species richness and evenness indices (± SE) for gillnet samples from the Zambezi, Kavango, and Kwando rivers. Letter superscripts denote significant differences (PERMANOVA, $P < 0.05$), * indicates heterogeneity of variance (PERMDISP $P < 0.05$).

	Zambezi	Kavango	Kwando
CPUE Number *	140.21 ± 18.36^{a}	115.85 ± 15.50^{a}	106.98 ± 7.05^{a}
CPUE Weight (kg)*	5.19 ± 0.46^{a}	12.52 ± 1.48^{b}	7.97 ± 0.46^{c}
Total number	10095	5759	10698
Total weight (kg)	374	853	797
Gillnet number	72	50	100
Total species	44	40	41
Species richness/net *	10.25 ± 0.32^{a}	9.26 ± 0.49^{ab}	10.35 ± 0.42^{ac}
Pielous evenness (J')	0.73 ± 0.01^{a}	0.78 ± 0.01^{a}	0.59 ± 0.02^{b}
Shannon-Weiner diversity (H')	1.64 ± 0.04^{a}	1.59 ± 0.04^{a}	1.33 ± 0.05^{b}
Simpsons diversity *	0.73 ± 0.01^{a}	0.75 ± 0.01^{a}	0.59 ± 0.02^{b}

Comparing assemblage structure by season

Differences in assemblage structure were detected between seasons (PERMANOVA *Pseudo-F* = 5.21, *P* = 0.001). Data was then split into rivers, PERMDISP used to test for homogeneity of variances, and PERMANOVA and CAP analyses were used to test for differences between seasonal assemblages within rivers (Table 2.5). The seasonal groupings for the Zambezi River did not have homogenous variances (PERMDISP *F* = 3.22, *P* = 0.04), with the rising season having the smallest average distance to centroid, while the Kavango and the Kwando river seasonal assemblage groupings had homogenous variances (Kavango PERMDISP *F* = 1.70, *P* = 0.233; PERMDISP *F* = 2.61, *P* = 0.108). PERMANOVA results (Table 2.5) and CAP analyses (Figure 2.10) revealed that the Zambezi and Kavango river seasonal assemblages were all significantly different, however in the Zambezi River, the differences between the rising and the high flood seasonal assemblages may have been an artefact of their unequal variances. The Kwando River seasonal assemblages were much more similar (Figure 2.10C), with the low and high water assemblages, and the high and falling water assemblages not significantly different from each other (Table 2.5).

Table 2.5: The PERMANOVA results (Pairwise tests *t* value, *P* value) and distances between centroids (in parentheses), for the comparison of fish assemblage structures between seasons within rivers (v = versus). All tests had one degree of freedom and used 997 – 999 permutations, * denotes significant differences.

River	Low v Rising	Low v High	Low v Falling	Rising v High	Rising v Falling	High v Falling
Zambezi	2.32, 0.001* (29.57)	3.15, 0.001* (35.23)	2.13, 0.001* (27.16)	1.53, 0.012* (20.33)	2.65, 0.001* (35.66)	2.54, 0.001* (34.43)
Kavango	2.31, 0.002* (34.26)	2.89, 0.001* (48.31)	1.98, 0.001* (31.34)	1.68, 0.029* (25.41)	1.82, 0.008* (23.42)	2.09, 0.001* (33.86)
Kwando	1.42, 0.042* (16.10)	1.33, 0.074 (12.50)	1.61, 0.009* (18.24)	1.78, 0.001* (20.33)	1.55, 0.006* (19.09)	1.32, 0.074 (15.18)

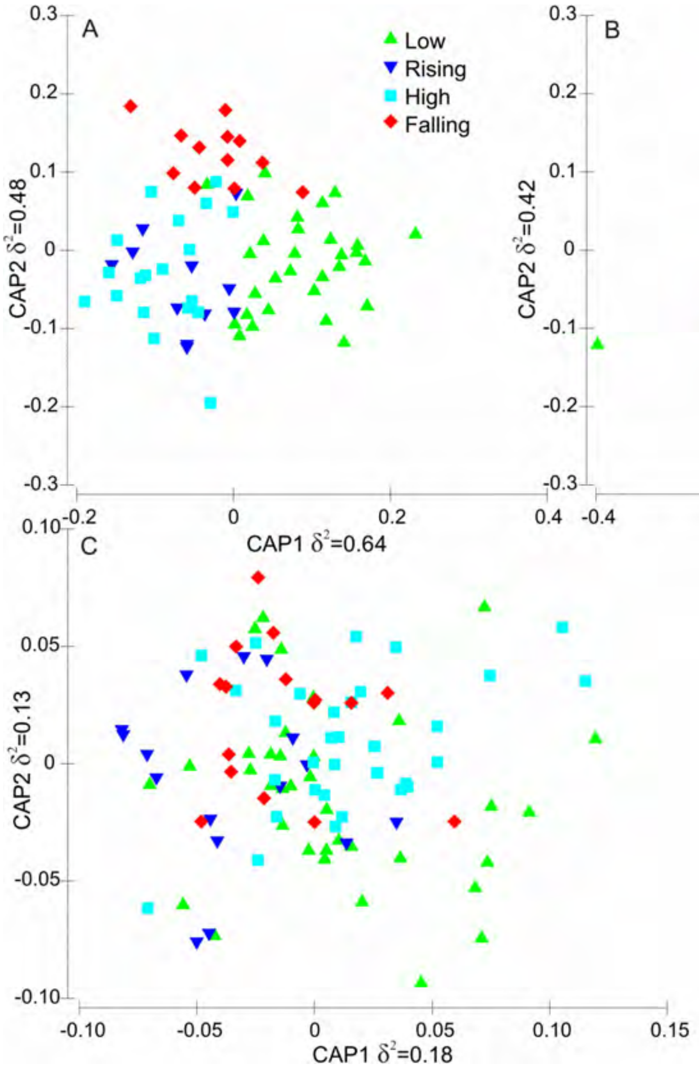

Figure 2.10: Canonical analysis of principal coordinates (CAP) ordinations of fish assemblage structures for A: the Zambezi, B: Kavango and C: Kwando rivers by hydrological seasons. δ^2 = the amount of variation explained by the canonical axis (see Anderson and Willis 2003).

Comparing assemblage structure between rivers

CPUE by biomass and number by river for all species sampled, used for multivariate analysis, are displayed in Appendix 2. PERMANOVA showed significant effects of river and season (river *Pseudo-F* = 31.23, $P = 0.001$; season *Pseudo-F* = 6.74, $P = 0.001$, both using 997 permutations), and a river × season interaction, (*Pseudo-F* = 3.45, $P = 0.001$, 999 permutations) indicating that changes in assemblages across seasons varied among rivers. PERMDISP analyses indicated that variances were homogenous for the low ($F = 3.10$, $P = 0.103$), high ($F = 1.76$, $P = 0.247$), and falling seasons ($F = 0.69$, $P = 0.575$), but not for the rising water season ($F = 8.90$, $P = 0.002$), where the Zambezi River had the lowest average distance to centroid. Post hoc PERMANOVAs indicated that all rivers differed within seasons (Table 2.6), even during rising water, illustrated by the CAP analyses (Table 2.7, Figure 2.11). The distances to centroids were greatest between the Kavango and Kwando rivers, followed by the Zambezi and Kwando rivers while the Zambezi and Kavango rivers were closest together (Table 2.6).

Table 2.6: The PERMANOVA results (Pseudo *F* and *P* values) and distances between centroids (in parentheses) for the comparisons of fish assemblage structure within seasons between rivers (v = versus). All tests had one degree of freedom and used 998 – 999 permutations.

Season	Zambezi v Kavango	Zambezi v Kwando	Kavango v Kwando
Low water	$F = 5.98$, $P = 0.001$ (35.72)	$F = 14.11$, $P = 0.001$ (35.47)	$F = 9.91$, $P = 0.001$ (45.99)
Rising water	$F = 6.62$, $P = 0.001$ (32.67)	$F = 14.34$, $P = 0.001$ (46.87)	$F = 16.28$, $P = 0.001$ (47.78)
High water	$F = 3.66$, $P = 0.001$ (29.30)	$F = 17.72$, $P = 0.001$ (46.20)	$F = 16.34$, $P = 0.001$ (60.13)
Falling water	$F = 4.98$, $P = 0.001$ (31.74)	$F = 7.80$, $P = 0.001$ (36.78)	$F = 11.19$, $P = 0.001$ (43.96)

Canonical analysis of principal coordinates (CAP) further separated fish assemblages within each season by river (Figure 2.11), with the degree of distinctiveness described by the high (> 83%) leave-one-out allocation success rates (Table 2.7).

Table 2.7: Canonical analysis of principal coordinates (CAP) of fish assemblage structure for each river by season illustrating the number of axes (m) the PCO used to explain a percentage of the data (m, % of the data explained), and the proportion of correct allocations (%).

Season	m, % explained	Zambezi	Kavango	Kwando
Low	9, 94.76	96.67	100	91.67
Rising	8, 98.38	90.91	100	100
High	4, 69.39	84.21	87.50	100
Falling	4, 67.89	83.33	92.86	87.50

Numerous species contributed to the observed differences in fish assemblage structure between rivers, depending on the season (Figure 2.11). Correlation of a species with a river on the graph, indicates a higher biomass of that species sampled in that river, compared to in the other rivers. *Hydrocynus vittatus* and *Micralestes acutidens* consistently correlated with both the Zambezi and Kavango rivers in all seasons, while *Schilbe intermedius*, *Brycinus lateralis*, *Marcusenius altisambesi,* and *Pharyngochromis acuticeps* correlated with the Kwando River for most seasons. For low, rising and falling water seasons *Synodontis nigromaculatus* correlated with the Kavango River.

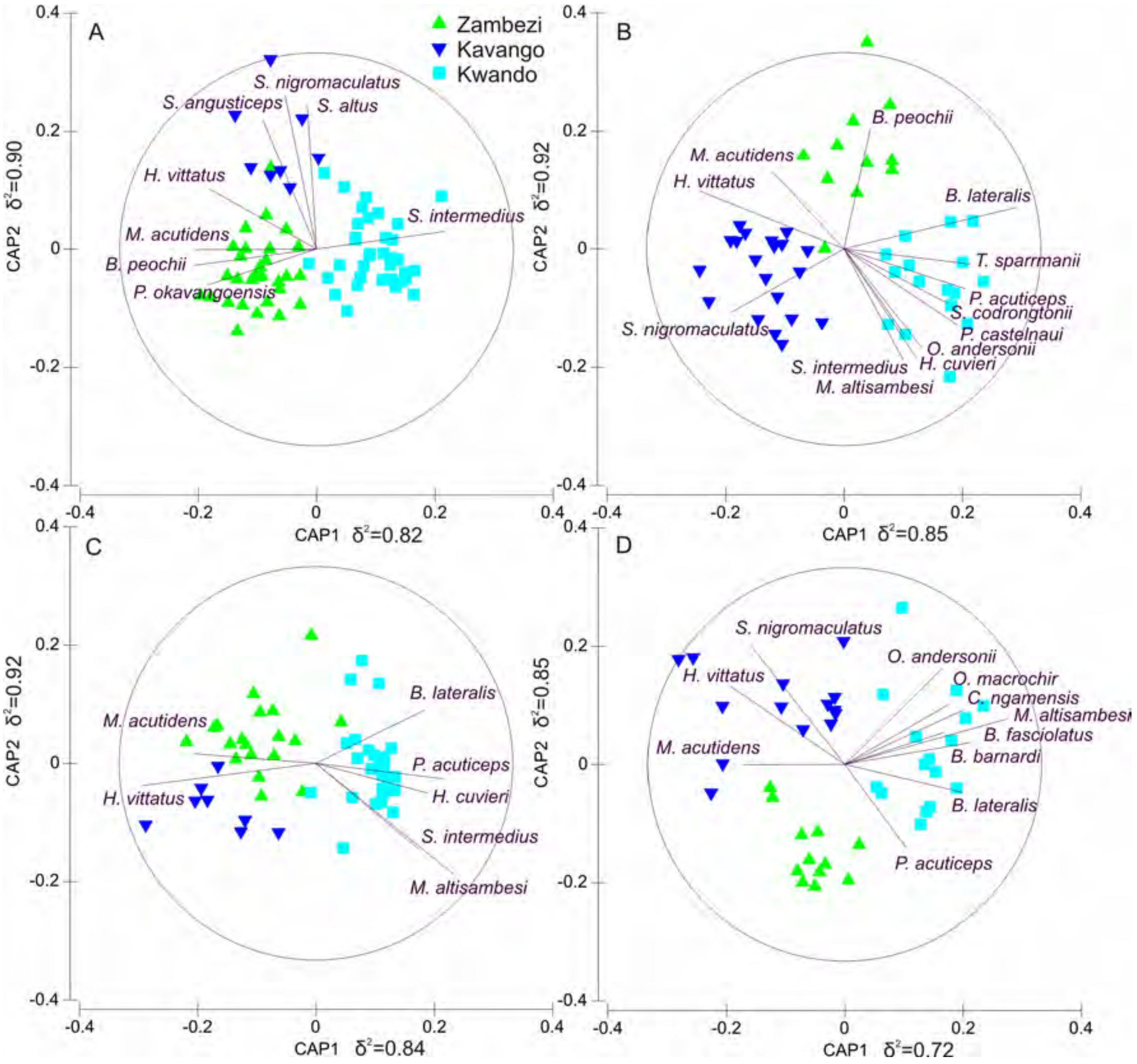

Figure 2.11: Canonical analysis of principal coordinates (CAP) ordination of fish assemblage structure for rivers in the varying seasons, A: low, B: rising, C: high, D: falling, and biplots of species correlations with the canonical axes (|r| = 0.5).

Discussion

When exploring fish community assemblages among and between seasons and rivers, it is important to consider the biotic and abiotic factors that may be influencing them. The first abiotic factor under consideration was temperature. Dallas (2008) attributed the thermal profile of rivers in general to hydrological, regional, climatological and structural characteristics, catchment and site. The Zambezi, Kwando and Kavango rivers in Namibia fall within a common climatic belt (Mendelsohn et al. 2003), illustrated by their similarities in weekly and annual fluctuations in surface water temperatures. As all three rivers are subject to similar regional (latitude, altitude) and climatological features, the lower winter temperatures of the Kavango and Kwando rivers compared to the Zambezi River were most likely a result of differing hydrological factors (i.e. flow rate), and structural features (i.e. river size and water depth). Descriptive metrics were used to explore the annual thermal features of the three rivers as no temperature thresholds are available for these natural systems, against which degree days, either below or above these limits could be calculated (Rivers-Moore et al. 2013). The minima (MiWMiT) of 16 and 17 °C recorded in the Kwando and Kavango rivers respectively, compared to 19 °C in the Zambezi River, are small differences unlikely to affect aquatic communities, as habitat heterogeneity translates into thermal structure among habitats, depths and substrate characteristics within rivers, resulting in an abundance of thermal refugia for poikilotherms (Tockner et al. 2000; Dallas 2008). With respect to the thermal toleranc, little other literature exists for this suite of species, besides *Coptodon rendalli,* a common cichlid of the Upper Zambezian ichthyofauna, that can tolerate temperatures from 11 to 37 °C (Whitfield and Blaber 1976). Additionally, when considering biological functioning, there are reports of some broadcast spawners in the southern Okavango Delta spawning in the winter months cued by the flood, where average monthly temperatures were 16 °C in June (Merron 1991), suggesting biological processes such as reproduction likely still occur at the minimal temperatures of the Kwando River in winter. Although this limited existing information suggests these fishes may have a wide temperature tolerance, future research should investigate the impacts of seasonal temperature fluctuations on these species.

The second abiotic factor influencing the three rivers was the magnitude and timing of the flood. The Zambezi River had the largest flood, followed by the Kavango River, peaking in May, and the Kwando River had the smallest flood which arrived later in the year in June -

July. Flood size has been directly correlated to fish growth, with larger floods resulting in increased growth rates of fishes (growth response), as a result of heightened primary and secondary production on the floodplain (Dudley 1974; Bayley 1988; Gomes and Agostinho 1997; Gutreuter et al. 1999; de Graaf 2003). Growth response has also been linked to the characteristics of the fish in question i.e. habitat preference and trophic position. Gutreuter et al. (1999) found a growth response in fishes with a high affinity with the moving littoral, while fishes less associated with this habitat had a less pronounced growth response. Bayley (1988) found that growth rates could be linked to hydrological regime in omnivores and not detritivores. In addition, although not directly translating into a growth response, Luz-Agostinho et al. (2008) found that fish diets varied with flood intensity and duration, and predators with different feeding strategies were affected differently.

The timing of the flood is also influential in the floodplain use by fishes, and for overall productivity, especially in temperate systems (Junk et al. 1989; Tockner et al. 2000). In the tropics, where annual temperature changes are less pronounced, it has been speculated that the flood is the main spawning cue for fishes (Welcomme 1985). The Okavango Delta, the panhandle of which is situated just 10 km south of the Kavango River Mahango sampling site, is subject to summer flooding in the north, and winter flooding in the south. It is therefore an ideal test site to understand differing utilisation of the floodplain by fishes in summer and winter. Merron (1991) found that non-guarding broadcast spawners such as *Clarias gariepinus* and *Schilbe intermedius* spawned on the floodplain during the flood in summer in the north, and towards the end of winter in the south. This however was not the case for *H. vittatus* (also a non-guarding broadcast spawner) and guarding species such as *Hepsetus cuvieri* and *Oreochromis andersonii*, which spawned in summer during warmer water temperatures regardless of hydrological season (Merron 1991). When flooding and spawning did not coincide, spawning occurred in the channels and juveniles migrated onto the floodplain with the increases in phytoplankton and zooplankton associated with the rising water (Hoberg et al. 2002). The use of the floodplain, although varying with species, would therefore most likely be extensive for all three rivers, despite differences in the timing of the flood.

When interpreting biotic responses to flood magnitude and timing however, it is important to consider that the flood pulse concept was developed in relation to large tropical floodplain rivers, with predictable flood pulses of long duration. Rivers which do not fit this description may be influenced by similar processes that drive productivity, but at substantially differing scales (Puckridge et al. 1998). Tockner et al. (2000), although working on temperate systems, highlighted the potential influences of below bankfull flow pulses and local rainfall contributions, which may significantly influence the productivity of smaller floodplain rivers such as the Kwando River. Therefore, the magnitude and timing of the flood pulse within each of the three rivers is likely to influence both the biology and ecology of their respective fish communities to varying extents.

Total dissolved inorganic nitrogen concentrations tended to be higher during the flood, compared to the low water period in the Zambezi and Kavango rivers. This is expected as inundation of the floodplain results in an initial flux of phosphate and nitrogen released by both soils and leaf litter and an increase in microbial activity, especially during summer (Baldwin and Mitchell 2000; Hoberg et al. 2002; Lindholm et al. 2007). In the Okavango Delta, Cronberg et al. (1995) found that nutrient levels increased with the flood, however at peak flood there was a dilution effect, but total dissolved inorganic nitrogen concentrations were still higher than at low water (Lindholm et al. 2007). The increase in nutrient concentrations observed in the Kwando River between May and August was coupled with a reduction in river level and an increase in river use by ungulates and elephants. It was observed that after cessation of the rains in April, by August few inland water sources remained, so elephants and other wildlife in the surrounding national parks frequented the river for not only water, but potentially food in the form of *P. mauritianus* stands (Pers. obs.). Dung from herbivores may contribute substantially to nutrient inputs (McLachlan 1971; Talling 1986; Lindholm et al. 2007), and the disturbance of settled detritus, which is known to play a big role in nutrient storage and cycling (Cronberg et al. 1995), may be contributing factors to both the increase in nutrient levels in the Kwando River between May and August, and the high nutrient content of this small river compared to the Zambezi and Kavango rivers. In the Kavango River a large contribution of nutrients to the floodplain that drains into the main channel can also be attributed to inputs of dung and potentially unsettling of detritus, resulting in heightened total dissolved inorganic nitrogen concentrations (mainly ammonium) downstream. In the Zambezi River total dissolved inorganic nitrogen concentrations were highest in the main channels compared to in backwater sites, where still waters could enhance sedimentation of nutrients, and higher concentrations of phytoplankton and aquatic macrophytes may result in the retention of nutrients (Olde Venterink et al. 2006).

As with nitrate concentrations, water quality variables were also influenced by the flood, with conductivity and total dissolved solids subject to the dilution effect, as was found in the Okavango Delta and the middle Zambezi River (Balon and Coche 1974; Cronberg et al. 1995). At the Kariba Dam inflow the conductivity reached higher maximum values than at Kalimbeza (Balon and Coche 1974), which is expected as one moves down the longitudinal gradient of a river (Vannote et al. 1980; Graça et al. 2001). Turbidity was found to increase with rising flood waters in a purging effect in the Okavango Delta (Cronberg et al. 1995), which may explain the fact that the turbidity was lowest for the Zambezi and Kavango Rivers at high water, increasing with falling and low water. Flood waters seemed slightly more acidic in the Zambezi and Kavango rivers, and pH increased with the falling water.

As was found by Cronberg et al. (1995), the chemical composition of the Kwando River differed from the Kavango River, with the former having a higher ionic content than the latter, while both rivers had relatively low total dissolved inorganic nitrogen concentrations. For example, the highest total dissolved inorganic nitrogen levels recorded in these rivers was 0.96 mg/l (0.66 mg/l NO_3, 0.30 mg/l NH_4), while nitrate levels recorded during two floods in the Ebro River in the Mediterranean ranged from 0.23 to 53 mg/l (Gallardo et al. 2012), total dissolved inorganic nitrogen measured in the lower Okavango Delta during two floods ranged from 1 to 2.5 mg/l (Lindholm et al. 2007), and in the Kafue River ammonium ranged from <0.01 to 5.22 mg/l and nitrate from 1.78 to 26.40 mg/l (Alsterhag and Petersson 2004). Cronberg et al. (1995) and West et al. (2015) attributed the poor nutrient contents of these systems to their catchment similarity, which is mineral poor Kalahari Sands, coupled with similar lithology and land use. Cronberg et al. (1995) suggested that the higher ionic concentrations of the Kwando River may be as a result of catchment morphology which produces higher runoff and overland flow. Although this small scale data collection cannot claim to be representative of all three rivers, as was stated by Cronberg et al. (1995), this information does add to the current knowledge on the total dissolved inorganic nitrogen concentrations and physicochemical characteristics of the Kavango, Kwando and Upper Zambezi rivers. As nutrient levels are positively correlated to primary productivity (Vanni 2002; Elser et al. 2007), differences in nutrient levels between rivers could be reflected in variations in food web structure and growth rates, which will be explored in subsequent chapters.

The typical Upper Zambezian floodplain ichthyofauna shared by these three rivers is made up of at least 100 fish species (Tweddle 2010). Assemblage structures differed between the three rivers, with the Zambezi and Kavango rivers having more similar assemblages than the Kwando River. These differences may be attributable to the varying flood regimes, and/or the absence of a dominant predator from the Kwando River.

The flood pulse is known to have a homogenising effect on ecosystems, including physicochemical characteristics and species composition (Thomaz et al. 2007). Since the Kwando River is subject to smaller, infrequent floods, this has created a heterogeneous environment that is not regularly reset by the flood to the same extent as the other two rivers, which are reset annually. As a result fish assemblages of the Kwando River did not change as much from season to season as did those from the Zambezi and Kavango rivers, and the Kwando assemblages were more distinct from those of the Kavango and Zambezi rivers throughout the year (Zambezi and Kavango rivers consistently had the lowest distance to centroid values throughout seasons, Table 2.6). In addition, the Kwando River had lower species richness and evenness (H’ and J’) diversity indices, compared to the Kavango and Zambezi rivers, also likely as a result of weaker flood pulse and subsequent ecosystem homogenisation. This homogenising effect has been demonstrated in fish assemblages in neotropical floodplain lakes (Tejerina-Garro et al. 1998; Gomes et al. 2012) where reduced variability of assemblages occurred after flooding, compared to after drawdown. In temperate environments homogenisation of zooplankton communities during flooding, and redevelopment of assemblages during flood recession, has also been well documented (Schöll et al. 2012). In the Upper Paraná River, Petry et al. (2003) found lower species richness, density and biomass of assemblage structure in lagoons connected to the main channel, compared to disconnected lagoons, which were dominated by opportunistic species. These differences were attributed to variations in nutrients and productivity, with higher values recorded in the shallow disconnected lagoons, as connected lagoons were drained of nutrients by the nutrient poor main channel, where nutrients and solids were filtered out by the many dams upstream (Petry et al. 2003). Although in the Zambezi and Kavango sampling sites all habitats were accessible from the main channel by boat, in the Kwando River large floating mats of *P. mauritianus* and *C. papyrus* have resulted in a much more heterogeneous environment (Pers. obs.), where selection factors of predation and competition (Vellend 2010) have theoretically allowed communities to develop over time.

The second potential driver of differences in assemblage structure between rivers was the abundance of *H. vittatus* in the Zambezi and Kavango rivers, and its relative absence from the Kwando River in all seasons (Figure 2.7). *Hydrocynus vittatus* is a large bodied piscivorous predator which uses the chase or pursuit strategy to catch prey in open water (Jackson 1961; Winemiller and Kelso-Winemiller 1994). Jackson (1961), Jackson (1986) and Winemiller and Kelso-Winemiller (1994) hypothesised that *H. vittatus* restricted all other fish species from open water main channel habitats by predation, confining them to backwaters and habitats with macrophyte refuges. This could have structured the Zambezi and Kavango assemblages by selection (Vellend 2010), while the Kwando River assemblage has not been subject to this same pressure.

In conclusion, the Zambezi, Kavango and Kwando rivers are influenced by differing flood regimes, and the nature and phase of the flood regime dictated the physiochemical structure of each river. It is suspected that peak flows have a homogenising effect on the river system, the extent of which may be directly proportional to the magnitude of the flood. Small floods, such as those experienced by the Kwando River, have potentially allowed fish assemblages time to develop in a heterogeneous landscape, so distinguishing it from the other river fish assemblages. In addition the abundance of *H. vittatus* in the Zambezi and Kavango rivers could have contributed to the differences in the fish assemblage structures of these rivers compared to that of the Kwando River. It is therefore likely that the varying flood regimes will result in other ecological processes differing between the Zambezi, Kavango and Kwando river systems which will be tested in the coming chapters.

CHAPTER 3: A comparison of the diets of six fish species from the Zambezi, Kavango and Kwando rivers

Introduction

Understanding food habits is essential when defining the functional role of fishes in aquatic ecosystems (Lévêque 1995; Link 2002; Pedreschi et al. 2015), and biologically, dietary analyses are important in understanding ecology because the food ingested by an organism directly influences its survival, growth rate and reproduction (Wootton 1990; Welcomme 2001). Stomach contents analysis is a standard practice used to determine fish diets (Hyslop 1980). This method has both advantages and disadvantages. It allows for high taxonomic resolution of prey items (Pinnegar and Polunin 2000; Kadye and Booth 2011) and although labour intensive, it does not require highly technical and/or expensive laboratory analysis, allowing for estimations of the energetic content of prey (Benoit-Bird 2004; White and Harvey 2007). However, there may be a strong temporal bias in stomach contents due to digestion rates, resulting in only a 'snapshot' of fish diets (Pinnegar and Polunin 2000). The rate of prey digestion may also affect prey identification and accurate measurements of prey weight or volume (Hyslop 1980; Stapp 2002). For stomach contents analysis on predatory fishes, sufficient sample sizes are difficult to obtain (Arrington et al. 2002), and prey accumulation curves are a well-developed method that tests sample size efficiency (Consoli et al. 2008; Esposito et al. 2009; Hallett and Daley 2011).

For this study, six predatory species were chosen for dietary analysis; *Brycinus lateralis, Clarias gariepinus, Clarias ngamensis, Hepsetus cuvieri, Serranochromis macrocephalus* and *Schilbe intermedius*. These species are widespread and abundant in all three rivers (Hay et al. 2000; Hay et al. 2002; Næsje et al. 2004; Peel 2012; Appendix 2) and they are representative of differing feeding modes and occupy varying habitats (Box 1). *Brycinus lateralis* is an opportunistic micro-carnivore, feeding in open water and at the water surface (Booth and McKinlay 2001), *C. gariepinus* and *C. ngamensis* are opportunistic omnivore/piscivores that feed in a number of habitats (Willoughby and Tweddle 1978; van der Waal 1985; Winemiller and Kelso-Winemiller 1996), and *H. cuvieri* is an ambush piscivore that prefers structured habitats (Winemiller and Kelso-Winemiller 1994). *Serranochromis macrocephalus* is a crepuscular piscivore and *S. intermedius* an omnivore, with both species inhabiting vegetated backwaters (van der Waal 1985; Winemiller 1991a; Merron and Mann 1995; Winemiller and Kelso-Winemiller 1996).

Only a few studies have described the diets of these fishes, with the exception of *C. gariepinus*, which has been studied extensively as a result of its invasive capabilities and its use in aquaculture (Henken et al. 1985; Kaiser et al. 1995; Cambray 2003; Ellender et al. 2014). Some work has been completed on the diets and feeding ecology of *C. gariepinus*, *C. ngamensis*, *H. cuvieri*, *S. intermedius* and *S. macrocephalus* on the Barotse floodplain in the Upper Zambezi River (Winemiller 1991a; Winemiller and Kelso-Winemiller 1994; Winemiller and Kelso-Winemiller 1996) and on Lake Liambezi (van der Waal 1985). The diets of *B. lateralis*, *C. gariepinus*, *C. ngamensis*, *H. cuvieri* and *S. intermedius* in the Okavango Delta (Merron 1993; Merron and Mann 1995; Booth and McKinlay 2001; Mosepele et al. 2012), and *B. lateralis* and *S. intermedius* from the Kavango River, Namibia (Hay 1995), have also been studied. Stomach contents analyses proved difficult for *B. lateralis* in the Okavango Delta as a result of prey mastication, which made prey identification very difficult (Booth and McKinlay 2001). Dietary information from these species has not been collected from the Kwando River, and comparisons between the Zambezi, Kavango and Kwando rivers are lacking.

The composition of a predator's diet results from both resource availability and feeding strategy (Wootton 1990; Spitz et al. 2006). Thus two scenarios are possible: i) diets vary between populations resulting from differing predator or prey abundances and habitat types, or ii) diets do not vary between populations due to preferential prey selection. With reference to the first scenario, Bruton (1979b) noted that *C. gariepinus* preyed upon the most abundant prey item available in Lake Sibaya, and Adite and Winemiller (1997) attributed differences in tropical West African fishes' diets to relative prey abundance and differing habitats. Pedreschi et al. (2015) found *Esox luscius* was highly opportunistic, feeding on a range of fish, vertebrate and invertebrate prey, in addition to the most abundant fish species (*Rutilus rutilus*).

With reference to the active selection for a preferred prey item, Potts et al. (2008) noted that in two reservoirs in South Africa, *C. gariepinus* actively selected for fish prey, and differences detected were attributed to fish size and differing sample compositions. Kadye and Booth (2011) found that diets of *C. gariepinus* did differ as a result of prey abundance and habitat types, however fish prey were also actively selected for. Since all three rivers considered here are periodically interlinked, all fish species evolved together (Tweddle 2010) and fish assemblage structure differs between rivers (see Chapter 2), it is hypothesised that differences in resource availability will dictate variations in diets between rivers.

The aim of this chapter is to describe and compare the diets of *B. lateralis, C. gariepinus, C. ngamensis, H. cuvieri, S. intermedius* and *S. macrocephalus* from the Zambezi, Kavango and Kwando rivers using stomach contents analysis. The hypotheses to be tested are i) *C. gariepinus*, *C. ngamensis* and *S. intermedius* are generalist omnivores, while *H. cuvieri* and *S. macrocephalus* are specialised piscivores, and ii) the diets of omnivorous fishes differ between rivers as a result of variations in prey abundance while the diets of piscivores do not differ between rivers as preferred prey fishes are actively selected for.

Methods

For stomach contents analysis, fish were collected using gillnets and baited longlines set overnight (6 pm – 6 am), from the Zambezi in October 2013 and July 2014, from the Kavango in June and August 2014, and from the Kwando in August 2013, January - April and July 2014. Any live fish were killed by concussion followed by destruction of the brain, measured to the nearest mm FL or TL and dissected. For *C. gariepinus*, *C. ngamensis*, *H. cuvieri*, *S. intermedius* and *S. macrocephalus*, stomach contents were identified, counted and weighed to the nearest 0.1 g after blotting dry on tissue. Bait from longlines was excluded from the stomach contents. *Brycinus lateralis* were preserved in formalin, and in the laboratory stomach contents were identified under a dissecting microscope, counted and weighed to the nearest 0.01 g after blotting dry. Fish remains were identified to species level, while insect remains were identified to family.

Stomach contents were sorted into specific prey categories: aquatic and terrestrial insects by order, fish by family, decapods (Atyidae, Potamonautidae), molluscs (snails, clams and mussels), and detritus.

Comparing sample compositions using fish length

To ensure that differences in diet were not due to ontogeny, an understanding of the size composition of the sampled fish was important. Length frequency distributions were compared to determine if the samples could have come from the same distribution using two-sample Kolmogorov Smirnov tests.

Describing diets

Dietary composition was assessed using an index of relative importance (*%IRI*) calculated from % weight, % number and % frequency of occurrence (Hyslop 1980) defined as:

$\%W_i = \frac{W_i}{\sum_{i=1}^{t} W_i} \times 100$, $\%N_i = \frac{N_i}{\sum_{i=1}^{t} N_i} \times 100,$ $\%FO_i = \frac{F_i}{\sum_{i=1}^{t} F_i} \times 100,$

where $\%W_i$ and $\%N_i$ are the percentage weight and number of prey i; W_i and N_i are the total wet weight and total number of prey item i from a total of t prey items. $\%FO_i$ is the percentage frequency of occurrence of prey item i, where $F_i = \frac{F_i}{\sum_{i=1}^{t} n_i}$, F_i is the frequency of item i from the stomachs containing prey item i, and n_i is the total number of stomachs examined. $IRI_i = (\%W_i + \%N_i) \times \%FO_i$, $\%IRI_i = \frac{IRI_i}{\sum_{i=1}^{t} IRI_i} \times 100,$

where IRI_i is the total *IRI* of prey item i, and $\%IRI_i$ is the percent IRI_i of item i from a total of t prey items. Each species was then grouped in length classes, and $\%IRI_i$ was tabulated per river system for each species for visual description of diet and comparison between river populations. $\%N_i$, $\%W_i$ and $\%FO_i$ for grouped length classes (total samples of each species per river) are tabulated in Appendix 3.

Using total stomach contents samples per river population, Schoener's (1970) index of overlap was used to calculate the diet similarity between river populations using $\%IRI_i$ of the specific prey categories. This index is calculated as: $\alpha_{jk} = 1 - 0.5\sum_{i=1}^{t} |p_{ij} - p_{ik}|$, where p_{ij} is the proportion of prey item i in population j, and p_{ik} is the proportion of prey item i in population k. Alpha (α) ranges from 0 (no overlap) to 1 (complete overlap).

Niche breadth for each population was calculated using the Shannon-Weiner index (Krebs 1989) using $\%IRI_i$ values of specific prey categories, defined as $H' = \sum_{i=1}^{n}(pi)(\ln pi)$, where *pi* is the proportion of a specific prey category for the *n* categories of prey listed. The higher the Shannon-Weiner index, the higher the number of species in the diet. Shannons index of evenness was also calculated using: $J' = \frac{H'}{Hmax}$, where $Hmax = \ln(S)$, and *H'* refers to the Shannon-Weiner index of dietary breadth, *S* represents the total number of prey categories. *J'* ranges between 0 (uneven) and 1 (completely even).

Multivariate analysis: Comparing diets between rivers and between species

Multivariate analyses were performed on the wet weights of stomach contents (biomass) which had been identified to order (invertebrates) and family (fishes). Categories which occurred in less than 5% of stomachs were categorised as rare prey and removed from the analyses (Duffy-Anderson et al. 2006). The data were then square root transformed to reduce the influence of the most abundant species (Clarke and Warwick 2001), and Bray-Curtis dissimilarity matrices were used for hierarchical clustering, as this resolves inter-species associations (Duffy-Anderson et al. 2006).

Permutational analyses of variance (PERMANOVA) were performed on all the biomass stomach data for all species with more than eight samples, to test if diets varied: i) within species between rivers; and ii) across species within rivers. Permutational analysis of multivariate dispersions (PERMDISP) were used to test for homogeneity of variances.

Similarity percentage (SIMPER) analyses were performed on the square root transformed biomass data, to compare diets of species between rivers and identify the prey items which contributed the most to fish diets.

When comparing diets between species, where PERMANOVA differences were detected, post hoc pairwise tests were used to test between species ($P < 0.05$). Unconstrained ordinations were performed using principal coordinate analyses (PCO) on the dissimilarity matrix to visualise the data, and ultimately canonical analyses of principal coordinates (CAP) were used to emphasise differences in diets between species. Diet categories were correlated with the canonical axes of the CAP to identify those categories driving the differences between species, using Pearson correlations of square root transformed diet biomass with canonical axes (Anderson and Willis 2003). A correlation of $|r| = 0.4$ was used as a cut off to display potential relationships between dietary categories and the canonical axes. All analyses were performed using PRIMER v6 with PERMANOVA add on (PRIMER-E Ltd, Plymouth United Kingdom; Clarke and Gorley 2006; Anderson et al. 2008).

Sample size sufficiency

To confirm sample size sufficiency for describing the diet of each species in each river in terms of specific prey category, cumulative prey curves were constructed using PRIMER v6 with PERMANOVA add on (PRIMER-E Ltd, Plymouth United Kingdom; Clarke and Gorley

2006; Anderson et al. 2008). Only stomachs containing identifiable prey items were used for these curves. Cumulative numbers of observed taxa across samples (Sobs) were calculated, as well as several non-parametric estimators of total prey category richness (Chao1 and 2, Jacknife1 and 2, and Bootstrap) (Colwell and Coddington 1994). Sobs is a negatively biased estimator of richness, and estimators differ in accuracy depending on the data in use, so multiple estimators were used to offset bias (Colwell and Coddington 1994; Hallett and Daley 2011). Sample order was randomised across 999 permutations, and averages (± SD) of permuted curves were plotted, removing the effect of sample order and producing smoothed curves (Hallett and Daley 2011). Since a visual assessment of sample size sufficiency (if an asymptote has been reached with Sobs) may be biased, the linear regression method of Bizzarro et al. (2007) was used to calculate the sufficiency of the sample size statistically. This method compares the slope for the regression of the last four stomach samples to a slope of zero using a Student's *t*-test of equality of the two population regression coefficients ($t = (b-0)/Sb$, b = slope of best fit line and S_b = standard error of the slope), with a p-value of > 0.05 demonstrating a sufficient sample size has been reached (Morris and Akins 2009).

Results

Comparing sample compositions using fish length

Length frequency analyses from all populations sampled are given in Figure 3.1, and results of the two-sample Kolmogorov-Smirnov tests comparing the length frequencies between rover populations are given in Table 3.1. No small *C. gariepinus* or *C. ngamensis* were sampled, while some small *H. cuvieri* and *S. macrocephalus* were sampled, and many small *S. intermedius* were sampled. The length frequency distributions of *C. gariepinus* from all rivers followed a similar trend and were not significantly different, while the Kavango River *C. ngamensis* sampled were generally larger than the Kwando River *C. ngamensis*. In the Zambezi River, the length frequency distributions of the *H. cuvieri* and *S. macrocephalus* sampled differed significantly from those sampled from the Kavango and Kwando rivers, as many small fish were sampled from the Zambezi River. *Schilbe intermedius* length frequency distribution different significantly in all three rivers, and those sampled from the Zambezi River were the smallest while those sampled from the Kwando River were the largest.

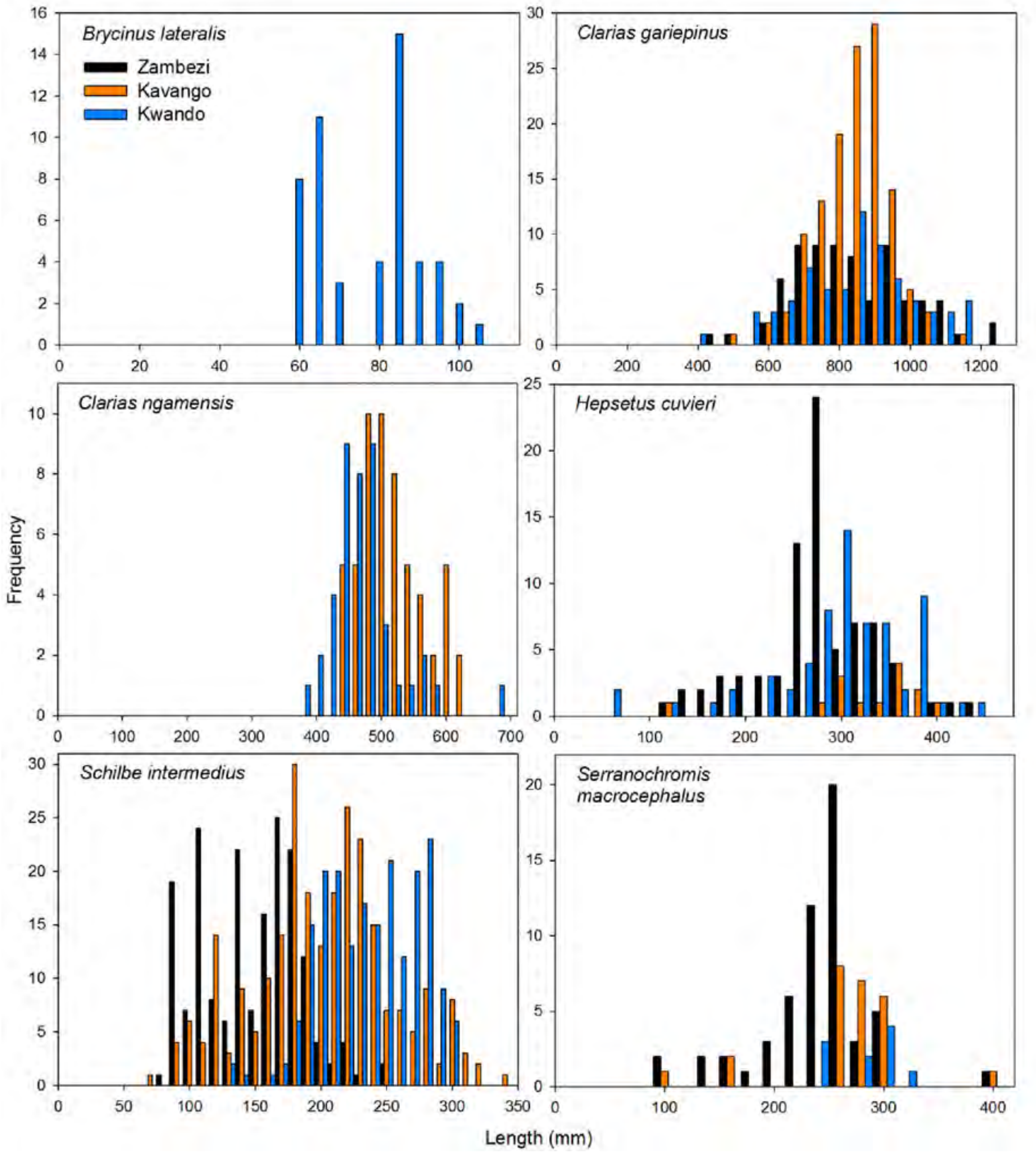

Figure 3.1: Length frequency distributions of a number of species from the Zambezi River (black bars), Kavango River (orange bars) and Kwando River (blue bars) populations.

Table 3.1: Results of the Kolmogorov-Smirnov two-sample tests comparing the length frequency distributions of the study species between the Zambezi, Kavango and Kwando rivers. Results are displayed as D statistic; Critical D value, and asterisks denote significant differences when D stat > Critical D.

Species	Zambezi v Kavango	Zambezi v Kwando	Kavango v Kwando
B. lateralis	-	-	-
C. gariepinus	0.16; 0.20	0.10; 0.23	0.13; 0.20
C. ngamensis	-	-	0.43; 0.28*
H. cuvieri	0.53; 0.39*	0.32; 0.23*	0.28; 0.40
S. intermedius	0.47; 0.13*	0.80; 0.14*	0.33; 0.13*
S. macrocephalus	0.40; 0.32*	0.54; 0.46*	0.22; 0.50

Diet composition

The diet of *B. lateralis* was described using % number (%N_i), % weight (%W_i), % frequency of occurrence (%FO_i) and % index of relative importance (%IRI_i). The diets of *C. gariepinus*, *C. ngamensis*, *H. cuvieri*, *S. intermedius* and *S. macrocephalus* are described using the % index of relative importance (%IRI_i); however % number (%N_i), % weight (%W_i) and % frequency of occurrence (%FO_i) are provided in Appendix 3.

Brycinus lateralis

Fifty two *B. lateralis* stomachs from the Kwando River were examined, and 21.2% were empty (Table 3.2).

Table 3.2: Stomach contents of *Brycinus lateralis* from the Kwando River. Terrestrial insect remains and aquatic insect remains in bold represent the total values for each category.

Order	Family	%N_i	%W_i	%FO_i	%IRI_i
Terrestrial insect remains		**14.80**	**86.92**	**68.29**	**74.88**
Unidentified remains		12.80	72.29	65.85	74.34
Ephemeroptera		2.00	14.63	2.44	0.54
Aquatic insect remains		**7.60**	**8.73**	**36.59**	**1.36**
Unidentified remains		2.00	1.60	12.20	0.58
Diptera	Chaoboridae	0.80	0.02	4.88	0.05
	Culicidae	0.40	0.23	2.44	0.02
Coleoptera	Gyrinidae	0.40	0.23	2.44	0.02
Trichoptera		0.40	0.02	2.44	0.01
	Psychomyiidae	0.40	2.97	2.44	0.11
	Hydropsychidae	0.80	0.23	4.88	0.07
	Philopotamidae	0.40	0.69	2.44	0.04
	Polymitarcyidae	2.00	2.74	7.32	0.46
Eggs		27.20	0.46	7.32	2.68
Seeds		50.40	3.89	29.27	21.08

The majority of *B. lateralis* stomach contents were masticated terrestrial insect remains, not identifiable to a lower taxonomic level, and as a result, stomachs from the Zambezi and Kavango rivers were not examined.

Clarias gariepinus

Of the 73 *C. gariepinus* stomachs examined from the Zambezi River, 63.0% were empty, while of the 127 examined from the Kavango River, 56.7% were empty and of the 69 examined from the Kwando River, 62.3% were empty.

Since no small *C. gariepinus* < 300 mm TL were sampled, fish were categorised into medium (≤ 750 mm TL) and large (> 750 mm TL) size classes. Medium *C. gariepinus* mainly ate unidentified fish prey in all rivers, while large *C. gariepinus* specialised on clariids, synodontids and crabs in the Zambezi, Kavango and Kwando rivers respectively (Table 3.3).

PERMANOVA found that the diets of the total samples of *C. gariepinus* were significantly different between rivers (*Pseudo* $F = 5.38$, $P = 0.001$; PERMDISP $F = 0.94$; $P = 0.54$). SIMPER analysis indicated the diet of *C. gariepinus* was dominated by clariids and synodontids (35.79% and 35.54%) in the Zambezi River, synodontids (89.74%) in the Kavango River and Decapoda (crabs 86.03%) in the Kwando River.

Table 3.3: Stomach contents of two size classes of *Clarias gariepinus* from the Zambezi, Kavango and Kwando rivers, illustrating the sample size (N), % of empty stomachs and $\%IRI_i$ of total prey including fish prey by family. Common prey items are shaded.

	Medium (≤ 750 mm TL)			Large (> 750 mm TL)		
	Zambezi	Kavango	Kwando	Zambezi	Kavango	Kwando
N	28	29	23	45	98	46
% empty	48.3	58.6	56.5	31.1	56.1	65.2
Insect remains	1.7	-	3.5	-	-	-
Fish remains	82.7	82.1	48.0	8.9	13.4	21.9
Alestids	0.2	-	0.4	0.7	-	0.9
Barbs	0.5	-	0.3	-	-	-
Cichlids	11.6	0.8	13.7	1.6	1.4	14.3
Clariids	2.1	-	-	58.8	-	-
Mormyrids	-	8.0	0.3	-	1.1	0.7
Silurids	-	-	-	-	3.4	-
Synodontids	1.1	4.5	-	30.0	77.7	-
Crabs	-	1.7	29.6	-	0.5	58.6
Detritus	-	2.9	0.3	-	2.5	0.7
Other	-	-	4.0	-	-	3.0

Clarias ngamensis

Of the 56 *C. ngamensis* stomachs examined from the Kavango River, 50.0% were empty, while 23.8% of the 42 stomachs examined from the Kwando River were empty. Only one *C. ngamensis* from the Zambezi River was sampled.

Clarias ngamensis of a medium size preyed upon insects (Odonata and Coleoptera), cichlids and detritus in the Kavango River, and insects (Trichoptera) in the Kwando River (Table 3.4).

Large *C. ngamensis* preyed upon crabs and insects (Hymenoptera) in the Kavango River and crabs and shrimps in the Kwando River.

Table 3.4: Stomach contents of two size classes of *Clarias ngamensis* from the Kavango and Kwando rivers, illustrating the sample size (N), % of empty stomachs and %IRI_i of total prey including insect prey by order and fish prey by family. Common prey items are shaded.

	Medium (≤ 500 mm TL)		Large (> 500 mm TL)	
	Kavango	Kwando	Kavango	Kwando
N	30	36	26	6
% empty	43.3	25.0	57.7	16.7
Insect remains (IR)	13.6	0.3	0.9	2.6
Terrestrial IR	1.2	-	-	-
Aquatic IR	0.4	3.0	-	2.0
Hemiptera	1.7	0.9	-	-
Odonata	8.6	7.9	-	2.3
Trichoptera	-	55.8	0.0	3.9
Diptera	-	0.0	2.0	-
Coleoptera	6.3	-	4.1	-
Ephemeroptera	0.7	4.3	-	-
Oligochaeta	-	0.2	-	-
Hymenoptera	-	-	26.8	-
Araneae	11.2	0.1	0.2	-
Fish remains	4.4	0.5	3.8	-
Cichlids	17.1	1.8	9.2	-
Clariids	1.0	-	-	-
Synodontids	-	-	10.5	-
Snails	1.7	5.1	0.0	4.0
Clams	-	10.9	-	-
Detritus	17.0	5.6	0.5	-
Crabs	0.4	-	42.5	67.1
Shrimps	14.9	3.6	-	17.9

PERMANOVA found that the diets of *C. ngamensis* were significantly different between rivers (*Pseudo* $F = 6.12$, $P = 0.001$), however this may have been due to the heterogeneity of variances between river samples (PERMDISP $F = 7.74$; $P = 0.011$). SIMPER analysis indicated the diet of *C. ngamensis* was dominated by Decapoda and cichlids (28.04% and 21.30%) in the Kavango River, and Trichoptera and Mollusca (51.54% and 18.28%) in the Kwando River.

Hepsetus cuvieri

Of the 80 *H. cuvieri* stomachs examined from the Zambezi River, 80.0% were empty, of the 14 examined from the Kavango River, 78.5% were empty, and of the 65 examined from the Kwando River 81.5% were empty.

All prey items from all systems were fish, and only two *H. cuvieri* of less than 100 mm FL were sampled, from the Kwando River, which preyed upon a top minnow and a cichlid. Small *H. cuvieri* were sampled from the Zambezi and Kwando rivers, which preyed upon fish remains and cichlids respectively (Table 3.5). Medium *H. cuvieri* preyed upon fish remains in both the Zambezi and Kwando rivers. Large *H. cuvieri* sampled from all three rivers had more specialised diets of cichlids in the Zambezi and Kwando rivers, and mormyrids, silurids and synodontids in the Kavango River. Grouped sample sizes of identified fish prey were too small from all three rivers for a multivariate comparison.

Table 3.5: Stomach contents of three size classes of *Hepsetus cuvieri* from the Zambezi, Kavango and Kwando rivers, illustrating the sample size (N), % of empty stomachs and %IRI_i of total prey. Common prey items are shaded.

	Small 100 - 200 mm FL		Medium 200 - 300 mm FL		Large > 300 mm FL		
	Zambezi	Kwando	Zambezi	Kwando	Zambezi	Kavango	Kwando
N	11	4	48	31	21	14	28
% empty	63.6	75	87.5	87.1	71.4	71.4	82.1
Fish remains	87.6	0	72.7	68.0	5.2	0	8.2
Alestids	0	0	0	12.1	0	0	10.5
Barbs	12.4	0	9.3	0	0	0	0
Cichlids	0	100	8.5	19.9	90.7	0	81.3
Mormyrids	0	0	4.8	0	0	32.9	0
Silurids	0	0	4.7	0	0	31.7	0
Synodontids	0	0	0	0	4.1	35.3	0

Schilbe intermedius

In the Zambezi River 180 *S. intermedius* were sampled, 69.4% of which were empty, in the Kavango River 257 were sampled of which 55.6% were empty, and in the Kwando River 203 were sampled of which 23.6% were empty.

Small *S. intermedius* mainly preyed on fish and insects in the Zambezi and Kavango rivers (Table 3.6), while in the Kwando River only three were sampled from this size class which preyed upon insects and Decapods. Medium *S. intermedius* preyed upon fish in the Zambezi (barbs) and Kavango (mormyrids) rivers, and insects (Odonata) in the Kwando River. Large

S. intermedius preyed upon mormyrids and insects in the Kavango and Kwando rivers respectively, and were not sampled in the Zambezi River.

Table 3.6: Stomach contents of three size classes of *Schilbe intermedius* from the Zambezi, Kavango and Kwando rivers, illustrating the sample size (N), % of empty stomachs and $\%IRI_i$ of prey including insects by order and fish by family. Common prey items are shaded.

	Small ≤150 mm FL		Medium 150 – 250 mm FL			Large >250 mm FL	
	Zambezi	Kavango	Zambezi	Kavango	Kwando	Kavango	Kwando
N	94	46	86	174	130	37	70
% empty	71.2	67.4	67.4	57.5	22.3	32.4	27.1
Insect remains (IR)	29.6	15.2	0.8	0.9	43.8	0.1	55.5
Aquatic IR	-	-	-	-	16.7	-	2.2
Terrestrial IR	0.4	0.7	-	0.4	11.5	0.1	10.2
Odonata	5.0	0.7	0.3	0.5	7.1	-	4.4
Ephemeroptera	0.3	-	10.2	0.1	1.7	-	3.1
Trichoptera	-	-	-	-	4.7	-	2.8
Coleoptera	-	-	-	-	-	-	-
Diptera	-	2.4	-	-	-	-	-
Hemiptera	-	-	-	-	0.1	-	-
Decapoda	2.9	2.7	7.1	0.1	2.8	-	1.0
Fish remains	44.4	70.6	45.7	44.8	8.0	13.0	10.3
Alestids	-	-	1.1	0.4	-	0.1	0.1
Barbs	7.0	-	30.4	-	0.1	-	-
Cichlids	9.1	1.5	0.6	0.2	3.0	0.1	9.8
Catfishes	-	-	-	0.7	-	0.2	-
Mormyrids	-	5.4	1.9	48.8	-	86.3	-
Topminnows	-	-	-	-	-	-	0.3
Detritus	1.3	0.9	1.7	3.1	-	-	0.1
Other	-	-	0.2	-	0.4	-	0.2

PERMANOVA found that the diets of the total samples of *S. intermedius* were significantly different between rivers (*Pseudo* $F = 13.28$, $P = 0.001$), however differences could have been due to heterogeneity of variances between samples (PERMDISP $F = 5.93$; $P = 0.015$). SIMPER analysis indicated the diet of *S. intermedius* was dominated by barbs and Decapoda (43.39% and 20.90%) in the Zambezi River, mormyrids (88.53%) in the Kavango River, and Odonata and Trichoptera (27.61% and 26.58%) in the Kwando River.

Serranochromis macrocephalus

Of the 57 *S. macrocephalus* sampled from the Zambezi River 63.2% were empty, in the Kavango River 25 were sampled of which 64.0% were empty, and in the Kwando River only 10 were sampled of which 60.0% were empty.

Serranochromis macrocephalus of less than 100 mm TL were sampled from the Zambezi River (N = 2), where they were empty, and from the Kavango river (N = 1) where the stomach contents were of insect remains. Medium fish of between 100 and 200 mm TL were sampled from the Zambezi (N = 8; 75% empty) and Kavango (N = 2, 100% empty) rivers and stomach contents included fish remains and a barb. The diets of *S. macrocephalus* from the large size class are illustrated in Table 3.7. Diets mainly consisted of barbs and fish remains in the Zambezi River, mormyrids in the Kavango River, and cichlids and alestids in the Kwando River. Sample sizes of total identified prey were too small from all three rivers for a multivariate comparison.

Table 3.7: Stomach contents of large *Serranochromis macrocephalus* from the Zambezi, Kavango and Kwando rivers, illustrating the sample size (N), % of empty stomachs and $\%IRI_i$ of prey. Common prey items are shaded.

	> 200 mm TL		
	Zambezi	Kavango	Kwando
N	47	22	10
% empty	59.6	63.6	60.0
Fish remains	30.3	16.1	9.9
Barbs	40.5	17.6	9.9
Cichlids	21.9	-	35.4
Citharines	1.8	-	-
Mormyrids	4.4	66.3	-
Alestids	0.9	-	39.6
Shrimps	-	-	5.1

Indices of diet overlap, dietary breadth and evenness

Diets of total samples overlapped the least between the Kavango and the Kwando rivers (Table 3.8), although small sample sizes limited the comparison.

For *C. gariepinus,* diets in the Zambezi and Kwando rivers overlapped the most, and diets were broad in these two rivers compared to in the Kavango River. *Clarias ngamensis* had a much more varied diet in the Kavango River compared to in the Kwando River, where its dietary niche was narrow. For *S. intermedius* dietary overlap was highest between the Zambezi and the Kavango rivers, and extremely low between the Kavango and the Kwando rivers. Dietary niches for this species were broad and relatively even in the Zambezi and Kwando rivers, and narrow and uneven in the Kavango River.

For *H. cuvieri* dietary niches were narrow, and there was a high level of overlap between the Zambezi and Kwando rivers where sample sizes were reasonable. *Serranochromis macrocephalus* had relatively narrow and very even dietary niches in the Zambezi and Kavango rivers, however diets overlapped very little.

Table 3.8: Schoener's index of dietary overlap between rivers (top half of table), Shannon-Weiner's index of dietary breadth and Shannon's index of dietary evenness (H', J' bottom half of table) of each species by river. * = N ≤ 10.

Species	Zambezi v Kavango	Zambezi v Kwando	Kavango v Kwando
C. gariepinus	0.49	0.57	0.36
C. ngamensis	*	*	0.20
H. cuvieri	*	0.76	*
S. intermedius	0.58	0.26	0.13
S. macrocephalus	0.23	*	*
	Zambezi	Kavango	Kwando
C. gariepinus	1.27, 0.58	1.03, 0.47	1.23, 0.49
C. ngamensis	*	2.07, 0.72	1.50, 0.59
H. cuvieri	0.62, 0.38	*	0.65, 0.60
S. intermedius	1.37, 0.55	0.95, 0.36	1.45, 0.54
S. macrocephalus	1.27, 0.71	0.99, 0.72*	*

Multivariate analysis: Comparing diets between rivers and between species

Dietary differences were found between species in each river using PERMANOVA (Table 3.9). In the Zambezi River the diet of *S. intermedius* differed from the diets of the other species, containing more Ephemeroptera (hatching mayflies) and Decapoda (Atyidae shrimps), while *C. gariepinus* and *H. cuvieri,* and *H. cuvieri* and *S. macrocephalus* had very similar diets (Table 3.9, Figure 3.2). PERMDISP indicated some differences may have been due to heterogeneity of variance (Table 3.9), although in combination with support from the CAP analyses, the detected differences are most likely real. *Clarias gariepinus* diet was characterised by higher proportions of synodontids and clariids, while *H. cuvieri* and *S. macrocephalus* diets contained mostly barbs and cichlids. Dietary distinctness of the assemblages however was not very high, as the leave – one –out allocation success rates of CAP analyses were low at 55 - 64% (Table 3.10).

In the Kavango River only *S. intermedius, C. gariepinus* and *C. ngamensis* were sampled in large enough numbers to describe and compare diets (see below). All three dietary assemblages had homogenous variances and were distinct, with *S. intermedius* positively correlating with mormyrids, *C. gariepinus* with synodontids and *C. ngamensis* with Araneae, Coleoptera (Dytiscidae) and Gastropods (Figure 3.2). The proportions of correct allocations were higher for the Kavango (Table 3.10) and hence the confidence in dietary distinctness greater.

Table 3.9: Results of PERMANOVA and PERMDISP tests on the diets of all species within river (*Pseudo* F, P value), and between species dietary differences using pairwise tests (PERMANOVA figures given, PERMDISP significant differences indicated using *). Distances between species diet centroids (in parentheses) are given, and all tests were done using 999 permutations.

	Zambezi	Kavango	Kwando
PERMANOVA	$F = 3.19, P = 0.001$	$F = 14.23, P = 0.001$	$F = 4.36, P = 0.001$
PERMDISP	$F = 4.28, P = 0.034$	$F = 2.20, P = 0.193$	$F = 2.81, P = 0.16$
Pair-wise tests			
S. intermedius, C. gariepinus	$t = 2.16, P = 0.001$ (40.31)	$t = 4.51, P = 0.001$ (51.95)	$t = 2.11, P = 0.001$ (37.53)
S. intermedius, S. macrocephalus	$t = 1.54, P = 0.022$* (31.16)	-	-
S. intermedius, H. cuvieri	$t = 1.77, P = 0.004$* (42.68)	-	$t = 1.84, P = 0.004$ (42.38)
S. intermedius, C. ngamensis	-	$t = 3.34, P = 0.001$ (46.40)	$t = 2.15, P = 0.001$* (28.19)
C. gariepinus, S. macrocephalus	$t = 1.98, P = 0.003$ (43.48)	-	-
C. gariepinus, H. cuvieri	$t = 1.44, P = 0.053$ (36.49)	-	$t = 1.50, P = 0.039$ (41.63)
C. gariepinus, C. ngamensis	-	$t = 3.07, P = 0.001$ (46.14)	$t = 2.27, P = 0.001$ (42.60)
S. macrocephalus, H. cuvieri	$t = 1.28, P = 0.179$ (32.45)	-	-
C. ngamensis, H. cuvieri	-	-	$t = 2.46, P = 0.001$ (56.63)

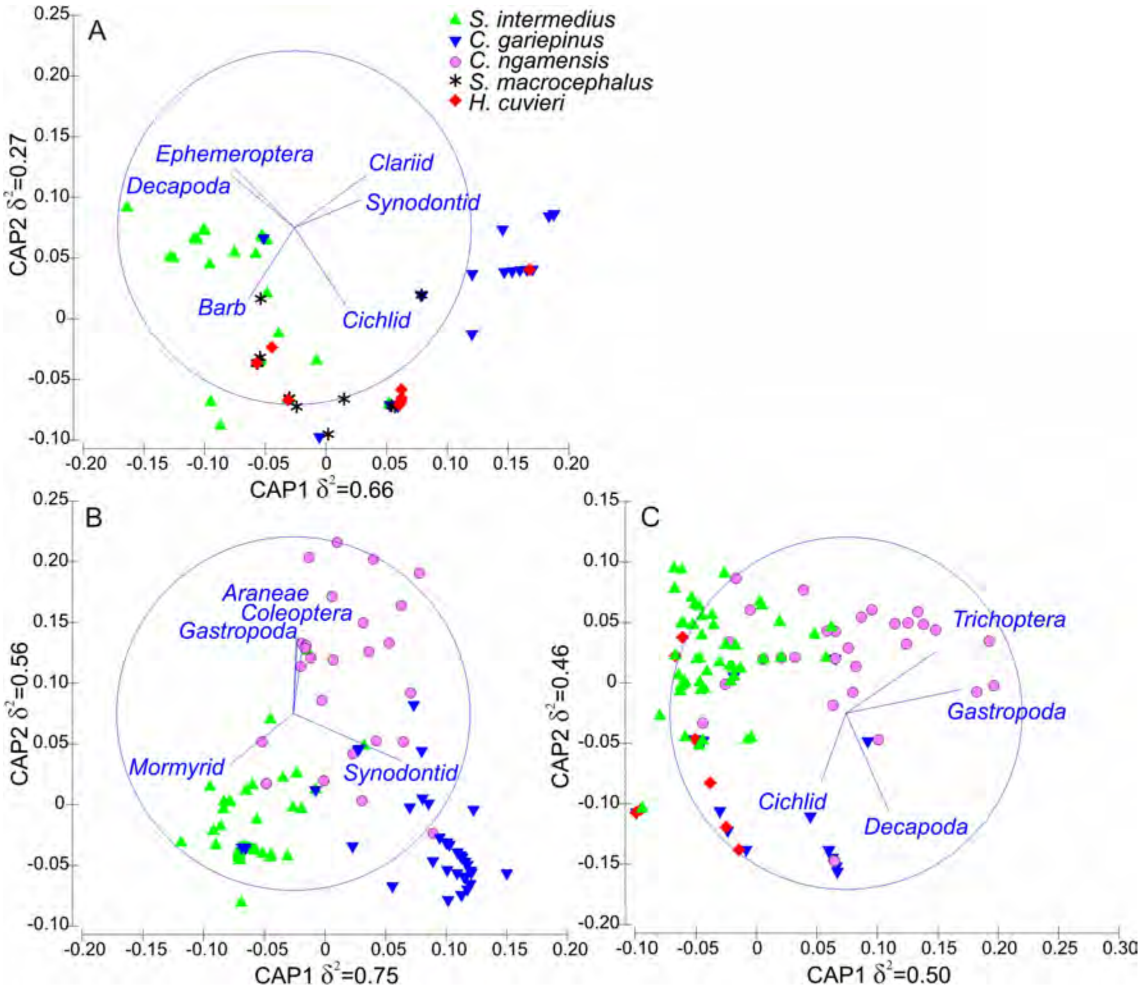

Figure 3.2: Canonical analysis of principal coordinates (CAP) ordination for species diets in the three rivers, A: Zambezi River, B: Kavango River, C: Kwando River, and biplots of diet category correlations with the canonical axes (|r| = 0.4).

In the Kwando River species diets were distinct, with *C. ngamensis* positively correlating with Trichoptera (caddisfly larvae) and Gastropoda (snails and clams), and *C. gariepinus* with Decapoda (Potamonautid crabs) and cichlids, however the correct allocation percentage was low (40%) (Table 3.10). The significant difference between *S. intermedius* and *C. ngamensis* detected using PERMANOVA may have been due to their heterogeneity of variance (PERMDISP Table 3.9).

Table 3.10: Canonical analysis of principal coordinates (CAP) for each species diet by river illustrating the number of axes (m) the CAP used to explain a percentage of the data (m, % of the data explained), and the proportion of correct allocations (%).

	m, % explained	*C. gariepinus*	*C. ngamensis*	*H. cuvieri*	*S. macrocephalus*	*S. intermedius*
Zambezi	9, 89.05	63.16	-	55.56	64.29	57.57
Kavango	16, 99.92	78.57	76.92	-	-	95.31
Kwando	10, 97.81	40	67.74	37.50	-	80.60

Sample size sufficiency

Sample sizes (N) used for accumulation curves were much reduced from the collected samples due to a high percentage of empty stomachs, and unidentified prey items which were removed for these analyses (Figure 3.3).

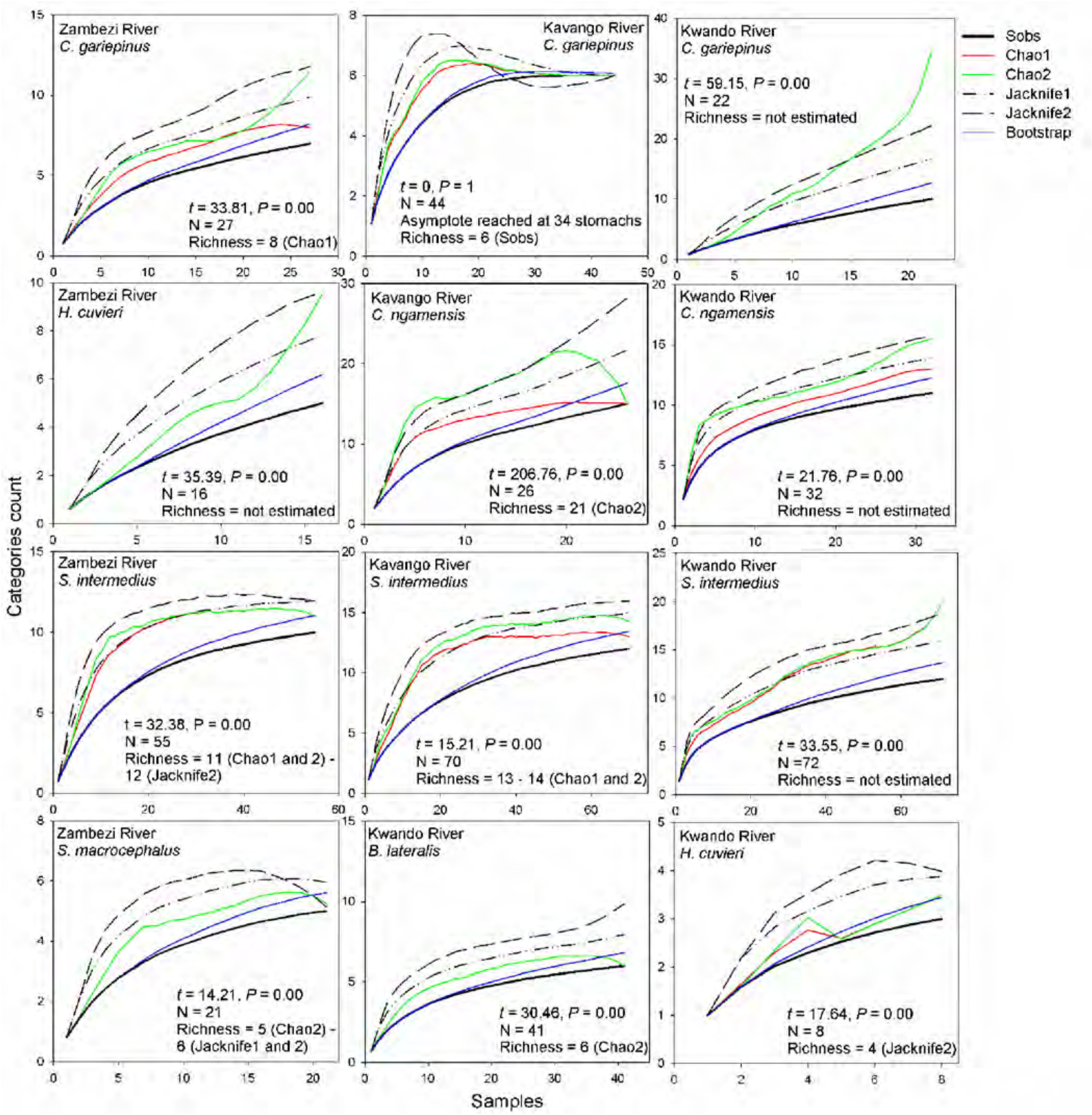

Figure 3.3: Prey accumulation curves for all species from all rivers, calculated for prey identified to family level categories. Curves are the averages of 999 permuted curves, constructed using randomised sample orders. Solid black lines are the observed prey species (Sobs) accumulation curves, while other curves are prey species richness estimators. *P* and *t* values comparing the regression of the last four samples to zero to define if the asymptote is reached are given, as well as the most likely prey richness and the defining estimators.

Cumulative prey curves of stomachs containing prey identified to family level categories illustrate sample size was only sufficient to accurately characterise the diet of *C. gariepinus* from the Kavango River (Figure 3.3). Many prey items were missing from the samples of *H. cuvieri* (Zambezi), *C. gariepinus* (Kwando), *C. ngamensis* (Kwando) and *S. intermedius* (Kwando), and as a result the estimators could not predict prey richness.

Discussion

Van der Waal (1985) described all of the species sampled in this study as predators in Lake Liambezi and suggested that *C. ngamensis* had omnivorous traits. In this study all species were characterised as predatory, with some feeding dominantly on fish (piscivores), or insects (invertivores), or on a combination of the two (omnivores), and all species showed some degree of plasticity. Differences in diets were detected, with Zambezi and Kavango river populations exhibiting more piscivorous feeding habits, compared to the Kwando River populations, which included more invertebrates in their diets.

This change in diet from piscivorous to partially invertivorous in *C. gariepinus*, *C. ngamensis*, *S. intermedius* is interesting, however not unheard of (e.g. Potts et al. 2008; Kadye and Booth 2011). *Clarias gariepinus* is known as a predacious generalist omnivore, and has been recorded feeding on a wide range of items including fish, molluscs, insects, plants, zooplankton, and detritus (Willoughby and Tweddle 1978; van der Waal 1985; Potts et al. 2008; Kadye and Booth 2011; Mosepele et al. 2012), or specialising on one particular item, from zooplankton (Dadebo 2009), to crustacea and zoobenthos (Bruton 1979b; Dorgeloh 1994; Yalcin et al. 2001), to detritus (Dadebo et al. 2014), or fish (Spataru et al. 1987; Winemiller and Kelso-Winemiller 1996). *Clarias ngamensis* is less studied, however it has been described as an omnivore (Willoughby and Tweddle 1978; Mosepele et al. 2012), a predator, an invertivore, a molluscivore (van der Waal 1985) and a macrophageous carnivore (Winemiller and Kelso-Winemiller 1996). *Schilbe intermedius* has most frequently been classified as an opportunistic predator, eating fish, aquatic and terrestrial insects, and crustaceans (van der Waal 1985; Hay 1995; Merron and Mann 1995; Winemiller and Kelso-Winemiller 1996; Mosepele et al. 2012). The diets of these three opportunistic species in all three rivers was therefore as expected, although the increase in invertebrates in the diets of *C. ngamensis* and *S. intermedius* in particular was accompanied by a large reduction in the percentage of empty stomachs sampled, a sign that less energy rich material was being consumed in the Kwando river when compared with the piscivorous diets of the Zambezi and Kavango populations (Arrington et al. 2002).

Stomach contents of *B. lateralis* were only sampled from the Kwando River, as mastication of prey items was so severe that identification beyond the categorisation of 'terrestrial insect remains' was impossible. Booth and McKinlay (2001) also noted mass prey mastication by *B. lateralis* from the Okavango Delta, attributing this to the two rows of sharp tricuspid and multicuspid teeth. In the literature *B. lateralis* has been categorised as an opportunistic macro-carnivore and an omnivore, feeding on zooplankton, invertebrates and seeds (Hay 1995; Booth and McKinlay 2001; Mosepele et al. 2012). In this study, the diet appeared to be similar, however with a lack of zooplankton. Seaman et al. (1978) found that zooplankton abundance was consistently low in areas where there was flow and/or macrophytes in Lake Liambezi, and that fish predation on zooplankton greatly reduced the abundance of the larger species. Lack of zooplankton in the diet of *B. lateralis* in the Kwando River could be as a result of low abundance of the large zooplankton species, while smaller species might not have been identified.

Hepsetus cuvieri and *S. macrocephalus* were almost exclusively piscivorous, preying mainly on cichlids and barbs, respectively, in all rivers, with significant dietary overlap in the Zambezi River where sample sizes were respectable. Cichlids have been noted as an important part of *H. cuvieri* diet by van der Waal (1985) and Winemiller and Kelso-Winemiller (1994), while barbs and mormyrids have been found in *S. macrocephalus* diets by Duerre (1969), van der Waal (1985) and Winemiller (1991a). Dietary overlap between these species may have resulted in competition and a consequent separation in feeding times, with *H. cuvieri* specialising as a diurnal ambush predator and *S. macrocephalus* as a crepuscular ambush predator (Winemiller 1991a; Winemiller and Kelso-Winemiller 1994). Inevitable interactions with other predatory species would complicate this scenario, and has not yet been assessed.

Fish diets have been found to change with season in response to the fluctuations in prey abundance (Angermeier 1982; Winemiller 1989a). The sampling periods in these rivers were similar, occurring in the cold season during falling water (June to August), and at low water in summer (September to November), with the exception of the Kwando River which was also sampled in the rising and high water periods (December to May) to improve sample sizes. Falling and low water periods often concentrate fishes in the main channel, providing an abundance of fish prey for predatory species (Bayley 1988; Wantzen et al. 2002). In the Kwando River during the rising and high water periods, there was a small rise in water level as a result of local rainfall (see Chapter 2). It is during this time of the year that the abundance of invertebrates in floodplain environments increases (Bayley 1988; Winemiller 1989a; Wantzen et al. 2002). However, many fishes spawn with rises in temperature and water level, and migrate onto the floodplain where food and suitable habitats are abundant (van der Waal 1996; Hocutt and Johnson 2001), and thus theoretically providing an abundance of invertebrate and fish prey. Moreover, the increases in habitat complexity and area inundated also creates a refuge from predation for spawning and juvenile fishes (Bayley 1988; van der Waal 1996). Therefore the differences in the diets of the Kwando River populations may be attributed to seasonally variable prey abundance.

Sample length composition could also influence diets as a result of ontogenetic shifts. Dietary shifts from invertebrates to vertebrates in relation to fish growth and development has been demonstrated in many freshwater piscivorous species (Winemiller 1989a; Mittelbach and Persson 1998; Pedreschi et al. 2015). This has been attributed to three main factors: the small size of juvenile fishes constrains their prey size range; spawning periods often coincide with an abundance of invertebrate prey, which is succeeded by fish prey as water levels drop; and lastly an increase in fish size often coincides with morphological adaptations, allowing feeding specialisation in adult fishes (Winemiller 1989a; Adriaens et al. 2001).

Although no small *C. gariepinus* or *C. ngamensis* were sampled from any of the rivers, there was a general increase in fish and crabs in the diets of large fishes, as has been recorded by Potts et al. (2008), Kadye and Booth (2011), and Dadebo et al. (2014 in a number of South Africa impoundments and an Ethiopian lake respectively. The proportion of cichlids in *Hepsetus cuvieri* diets in the Zambezi and Kwando rivers increased with fish length, as was found by Winemiller and Kelso-Winemiller (1994) in the Barotse floodplain on the Upper Zambezi River. Ontogenetic shifts in the diet of *S. macrocephalus* were difficult to detect in this study as a result of small sample sizes, however one individual less than 100 mm TL containing insects remains was sampled from the Kavango River indicating, if smaller fish had been sampled, a switch from insectivory to piscivory may have been detected. The diets of *S. macrocephalus* greater than 200 mm FL were dominated by barbs, mormyrids and robbers and cichlids in the Zambezi, Kavango and Kwando rivers respectively. In the Barotse floodplain on the Upper Zambezi River, Winemiller (1991a) found that smaller *S. macrocephalus* (< 150 mm TL) preyed upon more barbs than cichlids, while larger individuals (> 150 mm TL) preyed upon more cichlids than barbs. The diets of all size classes of *S. intermedius* from the Zambezi and Kavango were comprised of mainly fish prey, while in the Kwando River insects were dominant in the diet. This differed from the diet of *S. intermedius* in the Okavango Delta, Botswana, where the proportion of fish in the diet increased with fish length, while the proportion of insects in the diet decreased (Merron and Mann 1995).

Van der Waal (1985) described the fish fauna of Lake Liambezi as insectivore dominated, because of the abundant insects that lived on the detritus produced by large *Phragmites mauritianus* stands surrounding the lake (Seaman et al. 1978). Increased insectivory of *C. ngamensis* and *S. intermedius* in the Kwando River may thus be attributed to similar scenario, as this smaller river is overrun with *P. mauritianus* and *Cyperus papyrus* stands which produce large amounts of detritus, supporting an abundance of invertebrates (Pers. obs.). Alternatively a reduction of fish prey could cause an increase in alternative prey items in the diet. The optimal foraging theory predicts that fewer resources result in broader niche widths, and less specialised and more generalised foragers (Pyke et al. 1977). Angermeier (1982) found that as resources declined, fish ate more of the most common prey items. Although Kwando River populations fed on a more varied prey base, this only translated into broader dietary breadths for *H. cuvieri* and *S. intermedius*. For *C. gariepinus* and *S. macrocephalus* the Zambezi River populations had the greatest dietary breadth, and for *C. ngamensis* the Kavango River population had the greatest dietary breadth. The abundance of invertebrates in the diets of some predators from the Kwando River may just be as a result of their high natural abundance during the seasons sampled.

Since each constituent of stomach contents analysis (frequency of occurrence, percentage number and percentage weight) has its biases when used individually to describe diet (Hyslop 1980; Wootton 1990), an all incorporating index of relative importance is used to standardise results (Cortés 1997). Multivariate analysis is an alternative method for the quantification and comparison of diets based on identified prey wet weights (Cortés 1997). In this study, multivariate analysis of prey weights and stomach content analysis represented as the index of relative importance produced complementary results. For example for *C. gariepinus* in the Zambezi River, clariids and synodontids were the most important prey items identified by the index of relative importance and the SIMPER analysis. This corroboration held for all other species where multivariate analysis was performed, so strengthening the dietary descriptions of these species, despite their mainly insufficient sample sizes, a common problem when studying predatory species with high proportions of empty stomachs (Arrington et al. 2002).

In conclusion, the diets of *C. gariepinus, C. ngamensis*, and *S. intermedius* were highly plastic and often omnivorous and varied greatly between rivers, most likely reflecting prey abundance. Comparatively, the diets of *H. cuvieri* and *S. macrocephalus* were strictly piscivorous and did not vary to the same extent, potentially indicating preferential prey selection. Although a standard method for assessing fish diets, stomach contents analysis is not ideal, as was observed by Arrington et al. (2002); Kadye and Booth (2011) and Pedreschi et al. (2015); a large proportion of predatory fishes had empty stomachs, so reducing sample sizes and reducing the usefulness of this data to accurately describe fish diets. For species such as *B. lateralis* with multicuspid teeth and rasped pharyngeal pads (Booth and McKinlay 2001), prey identification was almost impossible. Stable isotope analysis has been used as an additional method to further understand the feeding and trophic ecology of fishes in the literature (Harrigan et al. 1989; Pinnegar and Polunin 2000; Renones et al. 2002; Cocheret de la Morinière et al. 2003; Kadye and Booth 2011; Pedreschi et al. 2015), and could aid in understanding the trophic ecology of fishes in the three rivers currently under study.

CHAPTER 4: Comparing food web structure and predator niches between fish communities using stable isotope analyses

Introduction

When describing and comparing biological communities, food web analysis adds another important dimension to the understanding gained by using common descriptors such as assemblage structure, species richness, abundance, and characteristics of individual species (Abrantes et al. 2014). Food web structure reflects the energetic processes of a community, identifies trophic links, elaborates on food chain length and highlights flows of carbon and nutrients throughout food chains (Polis and Strong 1996; Jepsen and Winemiller 2002).

Stable carbon and nitrogen ($\delta^{13}C$ and $\delta^{15}N$) isotope analysis reflects the assimilated food intake of an organism over a particular period of time and can be used to describe food web structure (DeNiro and Epstein 1978; DeNiro and Epstein 1981; Fry and Sherr 1984; Peterson and Fry 1987; Post 2002; Layman et al. 2012). Varying significantly with the photosynthetic pathway of primary producers, $\delta^{13}C$ is conserved throughout trophic transfers, on average displaying a 0 - 1‰ enrichment between consumer and food source, thus preserving information on primary producers at the base of the food web (DeNiro and Epstein 1978; Fry and Sherr 1984; Peterson and Fry 1987). Comparatively, $\delta^{15}N$ increases predictably in a step wise fashion (enrichment of ± 3‰) with trophic transfers as a result of the retention of heavier isotopes and the excretion of lighter isotopes (DeNiro and Epstein 1981; Minagawa and Wada 1984; Peterson and Fry 1987; Layman et al. 2012). This allows inferences to be made about the trophic level of consumers (Post 2002), as well as adding information on food sources (Vander Zanden and Rasmussen 1999).

The changes in $\delta^{13}C$ and $\delta^{15}N$ between food source and consumer are termed fractionation, and their estimation is essential for tracing energy flows and sources, determining trophic positioning and calculating food chain length (Vander Zanden and Rasmussen 2001). Fractionation varies on a number of scales, from ecosystem (marine and freshwater), to taxon (fish and invertebrates), to feeding strategy (herbivores and carnivores), to species and even tissue types within species. For example, Vander Zanden and Rasmussen (2001) found that carnivores demonstrated a significantly higher $\delta^{15}N$ fractionation of 3.2‰ compared to the

2.5‰ of herbivores, while Post (2002) found that herbivores and detritivores exhibited higher δ^{13}C fractionation than carnivores (0.50 vs. 0.05‰). Hussey et al. (2013) developed a scaled δ^{15}N fractionation framework from a meta-analysis of experimentally derived fish fractionation studies, concluding that δ^{15}N fractionation decreases with increased δ^{15}N. Gorokhova and Hansson (1999) found δ^{15}N fractionation factors of 3.6‰ and 2.7‰ for two species of mysids. Sweeting et al. (2007a) found that muscle tissue had higher δ^{15}N fractionation than heart and liver tissue in European sea bass. These differences in fractionation arise as a result of unequal assimilation of dietary components, fractionation or changing of dietary components by animal tissues, and the differential allocation of nutrients in the diet to different tissues (Gannes et al. 1997). Although average fractionation factors of 3.4‰ for δ^{15}N (Minagawa and Wada 1984; Post 2002) and 1‰ to 1.5‰ for δ^{13}C (DeNiro and Epstein 1978; Sweeting et al. 2007b) are used as standards, it is advised that ecosystem or species specific fractionation factors are estimated where possible (Gannes et al. 1997; Gorokhova and Hansson 1999; McCutchan et al. 2003; Sweeting et al. 2007a).

The position of an organism in δ^{13}C and δ^{15}N space, or its isotopic niche, although a distinct measure, can be used to estimate or interpret actual trophic niche space with caution, if care has been taken in understanding what an organism eats, its baseline isotopic signatures and sampling times (Bearhop et al. 2004; Newsome et al. 2007; Layman et al. 2007; Layman et al. 2012). Consequently, isotopic niches can be used to assess resource sharing, potential competition, predation, and, using recent developments in statistical Bayesian methodologies, describe the variations in isotopic space of communities, despite sample size disparities (Layman et al. 2007; Jackson et al. 2011; Jackson et al. 2012). It must be noted that although inference can be made regarding feeding and food web structure using relationships in isotopic space, diets cannot be characterised definitively as with stomach contents analysis (Layman et al. 2012). It is therefore often useful to use both direct observations of stomach contents and stable isotope analysis in conjunction to gain a more realistic understanding of food web structure and trophic processes over a time and space integrated scale (Post 2002; Kadye and Booth 2011; Layman et al. 2012).

This chapter aims to describe and compare the food web structure and trophic fish-community characteristics of the Zambezi, Kavango and Kwando rivers. In addition, isotopic niches and trophic positions of the predatory fish species sampled from these rivers will be compared, building on the information made available using stomach contents analysis in

Chapter 3. It is hypothesised that i) the Zambezi and Kavango river food webs will be based on terrestrial resources as a result of their large flood pulses, differing from the Kwando River food web which will be based on aquatic macrophytes as this river receives small flood pulses, and ii) the isotopic niches and trophic positions of the predatory species will support previously proposed hypotheses based on their habitat affinities and stomach contents analyses. These hypotheses are i) that the predation pressures imposed by *Hydrocynus vittatus* and *Hepsetus cuvieri* on all other fishes influences food web structure and fish community trophodynamics (Jackson 1961; Winemiller and Kelso-Winemiller 1994), and ii) that the Upper Zambezi serranochromines exhibit nearly complete ecological separation when considering habitat affinities and food habits (Winemiller 1991a).

Methods

Whole ecosystem stable isotope samples were collected in August 2013 from the Kwando River, September and October 2013 from the Zambezi River and in August 2014 from the Kavango River. The following samples were collected: fish white muscle tissue, whole bodies of insects and shrimps, muscle tissue of molluscs and crabs, fresh plant leaves, detritus collected by dredging, and particulate organic matter (POM) filtered through 0.45 µm pre-combusted glass fibre filters (Advantec). White muscle tissue is commonly used to assess fish trophodynamics as it is well studied and exhibits low variation in $\delta^{15}N$ values (Pinnegar and Polunin 1999; Sweeting et al. 2007a).

All tissue samples were rinsed in water and oven dried at 50 °C for 24 - 48 hours. All plant and detrital material was acid-washed in 1% HCl to remove carbonates which may be enriched in ^{13}C, before oven drying (DeNiro and Epstein 1978; Boutton 1991). Prior to analysis all samples were individually crushed to a homogenous powder with a pestle and mortar and weighed into tin capsules. The Zambezi and Kwando river samples were analysed using a Europa Scientific INTEGRA isotope ratio mass spectrometer at IsoEnvironmental cc, SAIAB, Grahamstown and the Kavango River samples were analysed on a Flash EA 1112 Series coupled to a Delta V Plus stable light isotope ratio mass spectrometer via a ConFlo IV system (all equipment supplied by Thermo Fischer, Bremen, Germany), housed at the Stable Isotope Laboratory, Mammal Research Institute, University of Pretoria.

All samples were calibrated against Vienna PeeDee Belemnite and atmospheric nitrogen for $\delta^{13}C$ and $\delta^{15}N$ respectively. The isotope values were expressed in the standard delta (δ) notation, defined as per mille (‰) deviation from a standard: $\delta X(‰) = \left(\frac{R_{sample}}{R_{standard}} - 1\right) x\ 1000$, where $X = {}^{13}C$ or ${}^{15}N$, $R = {}^{13}C/{}^{12}C$ or ${}^{15}N/{}^{14}N$, and standard = Peedee Belemnite (PDB) limestone or atmospheric nitrogen respectively.

Precision

For the Kavango River a laboratory running standard (Merck Gel: $\delta^{13}C = -20.57‰$, $\delta^{15}N = 6.8‰$, C% = 43.83, N% = 14.64) and blank sample were run after every 12 unknown samples. A number of samples were also done in duplicate, and analytical precision was <0.18‰ for $\delta^{13}C$ and <0.12‰ for $\delta^{15}N$.

For the Zambezi and Kwando river samples every batch of 96 combustions contained 29 internal standards of refmix2 = beet sugar and ammonium sulphate, and five certified protein standards of Casein (calibrated against IAEA-CH-6 and IAEA-N-1). For the Zambezi River samples analytical precision was <0.15‰ for $\delta^{13}C$ and for $\delta^{15}N$, and for the Kwando River samples analytical precision was <0.11‰ for $\delta^{13}C$ and <0.18‰ for $\delta^{15}N$.

Lipid correction

Carbon isotopes are commonly used to derive primary producer dietary sources of consumers, as carbon isotopes tend to change very little (± 1.5‰) with trophic level (Sweeting et al. 2007b). However, there is variation in the carbon value of different constituents of tissues – such as carbohydrates, lipids, and proteins (Post et al. 2007). Lipids tend to be ${}^{13}C$ depleted, so a high proportion of lipid in muscle tissue samples could complicate the relationship between an organism and its dietary sources (DeNiro and Epstein 1977; Focken and Becker 1998). Since the presence of lipids affects the carbon and not the nitrogen isotope value of the sample, there is a well-documented relationship between the amount of lipid a sample contains and the C:N ratio of the sample (McConnaughey and McRoy 1979). To reduce the effect of lipids on carbon isotope values, they are often chemically extracted from samples, or alternatively samples may be normalised using a mathematical correction. Chemical extraction is expensive, time consuming, and impacts the nitrogen isotope values of samples, whereas mathematical normalisation is cheap, and straightforward, however standard validated methods are lacking (Kiljunen et al. 2006).

For this study, approximately three samples from 18 of the most common fish species (53 samples in total) from the Kavango River were lipid extracted by soaking in a 2:1 chloroform: ethanol mixture, dried overnight at 70°C, and isotope analysis performed for both untreated and lipid extracted samples. The lipid extracted data were used to amend the commonly used McConnaughey and McRoy (1979) normalisation equation parameter *D* (isotope difference between protein and lipid) and constant *I*. This normalisation equation uses the proportions of C and N in the sample (C:N) to i) estimate the lipid content (*L*) of the sample:$L = \frac{93}{1+(0.246 \times (C{:}N)-0.775)^{-1}}$, and ii) correct the δ^{13}C value to produce the lipid normalised value δ^{13}C': $\delta^{13}C' = \delta^{13}C + D \times \left(I + \frac{3.9}{1+{}^{287}/_{L}}\right)$.

Values for *D* and *I* of 6‰ and -0.207 (McConnaughey and McRoy 1979) are commonly used, however Kiljunen et al. (2006) re-estimated them for a suite of freshwater, brackish water and marine fishes as 7.018 (*D)* and 0.048 (*I*).

For this study the McConnaughey and McRoy (1979) model was evaluated, and new *D* and *I* values were estimated from the Kavango River data. Differences between chemically lipid-extracted $\delta^{13}C_{\text{treated}}$ and original δ^{13}C values (observed), and between normalised δ^{13}C' and original δ^{13}C values (predicted), were plotted against the untreated C:N ratios. *D* and *I* were estimated by minimising the binomial negative log-likelihood function using: $-LL = Nln(\hat{\sigma})$, where $\hat{\sigma}$ is the maximum likelihood estimate of the model standard deviation described as: $\hat{\sigma} = \sqrt{\frac{\sum_i (L_i-\hat{L}_i)^2}{N}}$, and $\hat{L}_i$ is the predicted maximum δ^{13}C' with C:N ratio, L_i is the observed δ^{13}C lipid treated with C:N and *N* is the total number of lipid treated samples. The variability of the parameters was estimated using the conditioned parametric bootstrap resampling technique described by Efron (1980) (N = 1000 iterations).

Of the 18 species analysed from the Kavango river, δ^{13}C and C:N values varied both within and between species (Table 4.1). After lipid extraction, δ^{13}C values were higher for all species, and for those species where C:N > 4 before treatment, C:N decreased to below four and variation was reduced. Pre lipid extraction C:N values did not vary as much as those sampled in the literature (Kiljunen et al. 2006), indicating the lipid content of the species sampled was not variable or very high.

Table 4.1: Untreated and lipid treated $\delta^{13}C$ and C:N values, the difference between them (± SD), and the number of individuals subject to lipid extraction (sample size *N*), for 18 fish species from the Kavango River.

Species	*N*	Untreated		Lipid treated		$\delta^{13}C_{treated}$ - $\delta^{13}C_{untreated}$
		$\delta^{13}C$ (‰)	C:N	$\delta^{13}C$ (‰)	C:N	
Micropanchax johnstonii	3	-21.32 ± 0.60	4.25 ± 0.17	-20.23 ± 0.72	3.93 ± 0.03	1.10 ± 0.14
Brycinus lateralis	3	-22.39 ± 2.20	4.23 ± 0.38	-21.81 ± 2.03	3.96 ± 0.01	0.58 ± 0.17
Barbus poechii	3	-19.12 ± 0.40	3.93 ± 0.21	-18.55 ± 0.63	3.94 ± 0.02	0.58 ± 0.25
Clarias gariepinus	3	-22.47 ± 0.88	3.69 ± 0.09	-21.91 ± 0.73	3.94 ± 0.01	0.56 ± 0.16
Clarias ngamensis	3	-21.82 ± 0.54	4.05 ± 0.14	-20.77 ± 0.65	3.97 ± 0.01	1.05 ± 0.12
Marcusenius altisambesi	3	-23.32 ± 2.75	4.12 ± 0.55	-22.70 ± 3.29	3.99 ± 0.00	0.62 ± 0.55
Hepsetus cuvieri	3	-22.68 ± 0.66	3.84 ± 0.05	-22.01 ± 0.71	3.91 ± 0.04	0.67 ± 0.28
Hydrocynus vittatus	3	-22.64 ± 0.40	3.81 ± 0.12	-21.89 ± 0.46	3.89 ± 0.04	0.75 ± 0.06
Micralestes acutidens	3	-20.92 ± 0.58	3.99 ± 0.10	-20.13 ± 0.59	3.94 ± 0.04	0.79 ± 0.19
Oreochromis andersonii	3	-29.77 ± 0.69	4.41 ± 0.68	-27.97 ± 0.44	3.98 ± 0.03	1.80 ± 0.98
Oreochromis macrochir	3	-28.24 ± 0.42	4.44 ± 0.40	-26.14 ± 0.71	3.97 ± 0.03	2.11 ± 0.61
Pharyngochromis acuticeps	3	-22.15 ± 1.25	3.93 ± 0.15	-21.46 ± 1.28	3.91 ± 0.01	0.69 ± 0.16
Petrocephalus okavangoensis	3	-24.75 ± 0.65	4.18 ± 0.15	-23.65 ± 0.50	3.99 ± 0.07	1.10 ± 0.32
Serranochromis altus	3	-24.11 ± 2.45	4.01 ± 0.21	-23.32 ± 2.66	3.97 ± 0.02	0.79 ± 0.54
Serranochromis macrocephalus	3	-23.63 ± 0.49	3.97 ± 0.13	-22.83 ± 0.53	3.94 ± 0.00	0.80 ± 0.04
Schilbe intermedius	3	-21.38 ± 1.38	3.84 ± 0.26	-20.83 ± 1.38	3.93 ± 0.04	0.55 ± 0.04
Synodontis nigromaculatus	2	-24.16 ± 3.09	3.84 ± 0.01	-23.34 ± 3.05	3.96 ± 0.02	0.82 ± 0.04
Coptodon rendalli	3	-19.66 ± 1.11	4.39 ± 0.26	-18.44 ± 1.26	3.99 ± 0.01	1.22 ± 0.25

The predicted relationship (difference between $\delta^{13}C$'normalised and $\delta^{13}C$ untreated values) for the differences between $\delta^{13}C$ lipid-extracted and $\delta^{13}C$ untreated values, did not fit the McConnaughey and McRoy (1979) or the Kiljunen et al. (2006) formulae (Figure 4.1A). The McConnaughey and McRoy (1979) formula underestimated the difference between $\delta^{13}C$ lipid corrected and $\delta^{13}C$ untreated values, while the Kiljunen et al. (2006) formula overestimated the difference between $\delta^{13}C$ lipid corrected and $\delta^{13}C$ untreated values. New *D* and *I* parameters were estimated, which fit the observed data, so δ^{13}C'normalised and δ^{13}C lipid treated values coincided (Figure 4.1B). The amended relationship intersected the x-axis at 3, suggesting that fish muscle contained zero extractable lipid at a C:N ratio of 3.

Consequently, all fish samples were lipid normalised using the McConnaughey and McRoy (1979) equations, by using the estimated parameter D = 4.46 (95% CI: 2.62, 4.85) and constant I = 0 (95% CI: 0, 0.17), as calculated using this study's data (N = 53).

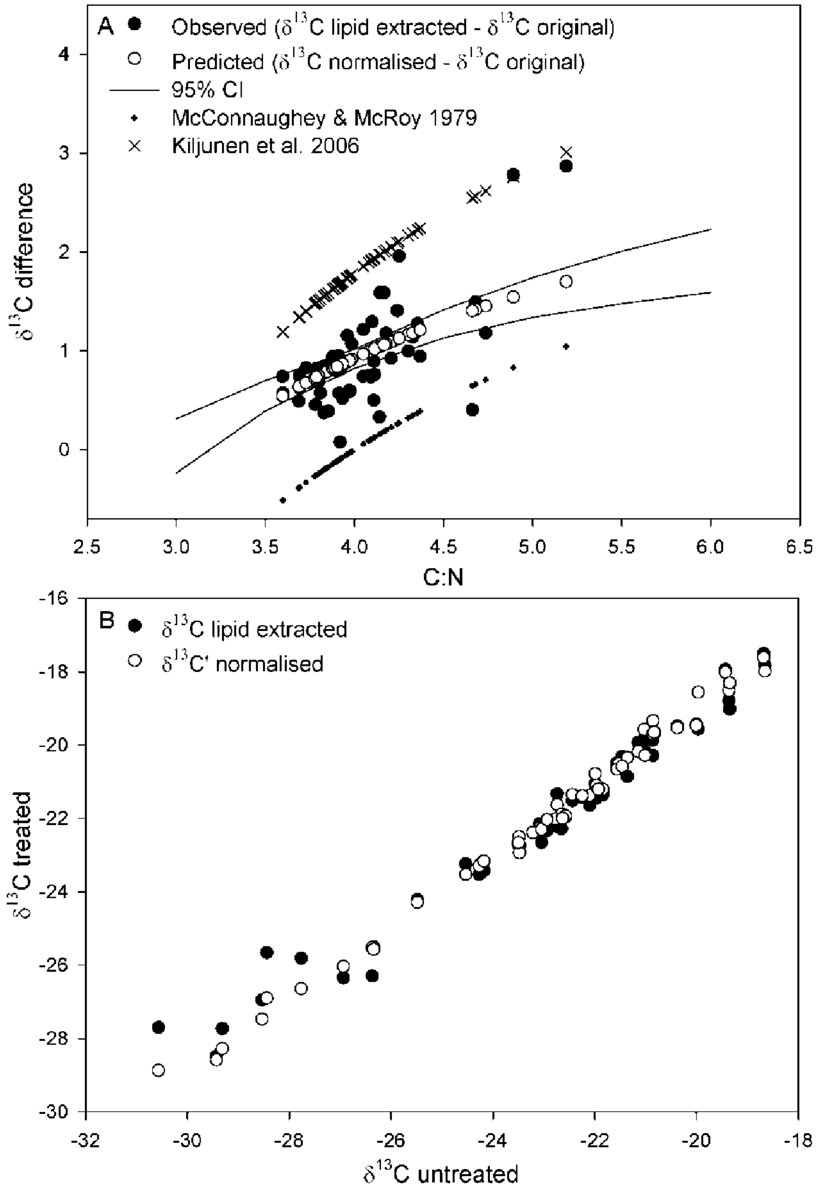

Figure 4.1: A: the δ^{13}C difference between lipid-extracted and δ^{13}C untreated values, and δ^{13}C'normalised and δ^{13}C untreated values and the 95% confidence interval in relation to the C:N ratios, for the McConnaughey and McRoy (1979) amended lipid normalisation equation. B: the δ^{13}C lipid extracted and δ^{13}C' normalised values in relation to the original δ^{13}C untreated values, illustrating the accuracy of the amended normalisation equation in calculating δ^{13}C' values which coincide with the δ^{13}C lipid extracted samples.

Fractionation factors
As an estimate of nitrogen fractionation (Δ^{15}N) is needed to standardise nitrogen values across systems relative to a baseline, Δ^{15}N values could either be acquired from the literature, or estimated for the systems under study. Values from the literature alone were deemed unsatisfactory as most of the field studies that have estimated fractionation factors have been from temperate northern hemisphere systems (Vander Zanden and Rasmussen 2001), and experimental studies have focused on species from these same systems (Post 2002). Literature values were therefore used for comparison with calculated values.

In order to summarise fractionation factors from the literature, the following were examined for Δ^{15}N values: experimental studies; field studies where diets were known from stomach contents analysis; and literature meta-analyses. Specifically, Vander Zanden and Rasmussen (2001), Post (2002), McCutchan et al. (2003) and Vanderklift and Ponsard (2003) were gleaned for Δ^{15}N values for muscle tissue samples of freshwater fishes. The mean Δ^{15}N values acquired were then averaged, producing a Δ^{15}N of 3.03‰ ± 0.67 (SD). A literature review by Sweeting et al. (2007) of 56 experimental studies published between January 1977 and November 2005, as well as his experimental study on European sea bass, estimated a similar average Δ^{15}N of 3.15‰ for fish muscle tissue.

Comparatively, the Δ^{15}N fractionations for this study were calculated using stomach contents data (see Chapter 3) from a number of predatory species from the Zambezi, Kavango and Kwando rivers according to the method of Sherwood and Rose (2005), using: $\Delta\delta^{15}N = \delta^{15}N - (\sum_{i=1}^{n} P_i \times \delta^{15} N_i)$, where $\delta^{15}N$ is the average $\delta^{15}N$ value of the consumer from a specific population, P_i is the mass proportion of the *i*th prey item in the diet of the consumer from that population, and $\delta^{15}N_i$ is the average $\delta^{15}N$ value of the *i*th prey item from the population sampled. Diet proportions (P values) for the stomach contents (described in Chapter 3) identified to family for fish and order for invertebrates were determined as: $P_i = \frac{W_i}{W_{tot}}$, where W_i is the total weight (g) of prey i consumed by all of the individuals of the consumer from a given population, and W_{tot} is the total weight (g) of all prey consumed by the consumer from the same population.

An average $\Delta^{15}N$ of 3.23‰ was calculated using the species from each river system which had N > 20 stomachs containing identified stomach contents (Table 4.2). *Schilbe intermedius* from the Kwando River was excluded as a $\Delta^{15}N$ of 6.09‰ was calculated, an extremely high value which was attributed to the high proportion of unidentified prey items (see Chapter 3 and Appendix 3).

This average $\Delta^{15}N$ of 3.23‰ was similar to both the $\Delta^{15}N$ of 3.03‰ and 3.15‰ estimated from the literature review and by Sweeting et al. (2007), and as a result was used as the $\Delta^{15}N$ value for subsequent calculations of trophic position for the baseline correction.

Table 4.2: The fractionation factors $\Delta^{15}N$ estimated using stomach contents analysis of predatory species from the three rivers. $N_{stomachs}$ are the number of stomachs which contained identified prey items used for this analysis.

River	Species	$N_{stomachs}$	$\Delta\delta^{15}N$
Zambezi	*Serranochromis macrocephalus*	21	2.57
Zambezi	*Schilbe intermedius*	55	3.19
Zambezi	*Clarias gariepinus*	27	2.23
Kavango	*Schilbe intermedius*	114	1.62
Kavango	*Clarias ngamensis*	28	2.72
Kavango	*Clarias gariepinus*	55	2.46
Kwando	*Clarias ngamensis*	32	5.29
Kwando	*Clarias gariepinus*	26	5.87
Kwando	*Brycinus lateralis*	41	3.13
		Average	3.23 ± 1.42

Baseline correction

Primary consumers are generally used to baseline ecosystems, so making them comparable across a spatial gradient (Cabana and Rasmussen 1996; Vander Zanden et al. 1997). These organisms are used as they are long lived, and generally feed on seston or detritus, so encompassing the main primary productivity driving ecosystems (Cabana and Rasmussen 1996; Post 2002).

This study aimed to use unionid mussels in baseline calculations however, these were not collected from all systems. Consequently all molluscs sampled from all rivers, including unionid mussels (N = 13), Thiaridae snails (N = 5), giant swamp snails (N = 6), a Corbiculidae clam (N = 1), and a Lymnacidae snail (N = 1), were used to calculate an average $\delta^{15}N_{baseline}$ of 3.16‰ ± 0.87, $\delta^{13}C_{baseline}$ of -27.69‰ ± 2.57, $\delta^{13}Cmax$ of -22.31‰, $\delta^{13}Cmin$ of -30.69‰, and a carbon range $CR_{baseline}$ of 8.38‰.

All organisms in all ecosystems were then adjusted based on the following equations for δ^{15}N and δ^{13}C. $Trophic\ position = \frac{\delta^{15}N_{organism} - \delta^{15}N_{baseline}}{\Delta^{15}N} + 2$, where 2 represents the trophic position of the baseline organism, Δ^{15}N represents the fractionation factor calculated as 3.23‰, $\delta^{15}N_{organism}$ is the isotope ratio of the organism, $\delta^{15}N_{baseline}$ is the isotope ratio (3.16‰) of the primary consumers used for the baseline (Post 2002). $\delta^{13}C_{corrected} = \frac{\delta^{13}C_{organism} - \delta^{13}C_{baseline}}{CR_{baseline}}$, where $\delta^{13}C_{corrected}$ is the corrected carbon isotope ratio of the consumer, $\delta^{13}C_{organism}$ is the uncorrected isotope ratio of the organism, $\delta^{13}C_{baseline}$ is the mean primary consumer isotope ratio -27.69‰, and $CR_{baseline}$ is the primary consumer carbon range (δ^{13}Cmax - δ^{13}Cmin = 8.38‰) (Olsson et al. 2009; Jackson and Britton 2014).

Comparing fish communities

Firstly, biplots of whole ecosystem stable isotope samples were compared visually. Fish species were categorised taxonomically and according to feeding habits as described in Table 4.3, as diets are often too flexible to be used solely for conclusive groupings (Jackson et al. 2001; Welcomme et al. 2006). Food resources were grouped as: POM, aquatic, floating and marginal plants, detritus, molluscs, crustaceans and aquatic insects (Table 4.3).

To identify differences between river fish communities, the Bayesian implementation of Layman's community metrics (Layman et al. 2007; Jackson et al. 2011) was used. This method estimates the error of the metrics and incorporates uncertainty, and is thus able to compare different numbers of groups, allowing comparisons between communities (Jackson et al. 2011). The metrics used to describe communities were: nitrogen range (NR) which describes trophic length; carbon range (CR) which depicts basal resource diversity; total area of the convex hull (TA) describing an overall measure of niche width; mean distance to centroid (CD) which adds information on niche width (trophic diversity) and species spacing (it is also less sensitive to outliers than TA); mean nearest neighbour distance (MNND) estimating density and clustering of species within the community and trophic redundancy; and standard deviation of the nearest neighbour distance (SDNND) measuring evenness of spatial density and packing (Layman et al. 2007; Jackson et al. 2011). All metrics were bootstrapped (N = 10000), so comparisons could be made between populations with differing sample sizes (Hill et al. 2015). A minimum of five samples (individuals) per group were used to mitigate bias in underestimating the population value (Jackson et al. 2011). No labeos were sampled from the Kwando River, so this group was excluded from the Kwando River analysis. Metrics were calculated using the SIBER package (Stable Isotope Bayesian Ellipses in R; Jackson et al. 2011; R Core Team 2012).

The mean core isotopic niche widths of i) the entire fish communities for each river, and ii) the fish communities within each river (as set out in Table 4.3) were quantified by calculating the sample size corrected standard ellipse areas (SEAc) and their % overlap using the SIBER package (Stable Isotope Bayesian Ellipses in R; Jackson et al. 2011) in R (R Core Team 2012). As described by Jackson and Britton (2013), SEAc's are a bivariate measure of the distribution of individuals in isotopic space, and encircle about 40% of the data, so representing the core dietary niche or the typical resource use of a community or group of species (Jackson et al. 2011; Jackson et al. 2012). To compare the sizes of core niche areas (SEAc) by species groups between rivers, a chi squared test (χ^2) using an $m \times m$ contingency table were used to compare the sizes of core niche areas among populations. The test statistic: $\chi^2 = \sum_{i=1}^{m-1}\sum_{j=i+1}^{m}\frac{(n_{ij}-n_{ji})^2}{n_{ij}+n_{ji}}$, where *nij* = the observed frequency in the *i*th row and *j*th column and *nji* = the observed frequency in the *j*th row and *i*th column, is distributed as a chi-squared variable with *m(m-1)/2* degrees of freedom for a table that has no empty cells. Labeos were not included in this analysis as they were not sampled in all rivers.

Comparing predator communities

The mean core isotopic niches (SEAc) of the predatory fish species from the catfish, serranochromine and piscivore feeding strategy groups described in Table 4.3 and their % overlap were calculated using the SIBER package in R (R Core Team 2012). The relationships between species lengths and trophic position, and species lengths and $\delta^{13}C_{corrected}$ values by river were quantified using linear regression analyses. Average trophic positions per species were also calculated by river.

Table 4.3: The organisms collected for stable isotope analysis, with fishes grouped taxonomically and by feeding strategy (prey noted according to Skelton (2001) and Marshall (2011)) and resources grouped as defined. For groups of fish species, the names used to describe the group are given in brackets under feeding strategy. Species superscripts indicate sampling location 1 = Zambezi, 2 = Kavango, 3 = Kwando, * = all rivers.

Family	Genera	Species	Feeding strategy	Prey
Cyprinidae	*Barbus, Coptostomobarbus, Opsaridium*	*B. barotseensis*^{1}, *B. unitaeniatus**, *B. bifrenatus*^{1}, *B. thamalakanensis*^{1,2}, *B. barnardi**, *B. fasciolatus**, *B. radiatus**, *B. poechii*^{1,2}, *B. eutaenia*^{1,2}, *B. multilineatus*^{3}, *B. afrovernayi**, *B. kerstenii*^{1,2}, *B. barotseensis*^{1}, *C. wittei*^{3}, *O. zambezense**	Invertivore (Barbs)	Aquatic insects, terrestrial insects, crustaceans, shrimps, small fish, plankton, seeds, plant matter, algae, periphyton, detritus
	Labeo	*L. cylindricus*^{1,2}, *L. lunatus*^{1,2}	Herbivore (Labeos)	Aufwuchs, epilithic and epiphytic algae, filamentous algae, periphyton
Distichodontidae	*Hemigrammocharax, Nannocharax*	*H. machadoi*^{3}, *H. multifasciatus**, *N. macropterus*^{2}	Invertivore (Citharines)	Small invertebrates from plants or the water column, periphyton, epiphyton
Alestidae	*Brycinus, Micralestes, Rhabdalestes*	*B. lateralis**, *M. acutidens**, *R. maunensis**	Invertivore (Alestids)	Aquatic insects, terrestrial insects, zooplankton
Alestidae, Hepsetidae	*Hydrocynus, Hepsetus*	*H. vittatus*^{1,2}, *H. cuvieri**	Predator (Piscivores)	Fish
Parauchenoglanis, Amphiliidae, Mochokidae	*Parauchenoglanis, Zaireichthys, Synodontis*	*P. ngamensis*^{1,3}, *Z.* spp.^{3}, *S. nigromaculatus**, *S.* spp.*	Benthic invertivore (Synodontids)	Molluscs, crustaceans, aquatic insects, small fishes, detritus, algae
Schilbeidae, Clariidae	*Schilbe, Clarias*	*S. intermedius**, *C. gariepinus**, *C. ngamensis*^{2,3}, *C. theodorae*^{1,3}	Predator/ omnivore (Catfishes)	Fish, crabs, shrimps, molluscs, aquatic insects, terrestrial insects, small mammals, zooplankton
Poeciliidae (Aplocheilichthyinae)	*Micropanchax*	*M. johnstoni**, *M. katangae**	Invertivore (Topminnows)	Aquatic and terrestrial insects, zooplankton
Cichlidae	*Hemichromis, Pseudocrenilabrus,*	*H. elongatus*^{1,3}, *P. philander**, *P. acuticeps**, *S. codringtonii*^{1,3}, *S. carlottae**, *S. giardi**	Benthivore (Benthic cichlids)	Crustaceans, molluscs, aquatic insects, seeds, fish

	Pharyngochromis, Sargochromis			
	Serranochromis	_S. altus_*, _S. angusticeps_*, _S. macrocephalus_*, _S. robustus_[1,2]	Predator (Serranochromines)	Fish, insects, crustaceans
	Tilapia, Coptodon	_T. sparrmanii_*, _T. ruweti_[1], _C. rendalli_*	Herbivore (Herbivorous cichlids)	Algae, detritus, invertebrates, small fish
	Oreochromis	_O. andersonii_*, _O. macrochir_*	Detritivore (Oreochromines)	Detritus, zooplankton, phytoplankton
Mormyridae	_Mormyrus, Hippopotamyrus, Cyphomyrus, Marcusenius, Petrocephalus, Pollimyrus_	_M. lacerda_[1,2], _H. ansorgii_[1], _C. cubangoensis_*, _M. altisambesi_*, _P. okovangoensis_[1,2], _P. longicapitus_[1,3], _P. castelnaui_*	Invertivore (Mormyrids)	Aquatic insects, shrimps, molluscs, zooplankton, small fish

Resources

Group name	Contents
Aquatic insects	Odonata*, Oligochaeta[1,3], Ephemeroptera*, Trichoptera[3], Diptera[2,3], Coleoptera[2,3], Hemiptera*
Crustaceans	Potamonautid crabs*, Atyid shrimps*
Molluscs	Thiaridae[1,3], Unionidae[1,2], Lymnacidae[2], clams[3], giant swamp snails*
POM	Particulate organic matter*
Aquatic plants	_Ceratophyllum demersum_[1,2], _Lagarosiphon ilicifolius_[1,3], _Najas horrida_*, _Ottelia exserta_[2,3], _Potamogeton schweinfurt_[3], _P. nodosus_[2], Utricularia[1,3], eel grass[1], unidentified aquatic plants*, filamentous algae[2,3], biofilm[2]
Floating plants	Giant azolla[3], _Nymphaea lotus_[1,3], _Nymphaea nouchali_*, _Nymphoides indica_[1,3], _Salvinia molesta_[1], _Trapa natans_[1,2]
Marginal plants	_Cyperus papyrus_[2,3], _Vossia cuspidata_[2,3], _Phragmites mauritianus_*, _Thelypteris interrupta_[3], _Bacopa floribunda_[3]
Detritus	125 µm[2,3], 500 µm*, 1 mm*, 2 mm[1,2]

Results

Comparing fish communities

Food web structure

The mean $\delta^{13}C_{corrected}$ and trophic position ($\delta^{15}N$ values) of the fishes and potential resources from the Zambezi, Kavango, and Kwando rivers are illustrated in Figure 4.2. From the resources and fishes sampled, the food chain length was longest in the Kwando, followed by the Kavango and shortest in the Zambezi River. Fishes tended to overlap greatly within each ecosystem, which will be elaborated upon in the next section.

Molluscs, which were used for baseline corrections, were positioned similarly in all systems with respect to trophic position, above primary producers and below fishes. Aquatic insects, which encompassed all families sampled and as a result had large carbon and nitrogen ranges, were generally positioned above the primary producers and below the fishes in all rivers. Crustaceans were positioned near the herbivorous cichids in the Zambezi and Kavango rivers, however in the Kwando River crustaceans held much lower trophic positions. Primary producers such as plants had substantial carbon ranges in all rivers, with marginal plants more enriched in ^{13}C in the Kavango and Kwando rivers where *C. papyrus* and *V. cuspidata*, plants using the C_4 photosynthetic pathway, were common. Detritus in the Zambezi and Kavango rivers was not derived clearly from one plant group, while in the Kwando River its $\delta^{13}C$ position indicated it was likely derived primarily from marginal plants and was enriched in $\delta^{13}C$ in relation to other organisms.

Using the assumed 1.5‰ increase in $\delta^{13}C$ per trophic level, particulate organic matter (POM) was positioned at the base of the food web in the Zambezi and Kavango rivers. In the Kwando River POM was positioned in a higher trophic position with enriched ^{13}C values, and submerged plants were positioned at the base of the food web.

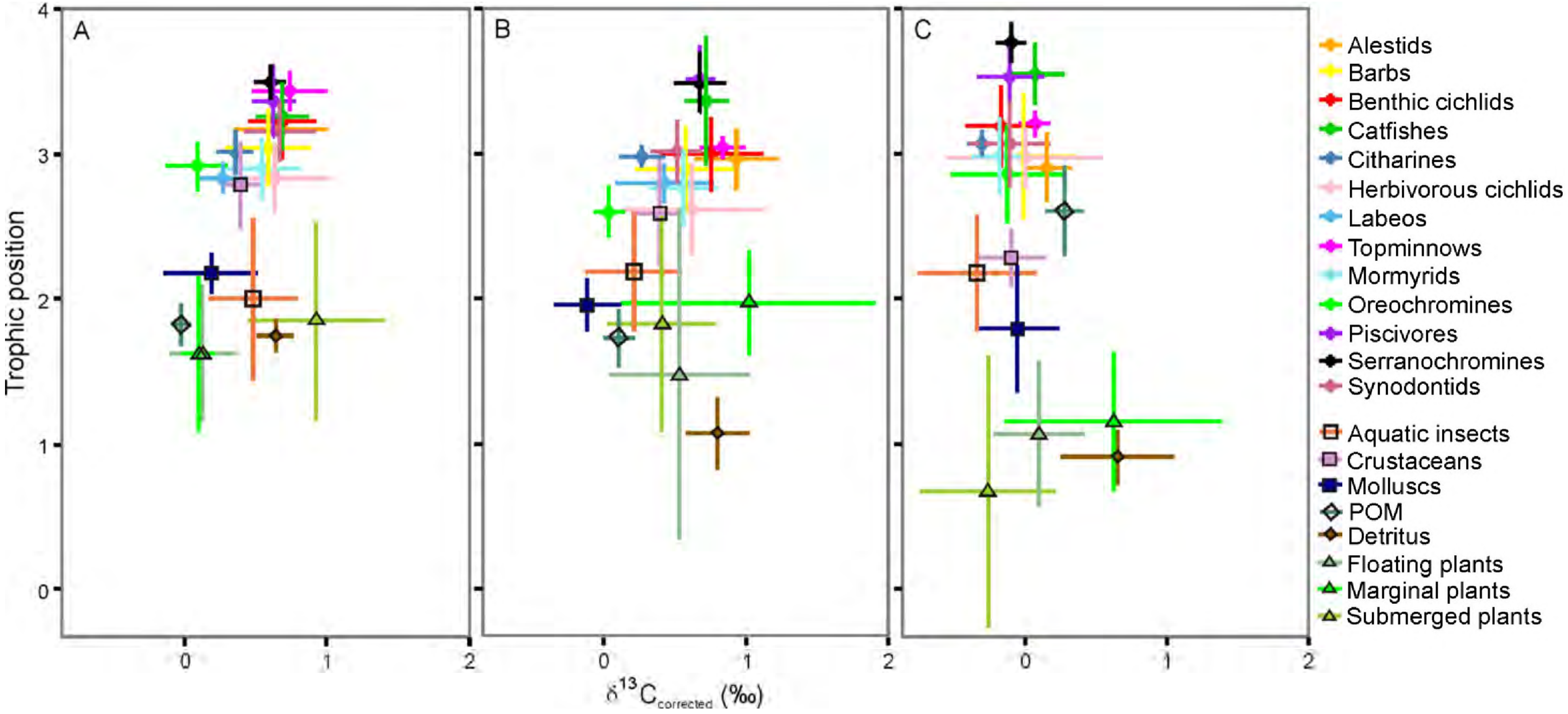

Figure 4.2: The mean $\delta^{13}C_{corrected}$ and trophic positions of fishes and resources from A: the Zambezi, B: the Kavango and C: the Kwando rivers.

Layman's Bayesian community metrics

As fishes were well sampled in all ecosystems, they were the focus of subsequent analyses. The Kavango and the Kwando river fish communities had the highest NR, so mirroring the ecosystem biplots illustrating high trophic diversity (Table 4.4). The Kavango and the Zambezi rivers had the highest CR, while the CR of the Kwando River was much lower suggesting the food web was based on a narrow range of primary producers. TA was largest in the Kavango, as a result of the high NR and CR values, followed by the Zambezi, and was smallest in the Kwando River. The lower CD's of the Zambezi and Kwando rivers suggests more generalist feeders and lower trophic diversity, while the Kavango River had the highest CD, implying more trophic specialisation within the community and greater niche differentiation. With low MNND values, the Zambezi and Kwando rivers had increased trophic redundancy, while the Kavango River had the greatest divergence in trophic niches, and the lowest trophic redundancy. The Kwando River had the lowest SDNND, suggesting an even distribution of trophic niches, while the Zambezi River trophic niches were distributed unevenly.

Table 4.4: Layman's Bayesian community metrics comparing the Zambezi, Kavango and Kwando rivers' fish communities (95% CI), and the total sample size (N) of all the fishes sampled.

Metric	Zambezi	Kavango	Kwando
NR	0.92 (0.62, 1.49)	1.09 (0.81, 1.54)	1.00 (0.68, 1.44)
CR	0.89 (0.45, 1.53)	0.98 (0.75, 1.39)	0.56 (0.36, 0.89)
TA	0.43 (0.20, 0.82)	0.57 (0.36, 0.91)	0.34 (0.20, 0.55)
CD	0.31 (0.23, 0.40)	0.37 (0.30, 0.44)	0.30 (0.24, 0.36)
MNND	0.15 (0.09, 0.22)	0.17 (0.12, 0.23)	0.15 (0.10, 0.21)
SDNND	0.13 (0.05, 0.28)	0.11 (0.05, 0.20)	0.09 (0.04, 0.18)
Total Sample N	273	347	274

Comparing whole fish community niche areas between rivers

The core isotopic niche areas (SEAc) of total fish communities was largest for the Kavango River (SEAc = 43‰^{2}) followed by the Kwando River (SEAc = 31‰^{2}), and smallest for the Zambezi River (SEAc = 26‰^{2}) (Figure 4.3). This suggests the fishes in the Kavango River utilised a broader range of resources, compared to the Zambezi and Kwando rivers. The Zambezi River SEAc overlapped 100% with the Kavango River, which shared 60% of its SEAc with the Zambezi. The Zambezi and Kavango rivers' SEAc values did not overlap significantly with the Kwando River SEAc, suggesting that the Kwando River fish community utilise different resources compared to those from the Zambezi and Kavango rivers.

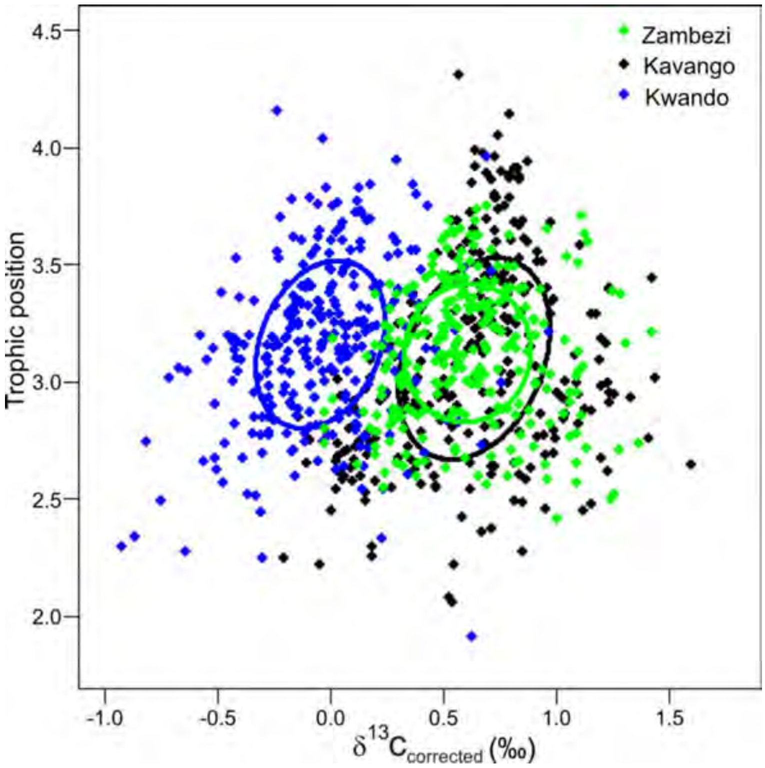

Figure 4.3: The core isotopic niche areas (SEAc) of the fish communities from the Zambezi, Kavango and Kwando rivers

Comparing fish group niche areas between rivers

By plotting and calculating the SEAc of all fish groups (defined in Table 4.3) by river, isotopic niche size and position could be compared between rivers in relation to surrounding fish groups (Figure 4.4). Separation by trophic position of predatory fishes (particularly the piscivore and serranochromine groups which are specialist feeders) compared to other fish groups was clear for the Kavango and Kwando rivers, while in the Zambezi River predatory fishes overlapped significantly with the other fishes, as was illustrated by the low NR (Table 4.4). Herbivorous and detritivorous fishes had the lowest trophic positions in the Zambezi and Kavango rivers, while in the Kwando River these groups overlapped significantly with invertivorous fishes.

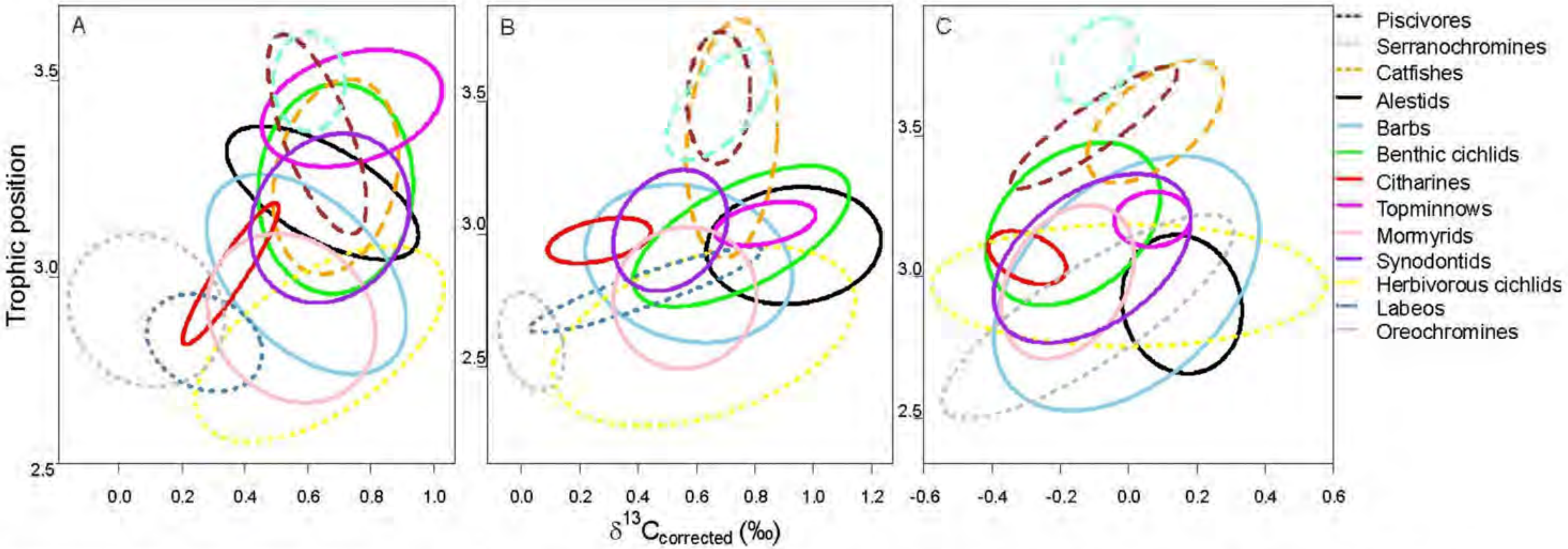

Figure 4.4: The core isotopic niche areas (SEAc) of the fishes grouped according to the example feeding strategy in Table 4.3 for the fish communities of A: Zambezi, B: Kavango and C: Kwando rivers. Dashed lines = predatory fish niches, solid lines = invertivorous fish niches, dotted lines = herbivorous/ detritivorous fish niches.

Core niche areas (SEAc) varied with species groups between rivers in a similar pattern; for example, barbs, benthic and herbivorous cichlids had large core niche areas, while citharines, labeos, piscivores and serranochromines had smaller core niche areas (Table 4.5). Statistically however, the distribution of group core niche areas (labeos excluded) differed significantly between rivers (χ^2 test, df = 22, $\chi^2 = 46.88$, $P = < 0.01$). The major differences were: barbs had a disproportionately large niche area in the Kwando River, topminnows had a large niche area in the Zambezi River, and the oreochromine niche areas were large in the Kwando River and small in the Kavango River.

Table 4.5: The core isotopic niche area (SEAc ‰^{2}) and sample size of individuals (N) per fish group (according to feeding strategy, Table 4.3) from the Zambezi, Kavango and Kwando rivers.

	Zambezi		Kavango		Kwando	
Fish groups	SEAc	N	SEAc	N	SEAc	N
Alestids	12.52	25	20.52	26	13.44	34
Barbs	22.37	54	32.61	61	49.69	23
Benthic cichlids	20.55	38	24.01	28	21.54	39
Catfishes	15.14	12	21.62	93	11.11	40
Citharines	3.15	5	4.31	10	3.09	13
Herbivorous cichlids	25.01	22	50.27	11	39.10	12
Labeos	6.94	7	8.22	5	-	0
Topminnows	12.70	10	4.08	10	3.38	18
Mormyrids	17.73	34	20.45	31	15.70	24
Oreochromines	15.00	5	6.16	21	26.76	11
Piscivores	9.04	18	8.39	10	7.29	14
Serranochromines	4.48	21	9.42	29	5.15	8
Synodontids	16.81	22	13.58	11	24.04	38

Comparing isotopic niche area overlap: the oreochromines overlapped with other groups in the Kwando River, while in the Zambezi and Kavango rivers this group had relatively distinct core niche areas (Table 4.6). Piscivores and serranochromines overlapped very little with other groups in the Kavango and Kwando rivers, while in the Zambezi River these groups overlapped with alestids, topminnows, synodontids, benthic cichlids and catfishes. Catfishes, which encompass large, mainly piscivorous predators such as *C. gariepinus*, and smaller, more invertivorous species such as *S. intermedius* (see Chapter 3), overlapped greatly with many other groups in the Zambezi, to a lesser extent in the Kavango, and overlapped very little in the Kwando. Overall the Kavango River fish groups had more distinct niche areas, with 53.8% of all possible group interactions resulting in overlap (Table 4.6), while in the Zambezi and Kwando rivers more group niche areas overlapped (60.2% and 60.6% of possible group interactions resulted in overlap, respectively).

Table 4.6: The core isotopic niche area (SEAc) % overlap between fish groups for the Zambezi, Kavango and Kwando rivers. Column headings indicate the group niche area being overlapped; for example in the Zambezi River 34.3% of alestids niche area was overlapped by barbs, while 19.2% of the barbs niche area was overlapped by alestids. B. cichlid = Benthic cichlids, H. cichlid = Herbivorous cichlids, Topm. = Topminnows, Oreochr. = Oreochromines, Serrano. = Serranochromines, Synod. = Synodontids, grey shading = areas of interest.

Groups	Alestids	Barbs	B. cichlid	Catfishes	Citharine	H. cichlid	Labeos	Topm.	Mormyrid	Oreochr.	Piscivore	Serrano.	Synod.
Zambezi River													
Alestids		19.2	50.9	54.1	3.1	1.9	0.0	13.8	0.0	0.0	45.5	0.0	55.9
Barbs	34.3		38.4	33.3	59.7	44.4	0.0	0.0	68.1	0.0	8.7	0.0	57.4
B. cichlid	83.5	35.3		98.2	10.5	8.8	0.0	52.0	15.1	0.0	72.7	34.4	88.9
Catfishes	65.4	22.5	72.4		1.8	1.9	0.0	47.2	7.1	0.0	67.5	27.7	64.7
Citharines	0.8	8.4	1.6	0.4		0.0	12.7	0.0	10.2	6.7	0.0	0.0	4.2
H. cichlid	3.8	49.6	10.7	3.1	0.0		34.6	0.0	69.9	0.4	0.0	0.0	17.7
Labeos	0.0	0.0	0.0	0.0	27.9	9.6		0.0	12.5	27.8	0.0	0.0	0.0
Topminnows	14.0	0.0	32.1	39.6	0.0	0.0	0.0		0.0	0.0	53.7	64.7	11.1
Mormyrids	0.0	54.0	13.0	8.3	57.1	49.6	32.0	0.0		4.1	0.0	0.0	25.0
Oreochromines	0.0	0.0	0.0	0.0	31.7	0.2	60.0	0.0	3.4		0.0	0.0	0.0
Piscivores	32.8	3.5	32.0	40.3	0.0	0.0	0.0	38.2	0.0	0.0		75.0	25.0
Serrano.	0.0	0.0	7.5	8.2	0.0	0.0	0.0	22.8	0.0	0.0	37.1		0.0
Synodontids	75.1	43.1	72.7	71.9	22.2	11.9	0.0	14.7	23.7	0.0	46.5	0.0	
Kavango River													
Alestids		24.0	50.6	12.8	0.0	15.7	16.2	100.0	12.6	0.0	0.0	0.0	5.1
Barbs	38.2		63.2	19.8	64.9	32.4	69.9	52.0	82.0	0.0	0.0	0.0	91.3
B. cichlid	59.2	46.6		24.7	0.0	15.7	53.5	100.0	46.0	0.0	0.0	0.0	50.9
Catfishes	13.4	13.1	22.3		0.0	0.4	2.4	38.9	4.3	0.0	90.4	83.7	21.5
Citharines	0.0	8.6	0.0	0.0		0.0	0.0	0.0	0.1	0.0	0.0	0.0	9.9
H. cichlid	38.5	49.9	32.9	0.9	0.0		73.8	0.0	79.6	6.3	0.0	0.0	14.4
Labeos	6.5	17.6	18.3	0.9	0.0	12.1		0.0	25.5	8.2	0.0	0.0	15.0
Topminnows	19.9	6.5	17.0	7.3	0.0	0.0	0.0		0.5	0.0	0.0	0.0	1.7
Mormyrids	12.6	51.4	39.2	4.1	0.5	32.4	63.6	2.3		0.0	0.0	0.0	42.4

Groups	Alestids	Barbs	B. cichlid	Catfishes	Citharine	H. cichlid	Labeos	Topm.	Mormyrid	Oreochr.	Piscivore	Serrano.	Synod.
Oreochromines	0.0	0.0	0.0	0.0	0.0	0.8	6.2	0.0	0.0		0.0	0.0	0.0
Piscivores	0.0	0.0	0.0	35.1	0.0	0.0	0.0	0.0	0.0	0.0		65.1	0.0
Serrano.	0.0	0.0	0.0	36.5	0.0	0.0	0.0	0.0	0.0	0.0	73.1		0.0
Synodontids	3.4	38.0	28.8	13.5	31.3	3.9	24.7	5.5	28.1	0.0	0.0	0.0	
						Kwando River							
Alestids		23.7	0.1	0.0	0.0	28.8	-	6.7	1.5	24.6	0.0	0.0	12.1
Barbs	87.6		61.4	7.6	59.0	70.3	-	100.0	98.1	84.3	0.0	0.0	93.3
B. cichlid	0.2	26.6		18.9	100.0	25.2	-	53.8	60.3	12.1	20.8	0.0	59.4
Catfishes	0.0	1.7	9.7		0.0	0.0	-	0.0	0.0	0.0	40.9	0.0	1.0
Citharines	0.0	3.7	14.3	0.0		7.4	-	0.0	12.8	0.1	0.0	0.0	10.0
H. cichlid	83.7	55.3	45.8	0.0	94.0		-	36.6	84.6	62.0	0.0	0.0	73.0
Labeos	-	-	-	-	-	-		-	-	-	-	-	-
Topminnows	1.7	6.8	8.4	0.0	0.0	3.2	-		1.6	3.8	0.0	0.0	14.1
Mormyrids	1.7	31.0	43.9	0.0	65.3	34.0	-	7.6		33.1	0.0	0.0	60.2
Oreochromines	49.0	45.4	15.1	0.0	0.8	42.5	-	30.1	56.5		0.0	0.0	47.1
Piscivores	0.0	0.0	7.0	26.8	0.0	0.0	-	0.0	0.0	0.0		1.1	0.0
Serrano.	0.0	0.0	0.0	0.0	0.0	0.0	-	0.0	0.0	0.0	0.8		0.0
Synodontids	21.6	45.1	66.3	2.2	78.1	44.9	-	100.0	92.2	42.3	0.0	0.0	

Comparing predator communities

The core niche areas of predators overlapped greatly in the Zambezi and Kavango rivers; however in the Kwando River, although less predators were sampled for stable isotope analysis, those sampled had more distinct trophic niches (Table 4.7; Figure 4.5). In the Zambezi River *H. vittatus* had a large core niche area (Table 4.7) that overlapped with all other predators sampled (Table 4.8), suggesting that this species shares resources with all other predators. In the Kavango River *S. intermedius* and *S. altus* had large core niche areas, and again *H. vittatus* niche area overlapped with those of many (75%) other predators. Smaller *H. vittatus* were sampled in the Zambezi River compared to the Kavango River, potentially influencing trophic position and niche area (Table 4.7). However, no significant relationship was detected between *H. vittatus* length and trophic position or $\delta^{13}C_{corrected}$ values in the Zambezi River, suggesting differences in fish lengths, at least in the range sampled, would not impact on isotopic niche position. However, a significant negative relationship between $\delta^{13}C_{corrected}$ values and fish length in the Kavango River, combined with the smaller niche width for *H. vittatus* suggests a potential specialisation of feeding habits (i.e. a decrease in used food resources) with an increase in fish length. In the Kwando River, *H. cuvieri* had a larger core niche area which overlapped with multiple predators, compared to those in the Zambezi and Kavango rivers.

In general, the *Serranochromis* spp. had small niche areas implying specialised diets, with the exception of *S. altus* in the Kavango River which fed opportunistically. *Schilbe intermedius* tended to occupy lower trophic positions in all rivers with a comparatively wide niche area, while *C. gariepinus* occupied the position of top predator, followed closely by *H. vittatus* and various *Serranochromis* spp. The Kwando River predators occupied higher trophic positions than in the Zambezi and Kavango rivers, with the exception of *C. gariepinus* which occupied similar trophic positions in the Kavango and Kwando rivers.

Small but significant increases in trophic position with fish length were found in the Zambezi River populations of *S. intermedius* and *S. altus*, in the Kavango River populations of *C. gariepinus, C. ngamensis, S. intermedius, S. altus,* and *S. macrocephalus*, and in the Kwando River *S. intermedius* population (Table 4.7). Significant changes in $\delta^{13}C_{corrected}$ values with fish length were found for *S. altus* from the Zambezi River, *H. vittatus* from the Kavango River, and *H. cuvieri* and *S. angusticeps* from the Kwando River (Table 4.7).

Table 4.7: The core isotopic niche areas (SEAc‰^{2}), sample sizes (N), mean length (mm TL/FL), minimum and maximum lengths (min, max mm TL/FL), slope and R^2 values describing the relationships between the trophic position and fish length (N-length), and between $\delta C^{13}_{corrected}$ values and fish length (C-length) (*=significant regression), and mean trophic position (TP) for the predatory fish species from the Zambezi, Kavango and Kwando rivers.

	C. gariepinus	*C. ngamensis*	*H. cuvieri*	*H. vittatus*	*S. intermedius*	*S. altus*	*S. angusticeps*	*S. macrocephalus*	*S. robustus*
Zambezi River									
SEAc	-	-	2.16	19.72	11.6	1.87	4.43	3.99	-
N	1	0	10	8	10	6	6	7	2
Length mean	723	-	196.3	156.1	131.2	144.7	162.7	155.7	272
min, max	-	-	145, 291	104, 295	79, 195	92, 202	79, 303	115, 182	144, 400
N-length	-	-	<0.01, 0.26	<0.01, 0.01	<0.01, 0.57*	<0.01, 0.83*	<-0.01, 0.36	<-0.01, 0.18	-
C-length	-	-	<-0.01, 0.22	<0.01, 0.02	<0.01, 0.23	<0.01, 0.94*	<0.01, 0.51	<0.01, 0.18	-
TP ± SD	3.69 ± 0	-	3.32 ± 0.08	3.42 ± 0.36	3.24 ± 0.20	3.60 ± 0.12	3.48 ± 0.09	3.42 ± 0.09	3.51 ± 0.17
Kavango River									
SEAc	5.1	4.92	6.04	9.2	20.02	10.99	1.41	5.36	2.5
N	30	19	3	7	44	7	6	11	5
Length mean	819.2	495.6	351.3	373.3	169.6	282.4	295.7	239.4	413.8
min, max	495, 1000	433, 600	314, 381	223, 536	55, 295	97, 442	270, 335	100, 299	362, 455
N-length	<0.01, 0.47*	<0.01, 0.40*	-	<0.01, 0.00	<0.01, 0.72*	<0.01, 0.82*	<0.01, 0.08	<0.01, 0.58*	<0.01, 0.33
C-length	<-0.01, 0.02	<0.01, 0.02	-	<-0.01, 0.57*	<0.01, 0.10	<0.01, 0.47	<0.01, 0.00	<0.01, 0.05	<-0.01, 0.14
TP ± SD	3.85 ± 0.17	3.40 ± 0.16	3.31 ± 0.13	3.60 ± 0.21	3.01 ± 0.32	3.37 ± 0.37	3.55 ± 0.08	3.48 ± 0.11	3.60 ± 0.08
Kwando River									
SEAc	1.94	5.93	7.29	-	6.75	-	5.22	-	-
N	4	13	14	0	22	2	5	1	0
Length mean	623.2	539	301.8	-	211.4	287	283	212	-
min, max	568, 695	435, 665	226, 384	-	123, 282	284, 290	191, 378	-	-
N-length	<-0.01, 0.07	<0.01, 0.22	<0.01, 0.27	-	<0.01, 0.33*	-	<0.01, 0.63	-	-
C-length	<-0.01, 0.45	<0.01, 0.13	<0.01, 0.45*	-	<0.01, 0.02	-	<0.01, 0.78*	-	-
TP ± SD	3.82 ± 0.10	3.72 ± 0.12	3.53 ± 0.21	-	3.40 ± 0.14	3.71 ± 0.10	3.82 ± 0.13	3.56 ± 0	-

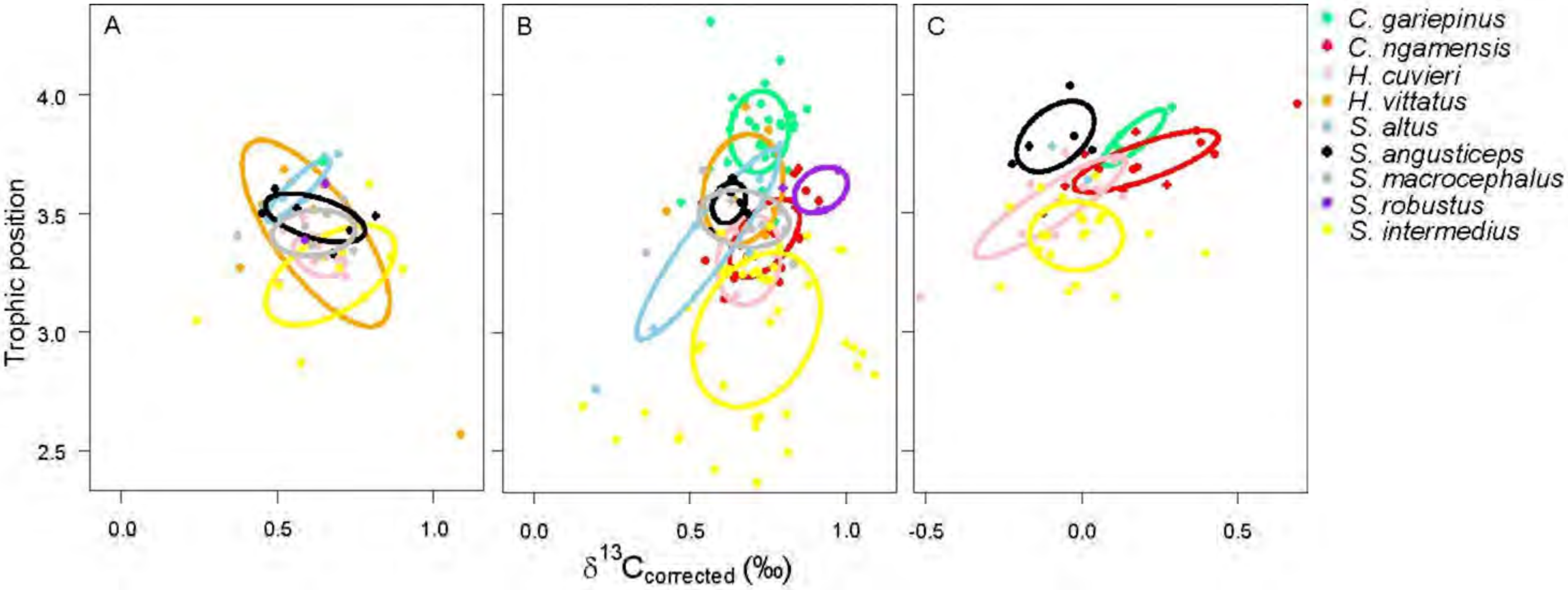

Figure 4.5: The core isotopic niche areas (SEAc) of the predatory fishes from A: the Zambezi, B: Kavango and C: Kwando rivers.

Table 4.8: The core isotopic niche area (SEAc) % overlap between predatory fishes from the Zambezi, Kavango and Kwando rivers. Column headings indicate the species niche area being overlapped. *C. gar* = *Clarias gariepinus*, *C. nga* = *Clarias ngamensis*, *H. cuv* = *Hepsetus cuvieri*, *H. vit* = *Hydrocynus vittatus*, *S. int* = *Schilbe intermedius*, *S. alt* = *Serranochromis altus*, *Serranochromis ang* = *Serranochromis angusticeps*, *S. mac* = *Serranochromis macrocephalus*, *S. rob* = *Serranochromis robustus*.

Species	*C. gar*	*C. nga*	*H. cuv*	*H. vit*	*S. int*	*S. alt*	*S. ang*	*S. mac*	*S. rob*
	Zambezi River								
C. gar		-	-	-	-	-	-	-	-
C. nga	-		-	-	-	-	-	-	-
H. cuv	-	-		11.0	15.6	0.0	2.2	24.2	-
H. vit	-	-	100.0		61.8	85.5	98.9	100.0	-
S. int	-	-	83.8	36.3		0.0	15.3	28.7	-
S. alt	-	-	0.0	8.1	0.0		16.1	0.0	-
S. ang	-	-	4.4	22.2	5.8	38.3		58.7	-
S. mac	-	-	44.7	20.3	9.9	0.0	52.9		-
S. rob	-	-	-	-	-	-	-	-	
	Kavango River								
C. gar		0.0	0.0	19.8	0.0	5.9	0.0	0.0	0.0
C. nga	0.0		52.5	13.4	4.7	1.9	0.0	42.3	0.0
H. cuv	0.0	64.4		12.7	14.2	7.7	0.0	32.6	0.0
H. vit	35.7	25.0	19.3		0.0	41.6	100.3	75.0	0.0
S. int	0.0	19.0	47.1	0.0		0.0	0.0	0.0	0.0
S. alt	12.7	4.2	14.0	49.7	0.0		94.1	55.1	0.0
S. ang	0.0	0.0	0.0	15.4	0.0	12.1		22.3	0.0
S. mac	0.0	46.1	29.0	43.7	0.0	26.9	84.6		0.0
S. rob	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	
	Kwando River								
C. gar		7.2	3.0	-	0.0	-	0.0	-	-
C. nga	21.8		21.6	-	0.0	-	0.0	-	-
H. cuv	11.1	26.5		-	18.5	-	0.0	-	-
H. vit	-	-	-		0.0	-	0.0	-	-
S. int	0.0	0.0	17.1	-		-	0.0	-	-
S. alt	-	-	-	-	-		0.0	-	-
S. ang	0.0	0.0	0.0	-	0.0	-		-	-
S. mac	-	-	-	-	-	-	-		-
S. rob	-	-	-	-	-	-	-	-	

Discussion

Stable isotope analysis allowed for i) the comparisons of food web structure and trophic dynamics between fish communities, and ii) the characterisation and comparison of isotopic niches and trophic positions of predatory fish species, from the Zambezi, Kavango and Kwando rivers.

Comparing fish communities

The flood pulse concept predicts that production sources of terrestrial materials from the floodplain drive food webs in large floodplain rivers (Junk et al. 1989). This was supported by Wantzen et al. (2002) who found C_3 macrophytes of riparian origin were the main component of the food web basal resources, followed by floodplain C_4 macrophytes, which were hypothesised to increase in importance during flooding. Zeug and Winemiller (2008) found that contributions of terrestrial and algal resources depended on patterns of flooding, with terrestrial resources such as riparian C_3 macrophytes and floodplain C_4 macrophytes increasing in importance during high water events, while algal resources increased in importance during low flow periods. Hoeinghaus et al. (2007) found that for low gradient rivers, C_3 macrophytes were most important followed by phytoplankton. These views were contrary to those of Lewis et al. (2001) and Thorp and Delong (2002) who found that algae were the dominant source of productivity in large river food webs. In the Okavango Delta, Lindholm et al. (2007) found that during a small flood the food web was depleted in ^{13}C, as a result of higher methane concentrations on the floodplain, while during a large flood the food web was ^{13}C enriched. They attributed this enrichment in ^{13}C to the abundance of biofilm on submerged floodplain vegetation (Lindholm et al. 2007), however C_4 grasses may have contributed.

Food web structure of the fish communities and resources sampled were similar between the Zambezi and Kavango rivers, where the fish communities occupied overlapping niche areas (SEAc), and POM was positioned as the most likely primary producer driving the food webs. The Kwando River fish community occupied a discrete niche area, depleted in $^{13}C_{corrected}$, and submerged plants were positioned near the base of the food web. As the Zambezi and Kavango rivers receive large flood pulses annually (see Chapter 2), and their fish communities were characterised by enriched $^{13}C_{corrected}$ values, it was hypothesised that C_4 inputs from the floodplain contributed largely to these food webs. In the study sites, the dominant C_4 plant species present on the floodplain was *V. cuspidata*, while *C. papyrus* bordered marginal swamps. *Vossia cuspidata* was dominant in all three rivers, although not sampled from the Zambezi River, while *C. papyrus* was abundant in the Kavango and Kwando rivers, but not in the Zambezi River at Kalimbeza. In addition, Abrantes et al. (2013) found that in the Zambezi River estuary, terrestrial C_3, C_4 and phytoplankton productivity sources contributed significantly to the aquatic food web.

The Kwando River receives very small floods, if at all (see Chapter 2), and the fish community there was characterised by depleted $^{13}C_{corrected}$ values, indicating an algal or aquatic macrophyte based food web. *Vossia cuspidata* and *C. papyrus* were both abundant in the Kwando River, however small floods may reduce the inundation of the floodplain so restricting the influx of enriched ^{13}C into the river annually. In addition, filamentous algae, which is depleted in ^{13}C with values averaging -1‰ corrected (-36‰ uncorrected), is often found in abundance covering lily beds lining the main channel (Pers. obs.). The enriched POM samples from this river may be indicative of the high inputs from hippopotami dung, which tend to be ^{15}N enriched (Jackson et al. 2012), and high in nutrients (McLachlan 1971; Kilham 1982). The fast turnover rates of phytoplankton (Setaro and Melack 1984; Train and Rodrigues 1997), generally a major constituent of POM (Bukaveckas et al. 2011), and since all other submerged macrophytes were not similarly enriched in ^{15}N, could indicate that the enriched position of POM was as a result of recent episodic ^{15}N enrichment.

The importance of terrestrial versus algal resources in river food webs is also influenced by the sampling season (Zeug and Winemiller 2008). Since the isotopic turnover of fish white muscle tissue is approximately three months (MacAvoy et al. 2001; Weidel et al. 2011), and the Zambezi and Kavango river fish communities were sampled between August and October in the falling water period, diet assimilation most likely coincided with the high water period when terrestrial inputs may have peaked (Zeug and Winemiller 2008). In the Kwando River, fish community tissue samples were collected in August during high water, meaning diet assimilation may have occurred either at the end of the small rise in river water associated with local rainfall, or during the low water period before the main flood arrived in July (see Chapter 2) when algal contributions may have dominated (Zeug and Winemiller 2008). Therefore, both flood magnitude and sampling season would have influenced the primary productivity resource inputs into the rivers. Future research should focus on testing these hypotheses regarding the basal resources driving these systems, and determining the isotopic turnover of tropical freshwater fish muscle tissue.

Nitrogen range and the position of predatory fishes within the food web also differed between rivers. In the Zambezi River the predatory fish groups overlapped significantly with invertivorous fishes, so reducing the nitrogen range of this river, unlike in the Kavango and Kwando rivers where these groups had higher trophic positions than the other fish groups and nitrogen ranges were higher. In addition, the trophic position of the top predatory species *C.*

gariepinus or the maximum trophic position, a value similar to mean food chain length (Briand and Cohen 1987; Post et al. 2000), was highest in the Kavango River, followed by the Kwando River, and lowest in the Zambezi River, although only one *C. gariepinus* was sampled from this river. Layman et al. (2005) hypothesised that fishing pressure that targets large bodied herbivore-detritivores should result in an increase in the length of the food web as predators that previously targeted these fishes shift their diets towards smaller bodied predatory fishes. Alternatively fisheries targeting large top predators should not reduce food chain length if there are smaller predators in the system that are not fished and that feed at similar trophic positions (Layman et al. 2005).

The Caprivi Floodplains in the Upper Zambezi River are considered heavily exploited, with commercial fishers targeting large bodied herbivorous-detritivorous cichlids, and overfishing is now apparent due to declines in commercial and subsistence catches (Tweddle 2010; Tweddle et al. 2015). Once the targeted cichlid fishery was depleted, fishers increased their effort and improved their catch efficiency by using more effective and often illegal fishing gears and methods (Tweddle et al. 2015). Large top predators such as *H. vittatus* and *C. gariepinus* were actively fished for (Winemiller and Kelso-Winemiller 1996; Pers. obs.), while smaller predators such as the serranochromine cichlids, *H. cuvieri* and *S. intermedius* were caught using smaller meshed gillnets than those previously targeting herbivorous-detrivorous cichlids. The consequence of this fishing pressure aimed at both the apex and the base of the food web, could be construed as fishing up and down the food web, and may have resulted in a reduction in food chain length (Pauly et al. 2001; Jennings et al. 2002), estimated as maximum trophic position in this study. The reduction in food chain length and the removal of predatory fishes might explain the higher trophic positioning of various invertivorous groups (benthic cichlids, topminnows, alestids and synodontids) in the Zambezi River compared to in the Kavango and Kwando rivers.

Overall the Kavango River had high trophic specialisation, and great divergence in trophic niches, as was indicated by the large CD, MNND and SEAc values (Rigolet et al. 2015). According to Rigolet et al. (2015) this may translate into a greater ecosystem resilience to change. The Mahango sampling site on the Kavango River is situated within national parks, which at the time of the study were protected from all types of fishing, a feature reinforced by the abundance of wild animals, particularly hippopotami. The river is subject to large annual floods, and the area sampled is bounded by floodplains (see Chapter 2). These reasons may all contribute towards the Kavango River food webs resilience to potential change.

Comparing predator communities

Stable isotope analysis allowed for the testing of several previous hypotheses proposed by Jackson (1961), Winemiller (1991a) and Winemiller and Kelso-Winemiller (1994; 1996) based on their observations on the habitat affinities and stomach contents analyses of fishes.

The first set of hypotheses relate to the predation pressures imposed on fish communities by *H. vittatus* and *H. cuvieri*. Jackson (1961) hypothesised that the number of species inhabiting main channel habitats is restricted by threats of competition with or predation by *H. vittatus*. Winemiller (1991a) observed that the large size classes of *S. robustus, S. altus, S. giardi, O. andersonii, O. macrochir,* and *C. rendalli* coexist in the main channel with *H. vittatus*; Winemiller and Kelso-Winemiller (1994) hypothesised that the threat of predation by *H. vittatus* in the main channel and *H. cuvieri* in backwaters and marginal habitats imposes considerable pressure on community food web structure in the Upper Zambezi, forcing small fishes (Cyprinodontidae, Cyprinidae and Alestidae) to occupy very shallow shoreline areas or vegetated microhabitats.

Predatory fish communities differed in all three rivers. In the Zambezi and Kavango rivers *H. vittatus* had large core niche areas positioned near the top of the food web, which overlapped with the other predators sampled. The variation in both trophic position and $\delta^{13}C_{\text{corrected}}$ values of *H. vittatus* suggests this is an opportunistic predator (Woodborne et al. 2012), which would compete with the other predators if resources were limiting. *Hepsetus cuvieri*, an ambush predator which prefers vegetated backwaters (Winemiller and Kelso-Winemiller 1994), occupied a very small core niche area in the Zambezi River that completely overlapped with *H. vittatus*, and in the Kavango River fed on similar resources to *H. vittatus* (similar $\delta^{13}C_{\text{corrected}}$ values), however at a slightly lower trophic position. In the Kwando River, where very few *H. vittatus* were sampled, *H. cuvieri* occupied a slightly larger isotopic niche area, and had a higher trophic position compared to the other populations. There is therefore evidence to support the hypotheses proposed by Jackson (1961) and Winemiller and Kelso-Winemiller (1994), that *H. vittatus* is a dominant predator which competes with other predators. Winemiller and Kelso-Winemiller (1994) noted differences in diet and habitat utilisation by sympatric *H. vittatus* and *H. cuvieri* as a result of threats of predation by *H. vittatus*, interspecific variation in foraging mode (*H. vittatus* is primarily a pursuit predator while *H. cuvieri* is an ambush predator), and differential foraging efficiencies in open waters and structured habitats. In the absence of *H. vittatus* in the Kwando River, there is evidence that *H. cuvieri* may be less confined to heavily vegetated backwaters and margins, so allowing this species to utilise a wider range of prey, hence the increase in trophic position and the expanded niche area. Future research should focus on the habitat utilisation of *H. cuvieri* and other predator species in the Kwando River in the absence of *H. vittatus*, compared to in the Zambezi and Kavango rivers where *H. vittatus* are abundant.

The second set of hypotheses relates to the predatory serranochromines. Winemiller (1991a) hypothesised that the Upper Zambezi serranochromines exhibit nearly complete ecological separation during the low water season, when considering habitat affinities and food habits. *Serranochromis altus* and *S. robustus* are known to utilise main channel habitats, while *S. angusticeps* and *S. macrocephalus* are commonly found in backwater habitats (Winemiller 1991a; Winemiller and Kelso-Winemiller 1991). In the Kavango River, where both *S. altus* and *S. robustus* were sampled, these species occupied discrete isotopic niche areas. This supports findings by Winemiller (1991a) and Winemiller and Kelso-Winemiller (1991) who observed *S. altus* foraging crepuscularly for mormyrids, while *S. robustus* preyed mainly on synodontids and crabs (Winemiller 1991a; Peel unpubished data). In backwater habitats, *S. macrocephalus* and *S. angusticeps* core isotopic niche areas did overlap in the Zambezi and Kavango rivers where they were sampled. Winemiller (1991a) documented that *S. macrocephalus* fed crepuscularly on mormyrids and benthic cichlids, while *S. angusticeps* fed diurnally on barbs and alestids. This was supported by stomach contents data presented in Chapter 3 demonstrating *S. macrocephalus* fed on mormyrids, barbs and cichlids. Since there was significant niche overlap between alestids, barbs and benthic cichlids in the Zambezi and Kavango rivers, this could explain the overlap in niche areas of *S. macrocephalus* and *S. angusticeps* despite their differing diets. Mormyrids occupied lower positions in isotopic space compared to alestids and barbs, which could explain the slightly lower position in isotopic space of *S. macrocephalus* compared to *S. angusticeps*. This stable isotope based food web analysis therefore supports the hypothesis proposed by Winemiller (1991a) that these cichlids are ecologically separated by habitat affinity and feeding habits.

Lastly, Winemiller and Kelso-Winemiller (1996) segregated the catfishes of the Upper Zambezi River into four size/trophic guilds: large carnivores (*Clarias gariepinus, C. ngamensis*); medium-sized carnivores (*C. stappersii, C. theodorae, Parauchenoglanis ngamensis, Clariallabes platyprosopos, Schilbe intermedius*), medium-sized omnivores (*Synodontis nigromaculatus,* and *Synodontis leopardinus, S. woosnami, S.* sp. cf. *woosnami, S. macrostigma, S. macrostoma* which are grouped as *Synodontis* spp. for this thesis), and small omnivores (*Amphilius uranoscopus, Chiloglanis neumanni* (now *C. fasciatus*), *Leptoglanis rotundiceps* (now *Zeirichthys* spp.)). *Clarias gariepinus, C. ngamensis*, and *S. intermedius* will be assessed with respect to this finding.

Clarias gariepinus occupied small niche areas at the top of the food chain in the Kavango and Kwando rivers where it was adequately sampled. Its small niche area was surprising as this large bodied species (Bruton 1976) has highly plastic feeding habits (Willoughby and Tweddle 1978; Bruton 1979b; Winemiller and Kelso-Winemiller 1996; Kadye and Booth 2011) and thrives in a variety of habitats (Bruton 1979c; Winemiller and Kelso-Winemiller 1996; van der Waal 1998; Kadye and Booth 2013). Feeding on a number of prey items, from fishes (Willoughby and Tweddle 1978; van der Waal 1985; Winemiller and Kelso-Winemiller 1996; Kadye and Booth 2011), to crustaceans (Bruton 1979b), invertebrates (Yalcin et al. 2001), plankton (Dadebo 2009) and detritus (Mosepele et al. 2012; Dadebo et al. 2014), this diverse feeder has even been recorded pack hunting with *C. ngamensis* in the Okavango Delta (Merron 1993). Core niche areas of *C. gariepinus* and *C. ngamensis* overlapped little as a result of the latter species preference for molluscs and invertebrates (see Chapter 3, Willoughby and Tweddle 1978; van der Waal 1985); however *C. ngamensis* occupied similar trophic positions compared to the other predatory species such as *H. cuvieri* and *S. altus.* This supports the findings of Winemiller and Kelso-Winemiller (1996), classifying *C. gariepinus* and *C. ngamensis* as large carnivores.

Schilbe intermedius occupied broad core niche areas at lower trophic positions compared to most other predators, supporting stomach contents findings from Chapter 3 describing them as either omnivores rather than piscivores, feeding on invertebrates, barbs, mormyrids and cichlids, or as medium-sized carnivores as hypothesised by Winemiller and Kelso-Winemiller (1996). Winemiller and Kelso-Winemiller (1994) surmised that the diurnal predation by *H. cuvieri* and crepuscular predation by *S. intermedius* might competitively exclude *H. vittatus* from backwaters. Synodontids and *P. ngamensis,* although not studied in detail, did occupy lower trophic positions compared to the other catfishes in the Kavango and Kwando rivers (Figure 4.4), so supporting the hypothesis proposed by Winemiller and Kelso-Winemiller (1996) describing them as medium sized omnivores. The small omnivores were not sampled in this study and therefore cannot be assessed.

Increases in trophic position with fish length were found for *S. intermedius* from all rivers, and for *C. gariepinus, C. ngamensis, S. altus,* and *S. macrocephalus* from the Kavango River, while changes in $\delta^{13}C_{corrected}$ values with fish length were found for *S. altus* from the Zambezi River, *H. vittatus* from the Kavango River, and *H. cuvieri* and *S. angusticeps* from the Kwando River. Ontogenetic niche shifts are well documented (see Chapter 3; Werner and Gilliam 1984; Scharf et al. 2000; Hammerschlag-Peyer et al. 2011), with fishes often feeding at higher trophic levels with increases in size as a result of selection for larger prey (Beaudoin et al. 1999; Jennings et al. 2002; Cocheret de la Morinière et al. 2003), while complete changes in diet with fish size have also been documented (Kolasinski et al. 2009; Yasuno et al. 2012; Pedreschi et al. 2015). Kadye and Booth (2011) found increases in trophic position of *C. gariepinus* with size in South Africa, so supporting the data from the Kavango River population, while the South African populations also switched from invertebrates to fish prey at around 25 cm TL, a size not sampled in this study. Winemiller and Kelso-Winemiller (1994) found that both *H. cuvieri* and *H. vittatus* changed their diets between fish groups with growth, as was found with changes in $\delta^{13}C_{corrected}$ values in this study. Winemiller (1991a) found that the serranochromine cichlids shifted their diets, changing the proportions of the same species in the diets of small and large individuals; for example, juvenile *S. robustus* preyed mainly on barbs (44%) and synodontids (3%), while adults preyed on synodontids (55%) and barbs (16%). This most likely resulted in increases in trophic position with fish length, with potentially small changes in $\delta^{13}C$ values. This is corroborated by the changes in isotope values of *S. altus* from the Zambezi and Kavango rivers, and *S. angusticeps* from the Kwando River. Greater changes in isotope values with predatory fish length would be expected with increases in sample size, and could be a focus of future research.

Dietary overlaps described using stomach contents analyses (see Chapter 3) and stable isotope analyses were generally complementary. For example, in the Zambezi River both stomach contents analysis and stable isotope analysis indicated dietary overlap or niche overlap between *S. macrocephalus* and *H. cuvieri*. In the Kavango River, diets of *C. gariepinus*, *C. ngamensis* and *S. intermedius* were distinct using stomach contents analysis, while isotopic niches of *S. intermedius* and *C. ngamensis* overlapped slightly using stable isotope analysis, and *C. gariepinus* occupied a different isotopic space. In the Kwando River, results from both methods suggested that *C. gariepinus* and *C. ngamensis* overlapped very slightly, while *S. intermedius* had a different core isotopic niche. Contrary to the general agreement between methods, *S. intermedius* and *H. cuvieri* diets in the Zambezi River did not overlap using stomach contents analyses, however their isotopic niches overlapped. With overall complementary results, it must be remembered that differing combinations of prey items may result in similar positions in the isotopic space of predators, while differing fractionation factors and isotopic turnover rates further complicate the isotopic relationships between predators and their prey, so emphasising the low taxonomic resolution of stable isotope analysis (Jepsen and Winemiller 2002), and its strength when used in combination with stomach contents analysis (Harrigan et al. 1989; Renones et al. 2002; Kadye and Booth 2011).

In conclusion, stable isotope analysis is useful when comparing ecosystems on a broad scale (Jepsen and Winemiller 2002). Basal resources driving the Zambezi and Kavango food webs were similar, with enriched ^{13}C indicative of C_4 plants on the floodplain, differing from the depleted autochthonous basal resources driving the Kwando River food web. The Kavango and Kwando river predators occupied discrete elevated trophic positions compared to the other fish groups, while the Zambezi River predatory fishes were positioned at lower trophic positions, overlapping significantly with other fish groups. This reduction in nitrogen range and the significant overlapping of the predatory fishes with invertivorous fishes could be a symptom of the increasing fishing pressure imposed on this river system.

When looking at species' isotopic niches, additional information on diet from stomach contents analysis (Chapter 3), and habitat, are essential for a true understanding of trophic relationships, as trophic pathways may be distinct even if isotope values are similar (Layman et al. 2012). For example, *H. vittatus* niche area overlapped with many other predators in the Zambezi and Kavango rivers, implying competition if resources were limiting and supporting the hypotheses proposed by Jackson (1961) and Winemiller and Kelso-Winemiller (1994). In the Kwando River where *H. vittatus* were not sampled, the predatory species tended to have more discrete isotopic niches, so implying less potential competition for resources. The serranochromine cichlids, as hypothesised by Winemiller (1991a), could be separated ecologically by habitat preference and feeding habits. The catfishes were separated into similar size/trophic guilds as proposed by Winemiller and Kelso-Winemiller (1996), although there was evidence that *P. ngamensis* was more of an omnivore than a carnivore. In general stable isotope and stomach contents analyses were complementary in describing the trophic dynamics of the predatory species sampled from the Zambezi, Kavango and Kwando rivers.

Since diet and fishing pressures directly (Weatherley and Gill 1987) and indirectly (Enberg et al. 2012) influence fish growth rates respectively, it is hypothesised that differences in these two factors in the three rivers should be reflected in variations in fish growth rates. Consequently, comparisons of growth rates will be assessed in Chapter 5.

CHAPTER 5: The age and growth of six species from the Zambezi, Kavango and Kwando rivers

Introduction

Growth is an important aspect of the ecology and life history of fishes, and quantification of growth is a crucial part of fisheries research and management (Summerfelt and Hall 1987; Weatherley and Gill 1987). The six species studied in Chapter 3 (*Brycinus lateralis*, *Clarias gariepinus*, *Clarias ngamensis*, *Hepsetus cuvieri*, *Schilbe intermedius* and *Serranochromis macrocephalus*), will be used for a comparison of growth rates between rivers. In addition to their high relative abundance, their employment of varying feeding strategies and their use of multiple habitats, these species are also representative of the three life history strategies described by Winemiller and Rose (1992). *Brycinus lateralis* is short lived, matures early, and spawns few eggs, often, over a protracted period, so it can be classified as opportunistic and thrives in environments with unpredictable disturbances (Hay 1995; Booth and McKinlay 2001). Comparatively, *C. gariepinus*, *C. ngamensis* and *S. intermedius* are classified as periodic strategists, because they are typically long lived, have high fecundities and low juvenile survivorship, and inhabit environments with predictable variability (Willoughby and Tweddle 1978; Bruton 1979a; van der Waal 1985; Merron and Mann 1995; Wartenberg et al. 2013). *Hepsetus cuvieri* and *S. macrocephalus* are classified as equilibrium strategists, which are typically medium to long lived, maturing at a moderate age, with low fecundity and high juvenile survivorship as a result of some parental care (van der Waal 1985; Merron et al. 1990; Winemiller 1991a). Equilibrium strategists usually do well in stable environments where competition and predation are important ecological drivers (Winemiller and Rose 1992). These life history strategies group similar species together with respect to their reproductive guild, longevity and body size, as well as their response to environmental disturbance (Winemiller and Rose 1992). It is hypothesised that species of similar life history strategies might demonstrate similar growth rate trends with varying environmental conditions.

Variation in fish growth rates have been attributed to factors influencing feeding rates, the nutritional value and availability of prey items (Welcomme 2001), and anthropogenic factors such as overfishing (Law 2000; Enberg et al. 2012). In floodplain rivers, the magnitude and duration of the flood pulse is a major factor controlling the availability and abundance of food resources (Junk et al. 1989; Smith 1991; Bayley 1995), and peaks in fish body condition during flooding has been documented (Welcomme 1975; Gomes and Agostinho 1997). As a result, seasonal growth has been documented, for example *Labeo dussumieri* were able to utilise the food resources and productivity associated with increased water levels and flow during the two monsoon seasons in the Mahaweli Ganga, Sri Lanka (Smith 1991). Bayley (1988) found faster growth during the rising water season in omnivorous fishes in the central Amazon floodplain, as a result of an increase in food availability. De Graaf (2003) found that growth and fisheries yields of *Colisa fasciatus* and *Channa punctata* correlated positively with flood magnitude most likely as a result of the promotion of primary and secondary production on the River Brahmaputra floodplain, Bangladesh. Gutreuter et al. (1999) found that the growth of fishes such as *Micropterus salmoides* and *Lepomis macrochirus* which exploited the littoral areas of the Upper Mississippi floodplain, increased in years of large floods and decreased in years of smaller floods. Dudley (1974) found that growth of young *Oreochromis andersonii*, *Oreochromis macrochir* and *Coptodon rendalli* was correlated with flood magnitude as a result of the increase in resources available, due to the abundant solar input into the shallow flooded areas during inundation of the Kafue River, Zambia. He also surmised that a reduction in inter and intraspecific competition during the flood could contribute to this increase in fish growth rates with increases in flood magnitude (Dudley 1974).

Anthropogenic manipulation in aquatic ecosystems through fisheries is a complex process that may have short and long term impacts on the phenotypic expression of traits (Law 2000; Enberg et al. 2012). Growth rate is one trait that is expected to change in response to fishing pressure (Enberg et al. 2012). Previous studies have reasoned that overfishing selects against fast growing, large fish, resulting in slower growth rates of the population (Favro et al. 1979; Kristiansen and Svåsand 1998; Edeline et al. 2007; Enberg et al. 2012). Alternatively, fishing may reduce the biomass of a population or stock, so reducing competition and consequently increasing growth rates (Boehlert et al. 1989; Law 2000). To complicate matters, Arantes et al. (2010) found that at high densities, *Arapaima* sp. in the Solimo˜es River, Brazil grew faster and matured earlier than at lower densities under heavy fishing pressure. They attributed this anomaly to an abundance of unlimited prey, a lag response to density dependent pressures, the complicated influence of overfishing on life history characteristics, and the potential that density dependent effects are less common in floodplain systems

(Arantes et al. 2010). Therefore, the effects of overfishing on fish growth rates are difficult to isolate from those of environmental variation as fishing pressure is rarely the only impacting factor (Rose et al. 2001; Arantes et al. 2010).

Relatively few studies have explored the age and growth of *B. lateralis*, *C. ngamensis*, *H. cuvieri*, and *S. macrocephalus*, despite their importance in subsistence, commercial and recreational fisheries in southern Africa (Duerre 1969; Willoughby and Tweddle 1978; Merron et al. 1990; Winemiller 1991a; Winemiller and Kelso-Winemiller 1994; Hay 1995; Winemiller and Kelso-Winemiller 1996; Booth and McKinlay 2001). These studies have focussed on Lake Liambezi (van der Waal 1985), the Shire Valley, Malawi (Willoughby and Tweddle 1978), the Barotse Floodplain of the Upper Zambezi River (Winemiller 1991a; Winemiller and Kelso-Winemiller 1994), and the Kavango River (Hay 1995); the age and growth of these species has not been assessed in the Caprivi Floodplain of the Upper Zambezi River or the Kwando River. In addition, previous studies have used for example, scales and length frequency analyses for the age and growth analysis of *B. lateralis* (van der Waal 1985; Hay 1995), pectoral spines and vertebrae for *C. ngamensis* (Willoughby and Tweddle 1978; van der Waal 1985), scales for *H. cuvieri* (van der Waal 1985; Winemiller and Kelso-Winemiller 1994), and scales for *S. macrocephalus* (Duerre 1969; van der Waal 1985; Winemiller 1991a), rather than metabolically inert otoliths which grow continually and have been proven as the most reliable structures for age estimation and consequently growth analyses (Campana and Neilson 1985; Campana and Thorrold 2001).

There is literature available on the age and growth of *S. intermedius* because of its high relative abundance and underutilisation in subsistence and commercial fisheries (Hecht 1980a; Merron and Mann 1995; Booth and Khumalo 2009); however, again the use of vertebrae (Balon and Coche 1974; Kolding et al. 1992), pectoral spines (Gaigher 1969; van der Waal 1985) and length frequency analysis (Hay 1995) for estimating age outweighs the use of otoliths (Hecht 1980a; Booth and Khumalo 2009). In addition, previous studies have assessed the age and growth of *S. intermedius* in Lake Kariba (Balon and Coche 1974; Kolding et al. 1992), Lake Liambezi (van der Waal 1985), the Kavango River (Hay 1995), two impoundments in South Africa (Gaigher 1969; Hecht 1980a) and one impoundment in Swaziland (Booth and Khumalo 2009), while information on the Caprivi Floodplain of the Upper Zambezi River and the Kwando River is lacking.

As a result of the importance of *C. gariepinus* in commercial fisheries (Willoughby and Tweddle 1978; Winemiller and Kelso-Winemiller 1996; Bokhutlo et al. 2015), studies on the age and growth of this species are abundant, focussing on a number of impoundments (van der Waal and Schoonbee 1975; Clay 1982; Clay 1984; Quick and Bruton 1984; Potts et al. 2008; Weyl and Booth 2008; Richardson et al. 2009; Wartenberg et al. 2013) and Lake Sibaya (Bruton and Allanson 1980) in South Africa, the Shire Valley (Willoughby and Tweddle 1978), the Okavango Delta (Chimatiro 2004; Bokhutlo et al. 2015), Lake Kariba (Kolding et al. 1992), Lake Liambezi (van der Waal 1985), and impoundments in Zimbabwe and Namibia (Clay 1982). Older studies used vertebrae (Willoughby and Tweddle 1978; Clay 1982; Clay 1984; Kolding et al. 1992) and pectoral spines (van der Waal and Schoonbee 1975; Bruton and Allanson 1980; Quick and Bruton 1984; van der Waal 1985) for age estimation, while more recent studies have used otoliths (Chimatiro 2004; Potts et al. 2008; Weyl and Booth 2008; Richardson et al. 2009; Wartenberg et al. 2013; Bokhutlo et al. 2015). Literature on the age and growth of *C. gariepinus* in the Caprivi Floodplains of the Upper Zambezi River, and the Kavango and Kwando rivers is not available.

The aim of this chapter is to assess, using otoliths as the hard structure for age estimation, the age, growth, relative condition and total mortality of the six study species and compare them between the Zambezi, Kavango and Kwando river systems in order to test two hypotheses. The first hypothesis is that fish growth rates will be influenced by the varying flood magnitudes of the three rivers, so fishes will grow fast in the Zambezi and Kavango rivers which receive large annual floods, and slower in the Kwando River, which receives small inconsistent annual floods. Secondly, I hypothesise that the intense fishing pressure imposed on the Zambezi River fishes will influence their growth and total mortality rates. Growth rates will either increase as a result of a reduction in competition, as hypothesised by Peel (2012) when comparing the growth rates of the three commercially important cichlids *O. andersonii*, *O. macrochir* and *C. rendalli* between the Zambezi, Kavango, and Kwando rivers and Lake Liambezi, or growth rates will decrease as a result of the selection and removal of fast growing individuals from the population, while total mortality rates will increase.

Methods

Sampling

Brycinus lateralis, *C. gariepinus*, *C. ngamensis*, *H. cuvieri*, *S. intermedius* and *S. macrocephalus* were caught using multifilament experimental gillnets, and floating 80 m longlines, with one meter snoods containing baited 9/0 circle hooks every four meters, both set at 6 pm and lifted at 6 am. This sampling was supplemented by D-net collections and rod and line angling. Three major otolith sampling events were conducted: July 2014 on the Zambezi River at Kalimbeza; June 2014 on the Kavango River at Mahango and January-February 2014 on the Kwando River at Nakatwa; where all of the *S. intermedius* and most of the *B. lateralis* were collected. Collection of a complete sample of otoliths from each species for age and growth analysis was attempted during these trips; however, for the less abundant species additional sampling events in 2014 (August 2014 on the Kavango River, July, August and November 2014 on the Kwando River) were used to supplement this data. In addition, *S. macrocephalus* were collected during bimonthly sampling trips to each river system in 2010 and 2011 as a part of a previous research project.

Fish were measured to the nearest mm fork length (FL) or total length (TL), weighed to the nearest gram and sexed. Using adult fish, sex ratios were compared to unity using chi squared tests (see Chapter 3). Either sagittal or asteriscus otoliths were removed, depending on species, cleaned and stored dry in labelled Eppendorf tubes. For *C. gariepinus, C. ngamensis, S. macrocephalus* and *S. intermedius* sagittal otoliths were set in clear polyester casting resin, and sectioned transversely through the nucleus at a thickness of 0.3 mm using a double bladed diamond edge saw. The sections were mounted on slides using DPX mountant and read using a dissecting microscope under transmitted light (Taylor and Weyl 2013). For *B. lateralis* and *H. cuvieri* whole asteriscus otoliths were immersed in methyl salicylate to improve the clarity of growth zones, and read using a dissecting microscope under transmitted light (Winker et al. 2010a; Winker et al. 2010b).

Growth zones were visible as alternating translucent and opaque zones. Growth zone counts were determined by counting the number of continuous opaque zones visible from the nucleus to the margin of the structure (Figure 5.1). Otoliths were read twice by one reader, and where these two readings differed, and a third time by an independent reader. Readings by the first reader were separated by a period of at least two weeks to avoid bias through memory of individual structures, and readings were conducted with no reference to biological data. An age estimate was accepted as the mode of the three readings if two were the same, or the median if the three readings were consecutive. If the readings differed by more than two, or if the structure was deemed unreadable by one reader, the otolith was rejected.

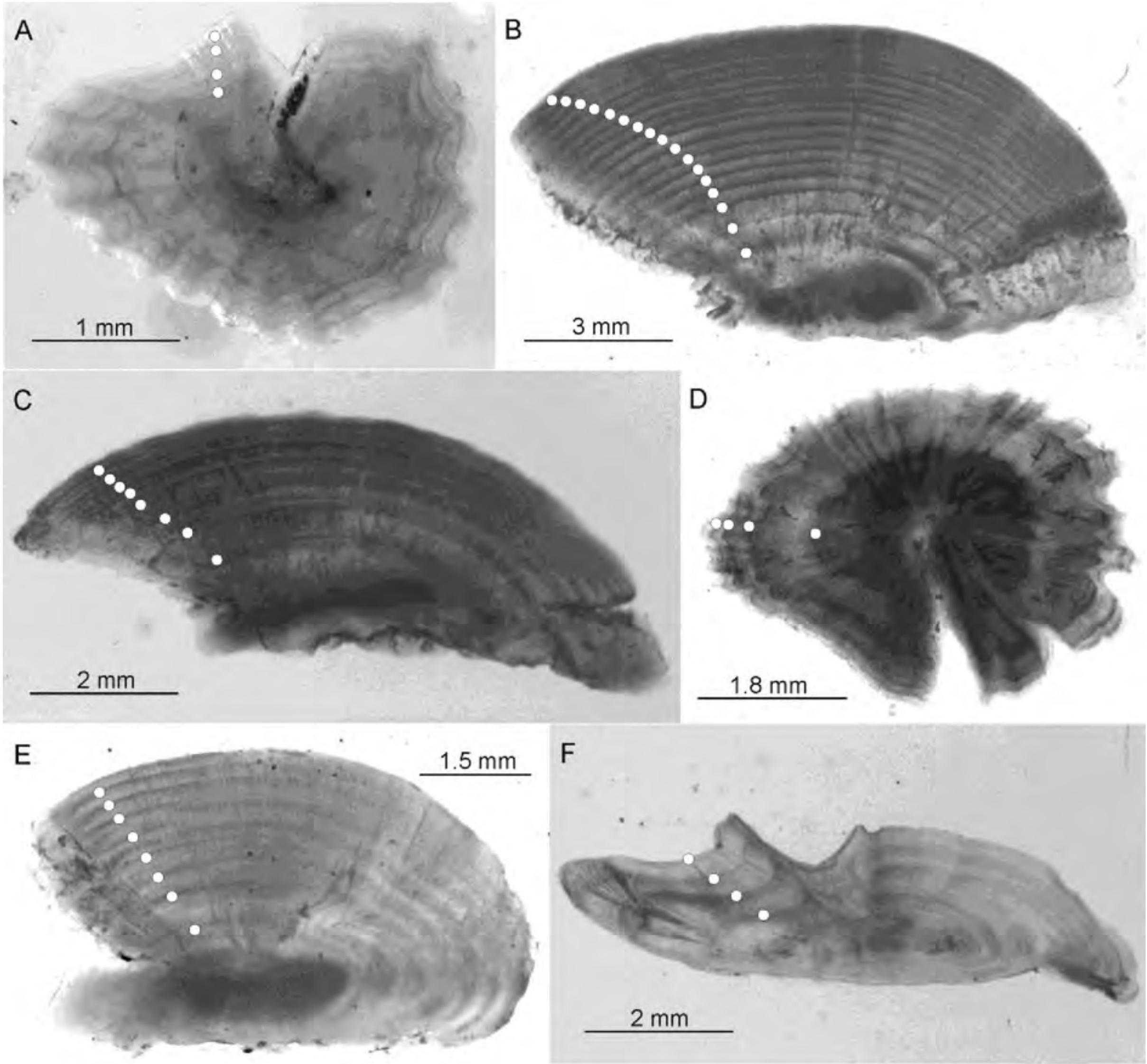

Figure 5.1: Photomicrograph illustrating the alternating opaque (marked) and translucent growth zones read using whole asteriscus otoliths for A: *Brycinus lateralis* and D: *Hepsetus cuvieri*, and using sectioned sagittal otoliths for B: *Clarias gariepinus,* C: *Clarias ngamensis,* E: *Schilbe intermedius* and F: *Serranochromis macrocephalus*.

Validation

Growth zone deposition has been validated as annual for *B. lateralis* using whole asteriscus otoliths by mark recapture of chemically tagged fish (MRCT) and edge analysis (EA), and for *S. macrocephalus* and *S. intermedius* using sectioned sagittal otoliths by edge analysis (EA) in Namibia (Taylor et al. 2016, Appendix 4). In addition, *S. intermedius* growth zone deposition was validated as annual using sectioned sagittal otoliths by marginal zone analysis (MZA) in an impoundment in Swaziland (Booth and Khumalo 2009), as annual using pectoral spines and as biannual using otoliths in two impoundments in South Africa by Hecht (1980a). For *H. cuvieri,* EA was used to validate growth zone deposition using whole asteriscus otoliths in Namibia (Taylor et al. 2016). Using sectioned sagittal otoliths, growth zone deposition of *C. gariepinus* has been validated as annual in two South African impoundments using MRCT (Weyl and Booth 2008; Wartenberg et al. 2013) and using EA in another South African impoundment (Potts et al. 2008), and in the Okavango Delta (Bokhutlo et al. 2015). In addition, *C. gariepinus* growth zone deposition has been validated as annual using pectoral spines or vertebrae by EA, marginal increment analysis (MIA), or known age fish (KA) in the Shire Valley, Malawi (Willoughby and Tweddle 1978), Elands River South Africa (van der Waal and Schoonbee 1975) and in a number of impoundments in Zimbabwe and one in Namibia (Clay 1982). Using vertebrae, growth zone deposition was validated as annual for *C. ngamensis* by MIA in the Shire Valley, Malawi (Willoughby and Tweddle 1978).

Therefore, aside from one study by Hecht (1980a) who found biannual deposition rates for *S. intermedius* in two impoundments in South Africa, growth zone deposition has been validated as annual for all of the study species. This is corroborated by 24 other validation studies on freshwater fishes in southern Africa (Table 5.1). From this literature review, only two other studies, one on a cichlid *Oreochromis mossambicus* (Hecht 1980b) and one on a cyprinid *Cyprinus carpio* (Winker et al. 2010b), recorded biannual growth zone deposition. Annual growth zone deposition is therefore assumed for most freshwater fishes in southern Africa, and as a result growth zone counts of the example species were approximated to age in years for growth analyses. This was not, however, tested within this chapter.

Table 5.1: Summary of validation studies on all freshwater fish species from southern Africa, including the ageing structure used, the growth zone deposition cycle, and the peak opaque zone detection period predicted by edge analysis. Validation methods include mark-recapture of chemically tagged fish (MRCT), mark recapture (MR), marginal increment analysis (MIA), edge analysis (EA), known age fish (KA), and corroboration of length frequency analysis (LFA) and tag recapture analysis (TRA).

Species	Location	Method	Structure	Cycle	Period	Reference
Oreochromis andersonii	Zambezi/Kavango, Namibia	MRCT, EA	Otoliths	Annual	Oct-Dec	Peel et al. 2016
	Kafue Floodplain, Zambia	EA	Scales	Annual	Oct-Jan	Dudley 1974
	Okavango Delta, Botswana	EA, MIA	Otoliths + Scales	Annual	Oct-Jan	Booth et al. 1995
Oreochromis macrochir	Zambezi/Kavango, Namibia	EA	Otoliths	Annual	Oct-Dec	Peel et al. 2016
	Kafue Floodplain, Zambia	EA	Scales	Annual	Oct-Jan	Dudley 1974
	Okavango Delta, Botswana	EA	Otoliths	Annual	Oct-Dec	Booth and Merron 1996
Coptodon rendalli	Zambezi/Kavango, Namibia	MRCT ,EA	Otoliths	Annual	Oct-Dec	Peel et al. 2016
	Kafue Floodplain, Zambia	EA	Scales	Annual	Oct-Jan	Dudley 1974
	Lake Chicamba, Mozambique	EA	Otoliths	Annual	Jun-Oct	Weyl and Hecht 1998
Oreochromis mossambicus	Lake Chicamba, Mozambique	EA	Otoliths	Annual	Jul-Oct	Weyl and Hecht 1998
	Venda Dams, SA	EA	Otoliths Scales	Biannual Annual	Feb-Mar, Jul-Aug Jun-Sep	Hecht 1980b
	Transval Dams, SA	MR	Scales	Annual	Aug	Le Roux 1961
	Mnjoli Dam, Swaziland	EA	Otoliths	Annual	Nov-Jan	Booth and Khumalo 2009
Serranochromis macrocephalus	Lake Liambezi, Kavango River, Namibia	MRCT, EA	Otoliths	Annual	Oct-Dec	Taylor et al. 2016
Clarias gariepinus	Okavango Delta, Botswana	EA	Otoliths	Annual	Jul-Sep	Bokhutlo et al. 2015
	Elands River, SA	KA	Pectoral spines	Annual	Nov-Dec	van der Waal and Schoonbee 1975
	Shire Valley, Malawi	MIA, LFA, TRA	Vertebrae	Annual	May-Aug	Willoughby and Tweddle 1978
	Glen Melville Dam, SA	MRCT	Otoliths	Annual		Weyl and Booth 2008
	Darlington Dam, SA	MRCT	Otoliths	Annual	Winter	Wartenberg et al. 2013
	Lake Mutirikwe, Zimbabwe	MIA	Vertebrae	Annual	Apr-Jul	Clay 1982
	Van der Kloof Dam, SA	MIA	Pectoral spines	Annual	Oct-Dec	Quick and Bruton 1984
	Kat and Laing Dams, SA	EA	Otoliths	Annual	May-Jun	Potts et al. 2008

Species	Location	Method	Structure	Cycle	Period	Reference
Clarias ngamensis	Shire Valley, Malawi	MIA	Vertebrae	Annual	May-Aug	Willoughby and Tweddle 1978
Schilbe intermedius	Mnjoli Dam, Swaziland	EA	Otoliths	Annual	Nov-Mar	Booth and Khumalo 2009
	Lake Liambezi, Namibia	EA	Otoliths	Annual	Sep-Nov	Taylor et al. 2016
	Venda Dams, SA	EA	Otoliths Pectoral spines	Biannual Annual	Jan-Mar, Jul-Aug Jan-Mar	Hecht 1980a
Brycinus lateralis	Lake Liambezi, Namibia	MRCT, EA	Otoliths	Annual	Aug-Oct	Taylor et al. 2016
Hepsetus cuvieri	Lake Liambezi, Namibia	EA	Otoliths	Annual	Oct-Nov	Taylor et al. 2016
Marcusenius pongolensis	Mnjoli Dam, Swaziland	EA	Otoliths	Annual	Mar-Jun	Booth and Khumalo 2009
Labeobarbus aeneus	Lake Gariep, SA	MRCT, EA	Otoliths	Annual	Jun-Sep	Winker et al. 2010a
Labeo capensis	Lake Gariep, SA	MRCT, EA	Otoliths	Annual	May-Aug	Winker et al. 2010a
Labeobarbus kimberleyensis	Lake Gariep, SA	MRCT, EA	Otoliths	Annual	Jul-Sep	Ellender et al. 2012b
Cyprinus carpio	Lake Gariep, SA	MRCT, EA	Otoliths	Biannual	Nov-Feb, Jun-Aug	Winker et al. 2010b
Micropterus salmoides	Eastern Cape Dams, SA	MRCT, EA	Otoliths	Annual	Sep-Jan	Taylor and Weyl 2013
	Lake Chicamba, Mozambique	EA	Otoliths	Annual	Jul-Oct	Weyl and Hecht 1999
	Lake Manyame, Zimbabwe	EA	Otoliths	Annual	Oct-Feb	Beamish et al. 2005
Myxus capensis	Binfield Dam, SA	KA	Otoliths	Annual		Ellender et al. 2012a
Mugil cephalus	Binfield Dam, SA	KA	Otoliths	Annual		Ellender et al. 2012a

Age estimation precision

Since growth zones have been validated as annual for the study species either by MRCT, EA, or both, opaque growth zones were equated to age in years for growth analysis. To assess the precision of the otoliths between species and systems, average percentage errors (APE) (Beamish and Fournier 1981) and coefficients of variation (CV) (Chang 1982) were calculated.

Average percent error was calculated for each species by river using:

$APE = \frac{1}{N}\sum_{j=1}^{N}\left[\frac{1}{R}\sum_{i=1}^{R}\frac{|X_{ij}-X_j|}{X_j}\right]$, where: N is the number of fish aged, R is the number of times each fish is aged, X_{ij} is the ith age estimation of the jth fish, X_j is the mean age of the jth fish. This was then multiplied by 100 to become the index of average percent error. The Coefficient of Variation (CV) was calculated as:

$CV_j = 100 \times \frac{\sqrt{\sum_{i=1}^{R}\frac{(X_{ij}-X_j)^2}{R-1}}}{X_j}$, where CV_j is the age precision estimate for the jth fish. The CV was averaged across all fish to produce a mean CV.

Age adjustment

Age adjustment theoretically provides a more accurate estimate of age than observed age data as it accounts for growth on a smaller temporal scale (Ballagh et al. 2011). It has been noted that this increase in accuracy can only be achieved if the spawning period and period of growth zone deposition are defined and discrete (e.g. DeVries and Grimes 1997). A protracted spawning period makes the allocation of a birth date inaccurate, while inaccuracies occur when the timing of annulus formation varies with year and location (e.g. Williams et al. 2005). However, even with a protracted spawning period, the inaccuracies are still less than if the exact number of growth zones are used. For example, *B. lateralis* spawns in the summer months between October and March, therefore the assigned birth date would be the median month of January. Using this birth date would mean the age estimates of those fish spawned in October and March would have an error of two months. Yet, if the number of opaque zones was used instead, this error could be up to 11 months for fish sampled immediately prior to growth zone deposition. Therefore, even though some of the species sampled had protracted spawning periods, their ages were adjusted according to the month of capture, the assigned "birth date" (median month of spawning) and the month of annuli deposition (Table

5.2). N refers to the number of complete annuli multiplied by 12. Months were given consecutive numbers from one (January) to 12 (December).

If $N = 0$, and the date of capture was between the birth date and the annulus deposition date, age was the number of months from the birth date to the date of capture. If the date of capture was between the annulus deposition date and the birth date, age was the number of months from the annulus deposition date to the date of capture.

If $N > 0$, the same principle to calculate months was applied; however for fish caught between the birth date and the annulus deposition date, N was added, while for fish caught between the annulus deposition date and the birth date, the number of months from the date of capture to the birth date were subtracted from N. All ages in months were converted to years by dividing by 12.

Table 5.2: The assigned birth month (modal month of spawning) and annuli deposition month used for age adjustment from each study species.

Species	Assigned birth date	Annuli deposition
B. lateralis	January [1,2,3]	September [4]
C. gariepinus	January [2,5,6]	August [7,8]
C. ngamensis	January [6]	August [6]
H. cuvieri	December [2,9]	October [4]
S. intermedius	January [2,10,11]	October [4]
S. macrocephalus	December [2,12]	November [4,13]

[1]Booth and McKinlay 2001, [2]van der Waal 1985, [3]Hay 1995, [4]Taylor et al. 2016, Appendix 4, [5]Bruton 1979a, [6]Willoughby and Tweddle 1978, [7]Bokhutlo et al. 2015, [8]Wartenberg et al. 2013, [9]Merron et al. 1990, [10]Booth and Khumalo 2009, [11]Merron and Mann 1995, [12]Kelley 1968, [13]Winemiller 1991a

Growth

Growth zone counts were approximated to age in years and age adjusted. Age and corresponding length data were fitted to the von Bertalanffy growth model of the form: $L_t = L_\infty(1 - e^{-K(t-t_o)})$, where L_t is the length at age t, L_∞ is the predicted asymptotic length, K is the Brody growth coefficient, and t_0 is the age at zero length (Ricker 1975). The parameters were estimated by minimising the binomial negative log-likelihood function using: $-LL = N ln(\hat{\sigma})$, where $\hat{\sigma}$ is the maximum likelihood estimate of the model standard deviation described as: $\hat{\sigma} = \sqrt{\frac{\sum_i (L_i - \hat{L}_i)^2}{N}}$ and $\hat{L}_i$ is the predicted total length-at-age, L_i is the observed length-at-age and N is the total number of observations. Since samples of *C. gariepinus* and *C. ngamensis* did not contain any small juveniles which could be used to estimate the t_0 parameter, this was set at zero so creating a two parameter von Bertalanffy growth equation. The variability of the parameters was estimated using the conditioned parametric bootstrap resampling technique described by Efron (1980) with 500 iterations. The percentile method (Buckland 1984) was applied to estimate 95% confidence intervals from resulting bootstrap vectors, where the 2.5% and 97.5% percentiles were used to obtain the lower and upper 95% confidence intervals, respectively.

To compare von Bertalanffy growth functions within rivers between sexes, and to compare combined sex von Bertalanffy growth functions between river systems, likelihood ratio tests (Kimura 1980) were used. In addition, to compare growth rates between systems the growth performance index phi prime (Φ') was calculated: $\Phi' = log10K + 2log10L_{\infty}$, where measurements in centimetres (Pauly and Munro 1984) were used. This index accounts for the interaction and dependence of the von Bertalanffy growth parameters L_{∞} and K and allows for comparisons of growth performance across populations (Winker et al. 2010b).

Average length-at-age was also calculated, and compared within each age class between river systems using a one way analysis of variance (ANOVA) and a Holm-Sidak pairwise multiple comparison procedure (three groups, data normally distributed and variance equivalent); Kruskal-Wallis one way ANOVA on ranks with a Dunns post hoc test (three groups, data not normally distributed or uneven variance); a student's *t*-test (two groups, data normally distributed); or a Mann-Whitney rank sum test (two groups, data not normally distributed). The significance level for all tests was $P < 0.05$.

Mortality

Total mortality was estimated using Hoenig's (1983) empirical equation as: $\ln(Z) = 1.44 - 0.982\ln(t_{max})$, where t_{max} is the maximum observed age, as mortality is inversely correlated to longevity across a diverse variety of taxa (Hoenig 1983; Hewitt and Hoenig 2005). Mortality could not be estimated using age-based catch curve analyses as adequate information was not collected.

Condition

Fish condition was quantified using the length-weight relationship of the form $W = aL^b$ where W is weight in grams and L is length as mm FL or TL. Length and weight were then linearly transformed, and their resulting regressions were compared using an analysis of covariance (ANCOVA). In addition the relative condition factor $Kn = \frac{W}{W'}$ (Le Cren 1951) was calculated where W is weight in grams and $W' = aL^b$, the length specific expected weight calculated from the grouped length-weight data from all populations under study. This relative condition factor displays fish condition around the value of one, whereby values greater than one indicate fish of a better than expected condition, while those with a condition factor of less than one indicate fish of a poorer condition than expected. To reduce bias in the calculation of the grouped length-weight relationship as a result of large sample size differences (for *B. lateralis*, *C. gariepinus* and *S. macrocephalus*), a subsample was chosen using a random number generator without replacement from the length-weight data of the populations with the largest sample sizes, so making all three population sample sizes equal. To compare relative condition factor between populations of each species, the ratio of the number of fish with a condition greater than one to the number of fish with a condition less than one was compared to the 1:1 relationship (unity) using chi squared tests (see Chapter 3).

Results

In total 2085 fish comprising 529 *B. lateralis*, 291 *C. gariepinus*, 113 *C. ngamensis*, 193 *H. cuvieri*, 662 *S. intermedius* and 297 *S. macrocephalus* were sampled from the three river systems for age and growth analyses.

Brycinus lateralis

The *B. lateralis* population structure was similar in the Zambezi (N = 210: 35 juveniles, 90 females, 84 males) and the Kavango (N = 107: 53 females, 53 males, one juvenile) rivers, while in the Kwando River significantly more females were sampled than males (N = 212: 12 juveniles, 142 females, 58 males; Table 5.3).

Ages were estimated by counting growth zones on whole asteriscus otoliths of *B. lateralis*, and the between reader precision was low for the Kavango River sample (APE > 8; CV > 10), which had the lowest average age, while precision in the Zambezi and Kwando rivers was high (Table 5.3; APE 1.75 – 2.36; CV 2.27 – 3.07).

Brycinus lateralis grew faster in the Zambezi River compared to in the Kwando River (likelihood ratio test; $\chi^2 = 354.83$; $P < 0.05$). In the Kavango River growth was more linear and exhibited high individual variability (Figure 5.2), especially within the first age class, and those fish of asymptotic lengths were not adequately sampled. As a result, the growth parameter t_0 for the Kavango River population was significantly different to that of both the Zambezi and the Kwando river populations (likelihood ratio test, Zambezi versus Kavango: $\chi^2 = 58.15$; $P < 0.05$; Kavango versus Kwando: $\chi^2 = 298.63$; $P < 0.05$). The Zambezi population had the best growth performance, followed by the Kwando and finally the Kavango populations (Table 5.3). Females grew faster than males and to larger sizes in the Zambezi and Kavango rivers (likelihood ratio test; Zambezi $\chi^2 = 24.75$; $P < 0.05$; Kavango $\chi^2 = 8.12$; $P < 0.05$), while in the Kwando River the growth rates of females and males were not significantly different (likelihood ratio test; $\chi^2 = 6.20$; $P = 0.10$).

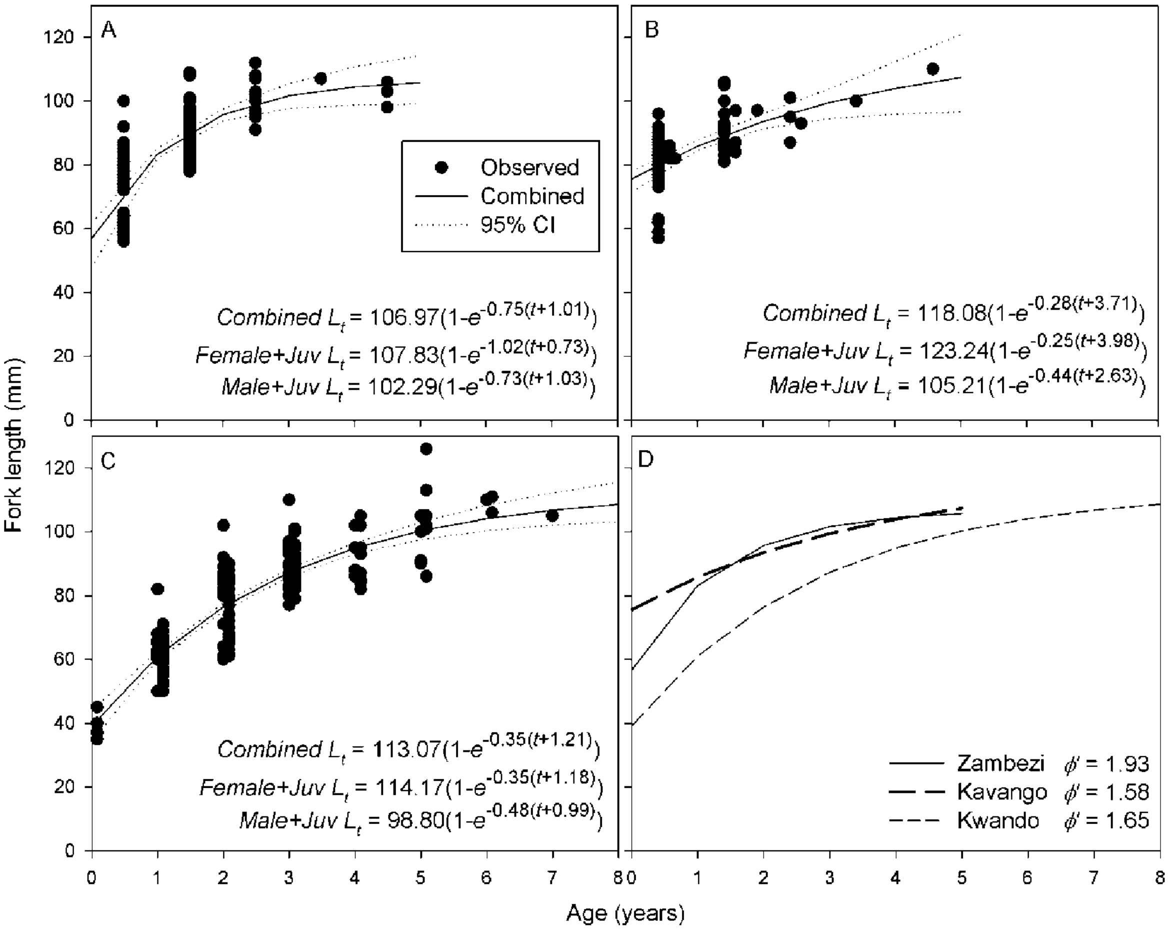

Figure 5.2: The observed lengths at age and von Bertalanffy growth model maximum likelihood estimates (MLE) for *Brycinus lateralis* populations for the combined sample, females (+juveniles) and males (+juveniles) from A: the Upper Zambezi River, B: the Kavango River, C: the Kwando River, Namibia, and D: a comparison of MLEs and phi prime values for all three rivers.

Table 5.3: Sample size (N), population structure (sex ratio males: females), age estimation precision (N rej. = otoliths rejected as unreadable, precision parameters APE and CV, mean age in years), life history characteristics (von Bertalanffy growth parameters, ϕ' = growth performance, $T_{\max}$ = maximum age, $L_{\max}$ = maximum length, Z = total mortality) and relative condition (above average condition: below average condition) for the six example species from the Zambezi, Kavango and Kwando rivers. Asterisks (*) = significantly different from unity (χ^2 tests; $P < 0.05$).

Species and location	N	Sex ratio (M:F)	N rej.	Precision APE(CV)	Mean age	t_o	L_∞	K	ϕ'	$T_{\max}$	$L_{\max}$	Z	Relative condition (>1:<1)
Brycinus lateralis													
Zambezi	210	1: 1.07	0	1.75 (2.27)	0.68	-1.01	106.97	0.75	1.93	4+	112	0.96	1: 1.12
Kavango	107	1: 1.02	0	8.41 (10.93)	0.41	-3.71	118.08	0.28	1.58	4+	110	0.95	2.31: 1*
Kwando	212	1: 2.45*	0	2.36 (3.07)	2.22	-1.21	113.07	0.35	1.65	7+	126	0.62	1: 3.31*
Clarias gariepinus													
Zambezi	85	1: 1.38	3	2.77 (3.69)	5.88	0	854.21	0.60	3.64	15+	1235	0.29	3.28: 1*
Kavango	133	1: 1.40	5	1.53 (2.03)	12.63	0	824.64	0.63	3.63	23+	1130	0.19	1: 1.59
Kwando	73	1: 1.12	7	3.59 (4.99)	8.98	0	890.44	0.32	3.40	16+	1130	0.28	1.17: 1
Clarias ngamensis													
Zambezi	1	-	0	-	-	-	-	-	-	-	-	-	-
Kavango	58	2.05: 1	5	4.26 (5.76)	6.21	0	514.73	0.91	3.38	16+	609	0.27	1: 4.20*
Kwando	54	1.70: 1	6	8.11 (10.30)	4.94	0	481.78	2.08	3.68	9+	675	0.48	2.83: 1*
Hepsetus cuvieri													
Zambezi	90	1: 1.07	0	0.74 (0.96)	0.93	-1.12	399.01	0.43	2.84	4+	425	0.95	1: 1.07
Kavango	14	1: 1.80	0	0.68 (0.88)	4.57	-2.33	385.82	0.29	2.63	8+	381	0.52	-
Kwando	89	1: 1.80	1	4.63 (6.12)	3.19	-0.75	362.00	0.48	2.80	8+	422	0.51	1: 4.69*
Schilbe intermedius													
Zambezi	200	1: 3.92*	1	5.13 (6.66)	0.69	-0.91	228.98	0.48	2.41	3+	222	1.23	1: 1.01
Kavango	260	1: 2.57*	1	7.79 (10.34)	2.57	-1.81	314.45	0.22	2.33	7+	331	0.58	1: 1.51*
Kwando	202	1: 1.22	2	8.07 (10.68)	3.39	-0.84	243.25	1.18	2.85	8+	300	0.54	1: 1.40
Serranochromis macrocephalus													
Zambezi	139	1: 1.02	1	25.28 (33.23)	1.02	-0.06	267.89	1.30	2.97	3+	388	1.15	1.05: 1
Kavango	112	1.10: 1	0	13.64 (18.61)	1.96	0.03	317.86	0.87	2.94	5+	396	0.75	1: 1.22
Kwando	46	2.46: 1*	0	6.59 (8.77)	3.63	0.08	267.16	0.97	2.84	8+	306	0.51	1: 5.43*

The average length-at-age data for ages 0+ to 4+ illustrates the fast growth rates of *B. lateralis* from the Zambezi and Kavango rivers compared to those from the Kwando River (Table 5.4).

Table 5.4: Average lengths (mm FL) at age ± SD (sample size) for the combined samples of *Brycinus lateralis* from the Zambezi, Kavango and Kwando rivers, Namibia. Significant differences of each age group between river systems are denoted using different letter superscripts.

Age (years)	Zambezi	Kavango	Kwando
0+	72.4 ± 10.6 (90)^a	80.2 ± 6.6 (73)^b	39.4 ± 8.1 (6)^c
1+	90.5 ± 5.9 (105)^a	90.0 ± 6.5 (27)^a	62.3 ± 4.5 (73)^b
2+	100.6 ± 6.4 (11)^a	94.2 ± 5.0 (5)^a	77.2 ± 10.4 (51)^b
3+	107 (1)	100 (1)	88.2 ± 6.3 (54)
4+	102.3 ± 4.0 (3)	110 (1)	91.5 ± 7.8 (13)
5+			101.7 ± 11.8 (11)
6+			109.0 ± 11.2 (3)
7+			105 (1)

The length weight relationships of *B. lateralis* from the Zambezi, Kavango and Kwando rivers are illustrated in Table 5.5. Relative condition was average in the Zambezi River, above average in the Kavango River, and below average in the Kwando River (Table 5.3). Total mortality rates were higher in the Zambezi and Kavango rivers where the maximum age was 4+ years, and low in the Kwando River where the maximum age was 7+ years (Table 5.3).

Clarias gariepinus

The *C. gariepinus* population structures were similar in the Zambezi, Kavango and Kwando rivers (Table 5.3) and overall only one juvenile *C. gariepinus* was sampled, from the Zambezi River.

Ages were estimated by counting growth zones on sectioned sagittal otoliths of *C. gariepinus*, and the between reader precision was high for the Zambezi, Kavango and Kwando river samples (APE 1.51 – 3.59; CV 2.03 – 4.99). Between three and seven otoliths were rejected as unreadable for this species (Table 5.3) as a result of stacking of growth zones on the edges of older otoliths.

Growth rates of *C. gariepinus* were highly variable in all river populations, as illustrated by the average lengths at age (Table 5.6), and due to the lack of small fish, t_0 was set to zero and two parameter von Bertalanffy growth models used for between river comparisons (Figure 5.3). The Zambezi and Kavango river *C. gariepinus* growth rates were not significantly different (likelihood ratio test; $\chi^2 = 1.37$; $P = 0.50$), while the Zambezi River population grew significantly faster than the Kwando River population (likelihood ratio test; $\chi^2 = 6.11$; $P = 0.047$). In addition, although the interaction of the variables did not differ significantly (likelihood ratio test; $\chi^2 = 4.76$; $P = 0.09$), the Kavango River population grew significantly faster than the Kwando River population (likelihood ratio test on K; $\chi^2 = 4.70$; $P = 0.03$). Phi prime values illustrated the fast growth of the Zambezi and Kavango river populations and the slow growth of the Kwando River population. Males reached longer maximum lengths than females in the Zambezi (males = 1235 mm TL, females = 1050 mm TL) and Kavango (males = 1130 mm TL, females = 939 mm TL) rivers, while in the Kwando River females grew to longer lengths (1130 mm TL) than males (1115 mm TL). The oldest fish sampled from all three rivers was a 23+ year old female from the Kavango River.

Table 5.5: The length-weight relationship parameters (a: intercept and b: slope), sample size (N) and correlation coefficients (R^2) for the example species from the Zambezi, Kavango and Kwando rivers. Letter superscripts denote the results of the analysis of covariance comparing the linearly transformed length weight relationships of each species between rivers.

Species		Zambezi	Kavango	Kwando
Brycinus lateralis	a	3.19E-06^{a}	7.37E-06^{ab}	2.24E-06^{b}
	b	3.34^{a}	3.16^{a}	3.40^{a}
	N	210	106	207
	R^2	0.90	0.92	0.95
Clarias gariepinus	a	1.53E-05^{a}	1.79E-06^{a}	1.80E-05^{a}
	b	2.90^{a}	3.19^{a}	2.86^{a}
	N	77	127	65
	R^2	0.95	0.89	0.95
Clarias ngamensis	a	-	2.24E-05^{a}	8.50E-05^{a}
	b	-	2.81^{a}	2.61^{a}
	N	-	52	46
	R^2		0.89	0.92
Hepsetus cuvieri	a	1.76E-06^{a}	2.81E-05^{b}	7.94E-06^{c}
	b	3.35^{a}	2.87^{b}	3.07^{c}
	N	87	14	74
	R^2	0.99	0.95	0.98
Schilbe intermedius	a	4.66E-06^{a}	1.02E-05^{b}	1.47E-06^{a}
	b	3.17^{a}	3.02^{b}	3.37^{a}
	N	199	254	199
	R^2	0.99	0.98	0.96
Serranochromis macrocephalus	a	2.65E-06^{a}	3.21E-05^{b}	5.63E-05^{c}
	b	3.34^{a}	2.88^{b}	2.76^{c}
	N	121	111	45
	R^2	0.98	0.96	0.92

Table 5.6: Average lengths (mm TL) at age ± SD (sample size) for the combined samples of *Clarias gariepinus* from the Zambezi, Kavango and Kwando rivers, Namibia. Significant differences of each age group between river systems are denoted using different letter superscripts.

Age (years)	Zambezi	Kavango	Kwando
0+	470 (1)		
1+			
2+	433 (1)	495.0 (1)	
3+	816.7 ± 203.4 (3)	1036.0 (1)	702.0 (1)
4+	809.3 ± 142.1 (20)	694.0 ± 125.9 (2)	805.3 ± 224.8 (3)
5+	801.9 ± 159.2 (17)^{a}	744.0 ± 106.0 (5)^{a}	726.6 ± 202.8 (9)^{a}
6+	818.0 ± 138.2 (20)^{a}	830.3 ± 69.4 (7)^{a}	786.8 ± 142.2 (6)^{a}
7+	867.0 ± 164.2 (9)^{a}	793.0 ± 151.9 (6)^{ab}	693.5 ± 164.8 (11)^{b}
8+	785.0 ± 28.3 (2)	742.3 ± 98.5 (4)^{a}	830.0 ± 99.4 (6)^{a}
9+	1022.5 ± 300.5 (2)	801.4 ± 95.7 (9)^{a}	769.5 ± 106.9 (4)^{a}
10+		828.4 ± 121.6 (9)	925.0 (1)
11+	800.0 ± 14.1 (3)	860.0 (1)	
12+	942.0 (1)	840.9 ± 90.7 (7)^{a}	799.7 ± 164.5 (6)^{a}
13+		885.3 ± 49.1 (4)^{a}	894.2 ± 118.1 (14)^{a}
14+	807.0 (1)	806.2 ± 84.7 (13)^{a}	1041.5 ± 131.3 (4)^{b}
15+	911.0 ± 213.5 (2)	830.9 ± 94.8 (20)	
16+		841.9 ± 105.3 (17)	950.0 (1)
17+		838.8 ± 88.0 (12)	
18+		824.7 ± 81.1 (7)	
19+		793.5 ± 40.3 (2)	
23+		700.0 (1)	

The length weight relationships are illustrated in (Table 5.5), and *C. gariepinus* were of above average condition in the Zambezi River, and of average condition in the Kavango and Kwando rivers (Table 5.3).

Total mortality rates were higher in the Zambezi and Kwando rivers where the maximum ages were 15+ and 16+ years respectively and low in the Kavango River where the maximum age was 23+ years (Table 5.3).

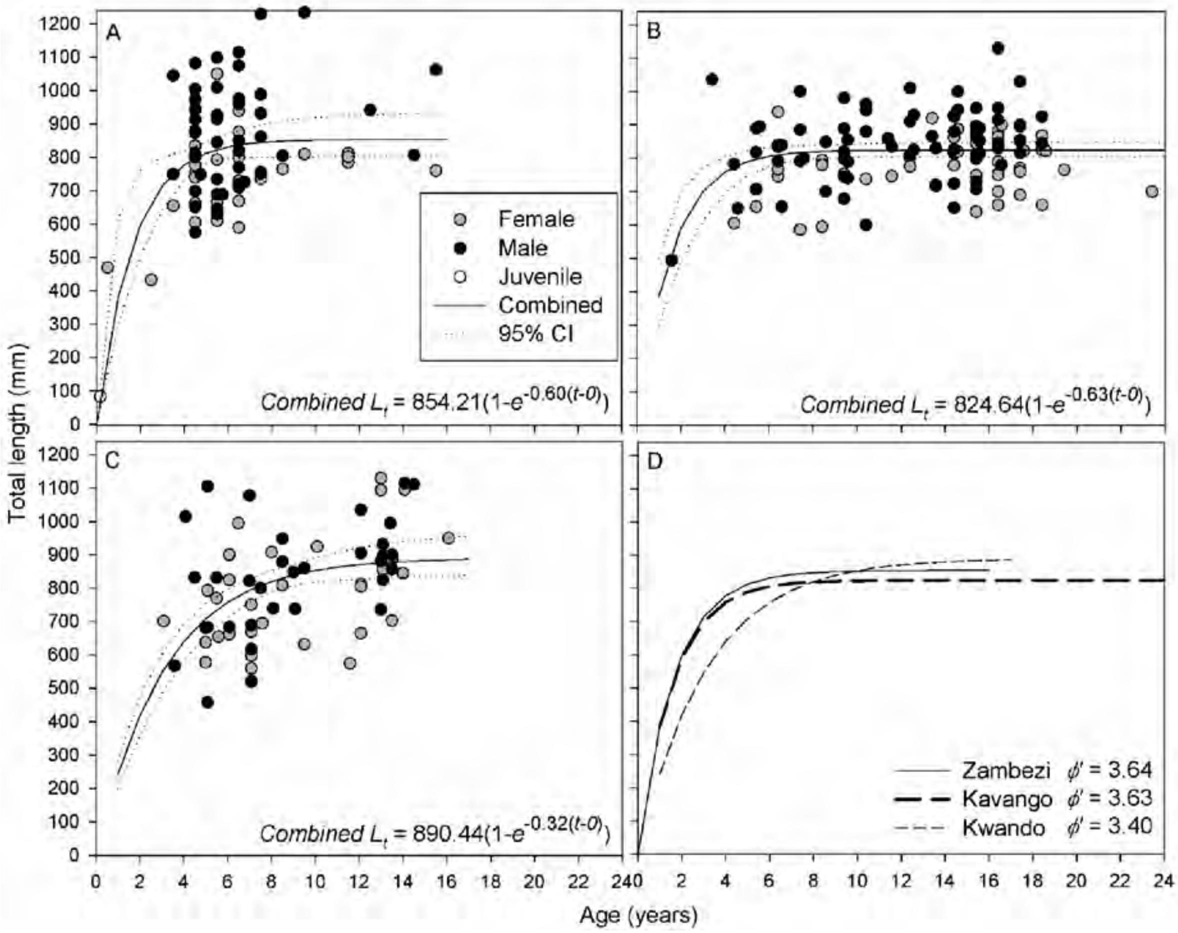

Figure 5.3: The observed lengths at age for females and males and von Bertalanffy growth model maximum likelihood estimates (MLE) for *Clarias gariepinus* populations for the combined sample from A: the Upper Zambezi River, B: the Kavango River, C: the Kwando River, Namibia, and D: a comparison of MLEs and phi prime values for all three rivers.

Clarias ngamensis

Samples of *C. ngamensis* were difficult to obtain from the Zambezi River, however in the Kavango and Kwando rivers, population structure was similar (Table 5.3) and no juvenile samples were collected.

Ages were estimated by counting growth zones on sectioned sagittal otoliths of *C. ngamensis*, and the between reader precision was high for the Kavango River samples (APE 4.26; CV 5.76), and lower for the Kwando River samples (APE 8.11; CV 10.30). Five and six otoliths respectively were rejected as unreadable for this species from the Kavango and Kwando rivers (Table 5.3).

Growth rates were estimated to be initially fast in both populations, although no juvenile fish were sampled (Table 5.7). Both populations exhibited considerable individual variation in growth, and the Kavango River population grew to a longer asymptotic length, while the Kwando River population grew at a faster rate than the Kavango River population (Figure 5.4). Overall growth described using a two parameter von Bertalanffy growth equation, was significantly different between populations (likelihood ratio test; $\chi^2 = 6.85$; $P = 0.03$). Phi prime values indicated the Kwando River population had better growth performance than the Kavango River population (Table 5.3). Similarly to *C. gariepinus*, the large individual variation in growth coupled with the lack of juvenile fish sampled for the *C. ngamensis* populations may have reduced the accuracy of the von Bertalanffy growth comparison, and average lengths at age were not significantly different between the ages of 3 and 6 years when sample sizes were sufficient for comparisons (Table 5.7). From the observed data females were smaller than males (Kavango River maximum lengths of 532 and 609 mm TL; Kwando River maximum lengths of 498 and 675 mm TL respectively), and the oldest fish was a 16+ years old female from the Kavango River (Figure 5.4; Table 5.3).

Table 5.7: Average lengths (mm TL) at age ± SD (sample size) for the combined samples of *Clarias ngamensis* from the Zambezi, Kavango and Kwando rivers, Namibia. Significant differences of each age group between river systems are denoted using different letter superscripts.

Age (years)	Kavango	Kwando
1+		456.7 ± 33.3 (3)
2+	473.0 ± 25.6 (4)	437.0 (1)
3+	493.3 ± 25.4 (6)^a	491.2 ± 34.6 (5)^a
4+	489.2 ± 46.2 (11)^a	466.6 ± 49.6 (7)^a
5+	496.8 ± 39.9 (5)^a	470.1 ± 69.8 (19)^a
6+	548.1 ± 29.5 (8)^a	508.1 ± 83.8 (9)^a
7+	532.3 ± 64.2 (8)	458.0 ± 31.1 (2)
8+	493.4 ± 46.1 (5)	665.0 (1)
9+	489.0 (1)	415.0 (1)
10+	497.0 (1)	
11+		
12+	507.0 ± 52.0 (3)	
16+	478.0 (1)	

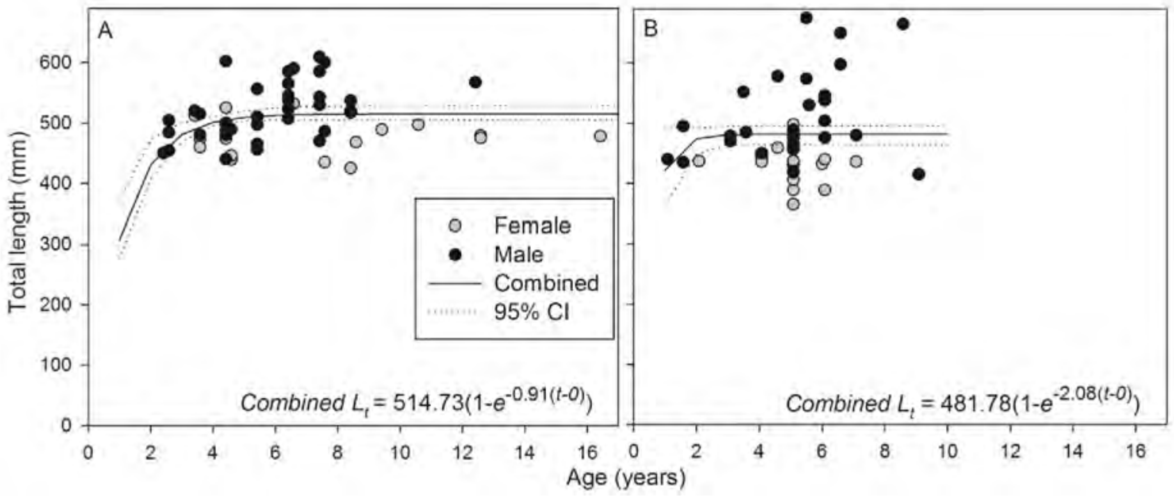

Figure 5.4: The observed lengths at age for females and males, and the von Bertalanffy growth model maximum likelihood estimates (MLE) for *Clarias ngamensis* populations for the combined sample from A: the Kavango River and B: the Kwando River, Namibia.

Clarias ngamensis had greater than average relative condition in the Kwando River and below average relative condition in the Kavango River (Table 5.3), and length weight relationships are illustrated in Table 5.5.

Total mortality rates were higher in the Kwando River compared to in the Kavango River as a result of the differences in maximum age (Table 5.3).

Hepsetus cuvieri

Population structures were similar in the Zambezi, Kavango and Kwando rivers (Table 5.3), however in the Kavango River *H. cuvieri* were difficult to sample and as a result a small sample size of 14 fish were collected.

Ages were estimated by counting growth zones on whole asteriscus otoliths of *H. cuvieri*, and the between reader precision was high (APE 0.68 - 4.63; CV 0.88 – 6.12) for all populations sampled (Table 5.3).

Growth rates for the *H. cuvieri* from the Kwando and Kavango rivers was not significantly different (likelihood ratio test; χ^2 = 2.40; P = 0.49) and both populations grew slower than the Zambezi River population (likelihood ratio test, Zambezi versus Kavango: χ^2 = 8.09; P < 0.05; Zambezi versus Kwando: χ^2 = 25.24; P < 0.05) (Figure 5.5). Phi prime values suggested the growth performance of the Zambezi River *H. cuvieri* population was highest, followed by the Kwando and Kavango river populations (Table 5.3). In the Zambezi and Kwando rivers where sample sizes were sufficient, females grew faster and to larger sizes than males (Zambezi River likelihood ratio test; $\chi^2 = 10.42$; $P < 0.05$; Kwando River likelihood ratio test; $\chi^2 = 14.44$; $P < 0.05$).

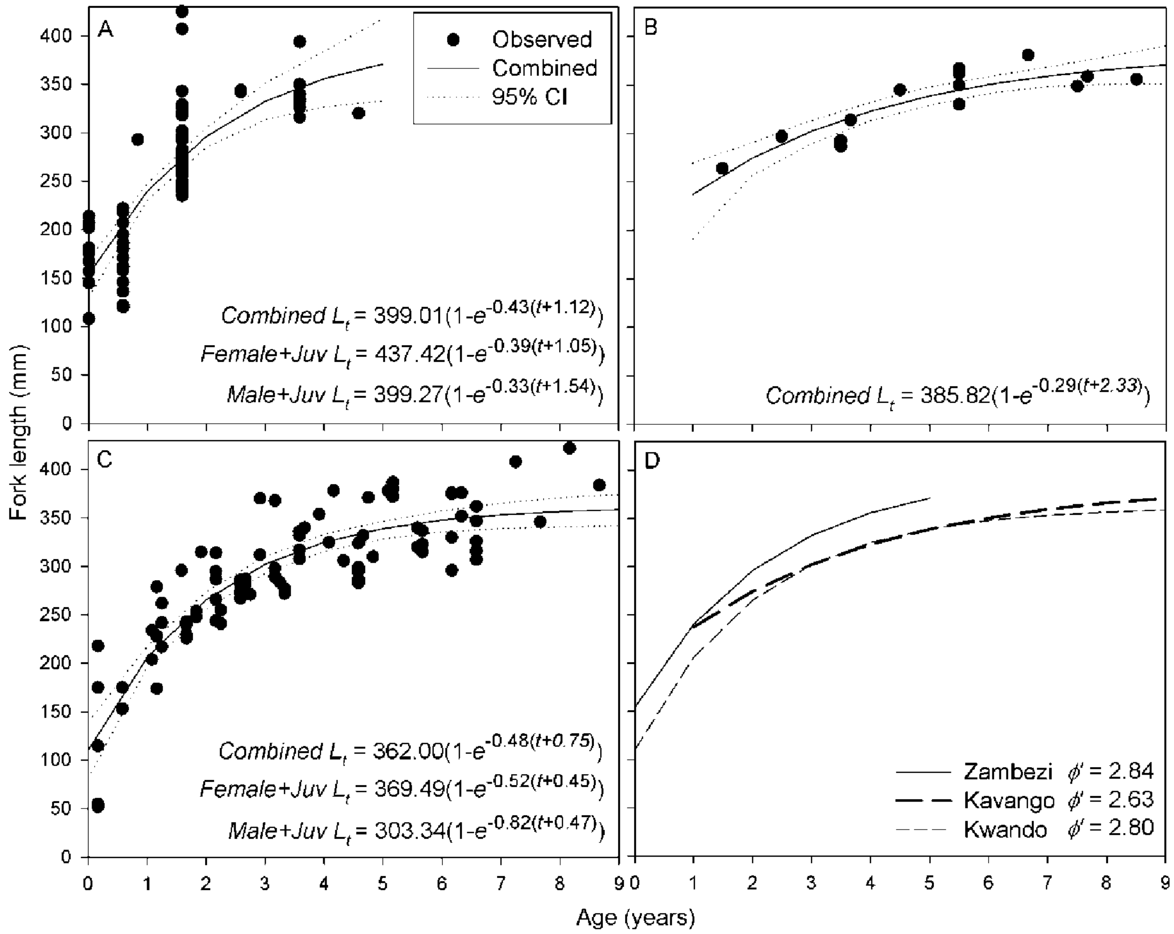

Figure 5.5: The observed lengths at age and von Bertalanffy growth model maximum likelihood estimates (MLE) for *Hepsetus cuvieri* populations for the combined sample, females (+juveniles) and males (+juveniles) from A: the Upper Zambezi River, B: the Kavango River, C: the Kwando River, Namibia, and D: a comparison of MLEs and phi prime values for all three rivers.

Average lengths at age for the Zambezi River population illustrated their faster growth rate compared to the Kavango and Kwando river populations for ages one and two, after which asymptotic growth was reached and sample sizes were small (Table 5.8). No significant differences between average lengths at age of *H. cuvieri* from the Kavango and Kwando river populations supported the results of the von Bertalanffy growth curve comparison.

Table 5.8: Average lengths (mm FL) at age ± SD (sample size) for the combined samples of *Hepsetus cuvieri* from the Zambezi, Kavango and Kwando rivers, Namibia. Significant differences of each age group between river systems are denoted using different letter superscripts.

Age (years)	Zambezi	Kavango	Kwando
0+	174.9 ± 32.5 (25)^{a}		134.7 ± 63.4 (7)^{a}
1+	281.1 ± 35.6 (55)^{a}	264 (1)	236.5 ± 31.2 (13)^{b}
2+	343.0 ± 1.4 (2)^{a}	297 (1)	274.4 ± 21.5 (18)^{b}
3+	341.7 ± 25.4 (7)^{a}	298.0 ± 14.2 (3)^{a}	313.8 ± 31.7 (14)^{a}
4+	320 (1)	345 (1)	323.1 ± 33.1 (11)
5+		352.3 ± 16.5 (4)^{a}	346.2 ± 30.0 (10)^{a}
6+		381 (1)	342.1 ± 28.9 (11)
7+		354.0 ± 7.1 (2)^{a}	377.0 ± 43.8 (2)^{a}
8+		356 (1)	403.0 ± 26.9 (2)

Length weight relationships are illustrated in Table 5.4, and *H. cuvieri* had average relative condition in the Zambezi River, and below average relative condition in the Kwando River (Table 5.3).

Total mortality rates were high in the Zambezi River where the maximum age of 4+ years was recorded, and low in the Kavango and Kwando rivers where the maximum age of 8+ years was recorded (Table 5.3).

Schilbe intermedius

Population structures were similar in the Zambezi and Kavango rivers where females outnumbered males and juveniles were sampled ($N_{juveniles} = 72$ and 20 respectively), while in the Kwando River the numbers of males and females were similar (Table 5.3) and only three juveniles were sampled.

Ages were estimated by counting growth zones on sectioned sagittal otoliths of *S. intermedius*, and the between reader precision was high for the Zambezi River samples (APE 5.13; CV 6.66) where average age was 0.69 years, and lower for the Kavango and Kwando river samples (APE >7; CV >10) where the average age was older than 2 years (Table 5.3).

Growth rates varied significantly between all three populations (likelihood ratio test, Zambezi versus Kavango: $\chi^2 = 8.56$; $P < 0.05$; Zambezi versus Kwando: $\chi^2 = 226.11$; $P < 0.05$; Kavango versus Kwando: $\chi^2 = 175.65$; $P < 0.05$), with the Kwando River population having the fastest growth rate (K), while the Kavango River population grew to the longest asymptotic length (L_{∞}) (Figure 5.6). The Zambezi River population grew relatively fast; however, older and larger fish were not present in the sample and therefore the asymptotic length was underestimated, while *S. intermedius* sampled from the Kavango and Kwando rivers exhibited large individual variation in growth (Figure 5.6). Phi prime indices (Table 5.3) and average length-at-age (Table 5.9) supported the superior growth performance of the Kwando River population, followed by the Zambezi and the Kavango river populations. Females grew significantly faster than males in the Zambezi (likelihood ratio test; $\chi^2 = 55.59$; $P < 0.05$), Kavango (likelihood ratio test; $\chi^2 = 107.12$; $P < 0.05$) and Kwando (likelihood ratio test; $\chi^2 = 224.56$; $P < 0.05$) rivers.

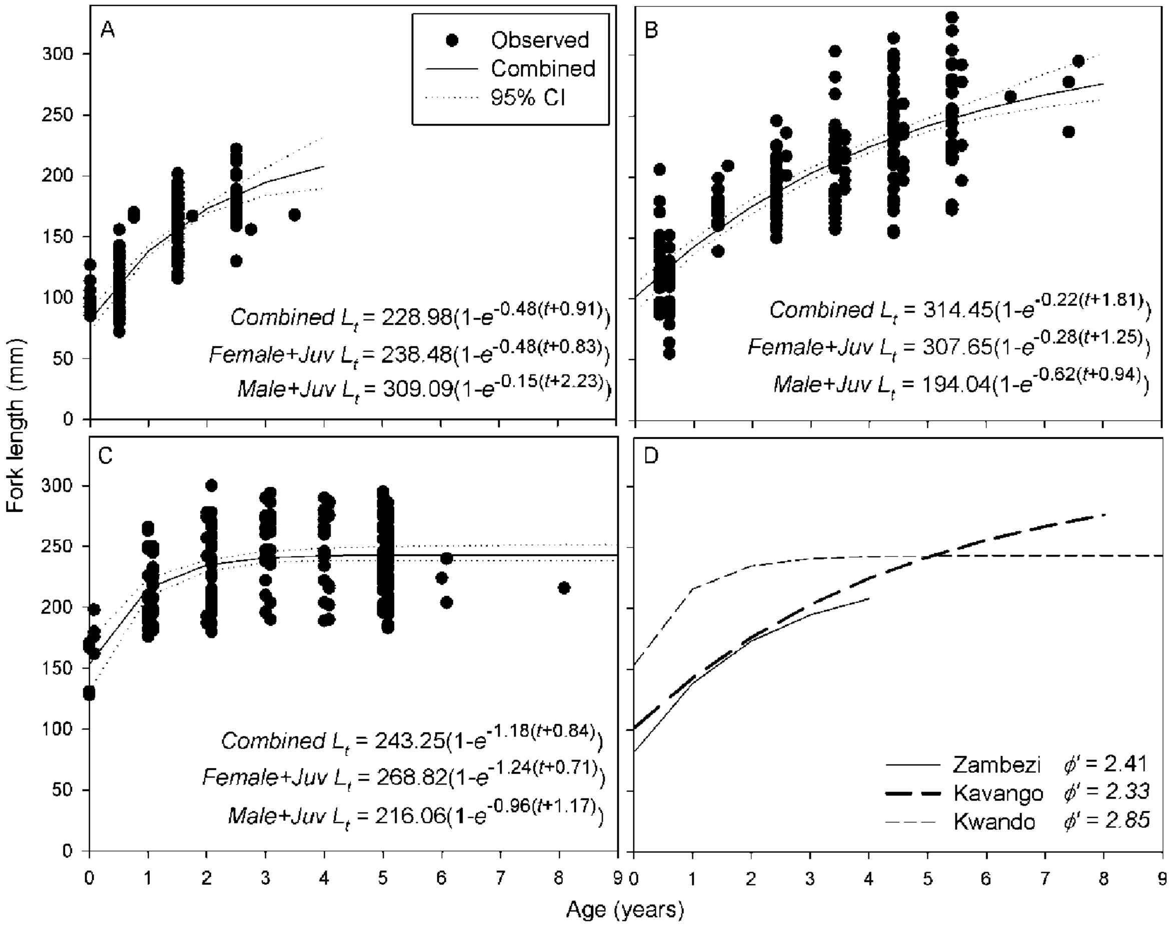

Figure 5.6: The observed lengths at age and von Bertalanffy growth model maximum likelihood estimates (MLE) for *Schilbe intermedius* populations for the combined sample, females (+juveniles) and males (+juveniles) from A: the Upper Zambezi River, B: the Kavango River, C: the Kwando River, Namibia, and D: a comparison of MLEs and phi prime values for all three river populations.

Table 5.9: Average lengths (mm FL) at age ± SD (sample size) for the combined samples of *Schilbe intermedius* from the Zambezi, Kavango and Kwando rivers, Namibia. Significant differences of each age group between river systems are denoted using different letter superscripts.

Age (years)	Zambezi	Kavango	Kwando
0+	104.8 ± 17.7 (86)^a	119.2 ± 27.4 (53)^b	160.2 ± 25.3 (9)^c
1+	161.9 ± 19.3 (91)^a	173.6 ± 15.8 (18)^a	213.5 ± 27.1 (32)^b
2+	181.6 ± 23.4 (20)^a	190.9 ± 22.2 (43)^a	236.7 ± 33.3 (37)^b
3+	162 ± 8.5 (2)^a	208.5 ± 29.6 (62)^b	251.0 ± 29.1 (25)^c
4+		231.5 ± 42.7 (46)^a	247.5 ± 34.0 (21)^a
5+		252.5 ± 38.8 (33)^a	239.9 ± 31.8 (72)^a
6+		266 (1)	222.7 ± 18.0 (3)
7+		270 ± 29.8 (3)	
8+			216 (1)

Schilbe intermedius from the Kavango River had significantly different length weight relationships (Table 5.5) and below average relative condition, compared to in the Zambezi and Kwando rivers where *S. intermedius* had average relative condition (Table 5.3). Mortality rates in the Zambezi River were much higher than in the Kavango and Kwando rivers, mirroring the low recorded maximum age of 3+ years compared to 7+ and 8+ years recorded in the other two rivers respectively (Table 5.3).

Serranochromis macrocephalus

In the Zambezi River, of the 138 *S. macrocephalus* sampled, 46 were males, 47 were females and 45 were juveniles, while in the Kavango River of the 112 *S. macrocephalus* sampled, 56 were males, 51 were females and five were juveniles. In the Kwando River, males outnumbered females (Table 5.3) and out of a total of 46 samples, 32 were males, 13 were females and one was a juvenile.

Ages were estimated by counting growth zones on sectioned sagittal otoliths of *S. macrocephalus,* and the between reader precision was low for the Zambezi and Kavango river samples (APE >10; CV >15) where the average age was between 1 and 2 years. In the Kwando River precision was higher (APE = 6.59; CV = 8.77) and the average age was 3.63 years.

Differences in growth rates were apparent between systems, with the Kavango River population growing significantly faster than both the Zambezi (likelihood ratio test; χ^2 =

15.67; $P < 0.05$) and Kwando (likelihood ratio test; $\chi^2 = 55.12$; $P < 0.05$) river populations. The Zambezi and the Kwando river populations did not show significant differences in growth (likelihood ratio test; $\chi^2 = 4.13$; $P = 0.25$) although the populations reached different maximum ages of 3+ and 8+ years respectively (Figure 5.7). This comparison was supported by the average length-at-age data (Table 5.10) and phi prime indices which highlighted the fast growth of Kavango and Zambezi river populations and the relatively slow growth of the Kwando River population where small fish were difficult to sample. In the Zambezi River males grew to a significantly longer asymptotic length than females (likelihood ratio test; $\chi^2 = 107.11$; $P < 0.05$), while there was no significant difference between the growth of females and males in the Kavango River (likelihood ratio test; $\chi^2 = 5.67$; $P = 0.13$). In the Kwando River the sample size was small, and as a result a comparison in growth rates between females and males could not be carried out with accuracy, although the maximum length reached of females (306 mm TL) was greater than males (252 mm TL).

The length weight relationships differed significantly between all river populations, and the Zambezi and Kavango river populations were of average relative condition, while the Kwando River population was below average condition (Table 5.3).

In the Zambezi River where a low maximum age of 3+ years was recorded, total mortality was highest, followed by in the Kavango River where the maximum age was 5+ years, and total mortality rates in the Kwando River were lowest and fish lived to the oldest maximum age of 8+ years (Table 5.3).

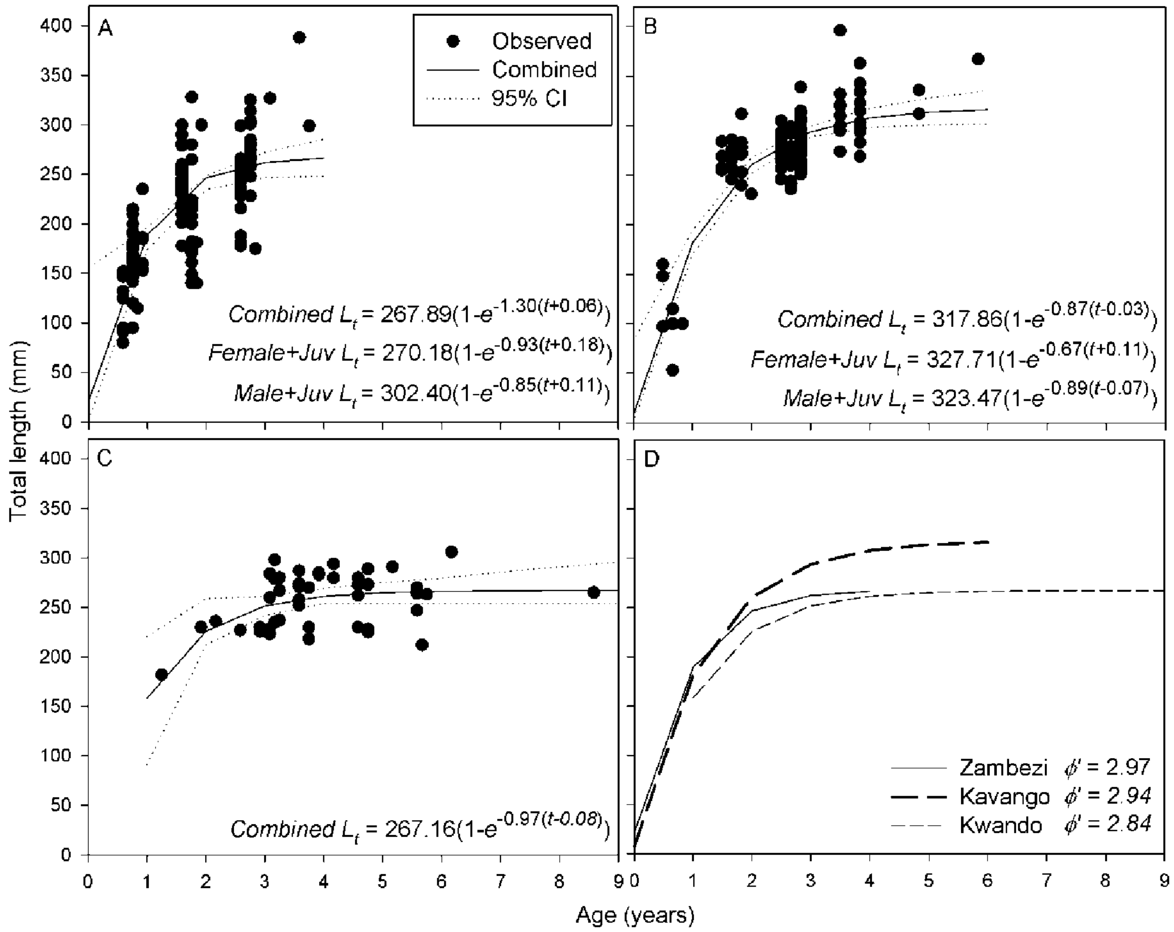

Figure 5.7: The observed lengths at age and von Bertalanffy growth model maximum likelihood estimates (MLE) for *Serranochromis macrocephalus* populations for the combined sample, females (+juveniles) and males (+juveniles) from A: the Upper Zambezi River, B: the Kavango River, C: the Kwando River, Namibia, and D: a comparison of MLEs and phi prime values for all three rivers.

Table 5.10: Average lengths (mm TL) at age ± SD (sample size) for the combined samples of *Serranochromis macrocephalus* from the Zambezi, Kavango and Kwando rivers, Namibia. Significant differences of each age group between river systems are denoted using different letter superscripts.

Age (years)	Zambezi	Kavango	Kwando
0+	153.8 ± 33.0 (42)^a	110.4 ± 35.6 (7)^b	
1+	230.2 ± 41.9 (54)^a	267.7 ± 18.2 (17)^b	182 (1)
2+	254.1 ± 38.5 (39)^a	277.9 ± 20.4 (65)^b	231.0 ± 4.6 (3)^a
3+	338.0 ± 45.5 (3)^a	315.4 ± 30.1 (20)^a	253.9 ± 25.3 (21)^b
4+		324.0 ± 16.9 (2)^a	266.8 ± 25.0 (12)^b
5+		367 (1)	259.1 ± 24.5 (7)
6+			306 (1)
7+			
8+			265 (1)

Discussion

Age estimation

The accuracy and precision of age estimates are directly related to the accuracy of growth estimates. There is strong support for the annual deposition of growth zones for all the study species in the literature (Willoughby and Tweddle 1978; Weyl and Booth 2008; Wartenberg et al. 2013; Taylor et al. In review), and as a result it can be assumed that age estimates are accurate. Measures of precision or the reproducibility of age estimates help quantify the error involved in age estimation (Beamish and Fournier 1981).

As a guideline for acceptable levels of precision, Campana (2001) reviewed 131 age estimation studies and found that the median CV was 7.6%, corresponding to an APE of 5.5%. In this study, for those species where age was determined using sectioned sagittal otoliths, precision improved with an increase in the average age of the population, as APE and CV were influenced to a greater extent by errors in age estimates of younger fish compared to older fish (Campana 2001). The low precision values calculated for *S. intermedius,* and *S. macrocephalus* in particular, were attributed to the difficulties in identifying the first annulus, a common problem in age estimation (Egger et al. 2004). In addition, incomplete and faint growth zones were present between *S. macrocephalus* annuli, most likely as a result of reproduction (Winemiller 1991a). Weak annuli and difficulty in identifying the first annulus have been noted by Bwanika et al. (2007) when determining the age of Nile tilapia using sectioned sagittal otoliths. Future studies on cichlids may consider burning otoliths to enhance the visibility of opaque zones (e.g. Booth et al. 1995; Booth and Merron 1996).

The lower precision of ages estimated using whole asteriscus otoliths from older populations of *H. cuvieri* may be attributed to the stacking of opaque zones on the otolith edge, which reduces the transparency of thicker, older otoliths. This is a common occurrence when whole otoliths are used for age estimation (Winker et al. 2010b), and future studies should consider sectioning the otoliths of older fish. This same phenomenon was not observed for *B. lateralis*, possibly because this species did not reach the same old ages as *H. cuvieri* (maximum ages of 7 and 8 years respectively); however this was most likely because the otoliths of *B. lateralis* were much thinner than those of *H. cuvieri* and as a result more transparent. Stacking of opaque zones on the edge of older otoliths was also found in *C. gariepinus* and *C. ngamensis* otoliths, and disagreement in age estimation between readers resulted in some otoliths being rejected. Since this disagreement occurred most commonly in older fish, the indices of precision were not affected and remained lower (maximum APE of 3.59%) than values of precision from other *C. gariepinus* populations sited in the literature (APE of 8-8.5%) (Richardson et al. 2009; Bokhutlo et al. 2015).

Growth

Brycinus lateralis

The life history characteristics of *B. lateralis* indicate a small, short lived species which produces few eggs, often, over an extended spawning season (Booth and McKinlay 2001). Growth was fast in the Zambezi and Kavango river populations, although growth performance in the latter was low, despite its good relative condition, possibly as a result of the absence of very small and large fish in the sample. The von Bertalanffy growth model for this population was linear. Growth was slower in the Kwando River population, despite the skewed sex ratio favouring females, the faster growing sex in the Zambezi and Kavango river populations. This skewed sex ratio has also been found by Booth and McKinlay (2001) in the Okavango Delta and by Hay (1995) in the Okavango River. Despite the slow growth and low condition of the Kwando River population, a maximum age and length of 7+ years and 126 mm FL was reached, making this the present longevity record for this species (Table 5.11), with a comparable maximum length to the Lake Kariba, Lake Liambezi and Okavango River populations (van der Waal 1985; Kolding et al. 1992; Hay 1995).

Hepsetus cuvieri

Hepsetus cuvieri have been described as a short lived, fast growing species (van der Waal 1985). This description was supported by the fast growing Zambezi River population; however, the Kwando River population grew slower to an older age of 8+ years despite being in poor relative condition. The sample size in the Kavango River was too small to estimate growth with any confidence. Previous studies show fast growth similar to that in the Zambezi River (van der Waal 1985; Winemiller and Kelso-Winemiller 1994), so making the Kwando River population the longevity record for this species (Table 5.11).

Table 5.11: A summary of studies that have described the age and growth of *Brycinus lateralis* (*B. lat*), *Clarias ngamensis* (*C. nga*), *Hepsetus cuvieri* (*H. cuv*), *Schilbe intermedius* (*S. int*) and *Serranochromis macrocephalus* (*S. mac*), the structure used for age estimation: otoliths (O), scales (S), vertebrae (V), pectoral spines (PS) and length frequency analysis (LF), their maximum age and length (mm), and their growth performance index phi prime (males, females).

Species	Location	Structure	max age	max length	Phi prime	Reference
B. lat	Upper Zambezi River	O	4	112	1.93	This study
B. lat	Kavango River	O	4	110	1.58	This study
B. lat	Kwando River	O	7	126	1.65	This study
B. lat	Lake Kariba	S	3	140		Balon and Coche 1974; Kolding et al. 1992
B. lat	Okavango River	S	4	135	1.99	Hay 1995
C. nga	Kavango River	O	16	609	3.38	This study
C. nga	Kwando River	O	9	675	3.68	This study
C. nga	Shire River	V	4	550	2.98, 2.94	Willoughby and Tweddle 1978
C. nga	Lake Liambezi	PS	6	590		van der Waal 1985
H. cuv	Upper Zambezi River	O	4	425	2.84	This study
H. cuv	Kwando River	O	8	422	2.80	This study
H. cuv	Lake Liambezi	S	5	470		van der Waal 1985
H. cuv	Upper Zambezi River	S	2	420		Winemiller and Kelso-Winemiller 1994
S. int	Upper Zambezi River	O	3	222	2.41	This study
S. int	Kavango River	O	7	331	2.33	This study
S. int	Kwando River	O	8	300	2.85	This study
S. int	Swaziland	O	8	280	2.44	Booth and Khumalo 2009
S. int	Venda Dams, SA	O	7	327	2.60	Hecht 1980a
S. int	Lake Kariba	V	6	340	2.08	Balon and Coche 1974; Kolding et al. 1992
S. int	Lake Liambezi	PS	5	330		van der Waal 1985
S. int	Okavango River	LF	5	290	2.25	Hay 1995
S. mac	Upper Zambezi River	O	3	388	2.97	This study
S. mac	Kavango River	O	5	396	2.94	This study
S. mac	Kwando River	O	8	306	2.84	This study
S. mac	Lake Liambezi	S	8	330		van der Waal 1985
S. mac	Barotse Floodplain	S	3	350		Winemiller 1991a
S. mac	Barotse Floodplain	S	5	360		Duerre 1969

Serranochromis macrocephalus

For *S. macrocephalus*, growth was fast to longer maximum lengths in the Zambezi and Kavango rivers compared to in the Kwando River, where *S. macrocephalus* lived to an old age of 8+ years. In the Kwando River population smaller fish were difficult to sample, *S.*

macrocephalus were in poor condition and males outnumbered females significantly. Growth is comparable to previous age and growth studies which used scales for age estimation (Table 5.11).

Clarias gariepinus

Clarias gariepinus is a fast growing, long lived species that exhibits exceptional individual variation in growth rates (Clay 1982; van der Waal 1985; Richardson et al. 2009; Wartenberg et al. 2013; Bokhutlo et al. 2015). Initial growth is fast with individuals reaching between 200 and 426 mm TL in their first year of life (Willoughby and Tweddle 1978; Bruton and Allanson 1980; van der Waal 1985; Bokhutlo et al. 2015), and growing to maximum lengths of 2000+ mm (58.9 kg) to a maximum age of 25 years (Bruton 1976; Wartenberg et al. 2013). Growth of the three populations under study expressed similar characteristics, initially fast and highly variable. Very few individuals were collected less than 500 mm TL, presumably as a result of this extremely fast initial growth most likely fuelled by the abundance of food on the floodplain at the time of spawning (van der Waal 1974; Chimatiro 2004), allowing juveniles to reach a size refuge from predation by the low water period when all fish are restricted to the main river channel (Bayley 1995).

The Zambezi River population grew fast, whereas the Kavango River population grew slower to the oldest age of 23 years. The Kwando River population grew the slowest and had the highest individual variation in growth. Growth performance of the Zambezi and Kavango river populations was higher than all other populations from the literature (Table 5.12), except those from an impounded population in South Africa (Quick and Bruton 1984). The growth rates of all three study populations tended to reach the theoretical asymptote after about four years. This trend is markedly different to historic *C. gariepinus* growth studies which estimated age using pectoral spines, vertebrae and length frequency analysis, and described short lived populations that exhibited linear growth (van der Waal and Schoonbee 1975; Willoughby and Tweddle 1978; Bruton and Allanson 1980; Clay 1982; Quick and Bruton 1984; van der Waal 1985). More recent studies that used sectioned sagittal otoliths to age *C. gariepinus* have modelled similar growth patterns whereby an asymptote is reached within the lifespan of the much longer lived population (Potts et al. 2008; Richardson et al. 2009; Wartenberg et al. 2013; Bokhutlo et al. 2015). Interestingly, Clay (1982) determined age using both pectoral spines and vertebrae and found *C. gariepinus* grew linearly with the vertebrae age estimates and asymptotically with the pectoral spine age estimates. Pectoral spines, vertebrae and length frequency analysis tend to underestimate age: as the lumen enlarges with age so engulfing or obscuring early annuli in pectoral spines (Clay 1982; Quick and Bruton 1984); a stacking of annuli occurs at the margin in vertebrae (Phelps et al. 2007); both pectoral spines and vertebrae may be resorbed (Weyl and Booth 2008); and length frequency analysis can only be used to estimate younger age classes (Chilton and Beamish 1982). Otoliths are generally considered the most reliable structure for age estimation (Campana and Neilson 1985; Campana and Thorrold 2001), and consequently asymptotic growth for *C. gariepinus* is more realistic than linear growth.

Table 5.12: A summary of studies that have described the age and growth of *Clarias gariepinus*, the structure used for age estimation: otoliths (O), scales (S), vertebrae (V), pectoral spines (PS) and length frequency analysis (LF), their maximum age and length (mm), and their growth performance index phi prime (males, females).

Location	Structure	max age	max length	Phi prime	Reference
Upper Zambezi River	O	15	1235	3.64	This study
Kavango River	O	23	1130	3.63	This study
Kwando River	O	16	1130	3.40	This study
Lower Okavango Delta	O	8	731	3.30	Bokhutlo et al. 2015
Xonxa Dam, SA	O	12	1260	3.40	Richardson et al. 2009
Shire Valley	O	9	630	2.89	Chimatiro 2004
Glen Melville Dam, SA	O	15	1310		Weyl and Booth 2008
Darlington Dam, SA	O	25	1240	3.11	Wartenberg et al. 2013
Kat River Dam, SA	O	10	1221	3.22	Potts et al. 2008
Laing Dam, SA	O	15	1230	3.53	Potts et al. 2008
Shire River	V	7	1000	3.22, 3.02	Willoughby and Tweddle 1978
Hardap Dam, Namibia	V	9	1480	3.16	Clay 1982
Lake Kyle, Zim	V	10	1020	3.06	Clay 1982
Lake Kariba, Zim	V	9	860	2.96	Clay 1982
Lake Mcllwayne, Zim	V	7	990	3.20	Clay 1982
Rynfield Dam, SA	V	7	620	3.11	Clay 1984
Lake Gariep, SA	V	8	1250	3.58	Clay 1984
Lake Kariba	V	11	820		Balon and Coche 1974; Kolding et al. 1992
Lake Liambezi	PS	8	1200		van der Waal 1985
Elands River, SA	PS	10	1105		van der Waal and Schoonbee 1975
Lake Sibaya, SA	PS	8	1088		Bruton and Allanson 1980
PJ le Roux Dam, SA	PS	8	1080	3.61, 3.67	Quick and Bruton 1984

Individual variation in growth has been attributed to environmental factors, genetic traits, social interaction/dominance hierarchies, and feeding behaviour (individual characteristics). As illustrated by van der Waal (1998), individual variation in growth could equip this species with two necessary strategies for survival under different environmental conditions: fast growers benefit under less variable weather conditions, while slow growers are able to survive under adverse conditions in shrinking water bodies by immersing themselves in mud. Similarly, Bokhutlo et al. (2015) attributed variation in growth to environmental factors, surmising that fish are isolated in floodplain microhabitats with differing prey abundance during the low water phase, essentially allowing fast growth in habitats with abundant prey and restricting growth in prey poor environments. Grobler et al. (1992) found that fast growing individuals had gained this advantage from an early age, and possessed consistently different enzyme allele frequencies compared to the slower growing individuals; however, they attributed individual variation in growth to a number of contributing factors, of which genetic, environmental and social interaction were the most probable. Martins et al. (2005) demonstrated how variation in growth was not as a result of social hierarchies, but rather due to differing feeding behaviours, where energetic active feeders grew faster than more docile inactive fish that chose to feed at the bottom of the tank, essentially a matter of individual preference. Individual variation in growth therefore may be as a result of a number of influential contributors, making *C. gariepinus* growth difficult to compare between river systems.

Clarias ngamensis

Clarias ngamensis has been described as a slow growing fish with a short life span (van der Waal 1985), however, as with *C. gariepinus*, *C. ngamensis* exhibited fast initial but highly variable growth. The Kwando River population had a higher growth performance and was in better relative condition than the Kavango River population; samples were not obtained from the Zambezi River. Growth performance was higher and *C. ngamensis* reached longer maximum lengths in the Kavango and Kwando river populations compared to those from Lake Liambezi and those from the Shire River (Table 5.11).

Schilbe intermedius

Schilbe intermedius grew fastest in the Kwando River reaching asymptotic lengths by 2 years of age, while in the Zambezi River growth was linear with no fish over 250 mm FL sampled. In the Kavango River growth was the slowest and *S. intermedius* were in poor condition, however fish reached the largest maximum length. Growth was highly variable for all three populations, as was found by Gaigher (1969). The growth performance of the Kwando River population was higher compared to all other studies from the literature (Table 5.11).

Female *S. intermedius* grew significantly faster than males in all three rivers, and the sex ratios of the Zambezi and Kavango river populations were skewed in favour of females. It may be surmised that if the sex ratio was skewed in the Kwando River population, growth would have been even faster to a larger maximum size due to the abundance of the faster growing females. A similar skewed sex ratio with females outnumbering males exhibited by *S. intermedius* has been reported in the Okavango Delta, Botswana (1 male: 3.8 females) (Merron and Mann 1995); in Lake Kainji, Nigeria (1 male: 7.8 females) (Olatunde 1978); in Pendjari River, Benin (1 male: 1.8 females) (Ahouansou Montcho et al. 2011); and in two South African impoundments (1 male: 19.7 females; 1 male: 14 females) (Hecht 1980a). Hecht (1980a) attributed differing sex ratios to the time of the year and the behaviour of male *S. intermedius*. He found that the sex ratio was lowest during the breeding season (October to March), and highest during the austral winter months (August in particular), potentially as a result of male *S. intermedius* migrating to deeper waters during winter and emerging into the shallow littoral areas at the onset of the breeding season to spawn (Hecht 1980a). This is supported by data from the current study which illustrates lower sex ratios in the Kwando River sampled in January and February and higher sex ratios in the Zambezi and Kavango rivers sampled from June to October. However, depths in the rivers do not vary as much as in an impoundment, and differing sex ratios may be as a result of behavioural differences between sexes, with the potential migration of one sex and not the other.

It must be noted that the use of relative condition as an underlying contributor to growth in this study may be complicated by two factors, i) sampling was not carried out at the same times of the year in all rivers, and ii) condition is greatly influenced by reproductive stage (Marshall and Frank 1999). As was found in Chapter 3 where diets were assessed using stomach contents analysis, Kwando River fishes tended to eat more invertebrates, while Zambezi and Kavango river populations were more piscivorous, potentially consuming more energy rich prey and as a result boosting condition. Dietary differences were attributed to the hydrological seasons sampled, with the Kwando River potentially housing abundant invertebrates during the sampling period of the small flood during summer (Bayley 1988; Winemiller 1989a; Wantzen et al. 2002). The Zambezi and Kavango rivers were sampled in falling and low water periods when fishes are concentrated in the main river channel, so allowing increased piscivory by predators (Bayley 1988; Wantzen et al. 2002). In addition, all of the study species spawn between August and May (Willoughby and Tweddle 1978; Bruton 1979a; van der Waal 1985; Merron et al. 1990; Merron and Mann 1995; Booth and McKinlay 2001), so were potentially reproductively spent and hence in poor condition in February-March when the Kwando River was sampled, while developing and in good condition during June and July when the Kavango and Zambezi rivers were sampled. Thus sampling period, which influenced the resources available (abundance of invertebrates) and reproductive stage of fishes (most were spent), may have resulted in the below average condition of three of the Kwando River species.

Addressing hypotheses

Overall young, fast growing populations of *B. lateralis*, *H. cuvieri*, *S. macrocephalus* were sampled from the Zambezi and Kavango rivers, while in the Kwando River populations were comprised of older individuals that were more slow growing. The growth of *C. gariepinus*, *C. ngamensis,* and *S. intermedius* was more variable, yet in the Zambezi River growth tended to be fast, while fishes lived to their oldest years in the Kavango River, and in the Kwando River growth was generally slower. Similarly, Peel (2012) found that the growth of three commercially important cichlids *O. andersonii*, *O. macrochir* and *C. rendalli* was fastest in the Zambezi River followed closely by the Kavango River, while those in the Kwando River grew slowly.

Other studies comparing growth rates between systems have speculated that the causes of these growth rate differences may be attributed to: temperature, hydrological regime, nutrients and productivity, and density dependent factors. Helser and Lai (2004) and Britton et al. (2010) attributed differences in the growth rates of a number of populations of *Micropterus salmoides*, to differences in latitude and temperature. Since the three areas under study are found within the same climatic belt (Mendelsohn et al. 2003) and temperatures differed less than 3 °C between rivers (see Chapter 2), growth rate differences are unlikely to be attributed to temperature.

In floodplain rivers, growth has been correlated to the magnitude and duration of the flood and/or the extent of the drawdown. Large and extended floods result in an abundance of resources on the floodplain so increasing growth of herbivorous or detritivorous fishes, while a large drawdown concentrates fishes in the river channel so increasing the growth of predatory fishes (Dudley 1974; Welcomme 1975; Bayley 1988; Gutreuter et al. 1999; Luz-Agostinho et al. 2008; Pérez and Fabré 2009). The Zambezi and Kavango rivers both experience large annual floods and subsequent drawdowns, while the Kwando River receives small infrequent floods (see Chapter 2). I therefore hypothesized that the annual inundation of the floodplain in the Zambezi and Kavango rivers sequesters allochthonous organic matter (Wissmar et al. 1981; Bayley 1988; Junk et al. 1989) and nutrients from the soil (Baldwin and Mitchell 2000; Hoberg et al. 2002; Valett et al. 2005), so driving productivity (Bayley 1988; Junk et al. 1989; Hocutt and Johnson 2001) and resulting in increased fish growth rates; whereas the Kwando River relies mainly on autochthonous inputs, so the fishes in this river do not grow as fast as those influenced by a large annual flood pulse. This is supported by growth rate trends of the example species, and by isotope analysis describing fish community niches (see Chapter 4), where the carbon sources driving the food webs of the Zambezi and Kavango rivers were similarly ^{13}C enriched suggesting allochthonous inputs, while the Kwando River carbon source was ^{13}C depleted.

Nutrients and productivity, although related to hydrological regime, can be an independent factor influencing growth rates. Higher nutrients and productivity can be translated into an abundance of prey fishes, which could be reflected in increased growth rates of predators, as was found in two impoundments in South Africa (Potts et al. 2008). Peel (2012) suggested that the Zambezi and Kavango rivers had elevated nutrient levels compared to the clear waters of the Kwando River, which could contribute to the detected differences in growth rates of the three cichlid species. In reality, the Kwando River had the highest total dissolved inorganic nitrogen concentrations (see Chapter 2), while the Zambezi and particularly the Kavango River were nutrient poor (Cronberg et al. 1995). Across all rivers, nutrient levels were relatively low (< 0.9 mg/l total dissolved inorganic nitrogen), compared to fluctuations in nutrient concentrations recorded within river systems over time (Bate et al. 2004; de la Rey et al. 2004; Lindholm et al. 2007; Bere and Tundisi 2011; Triest et al. 2012; Gallardo et al. 2012; Dalu et al. 2015). It is therefore unlikely that the small differences in total dissolved inorganic nitrogen concentrations measured in Chapter 2 contributed to the differing growth rates.

Lastly, I hypothesized that the high fishing pressure imposed on the Zambezi River fishes would influence growth and mortality rates. Differences in relative abundance of fishes have been attributed to high fishing pressure (Tweddle et al. 2015), which can also influence life history evolution, resulting in the early maturation and fast growth rates of fishes, which do not reach large sizes or old ages before they succumb to fishing mortality (Jepsen et al. 1999; Law 2000; Enberg et al. 2012). Peel (2012) attributed the differences in growth rates of the cichlids to the impacts of fisheries and density dependent competition for resources. Specifically, he hypothesised that the fishing pressure targeting the three cichlids in the Upper Zambezi River fishery (Tweddle 2010; Tweddle et al. 2015) thinned the cichlid populations, so reducing competition for resources and resulting in fast growth of the remaining fish. In the Kavango and Kwando rivers, where fishing pressures were negligible (inside the protected National Parks) cichlids were abundant, and increased competition slowed growth rates. This is supported by the high relative abundance and biomass of *C. rendalli* and *O. andersonii* in the Kavango and Kwando River, compared to in the Zambezi River (see Appendix 2). This same trend was observed for *C. gariepinus*, *C. ngamensis* and *S. intermedius*, which were sampled in high biomass in the Kavango and Kwando rivers, while in the Zambezi River lower biomass and abundance, were recorded (Appendix 2). In addition, total mortality rates, which encompass both natural mortality and fishing mortality (Ricker 1975), were highest in the Zambezi River, compared to in the other two rivers; consequently fishing was the most likely cause of the reduction in longevity of the species studied. Therefore, it is likely that overfishing did have an impact on the growth and mortality of at least *C. gariepinus*, *C. ngamensis* and *S. intermedius,* however, environmental variables may complicate this relationship (Law 2000; Enberg et al. 2012), and this could be investigated in future research.

In conclusion, fast growth rates modelled for a number of Zambezi and Kavango river fish populations could be attributed to the large flood pulses experienced by these rivers, while slower growth rates in fishes from the Kwando River coincided with smaller infrequent flood pulses. Fishing pressures imposed on the Zambezi River populations explained the high total mortality rates and the resultant lack of older fishes sampled from this river, compared to the old ages recorded from the Kavango and Kwando river populations, and may have contributed to their increased growth rates as a result of density dependent factors.

CHAPTER 6: General Discussion

The aim of this thesis was to compare the biology and ecology of the fish communities in three interconnected floodplain rivers. The objective was to test the hypothesis that fish community composition and assemblage structure, fish diets, food web structure and trophic dynamics, fish growth rates, relative condition and total mortality are influenced by the differing flood magnitudes of the three rivers, in support of the flood pulse concept proposed by Junk et al. (1989). The flood pulse concept was developed as an explanation of the relationships between the biota and the environment of unmodified, large river floodplain systems, and states that the driving force behind the functioning of floodplain ecosystems is the flood pulse (Junk et al. 1989).

The study sites were situated within the three large interconnected floodplain rivers, the Upper Zambezi, Kavango and Kwando rivers, in Namibia. All three rivers rise in the Angolan highlands, which receive seasonal rainfall during the austral summer months between September and March, producing annual waves of floodwaters. The Upper Zambezi River is the largest of the three rivers, with an annual average flow rate of 1050 m^3/s (Mazvimavi and Wolski 2006), followed by the Kavango River (annual average flow rate of 296 m^3/s (Mazvimavi and Wolski 2006), while the Kwando River is the smallest of the three rivers with an annual average flow rate of 38 m^3/s (*sensu* Schlettwein et al. 1991). To further define the study areas, the main physicochemical parameters such as water temperature, flood pulse, total dissolved inorganic nitrogen concentrations and water quality parameters were compared between rivers in Chapter 2.

The magnitude and timing of the flood pulse differed between the rivers, while surface water temperatures, total dissolved inorganic nitrogen concentrations and water quality parameters were all mostly similar. The Zambezi River had the greatest flood pulse of 6.14 m peaking in May, while the Kavango River had an average flood pulse of 3.80 m peaking in April-May, and the Kwando River had the smallest flood pulse of 0.65 m peaking in July-August. Surface water temperatures fluctuated seasonally, peaking in January at between 30 and 31 °C, and the coldest temperatures of between 16 and 19 °C were recorded in June. The Zambezi River was slightly warmer than the other rivers, and temperature variations were attributed to differing flow rates, river size and water depth. Total dissolved inorganic nitrogen concentrations were elevated (0.5 – 1 mg/l) in the Kwando River where large ungulates frequent the river, depositing nutrient rich dung and unsettling sediments. In the Kavango River total dissolved inorganic nitrogen concentrations were much lower (0.1 – 0.4 mg/l), however these increased with inputs from the floodplain frequented by wildlife. In the Zambezi River total dissolved inorganic nitrogen concentrations were of intermediate levels (0.3 – 0.6 mg/l), and tended to be higher in the main channel compared to in backwater habitats where nutrients could be taken up by aquatic vegetation and phytoplankton, or lost to sedimentation. In comparison with annual nutrient fluctuations of other rivers (e.g. Alsterhag and Petersson 2004; Lindholm et al. 2007; Gallardo et al. 2012), the fluctuation of the Zambezi, Kavango and Kwando rivers' total dissolved inorganic nitrogen concentrations were minimal, and nutrient levels were low as a result of their mineral poor Kalahari Sands based catchments and lithology (Cronberg et al. 1995; West et al. 2015). Both total dissolved inorganic nitrogen concentrations and water quality parameters varied with hydrological season, with purging and dilution effects recorded during rising and high water periods respectively (Cronberg et al. 1995).

Once the study sites were more accurately defined with respect to their abiotic characteristics, it was important to investigate the fish community composition and assemblage structure of the three rivers known to house the Upper Zambezian floodplain ichthyofauna. In the Zambezi and Kavango rivers, fish assemblage structure differed significantly with hydrological season, while in the Kwando River assemblages were less distinct seasonally. Fish assemblages also differed significantly between rivers in all hydrological seasons, with the Zambezi and Kavango rivers' assemblages less distinct from each other, when compared to the Kwando River assemblages (see Chapter 2). With the flood pulse well documented as having a homogenising effect on assemblage structure (Thomaz et al. 2007; Gomes et al. 2012), I hypothesised that dispersal of fishes across the heterogeneous floodplain in the Zambezi and Kavango rivers was the leading mechanism driving the differences in assemblage structure of these two rivers compared to the Kwando River, which received smaller less homogenising floods. After the flood pulse, processes of selection (habitat selection, predation, competition) and dispersal (movement of fishes between habitats and migration) (Winemiller 1996a; Vellend 2010) most likely structured assemblages on the floodplain and in the main channel, so creating the differing assemblage structures by season documented in the Zambezi and Kavango rivers. In the Kwando River, since the initial large flood pulse was not present to result in dispersal of fishes across the floodplain, the processes of selection and drift most likely structured assemblages, resulting in less distinct assemblage structures between hydrological seasons.

The species responsible for the differences in assemblage structure detected between rivers in all hydrological seasons was *Hydrocynus vittatus*, a large bodied, open water predator (Jackson 1961; Winemiller and Kelso-Winemiller 1994). This species was mostly absent from the Kwando River and abundant in the Zambezi and Kavango rivers. Among other species, *H. vittatus* most likely imposed heavy predation (selection) pressures upon the fish assemblages of the Zambezi and Kavango rivers during the falling and low water seasons, when prey fishes were restricted to the main river channel or moving off the floodplain (Winemiller 1989a; Winemiller 1990; Wantzen et al. 2002; Winemiller 2005a). This hypothesis, posed previously by Jackson (1961) and Winemiller and Kelso-Winemiller (1994), was supported by stable isotope data presented in Chapter 4, illustrating the position of *H. vittatus* as one of the top fish predators in the Zambezi and Kavango river food webs. In addition, *H. vittatus*'s core isotopic niche overlapped significantly with the core isotopic niches of a number of other predatory species in both the Zambezi and Kavango rivers, suggesting that if resources were limiting, this species would compete with other predators. The influence of predation pressures in structuring fish assemblages has also been documented in floodplain lakes of the Orinoco and Araguaia rivers (Rodríguez and Lewis 1997; Tejerina-Garro et al. 1998).

This suggested that, at least in falling and low water seasons, the Zambezi and Kavango rivers could be driven by top-down predatory forces controlling other consumers, while during the rising a high water seasons, when productivity was boosted by the flood pulse, these systems were driven by bottom-up processes controlling primary consumers. Winemiller et al. (2006) and Winemiller et al. (2014) noted seasonal changes in top-down and bottom-up control on benthic algae and detritus, with a number of large herbivorous/detritivorous species imposing top-down grazing control on benthic sediments during low water periods in the Cinaruco River, while during high water these species migrated elsewhere. The influence of top-down versus bottom-up consumer control on the dynamics of these complex food webs is difficult to decipher however, as multiple spatially and temporally dynamic trophic links exist, and omnivory is common (Polis and Strong 1996; Winemiller 1996b; Post 2002).

Although there is evidence for the predatory impacts of *H. vittatus,* this is of course not the only abundant predatory species within these river systems, and *Clarias gariepinus* is abundant in all three rivers. This predatory catfish was positioned at the top of the food web in all three rivers (see Chapter 4), had highly plastic feeding habits (see Chapter 3), occupied various habitats (Winemiller and Kelso-Winemiller 1996; van der Waal 1998; Ellender et al. 2014), and grew to large sizes and old ages (see Chapter 5). In the Kwando River, without the large flood pulse to promote productivity, top-down forces from the suite of predatory fishes including *C. gariepinus*, *Clarias ngamensis*, various serranochromine cichlids and *Schilbe intermedius*, could structure this ecosystem regardless of hydrological season. Consequently, a combination of the physical flood pulse and the ecological processes applied by abundant species, most likely structured assemblages in each river system.

Since floodplain systems are highly dynamic and complex, it is not surprising that life history strategy, interlinked with habitat selection and predation pressures, all influence food web structure (Winemiller 1996b; Winemiller 2007). Life history strategy is depicted as a trilateral continuum determined by trade-offs between fecundity, age and size at maturation and juvenile survivorship (Winemiller 1989b; Winemiller and Rose 1992; Winemiller 2005b). Periodic strategists prefer seasonal environments, due to their late maturing, high fecundity, pulsing reproductive strategy (Winemiller and Rose 1992; Winemiller 1996b). Equilibrium strategists, which invest heavily in small clutches, prefer crowded habitats with relatively stable resources, and opportunistic species tend to rapidly colonise frequently disturbed environments as a result of their early maturation and opportunistic reproductive traits (Winemiller and Rose 1992; Winemiller 1996b). As a result, the regular annual flood pulse disturbance of the Zambezi and Kavango rivers, supports long lived periodic strategists such as *H. vittatus* and *C. gariepinus*, which compensate for large losses of eggs in unfavourable years with good recruitment in favourable years (the storage effect) (Winemiller 1996b). More stable environments subject to density dependent ecological factors that encounter less frequent flood disturbances, such as the Kwando River, would be favourable to equilibrium type strategists such as cichlids and *Hepsetus cuvieri* (Winemiller 1996b). Opportunistic species tend to favour unpredictable conditions, and as a result are known to colonise floodplain environments, hence Winemiller (1996b) found Barotse floodplain environments supported abundant opportunistic and periodic strategists, while the main channel was dominated by equilibrium strategists.

Fish diets were also influenced by the flood pulse, known as the driver of productivity in floodplain systems (Junk et al. 1989). This was illustrated in Chapter 3 where the diets of *C. gariepinus*, *C. ngamensis* and *S. intermedius* were similar in the Zambezi and Kavango rivers, while in the Kwando River more invertebrates were consumed. This was attributed to the differing seasons sampled, with the Zambezi and Kavango rivers sampled between June and October when water levels were falling and low, so prey fishes were moving off the floodplain into the main channel for easier consumption by predators (Ward and Stanford 1995; Hoeinghaus et al. 2003; Winemiller 2005a). Alternatively, the Kwando River was sampled in January-April when water levels were slightly elevated as a result of local rainfall, creating ideal conditions for invertebrates (Winemiller 1989a; Bayley 1995). Hence basal productivity originating on the floodplain may support floodplain river food webs during flooding, while during falling and low water seasons consumers may be supported by basal resources originating from the main channel (Winemiller 1990; Wantzen et al. 2002; Winemiller 2005a; Zeug and Winemiller 2008). This was supported by stable isotope analyses that identified enriched carbon sources such as terrestrial C_4 grasses and riparian C_3 plants as the basal productivity driving the food webs in the Zambezi and Kavango rivers, in contrast to the depleted carbon sources such as aquatic algae and other aquatic macrophytes which supported productivity in the Kwando River (see Chapter 4).

The other main difference in food web structure detected was a restriction of nitrogen range and potentially food chain length, and a reduction in trophic level of predatory fishes in the Zambezi River compared to the Kavango and Kwando rivers. This could be as a result of the intense fishing pressure imposed on the Zambezi River, targeting both detritivorous/herbivorous cichlids, and more recently large predatory fishes (Tweddle 2010; Tweddle et al. 2015). The restriction of food chain lengths in response to fishing pressures has been well documented in the literature (Pauly et al. 2001; Jennings et al. 2002; Estes et al. 2011), and can result in changes in the abundance of herbivores and ultimately impact on the abundance and composition of primary producers (Estes et al. 2011). This simplification of ecosystem changes is however complicated in this scenario, as fishers in the Zambezi River target both primary consumers (large herbivorous/detritivorous cichlids) and consumers at the top of the food web (e.g. *H. vittatus* and *C. gariepinus*). Further research is therefore needed to clarify the effects of the constantly increasing fishing pressure in the Zambezi River, and identify the impacts of this pressure on food web structure.

Growth rates were also found to differ between rivers, and *Brycinus lateralis*, *C. gariepinus*, *H. cuvieri* and *Serranochromis macrocephalus* had greater growth performance in the Zambezi River, compared to in the Kavango and Kwando rivers. Increased growth rates have also been correlated with larger flood pulses (Dudley 1974; Bayley 1988; Gutreuter et al. 1999; de Graaf 2003). Alternatively, the evolution of both fast and slow growth rates has been attributed to fishing pressure, however difficulties arise when separating fishing effects from environmental effects (Enberg et al. 2012). It is therefore likely that the growth response was attributable to flood magnitude rather than fishing pressure, although the high total mortality rates calculated for all species sampled in the Zambezi River was attributable to greater fishing pressures. Figure 6.1 illustrates graphically the growth performance and total mortality rates of the focus species from all rivers. Species that were heavily fished, such as *C. gariepinus*, *H. cuvieri*, *S. macrocephalus* and *S. intermedius*, demonstrated high mortality rates in the Zambezi River, and lower mortality rates in Kavango and Kwando rivers where fishes were sampled within protected areas. *Brycinus lateralis*, a small bodied species that was not heavily fished, did not have greater mortality rates in the Zambezi River, but rather similar mortality rates in the Zambezi and Kavango rivers where *H. vittatus* were sampled in abundance, and lower mortality rates in the Kwando River where *H. vittatus* were rarely sampled. Winemiller and Kelso-Winemiller (1994) found alestids (previously characids) in the diet of *H. vittatus*, suggesting differences in mortality rates of *B. lateralis* could be attributed to predation pressure.

The variation in both growth performance and total mortality for each species between river populations, or the area of the shaded triangles in Figure 6.1, was used to illustrate species response to the differing conditions in each river. For example, the area between populations of *C. gariepinus* and *C. ngamensis* (although not sampled from the Zambezi River) is small. These species grow extremely fast initially (van der Waal and Schoonbee 1975; Willoughby and Tweddle 1978; Bokhutlo et al. 2015) to large sizes (Bruton 1976) and old ages (see Chapter 5; Wartenberg et al. 2013). They are periodic strategists that demonstrate a storage effect as a result of their high fecundity (Willoughby and Tweddle 1978; Bruton 1979a; Winemiller 1996b). They also exhibit plastic feeding habits (Willoughby and Tweddle 1978; Bruton 1979b), and can utilise varying habitats and survive extreme environmental conditions (Winemiller and Kelso-Winemiller 1996; van der Waal 1998; Ellender et al. 2014). It is therefore understandable that the growth performance and mortality rates of these species are not influenced greatly by differences in environmental conditions, as their life history strategy is robust and effective. A similar example was described by Winker et al. (2012), who found the late maturing periodic strategist *Labeo capensis* did not demonstrate significantly different growth performance, age and length at maturity and mortality rates in an impounded environment, compared to in its usual seasonal riverine habitat. They attributed the success of *L. capensis* in this unlikely environment to the extreme water level fluctuations, floodplain availability and turbidity, conditions essential for the persistence of a periodic strategist, and the lack of fishing pressure, which this species would have been particularly sensitive to (Winker et al. 2012).

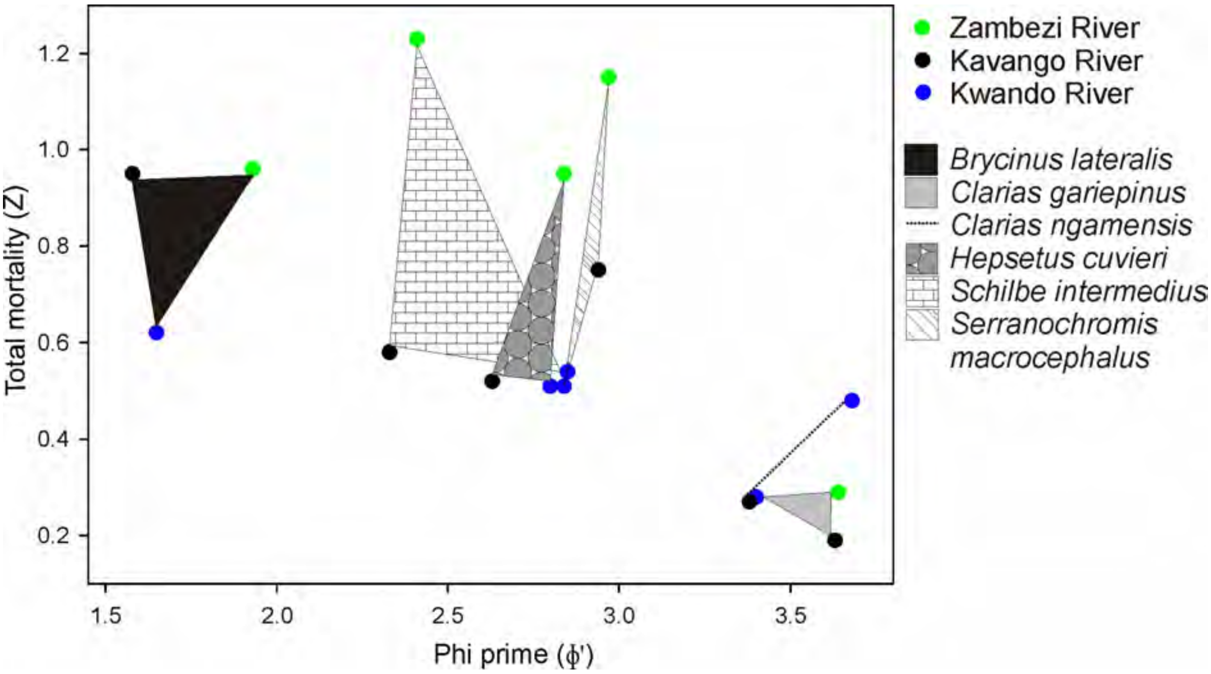

Figure 6.1: The growth performance (phi prime) and total mortality rates (Z) of all species studied from the Zambezi, Kavango and Kwando rivers. The variation in both parameters between rivers (shaded area) illustrates how each species adapts to the differing biotic and abiotic conditions of each river.

In contrast, *S. intermedius*, which is also a periodic strategist on account of its high fecundity, lack of parental care and single event spawning habits (van der Waal 1985; Merron and Mann 1995), illustrated great variation in total mortality and growth performance between river populations (Figure 6.1). Mortality rates were highest in the Zambezi River, potentially as a result of high fishing pressures, while growth performance was greatest in the Kavango River, perhaps as a result of an abundance of prey items. *Schilbe intermedius* does not reach large sizes or live to old ages (see Chapter 5), demonstrates adaptable feeding habits (see Chapter 3) although it is gape size limited, and has not been found to survive extreme environmental conditions. This may explain why this species exhibits less plastic and more variable total mortality and growth performance rates, compared to the highly adaptable clariids.

The equilibrium strategists, *H. cuvieri* and *S. macrocephalus*, had higher growth performance and mortality rates in the Zambezi River compared to in the Kavango and Kwando rivers (Figure 6.1). Again high mortality rates were attributed to the increased fishing pressures observed in the Zambezi River, and the greater growth performance in the Zambezi River was attributed to the larger flood pulse. As a result, these equilibrium strategists were more sensitive to differing environmental conditions than the periodic clariid species (Mims and Olden 2013). Peel (2012) found the growth performance indices of the Zambezi and Kavango river populations of three equilibrium strategists *Oreochromis andersonii*, *Oreochromis macrochir* and *Coptodon rendalli,* were much higher compared to the growth performance of the Kwando River populations. In addition, Merron (1991) found that *O. andersonii* sampled from perennially versus seasonally flooded habitats in the Okavango Delta exhibited precocial and altricial traits respectively. Referring mainly to reproductive traits such as fecundity, egg size and maturity, Merron (1991) highlighted the flexibility of this equilibrium strategists' life history characteristics with varying environmental conditions within an ecosystem. Although reproductive characteristics were not investigated in this study, results indicate that *S. macrocephalus* and *H. cuvieri* exhibited growth performances expected from equilibrium strategists in response to variations in hydrological regime and general environmental conditions.

Similarly, as opportunistic species typically thrive in unpredictable environments (Mims and Olden 2012) such as floodplains, it was expected and observed that the growth performance of *B. lateralis* was highest in the Zambezi River which experiences the largest annual flood. In addition, Tockner and Stanford (2002) predicted that one of the ecological consequences of increased anthropogenic impacts on floodplain rivers was the predominance of opportunistic species. With overfishing documented in the Zambezi River (Tweddle 2010; Tweddle et al. 2015), an abundance of this opportunistic species, which occupied a higher trophic position compared to in the other rivers (see Chapter 4), was not surprising. Interestingly, opportunistic species are generally short lived, however *B. lateralis* lived to the old age of seven years in the Kwando River, and four years in the Zambezi and Kavango rivers. It must be noted that the periodic, equilibrium and opportunistic strategies are endpoints on a life history continuum, and as a result some species may exhibit characteristics incorporating more than one endpoint (Winemiller 1989b; Winemiller and Rose 1992; Winemiller 2005b). Consequently, compared to the other species in the Upper Zambezi River ichthyofauna, *B. lateralis* lies between the periodic and opportunistic strategy in the life history continuum.

Conclusions

The fish communities and floodplain fish ecology in the Zambezi, Kavango and Kwando rivers differed. Differences in assemblage structure, feeding habits, food web structure, trophic dynamics and growth rates were attributed to the variation in flood magnitude between rivers and the resulting adaptations of fish life history strategies. This is in accordance with the flood pulse concept, which predicts that floodplain river productivity is driven by annual flood pulses. The Kwando River, which was the smallest of the three rivers and experienced small and unpredictable floods, demonstrated differences in fish ecology when compared to the Zambezi and Kavango rivers, which both received larger, predictable annual floods. Differences in assemble structure and positioning in isotopic space provided support for previously proposed hypotheses depicting *H. vittatus* as a top predator capable of structuring assemblages within the main channel environment of the Zambezi and Kavango rivers. In the Zambezi River, where fishing pressures are high, differences in food web structure, and high total mortality rates were detected.

This thesis contributes greatly to the ecological understanding of fish communities, and their response to seasonal floods of three southern African floodplain rivers. Information on the Kwando River ecosystem was novel and interesting, as the ecology of this rivers' fish community differed from that of the Zambezi and Kavango rivers. With small floods and consequently slow growing fishes, the Kwando River's fish community is potentially the most vulnerable to exploitation, and as a result more information is still needed for the effective management of this ecosystem. A broad understanding of food web structure in these three rivers was achieved however; more information is still needed to generate a comprehensive understanding of the complex floodplain processes controlling the seasonal productivity and ecology of the three rivers.

Implications for resource management and conservation

From this thesis it is clear that i) flood pulses drive the productivity and influence the ecology of the fishes in the Upper Zambezi, Kavango and Kwando rivers, and ii) increased fishing pressures on the Upper Zambezi River has impacted the fish community of this river and influenced fish ecology. There are a number of implications of this information on the future of these resources in relation to climate change, water abstraction and fisheries management.

The implications of climate change are variable and uncertain, however there is a general consensus that there is likely to be an increase in the frequency of extreme weather events, while some regions of the world will receive more rainfall, and some will receive less rainfall (Magadza 1994; Rosenzweig et al. 2001; Jentsch et al. 2007). Climate change models for western Southern Africa in the Upper Zambezi, Kavango and Kwando river catchments predict an increase in temperature and a reduction in rainfall of up to 10% by the end of the 21st century (Magadza 1994; Hulme et al. 2001; de Wit and Stankiewicz 2006; Beck and Bernauer 2011). This would most likely result in increases in water temperature, reductions in river flows, smaller and potentially shorter annual flood pulses, and an increase in evaporation of up to 40% in the Okavango Delta (Magadza 1994). Similarly, the demand on water resources from the Kavango River by Angola, Namibia and Botswana is ever increasing and proposals for irrigation schemes, hydroelectricity impoundments, and a water transfer pipeline have been put forward (Swatuk 2003; Kgathi et al. 2006). An increase in water abstraction and the building of impoundments will also result in reductions in river flow and flow variability (Andersson et al. 2006), while agricultural expansion and urbanisation could affect water quality, pollution and eutrophication (Mbaiwa 2004). To add to this, the demand for fish will only grow in the future, and as fish stocks are depleted in the Upper Zambezi River (Tweddle 2010; Tweddle et al. 2015), so fishers are moving west to the Kwando and Kavango rivers (Pers. obs.).

The impacts of reductions in river flow, flood magnitude, and flow variation on the species composition, assemblage structure, food webs and growth rates of the Upper Zambezi floodplain ichthyofauna are likely to be considerable (Poff and Zimmerman 2010). Xenopoulos et al. (2005) estimated that with decreases in water discharge of between 5 and 50%, fish community structure would be influenced significantly, and up to 9% and 22% of the fishes from Zambezi and Kavango rivers respectively would be lost. These species may include those that rely on large floods for gonad development, spawning and recruitment success (Bailly et al. 2008).

Changes in flow variability would influence fish assemblage structure, as was observed in Chapter 2. Mims and Olden (2013) found that the reduction in flow variability associated with the construction of impoundments resulted in an increase in the representation of equilibrium life history strategists, and a decrease in the representation of opportunistic strategists. This is consistent with life history theory which predicts that equilibrium strategists favour low disturbance environments, while opportunistic strategists favour high disturbance, unpredictable environments (Winemiller and Rose 1992; Winemiller 2005b). Periodic strategists are likely to be unaffected by alterations in flow regime as their longevity and high fecundity allows them to benefit from a storage effect, where high recruitment in good flood years can compensate for poor recruitment in bad flood years (Winemiller 1996b). Consequently in the Kavango River, the relative contribution of cichlids may increase in impounded river sections as well as downstream of impoundments. The abundance of some alestids and barbs my decrease downstream of impoundments, while the abundance of clariids, synodontids and *Hydrocynus vittatus* may not change.

Fish diets vary seasonally in floodplain rivers (see Chapter 3). During the high water level season insects and detritus are in abundance (Bayley 1988; Winemiller 1989a; Wantzen et al. 2002), and as flood waters recede, small fish species are concentrated in the main channel for easy consumption by predators (Bayley 1988; Wantzen et al. 2002). Reductions in river flow at low water levels would concentrate prey fishes in deep sections of the main channel allowing for easy consumption by predators. Small flood pulses may restrict the diets of some insectivorous and detritivorous fishes or juvenile fishes that rely on the inundation of floodplain as nursery habitat. Since the productivity of floodplain systems is driven by the annual inundation of the floodplain (Junk et al. 1989), and consequently terrestrial carbon significantly contributes to production inputs (see Chapter 4), reductions in flood magnitude are also likely to affect food web structure. Food webs may shift from terrestrial allochthonous primary production to algal based autochthonous primary production (Robertson et al. 1999; Morrongiello et al. 2011). With reductions in flood magnitude, Murray-Hudson et al. (2006) suggested that short life-cycle herbaceous species such as *Cyperus papyrus* and *Phragmites mauritianus*, would be gradually replaced by woody species such as *Vachellia* spp. (previously *Acacia* spp.) in the Okavango Delta. This change would be accompanied by a reduction in nutrients released by the annual inundation of organic matter and dung, and a reduction in structural habitat produced by these reeds. Ultimately, reductions in the nutrient inputs and primary productivity of these systems would result in slower fish growth rates and lower fisheries productivity (Bayley 1988; Bayley 1991; Gutreuter et al. 1999).

In addition, a more obvious impact of impoundment construction is the restriction of fish migrations. This has been widely documented (Halls et al. 1998; Halls et al. 1999; Daufresne and Boët 2007; Dugan et al. 2010), and in the Kavango River may restrict, for example, *H. vittatus* from finding suitable spawning or feeding grounds (Jackson 1961; Økland et al. 2005).

Changes in fish composition and assemblage structure, restrictions in the production inputs, changes in food web structure and reductions in fish growth rates would ultimately lead to a reduction in the ecosystems resilience to change, and an increased vulnerability to anthropogenic influences such as fishing, non-native species introductions, pollution and eutrophication (Palmer et al. 2008; Morrongiello et al. 2011). Although the impacts and implications of climate change are difficult to predict, any impacts would almost certainly be compounded by the presence of impoundments (Palmer et al. 2008). The most viable conservation strategy would be to reduce water consumption, however this will be difficult in developing countries, which are the most affected by reduced water discharges (Xenopoulos et al. 2005). Integrated water resource management of the Okavango River Basin is currently under way with the establishment of the Permanent Okavango River Basin Water Commission (OKACOM) in 1994 (Kgathi et al. 2006). This commission aims to manage this trans boundary resource using a number of legally binding principles developed in line with the Helsinki Rules and the United Nations Convention on the Non-Navigable Use of International Watercourses (Kgathi et al. 2006). Similarly in the Zambezi River Basin, the Southern African Development Community (SADC) has been instrumental in attempting to initialise institutions for Integrated Water Resource Management i.e. The Zambezi River Water Authority (Kirchhoff and Bulkley 2008). It is imperative that transboundary water resource management plans are updated and implemented for the management of these resources that are vital for the maintenance and growth of many countries.

The more immediate threats of non-native species introductions and overfishing also need to be addressed. The two non-native species threatening the Upper Zambezi and Kavango regions at present are the Nile tilapia *Oreochromis niloticus* (Tweddle 2010), and the Australian red- claw crayfish *Cherax quadricarinatus* (Nunes et al. 2016), both of which were introduced for aquaculture purposes. *Oreochromis niloticus* is widespread in most of southern Africa, and its main impacts include the competition and hybridisation with native congenerics (Zengeya et al. 2013; Ellender and Weyl 2014; Zengeya et al. 2015). As a result *Oreochromis andersonii* and *Oreochromis macrochir* are threatened by this species in the Upper Zambezi, Kavango and Kwando rivers (IUCN 2016). Although this species is already in this system, management measures could be directed towards the education of aquacaulturalists to stop any subsequent introductions, and the prevention of this species from entering the Kavango and Kwando systems. The impacts of *C. quadricarinatus* are currently under study, however may include the destruction of aquatic macrophytes, disruption of and competition with invertebrate communities, disruption of fish and amphibian reproduction, introduction of non-native parasites which could be detrimental to native Decapods, and ultimately the alteration of ecosystem functioning (Nunes et al. 2016). Management of this species include manual removal using traps, chemical removal using biocides, the hindrance of any subsequent introductions and movement through education of stakeholders, and the development of a barrier which inhibits this species movement into the Kwando River and particularly the Kavango River and Okavango Delta (Nunes et al. 2016).

The threat and impacts of intense fishing pressure, which has been demonstrated in the Upper Zambezi already (Tweddle 2010; Tweddle et al. 2015), and will most likely increase in the future, can be curbed with specific and adaptive management methods. In developing countries, following the failure of traditional governance, community based natural resource management (CBNRM) is often adopted as an effective method which empowers communities to manage their own resources more sustainably (Kuemlangan and Teigenem 2004; Abbott et al. 2007b). In Namibia, wildlife is often managed for hunting and tourism through conservancies, so producing revenue and providing an incentive for conservation (Jones and Weaver 2009). This same concept is currently being implemented with respect to fisheries, and the Namibian Nature Foundations EU funded Community Conservation Fisheries in the Kavango – Zambezi Transfrontier Conservation Area (KAZA) Project, in conjunction with the Sikunga and Impalila Conservancies have gazetted two fisheries protected areas (FPAs) (Tweddle et al. 2015). These FPAs are sections of river channel that are in effect ‘owned’ by the conservancy, and are guarded by conservancy employed fish guards. Revenue is generated through recreational angling permits which are bought by the local angling clubs and tourists from the local lodges, who pay to practice catch-and-release angling in the FPA. This conserves the fish resources within these channels, and local fishers are still permitted to fish within backwaters adjoining the channels. The FPAs theoretically work as refuge areas for fish reproduction and growth, and will replenish the surrounding backwaters and main channel sites for harvest by local fishers. Although not fully operational at present, these CBNRM endeavours are making progress towards the sustainable management of the regions fisheries, however support from Government ministries and tourist lodges is essential.

Recommendations for future research

Although this thesis contributes significantly to the understanding of southern African floodplain fish ecology and the influence of the flood pulse on fish communities, the limited field team and data collection period of two years, restricted the detail into which this thesis could delve. As a result, there is scope for future research to, i) improve the understanding of the physiological and behavioural adaptations of these fishes to seasonal fluctuations, ii) tease apart the drivers and dynamics of top-down versus bottom-up control of floodplain systems, and iii) gain an understanding of individual species on which little information exists.

As was explained by Winemiller et al. (2015), ecologists often categorise fishes into various niches without understanding basic aspects of their physiology. Information on the physiology of the Upper Zambezian floodplain ichthyofauna is lacking. Firstly, minimum average temperatures of 16 °C during the cold season were recorded in Chapter 2, temperatures that are colder than would be expected in tropical rivers. Although there is evidence of the influence of seasonal temperature fluctuations on fish physiology, such as the slowing of metabolism resulting in the deposition of opaque growth zones on fish otoliths (Peel et al. In review; Taylor et al. In review), there is also evidence that these low winter temperatures do not influence fish physiology as much as may be expected. For example, Merron (1991) observed *C. gariepinus* spawning with the delayed flood pulse, which only reaches the lower Okavango Delta in June-July when temperatures are 16 °C. In addition, information on the thermal tolerance of this suite of species is lacking, with only one study on *C. rendalli* (Whitfield and Blaber 1976) identified. Future studies on the thermal tolerance and the response of fishes to seasonal fluctuations in temperature would be valuable for a more comprehensive understanding of their ecology and vulnerability to potential change.

Secondly, with the aim to assess the seasonality of top-down and bottom-up drivers of food web structure, further investigation on the nutrient sources, basal resources (primary producers, detritus, plankton), and invertebrates, which were not extensively sampled in this thesis, is warranted. Regarding nutrient sources, it was hypothesised that the increase in total dissolved inorganic nitrogen concentrations in the Kavango and Kwando rivers was as a result of dung inputs and suspension of sediments by wildlife. Many studies, mostly on the Okavango Delta (e.g. Hocutt and Johnson 2001; Lindholm and Hessen 2007; Mosepele et al. 2009; Mosepele et al. 2012), have speculated on the nutrient inputs from wildlife dung on the floodplain, however not many have actually measured the fluctuations of these nutrients during the flood (e.g. Cronberg et al. 1995; Hoberg et al. 2002; Lindholm et al. 2007). This hypothesis needs to be systematically tested, and the importance of nutrients from these sources quantified, so an ecosystem approach to management can be adopted. The Caprivi Floodplain of the Upper Zambezi River is now populated by cattle and devoid of wildlife, and a comparison of the nutrient inputs associated with the two contrasting scenarios would be interesting.

In this thesis, evidence was presented for the dependence of the Zambezi and Kavango river food webs on allochthonous based resources, as opposed to the Kwando River which was based on autochthonous resources. This needs to be investigated further by seasonally collecting stable isotope samples from all basal resources available in the three rivers including plants, plankton and detritus, and perhaps using mixing models to quantify the contribution of differing basal resources to invertebrate and fish diets. This could test the seasonal influence of top-down versus bottom-up resource control in the three rivers, and explain the differing trophic positions of fish groups by river.

With respect to top-down control, the habitat utilisation of *H. cuvieri* and the other predators in the presence and absence *H. vittatus* could be investigated. As was touched upon in this thesis, changes in isotopic niche area with predator size could be investigated using larger sample sizes. In particular, the individual variation in growth rates of *C. gariepinus* and *C. ngamensis* implies, perhaps, differing utilisation of resources. This could be tested by collecting stable isotope samples and otoliths, to test the hypothesis that fast growing individuals occupy discrete trophic niches compared to slow growing individuals.

Lastly, there is still limited knowledge on the biology and ecology of a number of fishes within the Upper Zambezian floodplain ichthyofauna. In particular, very little biological and ecological information exists on the smaller barb, alestid, cichlid and mormyrid species, which are important components of subsistence fishers' catches at certain times of the year (Figure 6.2). With the fishing pressure on the Zambezi River currently high, and bound to increase in the future with the inevitable drying of the ephemeral Lake Liambezi, biological information on even small species is important.

Figure 6.2: A mixture of mormyrids, barbs, alestids, small cichlids, and synodontids caught by subsistence fishers on the Upper Zambezi River.

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Appendix 1: Fish poster illustrating the Upper Zambezian floodplain ichthyofauna


Serranochromis angusticeps - Thinface Largemouth - Mushuna


Serranochromis altus - Humpback Largemouth - Mushuna


Serranochromis macrocephalus - Purpleface Largemouth - Njenga


Serranochromis robustus jallae - Nembwe - Nembwe

Serranochromis thumbergi - Brownspot Largemouth - Nembwe

Serranochromis longimanus - Longfin Largemouth - Njenga


Sargochromis giardi - Pink Bream - Siyeo


Sargochromis cf. *codringtonii* - Dusky Bream - Siyeo


Sargochromis carlottae - Rainbow Bream - Mbuma


Sargochromis sp. - Green Bream - Mbuma


Oreochromis andersonii - Threespot tilapia - Njinji


Oreochromis macrochir - Greenhead Tilapia - Muu


Tilapia rendalli - Redbreast Tilapia - Mbufu


Tilapia sparrmanii - Banded Tilapia - Situhu


Tilapia ruweti - Okavango Tilapia - Situhu


Hemichromis elongatus - Banded Jewelfish - Liulungu


Pharyngochromis acuticeps - Zambezi River Bream - Impapati


Pharyngochromis sp. - Zambezi Rapids Bream - Impapati


Pseudocrenilabrus philander - Southern Mouthbrooder - Impapati

BAROTSE / UPPER ZAMBEZI RIVER AND FLOODPLAIN FISHES

Denis Tweddle


Ctenopoma multispine - Manyspined Climbing Perch
Mbundu, simungulungwe


Microctenopoma intermedium - Blackspot Climbing Perch
Mbundu, simungulungwe


Labeobarbus codringtonii - Upper Zambezi Yellowfish - Linyonga


Barbus paludinosus - Straightfin Barb - Mbaala


Barbus cf. *eutaenia* - Orangefin "eutaenia" - Mbaala


Barbus cf. *eutaenia* - Sharpsnout "eutaenia" - Mbaala


Barbus multilineatus - Copperstripe Barb - Mbaala


Barbus kerstenii - Redspot Barb - Mbaala


Barbus afrovernayi - Spottail Barb - Mbaala


Barbus poechii - Dashtail Barb - Mbaala


Barbus unitaeniatus - Longbeard Barb - Mbaala


Opsaridium zambezense - Northern Barred Minnow
Mbaala, Shiba


Barbus fasciolatus - Red Barb - Mbaala


Barbus radiatus - Beira Barb - Mbaala


Barbus bifrenatus - Hyphen Barb - Mbaala


Barbus barnardi - Blackback Barb - Mbaala


Barbus thamalakanensis - Thamalakane Barb - Mbaala


Barbus barotseensis - Barotse Barb - Mbaala


Barbus brevidorsalis - Dwarf Barb - Mbaala


Barbus haasianus - Sicklefin Barb - Mbaala


Coptostomabarbus wittei - Upjaw Barb - Mbaala


Labeo lunatus - Upper Zambezi Labeo - Iinwanga, linyonga


Labeo cylindricus - Redeye Labeo - Iinwanga, linyonga


Hepsetus cuvieri - African Pike - Molumesi


Hydrocynus vittatus - Tigerfish - Ngweshi


Brycinus lateralis - Striped Robber - Mbaala, Ikila


Micralestes acutidens - Silver Robber - Mbaala, Shiba


Rhabdalestes maunensis - Slender Robber - Mbaala, Shiba


Hemigrammocharax multifasciatus - Multibar Citharine


Hemigrammocharax machadoi - Dwarf Citharine


Nannocharax macropterus - Broadbar Citharine


Neolebias lozii - Banded Neolebias


Clarias gariepinus - Sharptooth Catfish - Ndombe, nsoho


Clarias ngamensis - Blunttooth Catfish - Ndombe, nsoho


Clarias stappersii - Blotched Catfish - Liwetete


Clarias theodorae - Snake Catfish - Silutupwi


Clariallabes platyprosopos - Broadhead Catfish - Ibozwe


Parauchenoglanis ngamensis - Zambezi Grunter
Siabela,Lihututu


Schilbe intermedius - Silver Catfish - Lubango


Amphilius uranoscopus - Common Mountain Catfish


Zaireichthys pallidus - Pallid Sand Catlet


Zaireichthys conspicuus - Blotched Sand Catlet


Synodontis nigromaculatus - Spotted Squeaker - Singongi


Mormyrus lacerda - Western Bottlenose - ndikusi


Hippopotamyrus szaboi (& *H. ansorgii*) - Slender Stonebasher
Ninga, inembele

Cyphomyrus cubangoensis - Okavango Parrotfish - Ninga


Mastacembelus frenatus - Longtail Spiny Eel - Musioka


Mastacembelus vanderwaali - Ocellated Spiny Eel - Musioka

Nothobranchius sp. - Caprivi Killifish


Chiloglanis spp - Suckermouth catfishes

Synodontis spp (taxonomy under investigation) - Singongi


Petrocephalus longicapitis - Longhead Churchill - Ninga, Inembele


Petrocephalus cf. *okavangensis* - Silver Churchill - Ninga, Inembele


Petrocephalus sp. - Spotfin Churchill - Ninga, Inembele


Pollimyrus marianne - Upper Zambezi Stonebasher - Ninga, Inembele


Pollimyrus cf. *castelnaui* - Dwarf Stonebasher - Ninga, Inembele


Micropanchax johnstoni - Johnston's Topminnow


Micropanchax sp. - Liambezi Topminnow


Micropanchax katangae - Striped Topminnow


Micropanchax hutereaui - Meshscaled Topminnow


Micropanchax sp. - Pigmy Topminnow

Notes on scientific names and current taxonomic status:

The studies undertaken on these fishes during Upper Zambezi fisheries programmes have revealed several new species. Taxonomic revisions of some species have been published since PH Skelton's second edition of "A complete Guide to the Freshwater Fishes of Southern Africa" was published in 2001. The names used here reflect the latest taxonomic information available in August 2013. Several species await description or revision and are here designated as sp. or spp. *Synodontis* species in particular remain unresolved with the exception of *S. nigromaculatus* and hence, instead of photos of numerous varieties, the illustrations of the other six "species" are used, with permission, from PH Skelton's guidebook .

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South African Institute for Aquatic Biodiversity (SAIAB)

Nwanyi Angling Club, Katima Mulilo

Appendix 2: Experimental gillnet catch per unit effort (CPUE) by biomass in grams/ net night (Biomass) and by abundance in number/ net night (Number) of all fish species sampled in the Zambezi, Kavango and Kwando rivers, Namibia in 2010 and 2011.

Species	Zambezi River		Kavango River		Kwando River	
	Biomass	Number	Biomass	Number	Biomass	Number
Brycinus lateralis	317.90	32.80	92.98	12.36	488.60	55.98
Barbus afrovernayi	-	-	0.05	0.06	-	-
Barbus barnardi	-	-	0.05	0.06	0.29	0.30
Barbus bifrenatus	-	-	-	-	0.35	0.30
Barbus eutaenia	1.12	0.83	0.47	0.34	-	-
Barbus fasciolatus	0.02	0.02	0.15	0.17	0.21	0.19
Barbus multilineatus	0.44	0.25	0.00		0.01	0.01
Barbus paludinosus	0.15	0.10	1.15	0.14	0.04	0.01
Barbus poechii	54.51	4.68	13.13	1.97	3.04	0.17
Barbus radiatus	7.05	2.93	1.62	1.28	3.23	0.66
Barbus thamalakanensis	0.17	0.07	-	-	-	-
Barbus unitaeniatus	1.14	0.35	0.10	0.07	1.81	0.24
Cyphomyrus cubangoensis	11.06	0.83	8.29	0.30	3.07	0.14
Clarias gariepinus	825.31	0.35	1649.82	0.81	1230.08	0.86
Ctenopoma multispine	0.39	0.03	-	-	-	-
Clarias ngamensis	19.59	0.02	586.26	0.61	448.11	0.61
Clarias stappersii	0.54	0.01	-	-	1.89	0.01
Clarias theodorae	-	-	-	-	4.10	0.01
Coptodon rendalli	3.17	0.06	91.93	0.22	63.73	0.19
Hemichromis elongatus	-	-	-	-	3.22	0.15
Hepsetus cuvieri	637.51	2.64	267.78	0.62	642.99	1.94
Hydrocynus vittatus	1438.22	10.72	2629.06	9.41	265.21	0.13
Labeo cylindricus	5.95	0.16	0.50	0.03	-	-
Labeo lunatus	50.13	0.37	145.75	0.51	-	-
Marcusenius altisambesi	118.47	4.86	758.54	31.93	761.26	9.46
Micralestes acutidens	12.09	4.82	13.51	4.62	0.03	0.01
Mormyrus lacerda	15.32	0.04	12.23	0.02	74.99	0.14
Oreochromis andersonii	25.55	0.04	118.87	0.14	288.69	0.57
Oreochromis macrochir	11.89	0.04	14.30	0.03	224.76	0.62
Opsaridium zambezense	0.11	0.03	-	-	-	-
Parauchenoglanis ngamensis	15.25	0.15	2.01	0.07	55.46	0.43
Petrocephalus okavangoensis	149.79	34.43	22.51	5.78	28.49	2.44
Pharyngochromis acuticeps	35.09	1.67	1.70	0.09	38.15	1.75
Pollimyrus castelnaui	4.61	1.35	2.30	1.13	1.53	0.36
Pseudocrenilabrus philander	0.27	0.13	0.08	0.03	1.39	0.14
Rhabdalestes maunensis	0.07	0.03	0.07	0.07	0.07	0.06
Sargochromis carlottae	32.03	0.23	38.96	0.21	48.00	0.34
Sargochromis codringtonii	13.37	0.08	39.53	0.09	97.65	0.64
Sargochromis giardi	5.38	0.07	181.15	0.46	69.82	0.19
Schilbe intermedius	677.84	21.07	2145.53	25.63	2476.48	22.86

Species	Zambezi River		Kavango River		Kwando River	
	Biomass	Number	Biomass	Number	Biomass	Number
Serranochromis altus	83.12	0.31	1211.21	1.58	121.31	0.26
Serranochromis angusticeps	58.22	0.62	548.29	0.88	77.39	0.28
Serranochromis macrocephalus	129.68	1.16	232.12	0.50	81.74	0.35
Serranochromis robustus	4.03	0.04	0.00	0.03	26.35	0.04
Synodontis nigromaculatus	39.22	0.48	1305.08	16.97	109.04	1.10
Synodontis spp.	205.03	7.19	345.36	7.63	152.07	1.54
Tilapia ruweti	0.01	0.01	-	-	-	-
Tilapia sparrmanii	177.43	4.04	36.21	0.70	73.74	1.53

Appendix 3: The % number ($\%N_i$), % weight ($\%W_i$) and % frequency occurrence ($\%FO_i$) used to calculate the % index of relative importance ($\%IRI_i$) of the prey items in the stomach contentss of the *Clarias gariepinus, Clarias ngamensis, Hepsetus cuvieri, Serranochromis macrocephalus,* and *Schilbe intermedius* sampled from the Zambezi, Kavango, Kwando rivers.

	Zambezi River			Kavango River			Kwando River		
	$\%N_i$	$\%W_i$	$\%FO_i$	$\%N_i$	$\%W_i$	$\%FO_i$	$\%N_i$	$\%W_i$	$\%FO_i$
Prey	*C. gariepinus*								
Insect Remains (IR)	2.99	0.08	7.41	-	-	-	-	-	-
Terrestrial IR	-	-	-	-	-	-	3.03	0.03	3.85
Odonata	1.49	0.10	3.70	-	-	-	6.06	0.25	3.85
Trichoptera	-	-	-	-	-	-	3.03	0.25	3.85
Fish Remains	46.27	11.21	44.44	33.77	22.84	30.91	33.33	14.32	42.31
Alestid	2.99	0.39	7.41	-	-	-	3.03	1.25	3.85
Barb	2.99	0.25	3.70	-	-	-	3.03	0.50	3.85
Cichlid	20.90	8.02	18.52	6.49	2.26	9.09	9.09	40.63	11.54
Clariid	11.94	51.58	22.22	-	-	-	3.03	0.25	3.85
Mormyrid	-	-	-	9.09	6.80	9.09	-	-	-
Silurid	-	-	-	5.19	12.06	7.27	-	-	-
Synodontid	10.45	28.38	22.22	35.06	37.13	45.45	-	-	-
Decapoda	-	-	-	3.90	4.35	5.45	18.18	35.62	23.08
Detritus	-	-	-	6.49	14.56	9.09	3.03	0.13	3.85
Other	-	-	-	-	-	-	15.15	6.77	7.69
	C. ngamensis								
Insect Remains	-	-	-	0.53	4.08	28.57	0.99	1.13	9.38
Terrestrial IR	-	-	-	0.59	0.14	3.57	-	-	-
Aquatic IR	-	-	-	0.07	0.38	3.57	2.32	4.42	21.88
Odonata	-	-	-	0.39	1.59	17.86	6.95	3.76	40.63
Trichoptera	-	-	-	0.07	0.09	3.57	-	-	-
Oligochaeta	-	-	-	-	-	-	3.31	0.47	3.13
Diptera	-	-	-	0.66	0.38	3.57	0.33	0.09	3.13
Coleoptera	-	-	-	0.92	5.84	17.86	-	-	-
Ephemeroptera	-	-	-	0.20	0.24	3.57	46.36	15.62	78.13
Hemiptera	-	-	-	0.26	0.09	10.71	0.66	4.42	6.25
Hymenoptera	-	-	-	88.64	4.27	3.57	-	-	-
Araneae	-	-	-	1.64	1.90	14.29	0.33	0.94	3.13
Fish Remains	-	-	-	0.46	3.47	21.43	1.32	0.56	12.50
Cichlid	-	-	-	0.53	18.42	21.43	0.99	5.83	9.38
Clariid	-	-	-	0.07	1.38	3.57	-	-	-
Synodontid	-	-	-	0.07	28.34	3.57	-	-	-
Citharine	-	-	-	0.07	0.09	3.57	-	-	-
Decapoda	-	-	-	3.55	1.54	7.14	11.92	42.05	28.13
Mollusca	-	-	-	0.72	23.71	35.71	22.85	9.41	40.63
Detritus	-	-	-	0.53	3.96	28.57	1.66	11.29	15.63

	Zambezi River			Kavango River			Kwando River		
	%N_i	%W_i	%FO_i	%N_i	%W_i	%FO_i	%N_i	%W_i	%FO_i
		H. cuvieri							
Fish Remains	41.18	32.47	43.75	-	-	-	25.00	11.60	25.00
Alestid	-	-	-	-	-	-	16.67	10.55	16.67
Barb	11.76	10.32	12.50	-	-	-	-	-	-
Cichlid	29.41	48.71	31.25	-	-	-	50.00	77.64	41.67
Mormyrid	5.88	1.91	6.25	33.33	32.54	33.33	-	-	-
Silurid	5.88	1.62	6.25	33.33	30.15	33.33	-	-	-
Synodontid	5.88	4.97	6.25	33.33	37.31	33.33	-	-	-
Micropanchax	-	-	-	-	-	-	8.33	0.21	8.33
		S. macrocephalus							
Insect Remains	-	-	-	8.33	0.03	11.11	-	-	-
Fish Remains	25.71	20.05	38.10	16.67	34.51	22.22	12.50	19.23	25.00
Alestid	2.86	6.50	4.76	-	-	-	12.50	19.23	25.00
Barb	42.86	27.64	33.33	25.00	11.31	33.33	25.00	38.46	50.00
Cichlid	17.14	26.29	23.81	-	-	-	37.50	19.23	50.00
Citharine	5.71	3.25	9.52	-	-	-	-	-	-
Mormyrid	5.71	16.26	9.52	50.00	54.15	44.44	-	-	-
Decapoda	-	-	-	-	-	-	12.50	3.85	25.00
		S. intermedius							
Insect Remains	13.33	2.33	20.00	5.71	0.29	10.53	28.49	31.62	33.55
Terrestrial IR	1.11	0.25	1.82	2.38	0.74	4.39	9.12	14.41	20.65
Aquatic IR	-	-	-	0.48	0.01	0.88	9.40	8.83	21.29
Odonata	4.44	3.71	7.27	2.86	0.43	5.26	9.97	6.03	16.13
Trichoptera	-	-	-	-	-	-	9.69	3.15	12.90
Ephemeroptera	13.33	2.50	12.73	0.95	0.01	1.75	8.55	1.30	9.03
Hemiptera	-	-	-	-	-	-	0.85	0.28	1.94
Coleoptera	-	-	-	0.48	0.10	0.88	-	-	-
Diptera	-	-	-	1.90	0.01	0.88	0.28	0.07	0.65
Fish Remains	24.44	30.59	38.18	27.62	13.22	46.49	8.26	11.85	17.42
Alestid	2.22	3.22	3.64	1.90	1.03	3.51	0.28	0.70	0.65
Barb	13.33	32.66	20.00	-	-	-	0.28	1.40	0.65
Cichlid	2.22	9.40	3.64	1.90	2.56	3.51	5.41	12.90	10.97
Citharine	1.11	0.74	1.82	-	-	-	-	-	-
Clariids	-	-	-	0.95	0.56	1.75	-	-	-
Cyprinid	-	-	-	-	-	-	0.28	1.05	0.65
Micropanchax	-	-	-	-	-	-	0.57	0.77	1.29
Mormyrid	3.33	11.38	5.45	43.81	78.50	46.49	-	-	-
Silurid	-			1.43	1.71	2.63	-	-	-
Decapoda	15.56	1.46	12.73	1.90	0.00	3.51	6.84	2.70	9.68
Detritus	5.56	1.76	9.09	5.71	0.82	10.53	0.57	1.05	1.29
Other	-	-	-	-	-	-	1.14	1.89	1.94

Appendix 4: Taylor GC, Peel RA, Hay CJ, Weyl OLF. In press. Validation of the periodicity of growth zone formation in the otoliths of four fish species from the Upper Zambezi Ecoregion, Southern Africa. *African Zoology*.

Validation of the periodicity of growth zone formation in the otoliths of four fish species from the Upper Zambezi Ecoregion, Southern Africa

Geraldine C Taylor[1,2*], Richard A Peel[1,2,3], Clinton J Hay[4,3] and Olaf LF Weyl[2,1]

[1]*Department of Ichthyology and Fisheries Science, Rhodes University, Grahamstown, South Africa*

[2]*South African Institute for Aquatic Biodiversity (SAIAB), Grahamstown, South Africa*

[3]*NNF/EU Community Conservation Fisheries in KAZA Project, Katima Mulilo, Namibia*

[4]*Department of Biological Sciences, University of Namibia, Namibia*

*Corresponding author, email: gc88taylor@gmail.com

Abstract

In the Upper Zambezi and Okavango Ecoregions, *Brycinus lateralis*, *Hepsetus cuvieri*, *Schilbe intermedius* and *Serranochromis macrocephalus* are important in subsistence fisheries, while *S. intermedius* and *S. macrocephalus* are often caught in commercial catches. Despite their importance, there is little information on their age and growth and age validation. Growth zone deposition rate in otoliths of *Brycinus lateralis*, *Hepsetus cuvieri*, *Schilbe intermedius* and *Serranochromis macrocephalus* was validated as annual using edge analysis (EA) in this study. Annual deposition of growth zones was corroborated by a fluorochrome marking experiment. Both methods demonstrated that one growth zone was deposited annually. EA demonstrated the highest proportion of opaque zones was detected between August and December, most likely as a result of slow growth during lower temperature water during the preceding winter. With growth zone deposition validated as annual, future research should focus on determining the growth, maturity and mortality rates of these species, parameters which are important for their management.

Keywords: *Brycinus lateralis*, *Hepsetus cuvieri*, *Schilbe intermedius*, *Serranochromis macrocephalus*

Introduction

Age estimation is an important aspect of any biological and ecological study as it allows for the determination of rates of maturity, mortality and growth (Campana & Thorrold 2001; Campana 2001). Otoliths are currently considered to be the most suitable structure for the age determination of fishes because these metabolically inert structures grow continuously throughout the life of the fish (Campana & Neilson 1985; Campana & Thorrold 2001). In otoliths, age is most commonly estimated by counting alternating opaque and translucent growth zones laid down as a result of varying calcium metabolism influenced by environmental (seasonal temperature changes) and behavioural (feeding and spawning) factors (Campana 2001). The interplay of these factors may result in differences in the timing of growth zone deposition between species in the same location or within species between locations (Gauldie & Nelson 1990; Campana 1999; Winker et al. 2010a, 2010b). As a result, age validation (determining the accuracy of age estimates), or the establishment of the frequency of formation of a typical growth increment, is a fundamental requirement of age estimation studies (Campana 2001).

The direct method of mark-recapture of chemically tagged wild fish (MRCT) and the indirect method of edge analysis (EA) are commonly used to validate the periodicity of increment formation (Campana 2001). MRCT involves applying a rapidly incorporated calcium binding chemical such as oxytetracycline hydrochloride (OTC) through immersion, injection or feeding of live fish (Campana 1999, 2001). This chemical adheres to bones, scales, spines and otoliths (Campana 1999) so creating a permanent mark visible under fluorescent light in the increment being formed at the time. The number of increments formed distal to this mark can then be compared to the time at liberty to ascertain increment periodicity. Although optimal when fish are allowed to grow in their natural environment, experiments involving fish kept under laboratory conditions or in outside enclosures are logistically easier to carry out (Campana 2001). Edge analysis is often used to corroborate the results of the MRCT experiment, and is based on the assumption that the relative frequency of opaque edges is periodic when plotted against time (Campana 2001).

In the Upper Zambezi and Kavango regions of southern Africa, because of the intensive sampling effort associated with validation experiments, previous research on determining growth zone deposition rates in otoliths has focussed on the commercially important cichlids *Oreochromis andersonii* (Castelnau), *Oreochromis macrochir* (Boulenger) and *Coptodon rendalli* (Boulenger) (Booth et al. 1995; Booth & Merron 1996; Peel et al. 2016). The growing demand on the fisheries of the region, and the Upper Zambezi River in particular (Tweddle 2010; Tweddle et al. 2015), has increased the fishing pressure on smaller species for which little biological information exists. The lack of validated-age data on these species is a serious constraint to the understanding of their life history and the development of management strategies because important biological parameters such as the rates of growth, maturity and mortality cannot be estimated. As these parameters are also the basis for stock assessment (e.g., Booth and Weyl 2004; Weyl et al. 2005), the availability of data on the growth zone deposition rate in their otoliths would allow for more accurate estimates of age and thus would allow for their inclusion in fisheries assessments and facilitate better management. For this reason, the aim of this study was to determine growth zone deposition rate in otoliths of *Brycinus lateralis* (Boulenger), *Hepsetus cuvieri* Castelnau, *Schilbe intermedius* Rüppell and *Serranochromis macrocephalus* (Boulenger) which are important contributors to subsistence and commercial fisheries in the region (Duerre 1969; Merron et al. 1990; Winemiller 1991; Winemiller & Kelso-Winemiller 1994, 1996; Hay 1995; Merron & Mann 1995; Booth & McKinlay 2001; Peel et al. 2015).

Materials and methods

Study site

Fish were collected from the large (300 km^2), shallow (mean depth ~3.5 m) ephemeral natural lake, Lake Liambezi (Muyako 17°52’58.48”S 24°23’45.00”E), in the Zambezi Region of north-eastern Namibia (Figure 1). Lake Liambezi receives water during exceptional floods of the Zambezi and Kwando rivers, so water level is unpredictable, and in the present wet phase the lake has been inundated since 2007.

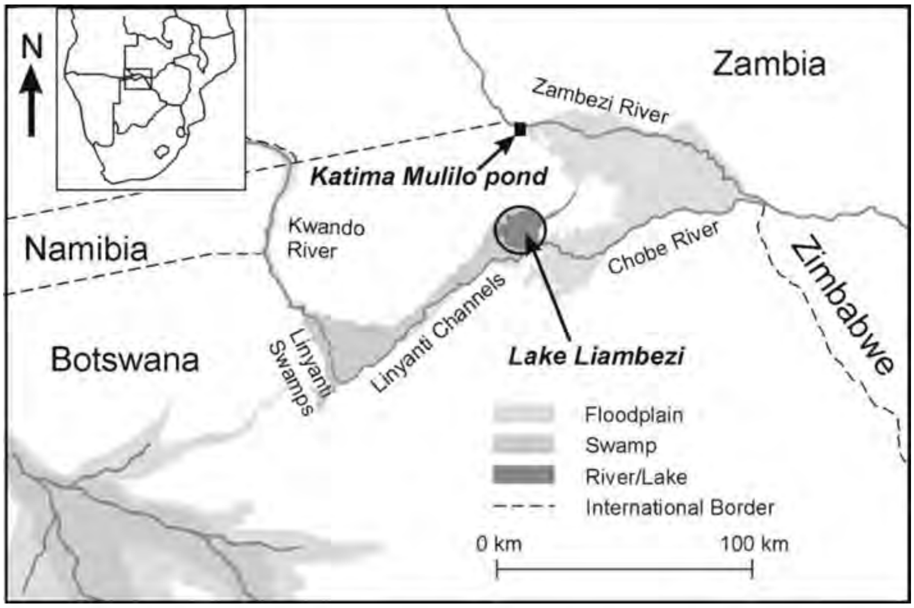

Figure 1: The locations of Lake Liambezi, the Upper Zambezi River, and the pond at Katima Mulilo, in the Upper Zambezi Ecoregion, Namibia.

Water temperature was recorded in each system using HOBO Pro v2 data loggers (Onset®, Bourne, MA, USA), programmed to log temperature at six hour intervals. Data were summarised to mean daily temperature, and the monthly averages plotted for comparison between systems. Temperature data encompassing the whole study period (April 2014 to March 2015) were collected from the pond, while data from the Upper Zambezi River and Lake Liambezi were collected between October 2013 and October 2014. The water temperatures of Lake Liambezi, the Katima Mulilo pond and the adjacent Upper Zambezi River followed a similar trend, with the lowest temperatures recorded in June and July (Figure 2).

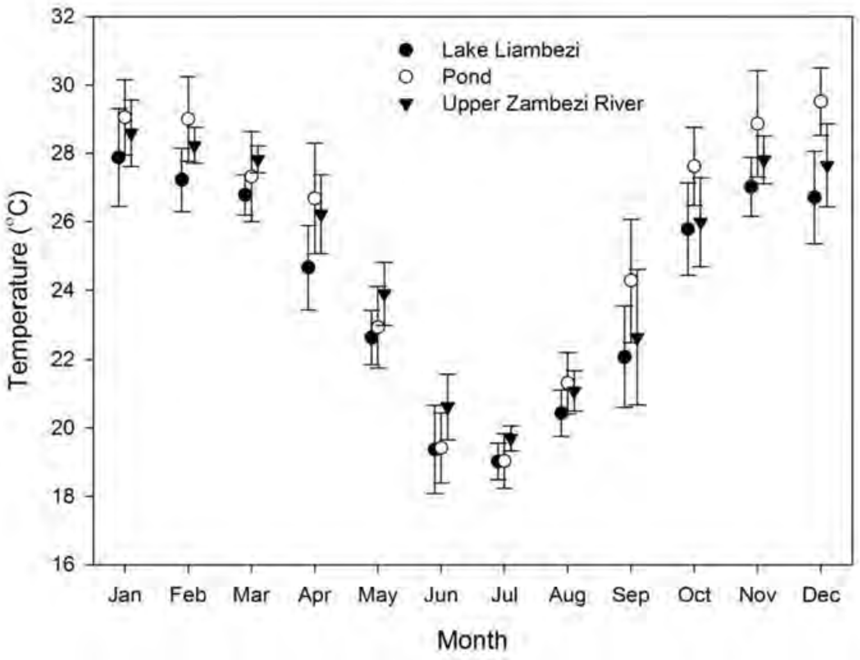

Figure 2: The mean monthly temperature (± SD) recorded from 27 March 2014 to 25 February 2015 from the Katima Mulilo pond, and from between October 2013 and October 2014 from Lake Liambezi and the Upper Zambezi River.

Edge Analyses

EA was carried out using fish from the four species captured during regular sampling of Lake Liambezi in 2013, 2014, and the beginning of 2015 using gill nets and seine nets. A sample of 457 *B. lateralis* between 35 and 131 mm fork length (FL), 176 *H. cuvieri* between 135 and 436 mm FL, 343 *S. intermedius* between 90 and 273 mm FL and 199 *S. macrocephalus* between 45 and 302 mm total length (TL) were used for the analysis (Table 1). Most fish from the gill nets were dead on retrieval, and any live fish were sacrificed by concussion followed by destruction of the brain. Ethical approval was granted by the SAIAB Animal Ethics Committee (Reference # 2013_07). All fish were measured to the nearest mm FL or TL and dissected to determine sex. The largest pair of otoliths was then collected: sagittal for *S. intermedius* and *S. macrocephalus*, and asteriscus for *B. lateralis* and *H. cuvieri*.

Table 1: The sampling dates, sample size, length range and sex structure (percentage juvenile, male, female) of the *Brycinus lateralis*, *Hepsetus cuvieri*, *Schilbe intermedius* and *Serranochromis macrocephalus* sampled for EA.

Species	Sampling date	Sample size (N)	Length range (mm)	Sex ratio (%J, %M, %F)
Brycinus lateralis	February 2015	29	73 - 111	0, 7, 93
	March 2015	30	86 - 107	0, 6, 94
	April 2014	94	47 - 128	9, 21, 70
	May 2015	30	68 - 86	0, 10, 90
	June 2014	109	45 - 126	18, 29, 53
	August 2014	86	45 - 131	27, 15, 58
	November 2014	32	35 - 109	6, 0, 94
	December 2014	47	47 - 131	23, 15, 62
Hepsetus cuvieri	February 2013	18	135 - 368	17, 72, 11
	March 2013	32	210 - 436	9, 56, 35
	April 2014	34	195 - 369	0, 53, 47
	June 2014	29	210 - 386	3, 45, 52
	August 2014	23	210 - 370	9, 52, 39
	October 2013	18	235 - 375	0, 50, 50
	December 2014	22	280 - 360	5, 36, 59
Schilbe intermedius	February 2013	54	119 - 246	4, 52, 44
	March 2013	45	122 - 255	2, 49, 49
	April 2014	53	141 - 253	2, 68, 30
	June 2014	45	90 - 264	0, 84, 16
	August 2014	53	170 - 255	0, 85, 15
	October 2013	51	155 - 273	0, 61, 39
	December 2014	42	152 - 248	0, 74, 26
Serranochromis macrocephalus	February 2013	21	71 - 262	5, 52, 43
	March 2013	33	104 - 252	3, 42, 55
	April 2014	23	141 - 302	4, 61, 35
	June 2014	16	120 - 295	6, 56, 38
	August 2014	8	166 - 248	0, 25, 75
	October 2010	23	140 - 285	9, 35, 56
	November 2010	7	122 - 234	57, 14, 29
	December 2014	9	182 - 267	0, 33, 66

Sagittal otoliths were set in clear polyester casting resin, sectioned transversely through the nucleus using a double bladed diamond edge saw at a thickness of 0.4 mm, and mounted on slides using DPX mountant following the procedure described by Taylor & Weyl (2013). Asteriscus otoliths were read whole immersed in methyl salicylate as described in Winker et al. (2010b). All otoliths were viewed under transmitted light at variable magnification (10–40 ×) and the optical appearance of the otolith edge was assessed and categorized as opaque zone present (1) or absent (0). All otoliths were read twice by an experienced reader, and a subsample of otoliths was read by an independent reader to confirm the appearance of an opaque edge. All readings were done blind without prior knowledge of the month of capture. Results were expressed as the monthly proportion of otoliths with an opaque zone at the edge and modelled using a periodic logistic regression (Flury & Levri 1999) of the form:

$$logit(\hat{O}_i) = \beta_0 + \beta_1 \sin\left(2\pi \frac{M_i}{P}\right) + \beta_2 \cos\left(2\pi \frac{M_i}{P}\right),$$

where *logit* is the link function for the binomial regression, $\hat{O}_i$ is the expected proportion of otoliths with an opaque zone present at the edge for each month M_i, P is the assumed periodicity of growth deposition (i.e. here 12 and 6 for an annual and biannual cycle, respectively) and β_0, β_1, β_2 the regression coefficients (Beamish et al. 2005).

Regression parameters were estimated by minimising the negated binomial log-likelihood function of the form:

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

where n_i is the number of otoliths examined in sample i and m_i represents the number of otoliths with an opaque zone present on the edge.

The null hypothesis that no seasonality was observed ($\mathrm{H}_0\ P = not\ restrained$), and the alternative hypotheses that growth zone deposition is annual ($\mathrm{H}_\mathrm{a}\ P = 12$), and biannual ($\mathrm{H}_\mathrm{a}\ P = 6$), were tested using a likelihood ratio test with a significance level of $P \leq 0.05$.

Mark-recapture of chemically tagged fish (MRCT)

The aim of this study was to validate the periodicity of growth zone deposition using both EA and MRCT for all species, however only *B. lateralis* were collected for MRCT. Since the likelihood of recapturing fish released into the large and heavily fished Upper Zambezi River and Lake Liambezi is low, fish were stocked into an earthen pond. *Brycinus lateralis* from Lake Liambezi were stocked into a 154 m^3 pond (14 m x 11 m x 1 m deep) in Katima Mulilo (17°29’15”S, 24°15’19”E) adjacent to the Upper Zambezi River. The fish were subject to the same climatic conditions as the Zambezi, Kwando and Kavango rivers and Lake Liambezi, with the exception of the annual flood. The pond was in a near-natural state and contained a variety of other fish species including *Tilapia sparrmanii* A. Smith, *O. macrochir*, *C. rendalli*, *Pseudocrenilabrus philander* (Weber), and *O. andersonii,* and had overhanging and floating aquatic vegetation. These conditions mimicked the natural habitat and no supplementary feeding was necessary.

During three collection events on the 27th and 29th March and the 4th April 2014, 183 *B. lateralis* (±70 – 100 mm FL) were sampled using a 5 mm meshed 5 m seine from Lake Liambezi at Muyako. These fish were immersed in oxytetracycline hydrochloride (OTC) at concentrations of between 570 and 700 mg OTC/l for between seven and eight hours in a 50-l opaque drum. Oxygen was provided and the drum was kept covered to prevent degradation of OTC by sunlight. Water quality parameters at Muyako, and at the Katima Mulilo pond were measured and summarised in Table 2. Conductivity (µS/cm), total dissolved solids (ppm), temperature (°C) and pH were measured using a Hanna HI98129 Combo pH and Electrical Conductivity meter, and turbidity (NTU) was measured using an AquaLytic AL250T-IR Turbidity meter.

Table 2: The average ± standard deviation of the water quality parameters of Lake Liambezi before the fish were sampled, and in the pond at the time the fish were released.

Parameter	Lake Liambezi	Pond
Temperature	27.9 ± 1.66	31.2 ± 0.77
Conductivity	284 ± 1.41	51.3 ± 5.13
Total dissolved solids	142	25.6 ± 2.08
pH	8.37 ± 0.10	7.94 ± 0.25
Turbidity	5.77	12.5

Six *B. lateralis* died during immersion, and as a result a total of 177 *B. lateralis* were released into the pond for the MRCT experiment. The pond was drained and fish were recaptured using a 5 m seine net of 5 mm mesh size at the end of February 2015 after 11 months at liberty.

Harvested fish were sacrificed by concussion followed by destruction of the brain, measured to the nearest mm, dissected to determine sex, and their asteriscus otoliths removed and stored in the dark to avoid degradation of the fluorescent OTC mark by ultraviolet light (Winker et al. 2010b). Otoliths were prepared as described for EA and viewed under reflected ultraviolet (460–490 nm) light to determine the position of the fluorescent mark, and under transmitted white light to count the number of growth zones proximal and distal to the mark.

Results

Edge Analyses

Observed and predicted data from Lake Liambezi for *B. lateralis*, *H. cuvieri*, *S. intermedius* and *S. macrocephalus* indicated that the highest proportion of otoliths had opaque edges from August to November (Figure 3). Periodic regression parameters for all species are provided in Table 3. Periodic logistic regression analyses failed to reject the alternative hypothesis that one opaque zone was deposited annually for *B. lateralis* (χ^2 = 2.59, d.f. = 3, P = 0.11), *H. cuvieri* (χ^2 = 0.00, d.f. = 3, P = 1), *S. macrocephalus* (χ^2 = 0.08, d.f. = 3, P = 0.78), and rejected the alternative hypothesis that growth zone deposition was biannual (*B. lateralis* χ^2 = 5.77, d.f. = 3, P = 0.016; *H. cuvieri* χ^2 = 61.73, d.f. = 3, P < 0.001; *S. macrocephalus* χ^2 = 21.04, d.f. = 3, P < 0.001). For *S. intermedius* both alternative hypotheses were rejected (H_1^0 χ^2 = 17.23, d.f. = 3, P < 0.001; H_2^0 $\chi2$ = 119.18, d.f. = 3, P < 0.001), however the observed data illustrate it is likely that one opaque zone was deposited annually.

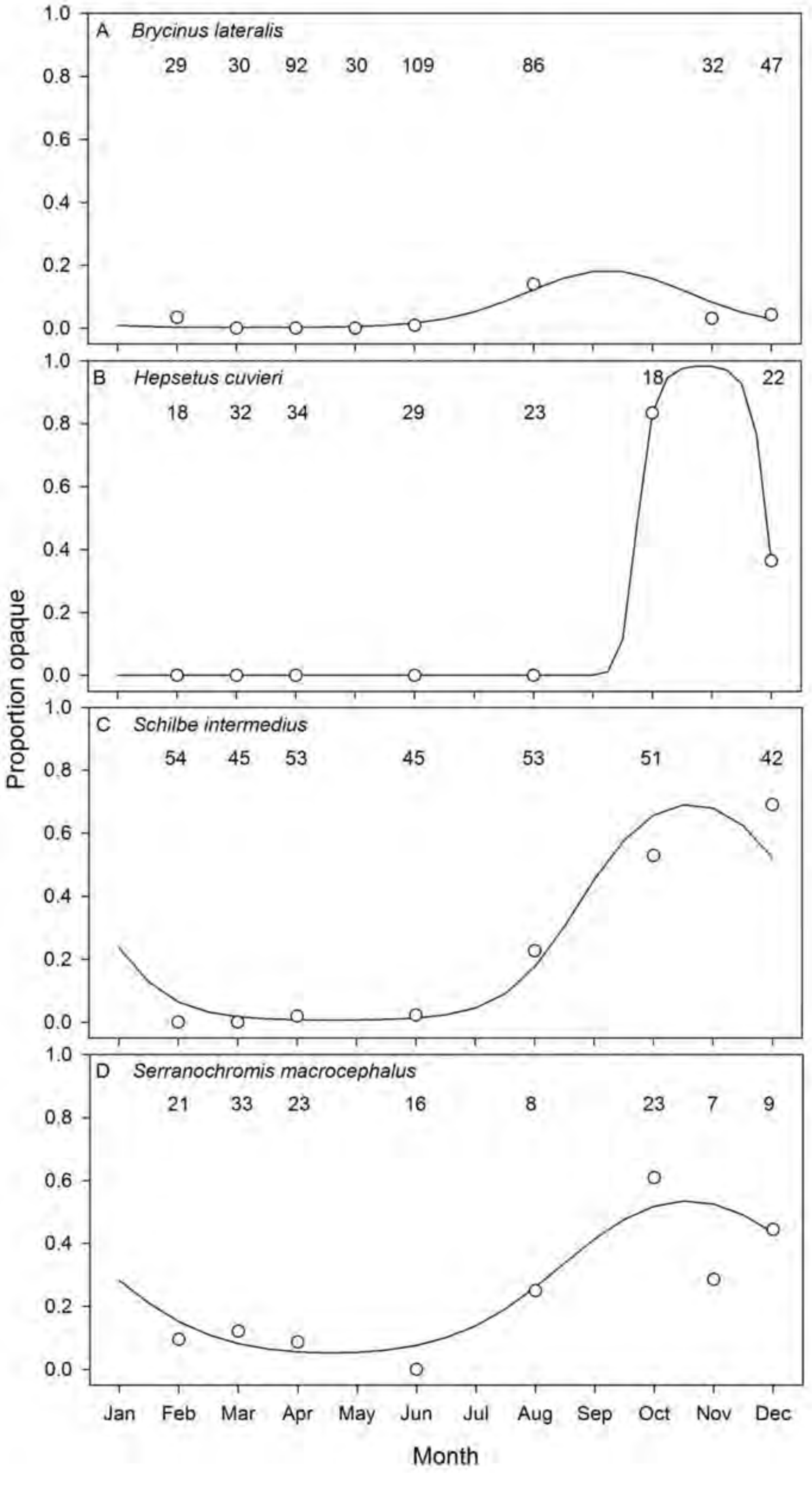

Figure 3: Proportion of opaque otolith edges from A) *Brycinus lateralis*, B) *Hepsetus cuvieri*, C) *Schilbe intermedius*, and D) *Serranochromis macrocephalus* from Lake Liambezi, Namibia. Solid line = predicted binomial periodic regression model; open circles = observed opaque proportions, sample sizes are given above each month sampled.

Table 3: Parameter estimates from logistic periodic analyses predicting temporal proportion of opaque zone deposition over a 1-year period for *Brycinus lateralis, Hepsetus cuvieri, Schilbe intermedius,* and *Serranochromis macrocephalus* from Lake Liambezi, Namibia. β_0, β_1, β_2 = regression coefficients, d.f. = degrees of freedom, *ln L* = log likelihood function.

		Periodic regression model coefficients		
Species	Statistic	Full	Annual	Biannual
Brycinus lateralis	β_0	-3.52	-3.79	-3.94
	β_1	-0.85	-2.28	2.24
	β_2	2.17	0.29	0.22
	Periodicity	9.78	12	6
	d.f.	4	3	3
	ln *L*	-59.26	-60.55	-62.14
Hepsetus cuvieri	β_0	-211.28	-21.84	-12.22
	β_1	211.64	-14.79	-19.15
	β_2	30.72	21.28	10.53
	Periodicity	47.18	12	6
	d.f.	4	3	3
	ln *L*	-22.53	-22.53	-53.40
Schilbe intermedius	β_0	-3.23	-2.11	-1.37
	β_1	0.62	-1.92	-0.72
	β_2	-4.01	2.20	0.81
	Periodicity	26.21	12	6
	d.f.	4	3	3
	ln *L*	-100.24	-108.86	-159.83
Serranochromis macrocephalus	β_0	-1.42	-1.38	-1.51
	β_1	-0.90	-1.04	-0.85
	β_2	1.29	1.11	0.00
	Periodicity	11.54	12	6
	d.f.	4	3	3
	ln *L*	-59.07	-59.11	-69.59

Mark recapture of chemically tagged fish

Of the 177 *B. lateralis* released in the Katima Mulilo pond, 20 were recaptured, ranging between 75 and 91 mm FL and encompassing both males and females. All *B. lateralis* recaptured had a fluorescent mark on their otoliths (Figure 4), with between zero and five opaque zones before the fluorescent mark and one opaque zone after the fluorescent mark (Table 4).

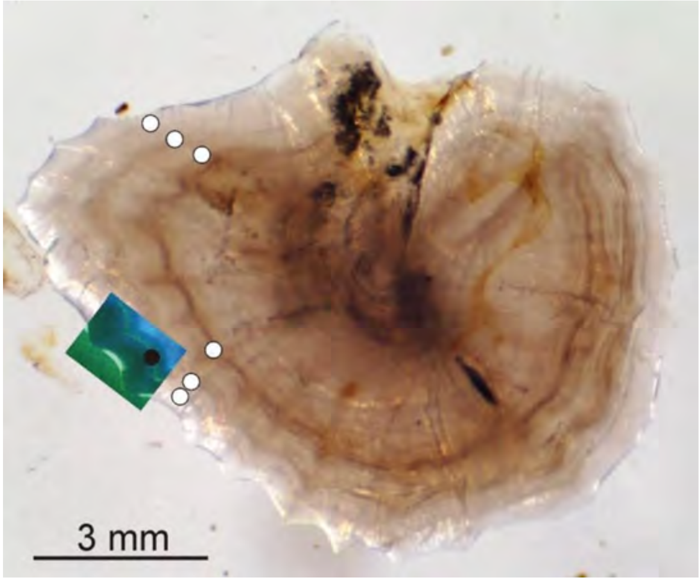

Figure 4: Three year old *Brycinus lateralis* asteriscus otolith immersed in oxytetracycline hydrochloride and grown in a pond for 11 months. Opaque zones counted under transmitted light = white circles, fluorescent mark = black circles.

Table 4: Fork length (mm), sex, and number of opaque bands of *Brycinus lateralis* before and after immersion in oxytetracycline hydrochloride and recaptured after 11 months in a pond.

Length (mm)	Sex	Opaque before	Opaque after	Age
82	F	2	1	3
84	F	3	1	4
83	F	5	1	6
86	F	1	1	2
80	F	2	1	3
90	F	3	1	4
86	F	2	1	3
91	F	4	1	5
82	F	1	1	2
75	F	1	1	2
77	F	2	1	3
86	F	3	1	4
85	F	2	1	3
80	F	2	1	3
84	F	3	1	4
76	F	2	1	3
80	F	2	1	3
75	M	0	1	1
75	M	2	1	3
87	F	3	1	4

Discussion

This study demonstrated that one opaque and one translucent growth zone was deposited annually for *H. cuvieri, S. macrocephalus* and *S. intermedius* using EA in the Upper Zambezi Ecoregion of Southern Africa. Opaque zone deposition was detected in samples collected between September and December for these species. This annual peak in opaque zone deposition was clear for all species, despite the bi-monthly sampling regime, and it is suspected that with a complete year of data, this annual peak in opaque zone deposition would have been even clearer. While the sample sizes over the opaque zone deposition period for *S. macrocephalus* were small, an increase in the relative abundance of opaque edges was still detected.

For *B. lateralis,* EA results were less convincing, with only a week, yet significant unimodal relationship detected. This might have been influenced by the absence of samples from two months over what appears might have been the peak deposition period. However, annual deposition of a growth zone was validated for *B. lateralis* using MRCT. Consistency of results from two independent techniques can be considered strong evidence of an annual growth zone deposition rate in this species. The results from this study are also consistent with findings from other validation studies conducted in the Upper Zambezi and Okavango Ecoregions of Southern Africa, where opaque zone deposition was detected between October and December for *C. rendalli, O. andersonii* and *O. macrochir* (Booth et al. 1995; Booth & Merron 1996; Peel et al. 2016).

Opaque zones are formed when metabolic rates are slowed, causing a reduction in growth rates as a result of one or a number of environmental or biological factors (Weatherley & Gill 1987; Gauldie & Nelson 1990). Dudley (1974) found that in the Kafue River, *O. andersonii*, *O. macrochir* and *C. rendalli* deposited one ring between October and January on scales. He attributed growth zone deposition to the slowing of fish growth rates as a result of a combination of factors: low temperatures during winter months, reproductive activity and associated behaviour at the onset of warm temperatures, and the lack of food supplies during low water periods. Peel et al. (2016), Booth et al. (1995) and Booth & Merron (1996) all confirmed that opaque zone formation was asynchronous with hydrological season, and Peel et al. (2016) suggested that cold winter temperatures were the most likely cause of opaque zone formation. With the temperature regimes of the experimental pond, Lake Liambezi and the adjacent Upper Zambezi River (Figure 2) all following a similar trend of low winter temperatures between June and August, fishes from these three systems may all deposit their opaque growth zones as a result of slow growth during this cold winter period.

Annual growth zone deposition is consistent with other validation studies conducted on southern African freshwater fishes (e.g. Willoughby & Tweddle 1978; Weyl & Hecht 1998; Bhokhutlo et al. 2015), except for *S. intermedius* in impoundments in South Africa where two growth zones were deposited each year (Hecht 1980). The biannual growth zones detected for *S. intermedius* by Hecht (1980) was however contrary to the annual deposition of growth zones by this species in Mnjoli Dam, Swaziland (Booth & Khumalo 2009) and in the Upper Zambezi region (this study). Such inconsistency suggests that regional validation should be carried out for this species.

With regards to *B. lateralis, H. cuvieri* and *S. macrocephalus*, the current study suggests the annual deposition of one opaque and one translucent zone each year. This effectively validates growth zone deposition rate as annual and thus age can be estimated from direct counts of growth zones. As growth zone deposition rate has now been validated, future biological assessments on these species can now be undertaken using samples derived from single surveys, allowing future research to focus on determining population age-structure and rates of growth, maturity and mortality. This will allow for a better understanding of their biology and facilitate better management.

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