

**COLONISATION AND SUCCESSION OF FISHES IN LAKE
LIAMBEZI, A SHALLOW EPHEMERAL FLOODPLAIN
LAKE IN SOUTHERN AFRICA**

Thesis submitted in fulfilment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

of

RHODES UNIVERSITY

by

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October 2016

Abstract

Lake Liambezi is a shallow ephemeral floodplain lake situated in north-eastern Namibia. It is fed on an irregular basis by the Upper Zambezi and Kwando rivers, which overflow into the lake during years of extremely high flooding. The lake dried up in 1985 following five years of low floods in the inflowing rivers. It remained largely dry until the early 2000s, whereupon it received several minor floods, but subsequently dried up on each occasion. In 2007 it received a larger flood that sustained the lake up until April 2009, when it received a major flood, filling for the first time since the late 1970s. The lake reached a peak surface area of around 370 km² during successive floods in 2010 and 2011. It has remained inundated since, despite having not received any significant inflow. The aim of this thesis was to contribute toward the understanding of fish colonisation patterns, and the drivers of community succession following flooding in Lake Liambezi. The study used field estimates of abundance/biomass, otolith-derived age, growth and maturity data, and gut contents and stable isotope data to test the central hypothesis that: the hydrological regime, life-history adaptations and trophic dynamics in Lake Liambezi interact to determine fish colonisation patterns and drive community succession.

The fish fauna of Lake Liambezi displayed remarkable resilience to drying, with a diverse range of species, representative of opportunistic, periodic and equilibrium life-history strategies, colonising in large numbers from the Upper Zambezi and Kwando rivers during each of three discrete flooding events in 2001, 2004 and 2007. The colonising fish communities differed significantly from their source populations on the Zambezi and Chobe river floodplains as a result of interspecific differences in the propensity and ability to undertake extensive lateral migrations. The colonising fish communities were consistently dominated by two opportunistic cyprinids *Enteromius paludinosus* and *Enteromius poechii*, and two catfishes with a periodic life-history strategy, *Schilbe intermedius* and *Clarias gariepinus*. The results largely supported the hypothesis that the colonising fish community composition would exhibit a high degree of determinism and low stochasticity.

Following inundation in 2007, the fish community underwent a succession, from a colonising assemblage dominated by floodplain specialists, to a lacustrine assemblage dominated by fishes adapted to more stable environments. Species diversity and abundance declined markedly in the year after inundation as the lake shrank from 65 km² to just 10 km². The

abundance distribution of individual taxa was far more even after the lake filled in 2009, with five species from different families (*E. paludinosus*, *S. intermedius*, *Brycinus lateralis*, *Marcusenius altisambesi* and *Tilapia sparrmanii*) each contributing more than 10% to the catch numerically. The greater magnitude and duration of the 2009 flood gave less prolific colonisers the opportunity to enter the lake in larger numbers. The vast open waters of the lake were quickly colonised by two small planktivorous alestids, *Rhabdalestes maunensis* and *B. lateralis*. The number of *R. maunensis* crashed later in 2010, but *B. lateralis* continued to increase rapidly in abundance, and came to dominate the fish community in 2011. Larger, later maturing species increased steadily in abundance, highlighted by the development of the fishery, based primarily on tilapiine cichlids. The fish community remained largely the same between 2011 and 2014, indicating that it may have reached maturity.

The life history strategies of eight common fish species were investigated, and their establishment success evaluated against life-history theory. *Brycinus lateralis* displayed life-history traits typical of an opportunistic strategist, enabling it to achieve rapid population growth. Key to its success was its ability to breed independently of the hydrological cycle. *Clarias gariepinus* and *S. intermedius* are periodic strategists. They were unable to breed successfully in the lake in non-flood years, but have been able to persist due to their greater longevity than other successful colonists such as the small opportunistic cyprinids. As predicted by life-history theory, the equilibrium strategists *Hepsetus cuvieri*, *Oreochromis andersonii*, *Oreochromis macrochir*, *Coptodon rendalli* and *Serranochromis macrocephalus* have been very successful at establishing in Lake Liambezi. The cichlids displayed fast growth and early maturity, contributing to rapid population growth potential.

Stable isotope analysis indicated that consumer biomass was supported by phytoplankton and, to a lesser extent, aquatic macrophytes. Three food chains were identified. The phytoplankton based pelagic food chain was longest, involving up to four trophic transfers. The benthic food chain based on detritus of planktonic origin was characterised by high levels of omnivory, and involved up to three trophic transfers. The food chain based on detritus derived from macrophytes was shortest, involving two trophic transfers. Predators fed across all three food chains, but more so on the benthic food chains. Food web dynamics were, for the most part, driven by species abundance patterns. Competition between *B. lateralis* and *R. maunensis* was, however, the most likely cause of the latter's decline.

Together, these results provided evidence that colonisation patterns and species successions in Lake Liambezi were significantly influenced by species life-history strategies and their adaptations to the irregular and unpredictable hydrological regime. Interspecific biotic interactions played a minor role in driving species abundance patterns.

Acknowledgements

First and foremost, I would like to thank my supervisors Professor Olaf Weyl, Dr Jackie Hill and Dr Clinton Hay. Olaf, thank you for your mentorship, guidance and support, not only for this thesis, but over the past eight years. It's been a long and rewarding relationship, and I hope that we can continue to work together on new and exciting research projects in the future. Jackie, thank you so much for taking me on after Sven tragically passed away. Your isotope knowledge was invaluable, and your positive feedback was always a great morale booster. Clinton, thanks for your interest and useful comments on the final draft of this thesis.

I would like to thank the Namibia Nature Foundation (NNF) for administering the project, and for providing logistical support for field work. Funding was provided through the NNF/EU Community Conservation Fisheries in KAZA Project, by the Southern African Scientific Service Centre for Climate Change and Adaptive Land Management (SASSCAL) and the Nedbank Namibia Go Green Fund. Additional funding and support were provided by the South African Institute for Aquatic Biodiversity (SAIAB) and the National Research Foundation of South Africa (NRF).

I would like to gratefully acknowledge the Ministry of Fisheries and Marine Resources, Namibia, for granting permission to carry out this research, for providing an office at Katima Mulilo, and for granting permission to use long-term monitoring data from lake Liambezi.

Geraldine Taylor, thank you for your love and support, your assistance in the field, and for proof reading this thesis. Denis Tweddle, thank you for giving us a home in Katima Mulilo and for supporting my research over the past six years. Michelle Jackson, thank you for teaching me the basics in SAIR. Osbert Simataa, thank you for your assistance in the field. Dick Sharpe and Robbie Sparg, thanks for fixing boats and trailers. Bruce and Christine, thanks for your friendship and support, and for opening your home to us in Grahamstown. Kim and Sashank, thanks for accommodating us when we were on the move.

Finally, I would like to thank my family, to whom this thesis is dedicated. Dad, Mum and Briony, thank you for your love and support throughout my studies, and for encouraging my passion in fish and fishing from an early age.

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CHAPTER 1

General introduction

Shallow lakes

Wetlands are diverse and productive systems (Ward *et al.* 1999, 2002) that provide many economically valuable goods and services, such as water purification, food supply and flood control, on which humans depend (Baron *et al.* 2002; Arthington *et al.* 2004). Among the most productive and important wetlands in Africa are large, shallow lakes (<5 m average depth) such as Chad and Chilwa (Kalk *et al.* 1979; Carmouze *et al.* 1983b), many of which occur in the drier tropics where surface water is scarce, making them extremely important both ecologically and economically (Kolding *et al.* 2016b).

The functioning of shallow tropical lakes is influenced by the interacting components of basin geomorphology, climate and biogenic processes (Talling 1992, 2001). These vary considerably across tropical Africa, creating a diverse range of shallow aquatic environments. One thing all shallow lakes have in common, however, is a high surface area relative to their volume. This means that the water replacement time in shallow lakes is generally short, making them especially sensitive to changes in water inputs (Talling 2001). As a consequence, water level fluctuations are a dominant force controlling ecological processes in shallow lakes (Dumont 1992; Wantzen *et al.* 2008; Kolding and van Zwieten 2012). Due to their extensive and gently sloping littoral areas, even small changes in water level can result in large changes in the area of inundation. Many other environmental factors vary concurrently with fluctuations in water level (Talling 1992), with important consequences for lake biota (Dumont 1992; Talling 2001).

On or near the equator, fluctuations in water level can be minimal. In Lake George, Uganda for example, seasonally bimodal rainfall and melt-water from glaciers and snow on the Rwenzori Mountains provide a high and continuous flow of water into the lake, the level of which is further buffered by outflow through the Kazinga Channel that flows slowly into Lake Edward (Viner and Smith 1973; Greenwood 1976). As a result of the climatic and hydrological stability, environmental conditions in Lake George vary more widely on a diel cycle than they do seasonally (Viner and Smith 1973). Seasonal variation in the hydrological regime of tropical lakes becomes more pronounced with increasing latitude, due to seasonal

variation in rainfall brought about by movement of the intertropical convergence zone (ITCZ) with the changing position of the thermal equator (Talling 2001). Large shallow lakes that are relatively stable in the long term, but experience marked seasonal fluctuations in water level include the exorheic lakes Bangweulu and Mweru in northern Zambia (Jul-Larsen *et al.* 2003), and the endorheic lakes Naivasha and Baringo in Kenya (Talling 1992). Water levels in the aforementioned endorheic lakes, which lack surface outflows, are buffered by seepage-out to underlying groundwater (Talling 2001). In addition to marked seasonal fluctuations in water level, many endorheic lakes in the drier tropics experience large interannual fluctuations. In extreme cases these are characterised by flooding and drying cycles, which can vary widely in duration from years to decades. Well studied examples of endorheic freshwater lakes that experience flooding–drying cycles, or are ephemeral in nature, include Lake Chilwa in Malawi (Kalk *et al.* 1979) and to some extent Lake Chad (Carmouze *et al.* 1983b).

Drying is a major disturbance in ephemeral lake ecosystems that has devastating consequences for populations of aquatic biota. However, many of the species that inhabit ephemeral lakes are able to survive prolonged droughts by aestivating (e.g. crocodiles) or adopting dormant stages in the sediment (e.g. zooplankton) (Dumont 1992). Others that survive in aquatic refugia may be specially adapted (short generation time, high reproductive effort and high demographic resilience) to exploit the ephemeral habitat (Winemiller and Rose 1992). Periodic drying may even be necessary for the maintenance of species diversity in ephemeral lakes as it increases habitat diversity, and promotes species coexistence by mediating biotic interactions (Dumont 1992; Ward *et al.* 2002; Wantzen *et al.* 2008). However, the frequency with which ephemeral lakes experience such intense disturbances means that they generally host fewer species, and fewer endemic species than lakes and rivers that experience less intense and more predictable disturbances (Dumont 1992). Understanding how biota respond to flooding and drying in ephemeral lakes is therefore essential for their conservation and management.

Ephemeral lakes

Gawne and Scholz (2006) reviewed the effects of flooding and drying on lakes and, using that information, proposed a conceptual model for understanding the functional processes of ephemeral deflation basin lakes in the Murray–Darling Basin of south-eastern Australia. The

model incorporates aspects of the Flood Pulse Concept (Junk *et al.* 1989), Trophic Cascade Model (Carpenter *et al.* 1985) and Geomorphic–Trophic Model (Hershey *et al.* 1999) as they apply to ephemeral lakes. It identifies five phases in the flooding–drying cycle that begin and end with a dry lake bed:

1. The first phase begins with the flooding of a previously dry lake bed, and is characterised by high levels of productivity, high structural habitat complexity and low predator densities; conditions that allow for the rapid development of an abundant, diverse consumer community.
2. The next phase is characterised by an increase in fish abundance, and a decrease in structural habitat complexity associated with the decomposition of flooded terrestrial vegetation and stranding of vegetation by the receding water level.
3. As water levels continue to recede, organisms become concentrated and the density of predators increases, exerting top-down pressure on consumers of lower trophic levels.
4. Avian predation becomes an important structuring force when the water level reaches a point at which fish can no longer take refuge in deeper areas. This continues until environmental conditions become too harsh for aquatic organisms to tolerate.
5. The lake eventually dries, becoming an important habitat for terrestrial plants and animals, during which time organic matter accumulates, ready to fuel the high productivity once floodwaters return.

The resilience and capacity for recovery of fish communities in ephemeral lakes depends on the availability of permanent aquatic refugia, such as marginal wetlands and inflowing rivers. Here, relict populations of lake fauna can survive periods of lacustrine desiccation, and recolonise the lake when floodwaters return (Dumont 1992; Wantzen *et al.* 2008). Recovery is generally very rapid, owing to the high levels of productivity associated with flooding. Upon flooding, a pulse of nutrients is released from sediments (Baldwin and Mitchell 2000; Scholz *et al.* 2002), vegetation and other organic material (McLachlan 1971; Furch and Junk 1997). This launches a period of increased productivity known as the ‘trophic upsurge’. The term was originally used in reference to post-impoundment productivity in man-made lakes (Baranov 1961), but is equally suited to describe the same phenomenon in ephemeral lakes.

Fish species that can reproduce in the new lentic environment increase rapidly in abundance as plentiful foods, ideal nursery areas among flooded terrestrial vegetation, and low predator densities contribute to enhanced juvenile survival and recruitment (Lowe-McConnell 1987;

Winemiller 1996a). Species increase in abundance at different rates, with smaller, opportunistic species being most rapid, followed by large bodied periodic strategists, and later, in the absence of further disturbances, equilibrium strategists (Winemiller and Rose 1992; Winemiller 1996b). Predator numbers increase progressively, and eventually they begin to exert top-down control on fishes and invertebrates of lower trophic levels (Lévêque 1995; Gawne and Scholz 2006). Their effects are compounded by reduced habitat diversity and receding water levels, which further increase predator densities (Jackson *et al.* 2001).

Fisheries, representing man's impact as a predator, also exert significant pressure on fish communities in many African lakes. Under the 'unselective' harvest regime of many African fisheries, where fishers employ a broad array of fishing methods and gears, their effect will be spread across a wide range of species of all age and size classes, apparently conserving the overall community structure (Kolding and van Zwieten 2014; Kolding *et al.* 2016a). However, not all fisheries are unregulated or have reached such high levels of exploitation. Some still selectively target the largest, most valuable fish species in a community (e.g. Peel *et al.* 2015). Selective fishing, especially of predatory species, can have indirect effects on fish community structure by altering trophic dynamics (Welcomme 1999; Jackson *et al.* 2001; Allan *et al.* 2005; Layman *et al.* 2005; Garcia *et al.* 2012).

As water levels recede further, environmental conditions such as salinity, turbidity, and fluctuations in oxygen concentration and temperature become increasingly harsh (Talling 1992). These conditions select for species that are tolerant of adverse environmental conditions, or are specially adapted to cope, through the use of an accessory air breathing organ (Furse *et al.* 1979; Benech *et al.* 1983). In southern Africa, the hardiest species that survive longest before drying usually comprise at least one cichlid species of the genus *Oreochromis*, together with a small cyprinid *Enteromius paludinosus*, and the hardiest of the three, the clariid catfish, *Clarias gariepinus* (Jackson 1989). These taxa are also among the first to recolonise ephemeral habitats when floodwaters return (e.g. Furse *et al.* 1979).

Lake Liambezi

Lake Liambezi (17.92° E, 24.32° S; 929 m amsl) is a shallow ephemeral floodplain lake situated in the Zambezi Region of Namibia in southern Africa (Figures 1.1 and 1.2). The Zambezi Region is a narrow strip of land, formerly known as Caprivi, which extends

eastwards from the north-east corner of the country, and is bordered by Angola, Zambia, Botswana and Zimbabwe. The region has a very flat topography, with elevations ranging from 1 100 m in the far west to 930 m in the east (Mendelsohn and Roberts 1997). Rain falls during austral summer from October to April. Rainfall in the region is highly variable, but averages approximately 700 mm in the north-east, declining gradually to 500 mm in the south-west (Mendelsohn and Roberts 1997). The annual average evaporation rate is as high as 2 500 mm (Mendelsohn and Roberts 1997). Vegetation in the Zambezi Region is influenced mainly by soil type and flooding. Soils around Lake Liambezi are predominantly clay-loam that, in higher areas, support Mopane woodlands, and in lower areas subject to occasional flooding, are covered by floodplain grasses (Mendelsohn and Roberts 1997).

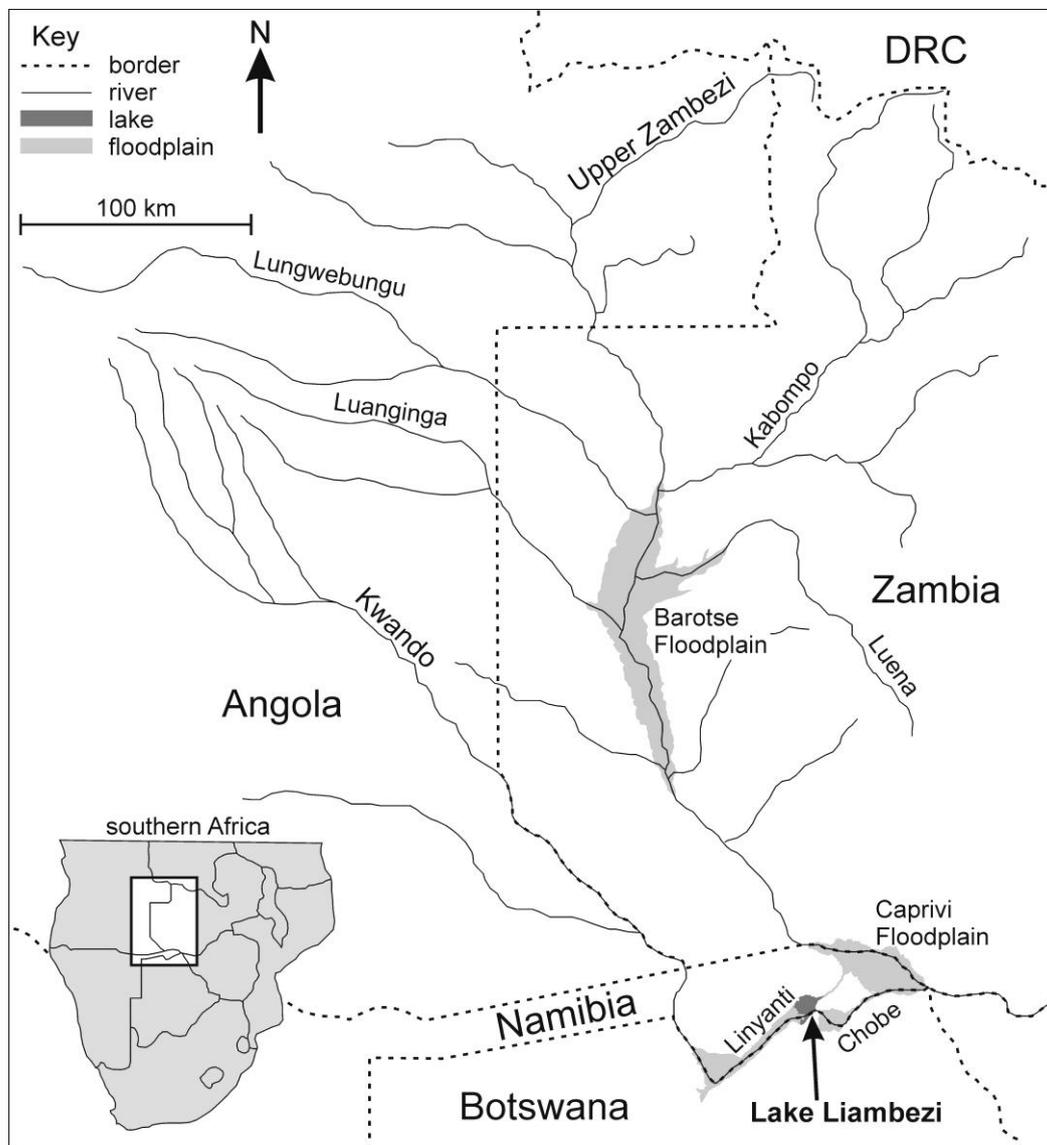


Figure 1.1. Lake Liambezi is situated in north-eastern Namibia, and is fed by floodwaters from the Upper Zambezi and Kwando rivers.

Hydrology

Lake Liambezi occupies a shallow depression on the Namibia–Botswana border (Figure 1.2). It is fed on an irregular basis by two unregulated floodplain rivers, the Upper Zambezi River and the Kwando River (Figure 1.1), which overflow into the lake during years of exceptionally high flooding. The Upper Zambezi River, which rises in north-western Zambia, forms the north-eastern border with Zambia for approximately 120 km, from Katima Mulilo town to the Chobe River confluence. Water from the Upper Zambezi River, the primary source, enters Lake Liambezi via two pathways (Figure 1.3). Annually, when the Zambezi floods, the Chobe River reverses flow direction and enters the lake in the south-east, while the Bukalo Channel flows from the Caprivi floodplain into the north-east of the lake. The smaller Kwando River rises in the central Angolan highlands. It bisects the Zambezi Region in the west, after which it forms the western border with Botswana, eventually flowing into the Linyanti Wetlands. Its waters percolate through the wetlands during years of high flooding and out via the Linyanti Channels, which flow north-eastward along the Namibia–Botswana border into the lake (Figure 1.3). Rainfall and runoff from the area north of the lake also contribute to water inputs. Outflow from the lake via the Chobe River when floodwaters recede is intermittent and dependent on lake level (Seaman et al. 1978).

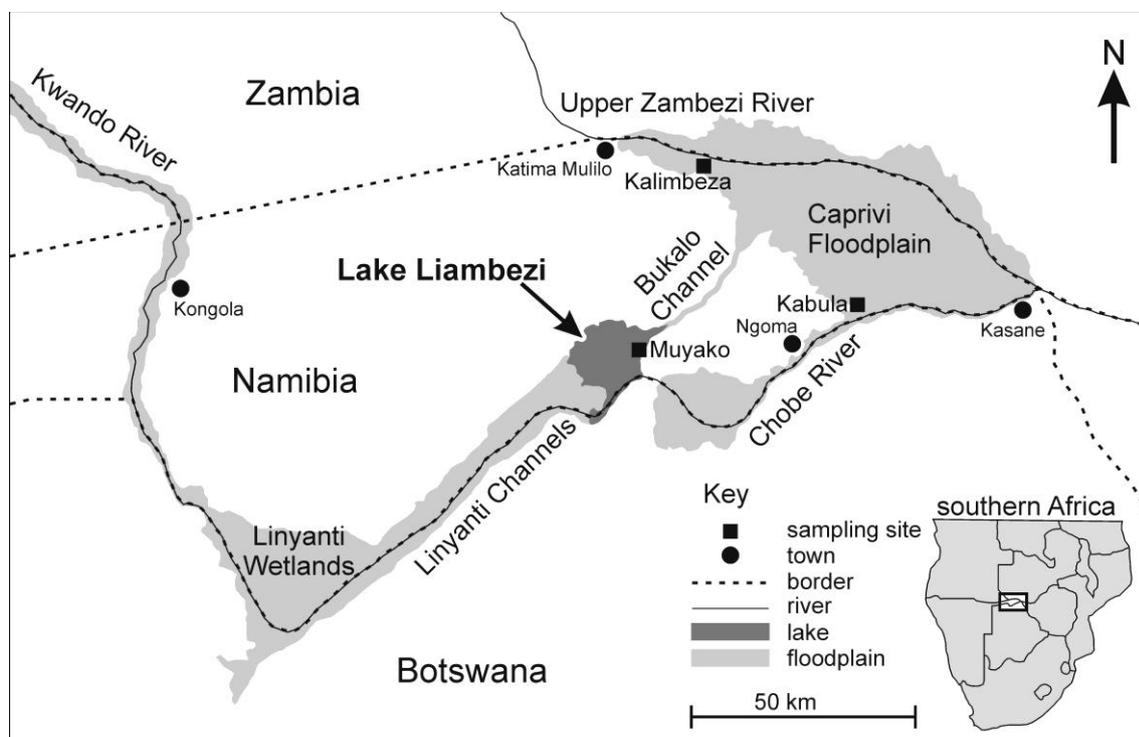


Figure 1.2. Map of north-eastern Namibia illustrating the rivers and floodplains feeding into Lake Liambezi, and the location of sampling sites on Lake Liambezi and the Upper Zambezi and Chobe rivers.

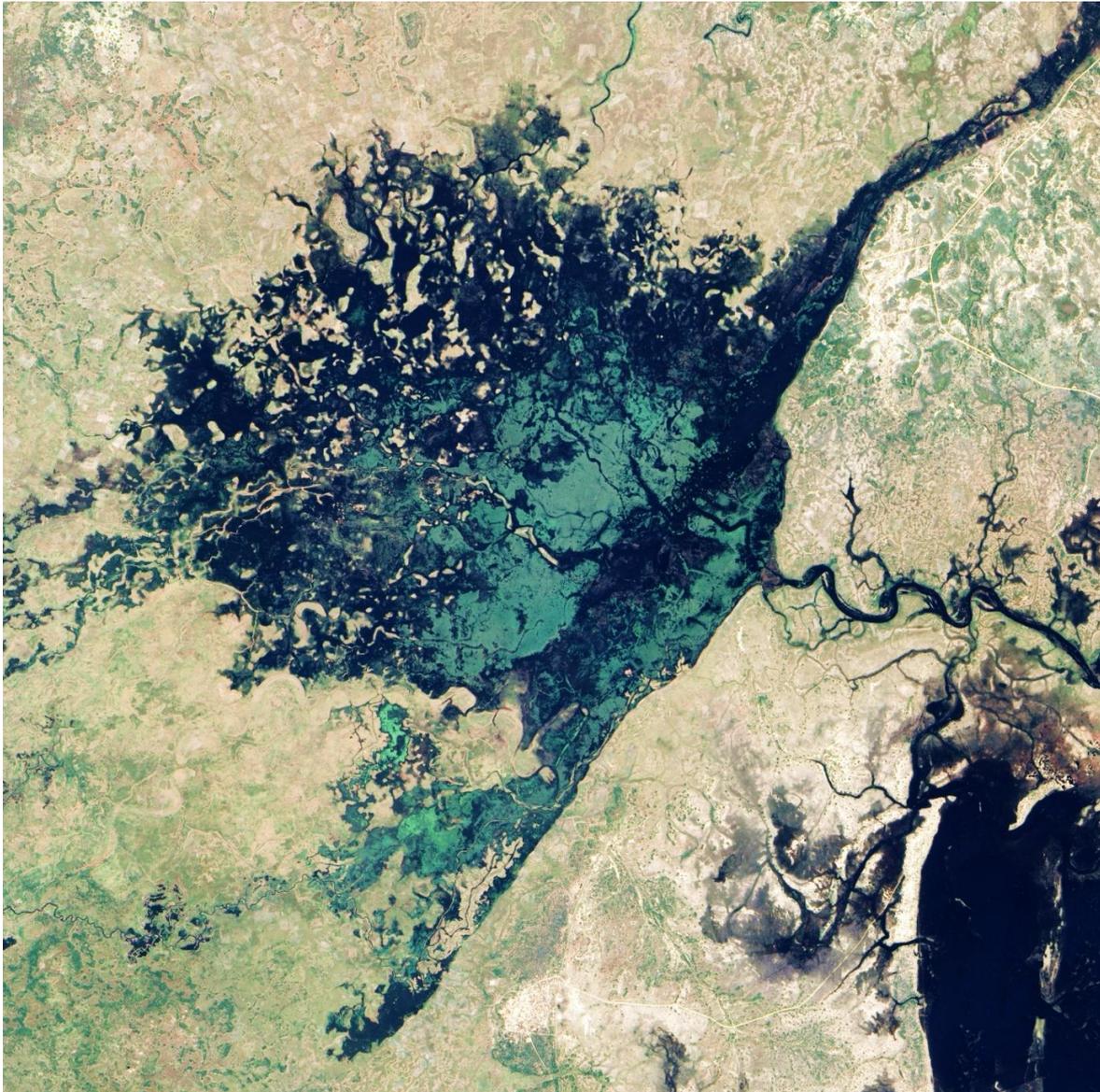


Figure 1.3. Satellite image of Lake Liambezi taken shortly after filling in April 2009 showing stands of established vegetation and numerous islands. The Bukalo Channel enters the lake in the north-east, the Chobe River in the east, and the Linyanti Channels in the south-west and west. The Chobe floodplain is visible in the south-east corner of the image. NASA Earth Observing-1 Advanced Land Imager (ALI).

Flood regimes differ markedly between the Upper Zambezi and Kwando rivers. In the Zambezi River, floodwaters derived from tributaries in north-western Zambia and east-central Angola usually spill onto the Caprivi floodplain in January–February. The flood waters peak in March–April, at which time they may overflow into Lake Liambezi, and subside from May to June (van der Waal and Skelton 1984). The average flood magnitude (calculated as the maximum water level minus the minimum water level of the previous dry season) in the Zambezi River at Katima Mulilo between 1965 and 2014 was 5.42 m, with a minimum magnitude of 2.38 m in 1992 and a maximum of 7.49 m in 1969 (data from

Namibia Hydrological Services, Ministry of Agriculture, Water and Forestry). The Zambezi River needs to reach a water level in excess of 6.30 m at Katima Mulilo, and remain above that level for several weeks for it to overflow into Lake Liambezi. The Zambezi River has exceeded the 6.30 m mark 19 times since 1965, on average once every 2.7 years. A more substantial flood, in excess of 6.80 m, is generally required to fill the lake. This has occurred 13 times since 1965, on average once every 4 years

Rainfall in the Kwando River catchment in south-eastern Angola occurs during the same season as that in the Zambezi River catchment, but the arrival of floodwaters in Namibia is delayed until June–July by the Silwana floodplains on the Angola–Zambia border. The Linyanti wetlands further delay the arrival of the peak flood at Lake Liambezi until August–September, during the dry season (van der Waal and Skelton 1984). The flood magnitude of the Kwando River at Kongola, near the Angolan and Zambian border, averages less than 1 m (van der Waal and Skelton 1984; Taylor 2016). The average annual discharge of the Kwando River at Kongola is equivalent to roughly 3% of the discharge of the Upper Zambezi River at Katima Mulilo (*sensu* Schlettwein *et al.* 1991). The Linyanti wetlands absorb a large portion of this, so that even in high flood years the Kwando River is only able to stabilise the receding water level in Lake Liambezi during the dry season (van der Waal and Skelton 1984).

The irregular nature of large flooding events in the Upper Zambezi River, and consequent inflow into Lake Liambezi, means that the lake experiences extreme fluctuations in water level, resulting in cyclical phases of flooding and drying that vary widely in duration from one year to several decades. The previous prolonged period of inundation lasted from ca. 1966 until, after five consecutive years of low floods in the inflowing rivers, it dried up in 1985 (Grobler and Ferreira 1990). The lake was partially inundated, but subsequently dried in 1989, 2001, 2003 and 2004 (Schlettwein *et al.* 1991; Mutelo 2013). In 2007 it received a larger flood that sustained the lake through 2008, and in April 2009 it received a major flood, filling for the first time since the late 1970s (Figure 1.4). The lake received further inflow in 2010 and 2011, but has not received any significant inflow since, and is likely to dry in the coming year (2017) in the absence of further inflow.

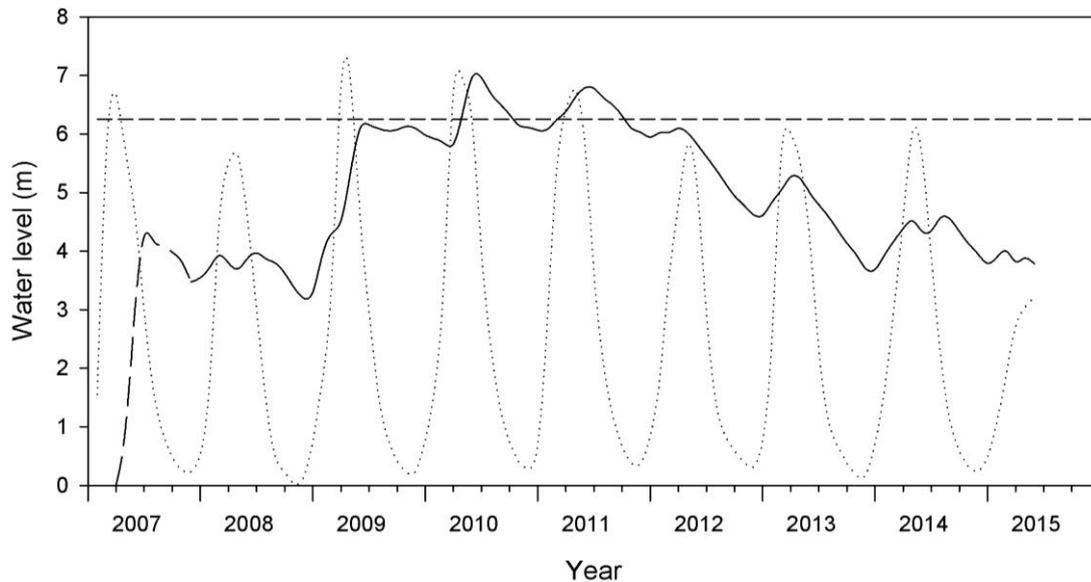


Figure 1.4. Water level of Lake Liambezi (—) since inundation in 2007. The annual flood cycle of the Zambezi River (····), and the level at which the Zambezi River spills into the lake (---) are illustrated to show when the lake received inflow.

Limnology

At its peak the lake has a maximum depth of 7 m, and an average depth of approximately 2.5 m (Peel *et al.* 2015b). The lake and surrounding wetland may cover between 300 and 400 km², approximately one third of which is usually open water (Seaman *et al.* 1978; Schlettwein *et al.* 1991; Mutelo 2013). The remainder is characterised by vast, fragmented stands of emergent macrophytes that are dominated by *Phragmites australis* and, to a lesser extent, *Typha capensis*, between which lie extensive beds of the submerged macrophytes *Lagarosiphon ilicifolius* and *Najas horrida* (Figure 1.5) (Seaman *et al.* 1978; Peel *et al.* 2015b). The open water area supports a diverse phytoplankton assemblage that is dominated by blue-green algae, especially *Microcystis* species (Seaman *et al.* 1978). The invasive floating weed *Salvinia molesta*, which covered 26% of the lake in 1975 (Seaman *et al.* 1978), was not recorded in the lake over the duration of the present study, although it persists in low densities in the inflowing rivers (Peel *et al.* 2015b).

Surface water temperatures in Lake Liambezi during 2013–2014 ranged between a high of 31.7 °C in January and a low of 17.3 °C in June (Figure 1.6). The annual average water temperature was 24.1 °C. Lake Liambezi, like other shallow tropical lakes, is polymictic, the shallowness of the lake preventing any stable thermal stratification (Seaman *et al.* 1978). Stratification occurs on calm days when wave action and turbulence is insufficient to transfer

the surface heat gain to the water column. This breaks down after sunset as surface heat is lost to the atmosphere. This situation is more common in the vegetated parts of the lake where emergent macrophytes provide shelter from the wind. In the open lake, wind assisted polymixis ensures that dissolved oxygen levels are high at all depths (Seaman *et al.* 1978). Low levels of dissolved oxygen were recorded by Seaman *et al.* (1978) under dense mats of floating *S. molesta*, now absent from the lake.



Figure 1.5. Habitat types in Lake Liambezi: (a) and (b) open water, (c) a reminder that the lake was recently dry, (d) and (e) dense stands of submerged, floating leaved and emergent macrophytes, and (f) the inflowing Bukalo Channel partially flooded in March 2013.

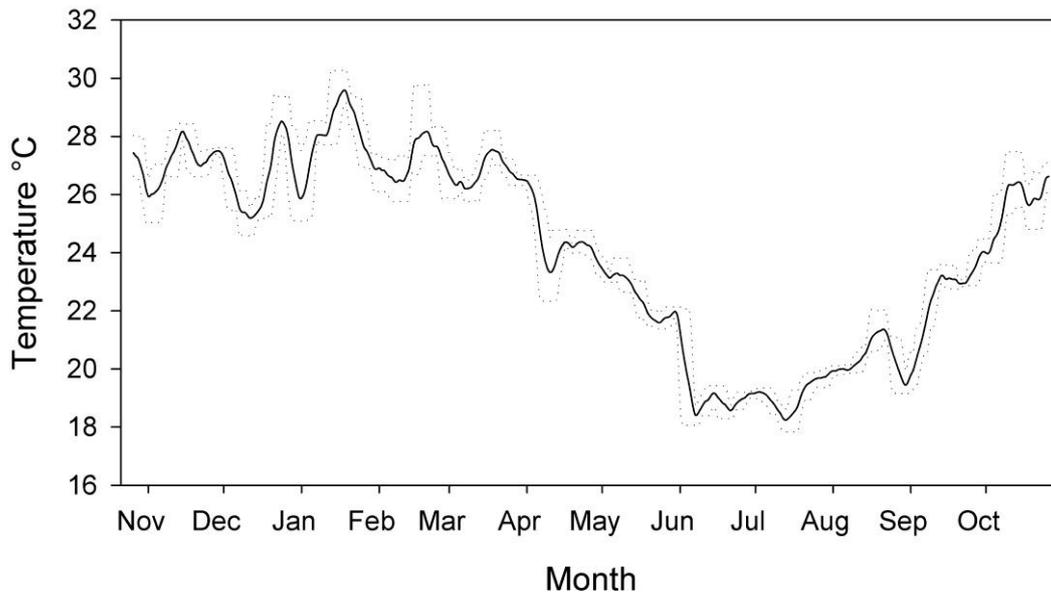


Figure 1.6. Seven day moving averages of mean daily water temperature (—) and 95% confidence intervals (·····) recorded in Lake Liambezi between October 2013 and October 2014 using a HOBO Pro v2 data logger (Onset[®], Bourne, MA, USA) programmed to log temperature at hourly intervals.

Regular flooding–drying cycles contribute to high levels of nutrient availability and productivity potential in ephemeral lakes through riverine inputs and sediment releases (Scholz *et al.* 2002). The Kalahari sands that cover much of the Upper Zambezi and Kwando river catchments are nutrient poor (Cronberg *et al.* 1995; Robertson 2005), so both rivers have relatively low conductivity and nutrient levels (Table 1.1). Lake Liambezi has moderate conductivity and nutrient levels (Table 1.1) as a result of nutrient release from sediments upon re-flooding, combined with evaporative concentration of nutrients and ions over time (Seaman *et al.* 1978). The conductivity of Lake Liambezi is much lower than that of most truly endorheic shallow lakes such as Rukwa and Chilwa (Ricardo 1938; McLachlan 1979). This may be due to several factors, including the low ion content of inflowing floodwaters, the infrequency with which Lake Liambezi receives inflow compared to the above mentioned lakes, and the fact that Lake Liambezi experiences outflow, and thus nutrient loss, via the Chobe River at high water levels. Water transparency varies considerably in Lake Liambezi depending on water level, but averages approximately 1 m in open water when the lake is full, and approximately 2 m in vegetated parts of the lake where turbulence in the water column is reduced and phytoplankton densities are lower (Seaman *et al.* 1978; Table 1.1).

Table 1.1. Water quality parameters and inorganic nitrogen concentrations (\pm standard deviation) measured in Lake Liambezi and the Zambezi and Kwando Rivers in August 2015.

Parameter	Lake Liambezi	Zambezi River	Kwando River
Conductivity ($\mu\text{S cm}^{-1}$)	304 \pm 42	83.4 \pm 0.6	85.7 \pm 5.7
Total dissolved solids (ppm)	152 \pm 20	41.4 \pm 0.4	43.7 \pm 3.7
pH	8.3 \pm 0.3	8.4 \pm 0.1	7.6 \pm 0.0
Turbidity (NTU)	3.8 \pm 2.2	4.6 \pm 0.5	6.93 \pm 0.09
NO ₃ (mg l ⁻¹)	2.16 \pm 0.70	0.19 \pm 0.10	0.41 \pm 0.12
NH ₄ (mg l ⁻¹)	0.58 \pm 0.09	0.12 \pm 0.04	0.33 \pm 0.05
Total inorganic N (mg l ⁻¹)	2.74 \pm 0.73	0.30 \pm 0.10	0.74 \pm 0.10

Fish fauna and fisheries

The fish fauna of the Upper Zambezi River floodplains is diverse, comprising at least 80 species (Tweddle 2010). Most of these are shared between the Upper Zambezi and Kwando rivers that feed Lake Liambezi. There are, however, some differences between the two rivers. For example, parapatric speciation in the mormyrid genus *Pollimyrus* has led to the evolution of distinct sibling species, *Pollimyrus marianne* and *Pollimyrus cuandoensis*, in the Upper Zambezi and Kwando rivers, respectively (Kramer *et al.* 2003, 2014). Lake Liambezi is naturally colonised by fishes from these two rivers during flooding events. The lentic conditions in Lake Liambezi are not suitable for all the species inhabiting the inflowing rivers, and consequently the fish fauna is generally dominated by limnophilic and eurytopic species, while most rheophilic species are scarce or even absent (van der Waal and Skelton 1984). Van der Waal (1980) recorded 43 fish species from Lake Liambezi between 1973 and 1976, and Peel *et al.* (2015) recorded 46 species between 2010 and 2012. A checklist of 48 species recorded from Lake Liambezi over the extended duration of this study (2007–2014) is given in Table 1.2.

Table 1.2. Fish species recorded from Lake Liambezi between 2007 and 2014, their scientific and common names, maximum lengths (cm), reproductive strategy according to Balon (1975), life-history strategy according to Winemiller and Rose (1992), and feeding group, derived from information summarised in Skelton (2001) and Marshall (2011). Life-history strategy: O = opportunistic, P = periodic, E = equilibrium; feeding group: Det = detritivore, Herb = herbivore, Omn = omnivore, Inv = invertivore, Pred = predator.

Taxon	Common name	Length (mm)	Reproductive strategy	Life-history strategy	Feeding group
Mormyridae					
<i>Marcusenius altisambesi</i> Kramer, Skelton, van der Bank & Wink, 2007	Bulldog	300	non-guarder	P	Inv
<i>Mormyrus lacerda</i> Castelnau, 1861	Western bottelnose	500	non-guarder	P	Inv
<i>Petrocephalus</i> cf. <i>okavangensis</i> Kramer, Bills & Skelton, 2011	Churchill	120	non-guarder	O	Inv
<i>Pollimyrus marianne</i> Kramer, van der Bank, Flint, Sauer-Gürth, Wink, 2003	Dwarf stonebasher	80	non-guarder	O	Inv
Cyprinidae					
<i>Enteromius barnardi</i> Jubb, 1961	Blackback barb	70	non-guarder	O	Inv
<i>Enteromius bifrenatus</i> Fowler, 1935	Hyphen barb	70	non-guarder	O	Inv
<i>Enteromius haasianus</i> David, 1936	Siclefin barb	30	non-guarder	O	Inv
<i>Enteromius multilineatus</i> Worthington, 1933	Copperstripe barb	40	non-guarder	O	Inv
<i>Enteromius paludinosus</i> Peters, 1852	Straightfin barb	150	non-guarder	O	Inv
<i>Enteromius poechii</i> Steindachner, 1911	Dashtail barb	130	non-guarder	O	Inv
<i>Enteromius radiatus</i> Peters, 1853	Beira barb	120	non-guarder	O	Inv
<i>Enteromius barotseensis</i> Pellegrin, 1920	Barotse barb	50	non-guarder	O	Inv
<i>Enteromius unitaeniatus</i> Günther, 1866	Longbeard barb	140	non-guarder	O	Inv
<i>Coptostomabarbus wittei</i> David & Poll, 1937	Upjaw barb	30	non-guarder	O	Inv
<i>Labeo cylindricus</i> Peters, 1852	Redeye labeo	230	non-guarder	P	Herb
<i>Labeo lunatus</i> Jubb, 1963	Upper Zambezi labeo	400	non-guarder	P	Herb
Alestidae					
<i>Brycinus lateralis</i> (Boulenger, 1900)	Stripped robber	140	non-guarder	O	Inv
<i>Hydrocynus vittatus</i> Castelnau, 1861	Tigerfish	700	non-guarder	P	Pred
<i>Micralestes acutidens</i> (Peters, 1852)	Silver robber	80	non-guarder	O	Inv
<i>Rhabdalestes maunensis</i> (Fowler, 1935)	Slender robber	60	non-guarder	O	Inv
Hepsetidae					
<i>Hepsetus cuvieri</i> Castelnau, 1861	African pike	470	nest guarder	E	Pred
Schilbeidae					
<i>Schilbe intermedius</i> Rüppell, 1832	Silver catfish	300	non-guarder	P	Pred
Clariidae					
<i>Clarias gariepinus</i> (Burchell, 1822)	Sharptooth catfish	1400	non-guarder	P	Pred
<i>Clarias ngamensis</i> Castelnau, 1861	Blunttooth catfish	700	non-guarder	P	Pred
<i>Clarias stappersii</i> Boulenger, 1915	Blotched catfish	410	non-guarder	P	Inv
<i>Clarias theodora</i> Weber, 1897	Snakehead catfish	350	non-guarder	P	Inv
Mochokidae					
<i>Synodontis nigromaculatus</i> Boulenger 1905	Spotted squeaker	300	non-guarder	P	Omn
<i>Synodontis</i> spp	Squeaker	250	non-guarder	P	Omn
Poeciliidae					
<i>Micropanchax hutereaui</i> (Boulenger, 1913)	Meshscaled topminnow	35	non-guarder	O	Inv
<i>Micropanchax johnstoni</i> (Günther, 1893)	Johnston's topminnow	50	non-guarder	O	Inv
<i>Micropanchax katangae</i> (Boulenger, 1912)	Striped topminnow	50	non-guarder	O	Inv
<i>Micropanchax</i> sp. "pygmy topminnow"	Pygmy topminnow	20	non-guarder	O	Inv
Cichlidae					
<i>Oreochromis andersonii</i> (Castelnau, 1861)	Threespot tilapia	500	mouth brooder	E	Det

Taxon	Common name	Length (mm)	Reproductive strategy	Life-history strategy	Feeding group
<i>Oreochromis macrochir</i> (Boulenger, 1912)	Greenhead tilapia	400	mouth brooder	E	Det
<i>Pharyngochromis acuticeps</i> (Steindachner, 1866)	Zambezi happy	220	mouth brooder	E	Inv
<i>Pseudocrenilabrus philander</i> (Weber, 1897)	Southern mouthbrooder	130	mouth brooder	E	Inv
<i>Sargochromis carlottae</i> (Boulenger, 1905)	Rainbow bream	260	mouth brooder	E	Inv
<i>Sargochromis giardi</i> (Pellegrin, 1903)	Pink bream	480	mouth brooder	E	Inv
<i>Sargochromis</i> sp. “green bream”	Green bream	290	mouth brooder	E	Inv
<i>Serranochromis altus</i> Winemiller & Kelso-Winemiller, 1990	Humpback largemouth	410	mouth brooder	E	Pred
<i>Serranochromis angusticeps</i> (Boulenger, 1907)	Thinface largemouth	410	mouth brooder	E	Pred
<i>Serranochromis macrocephalus</i> (Boulenger, 1899)	Purpleface largemouth	350	mouth brooder	E	Pred
<i>Serranochromis robustus jallae</i> (Günther, 1864)	Nembwe	450	mouth brooder	E	Pred
<i>Coptodon rendalli</i> (Boulenger, 1897)	Redbreast tilapia	400	nest guarder	E	Herb
<i>Tilapia sparrmanii</i> A. Smith, 1840	Banded tilapia	220	nest guarder	E	Herb
<i>Tilapia ruweti</i> (Poll & Thys van den Audenaerde, 1961)	Okavango tilapia	100	nest guarder	E	Herb
Anabantidae					
<i>Ctenopoma multispine</i> Peters, 1844	Manyspined climbing perch	150	nest guarder	E	Inv
<i>Microctenopoma intermedium</i> (Pellegrin, 1920)	Blackspot climbing perch	60	nest guarder	E	Inv

Van der Waal (1980) monitored the fishery on Lake Liambezi between 1973 and 1976. During this period the lake supported up to 120 fishers, most of whom were part-time, farming during the rainy season and fishing in the dry season. Fishers operated using traditional dugout canoes and large meshed (102–152 mm) multifilament gillnets. Catches comprised mainly large tilapiine cichlids (*Oreochromis andersonii*, *Oreochromis macrochir* and *Coptodon rendalli*) and clariid catfishes (*C. gariepinus* and *Clarias ngamensis*). The fishery yielded an estimated 640 tonnes at its peak in 1973/74. The fishery operating on Lake Liambezi during the present study was similar to that in the 1970s, except that multifilament gillnets had been replaced by more efficient monofilament gillnets, the preferred mesh size had fallen from 127 to 89 mm, and an estimated 340 full-time fishers were active (Peel *et al.* 2015b). When the lake filled in March/April 2009 catches were initially dominated by *C. gariepinus* and *C. ngamensis*, much of which were discarded because there was no local demand, and the external market links had not yet developed (D. Tweddle, personal communication). By November 2010, less than two years after filling, the lake supported a thriving fishery based on large, high-value tilapiine cichlids (Figure 1.7). The average catch per dugout canoe was estimated at 36 kg day⁻¹, and the annual yield for 2011/12 was calculated as 2 700 tonnes (Peel *et al.* 2015b).

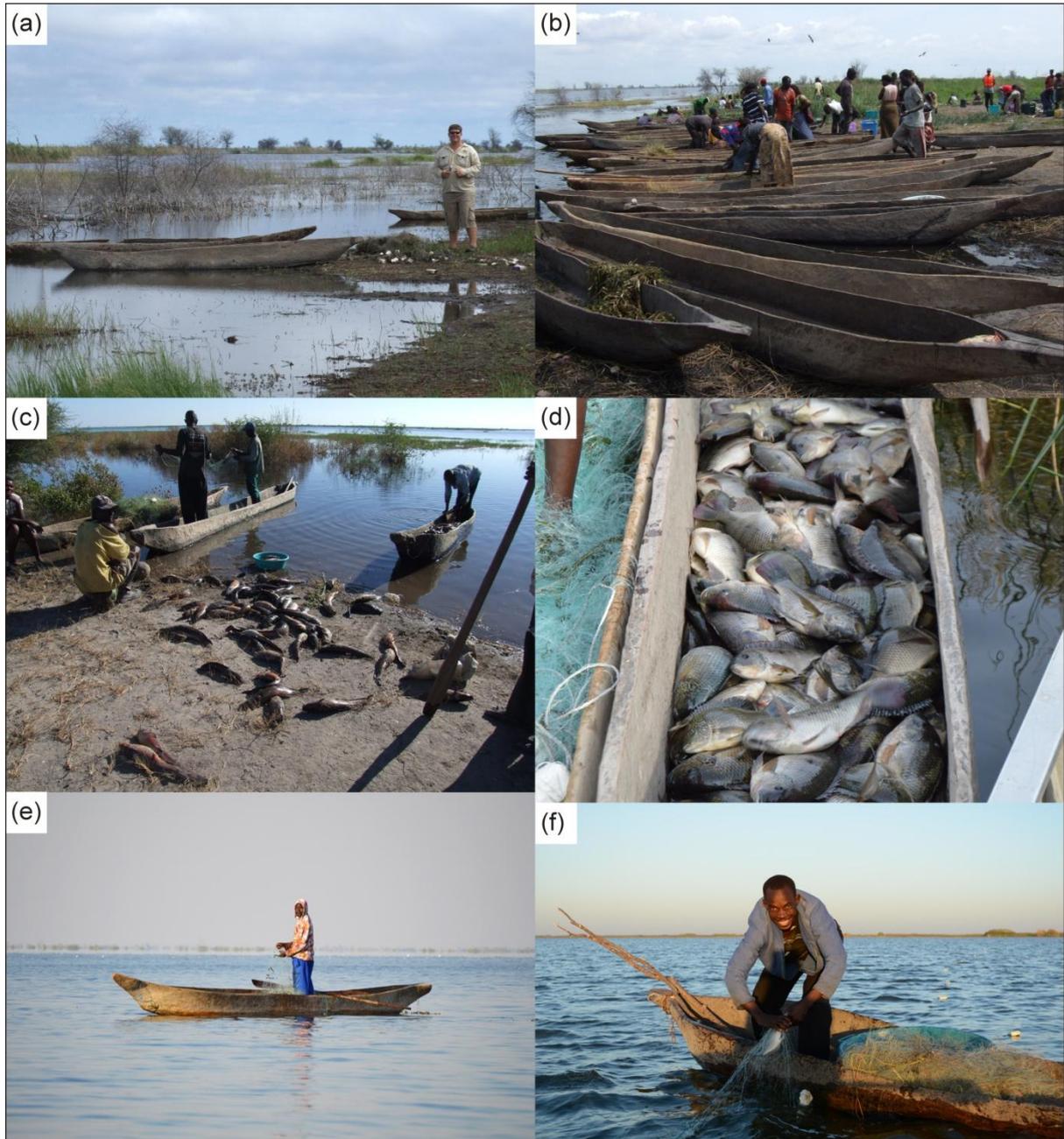


Figure 1.7. Fishing in Lake Liambezi: (a) Shamauka landing in February 2010 was sparsely populated, (b) the same landing in November 2010 was a hive of activity, (c) gill net catches were dominated by *Clarias* spp. after filling, much of which was discarded, (d) by late 2010 *Oreochromis* spp. supported a large fishery, (e) and (f) fishermen checking their gill nets in the open lake during the early morning. Images (a), (b) and (c) credit Denis Tweddle.

Lake Liambezi contributes significantly to the livelihoods of lakeside communities, and to the regional economy (Abbott *et al.* 2015). Management of this valuable ephemeral resource needs to be guided by a comprehensive understanding of the biology, ecology and temporal dynamics of the fish community. Apart from the work of van der Waal (published across several papers), there is very limited information on Lake Liambezi, and from ephemeral

freshwater lakes elsewhere in Africa, on which to base management recommendations. More recently developed techniques, such as the use of multivariate statistics to analyse assemblage structure, otoliths for ageing and stable isotopes for food web analysis, were used to update our knowledge, and provide new insights into the ecological functioning of Lake Liambezi since the lake was previously inundated and studied by van der Waal in the 1970s.

Thesis outline

The aim of this PhD thesis was to contribute toward the understanding of fish colonisation patterns, and the drivers of community succession following flooding in a large, shallow ephemeral floodplain lake in the tropics. The central hypothesis of the study is that: the hydrological regime, life-history adaptations and trophic interactions combine to determine fish colonisation patterns and drive community succession.

To understand fish colonisation patterns, the community structure of the colonising fish community was assessed following three separate flooding events of the previously dry lake bed in 2001, 2004 and 2007 (Figure 1.8) (Chapter 2). The chapter aimed to determine the relative contribution of stochastic and deterministic processes by comparing the colonising fish communities in Lake Liambezi with those of the source populations in the Zambezi and Chobe river floodplains, and by comparing the colonising fish communities between years. Chapter 3 examines the response of the colonising fish fauna, of riverine origin, to the lentic conditions facing them in Lake Liambezi. In it, a description is given of the temporal succession of fish species, and development of a lacustrine fish community over an eight year period of continuous inundation from 2007 to 2014 (Figure 1.8). The observed changes in diversity, composition and abundance are discussed in relation to Winemiller's (1996b) model predicting succession in the relative dominance of alternative life-history strategies in fish communities following major habitat disturbances. The life-history theme is carried over into Chapter 4, the aim of which was to assess the life-history strategies of eight common fish species in Lake Liambezi, and evaluate their establishment success against life-history theory in an effort to understand the drivers behind fish community successions. In Chapter 5, the food web structure and trophic dynamics of a mature lacustrine fish community are assessed. The aim of this chapter was to determine the sources of primary production supporting consumer biomass, and examine the trophic interactions among fish species in an attempt to elucidate their influence upon species succession. The main findings of these studies are

synthesised in Chapter 6, and suggestions are made towards further development of Gawne and Scholz's (2006) conceptual model of ephemeral lakes. Consideration is given to management implications of the findings, with particular reference to fisheries, and recommendations for future research are outlined.

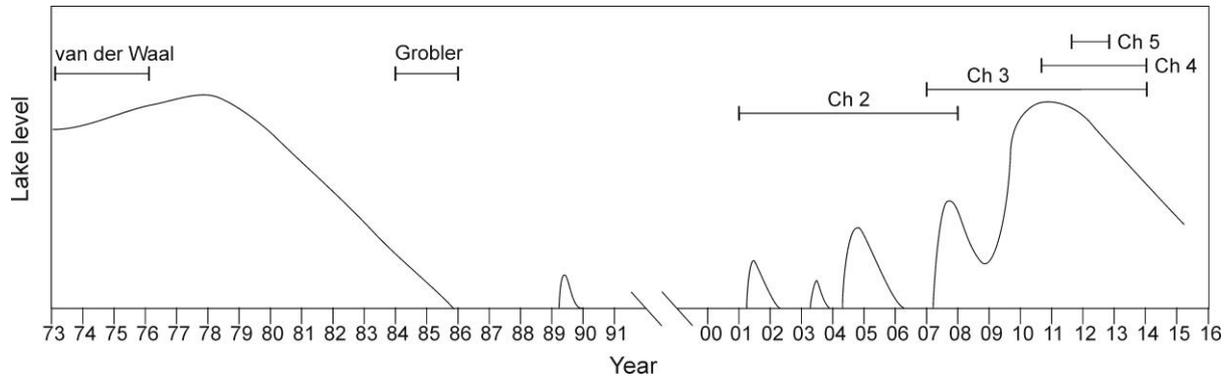


Figure 1.8. Graphical illustration of water level fluctuations in Lake Liambezi since 1973. Two previous studies were carried out on the lake before it dried in 1985; a PhD by B C W van der Waal during a high water period, and an MSc by H J W Grobler as the lake dried. This thesis uses data collected between 2001 and 2014, which included several discrete flooding events and a prolonged period of inundation. The years during which data were collected and analysed in each of the following data chapters are indicated.

CHAPTER 2

Fish colonisation patterns in Lake Liambezi following three discrete flooding events

Introduction

Floodplain rivers are highly dynamic ecosystems in which environmental conditions vary temporally and spatially (Ward *et al.* 2002). Fishes inhabiting these systems must move in order to exploit optimal habitats for spawning, feeding and refuge as environmental conditions change (Lucas and Baras 2001). Daget (1960) identified two broad types of migration in tropical African fishes: 1) longitudinal migrations, which take place within the main river channel; and 2) lateral migrations, which take place between the main river channel and adjacent floodplains. Blache (1964) and Williams (1971) separately classified movement patterns further by seasonality and local versus regional movements. Welcomme (1985) combined these classifications to come up with six phases in the distribution of fish, illustrated in Figure 2.1, that are broadly applicable to most species inhabiting floodplain river ecosystems. There is, however, a large degree of variation in the timing, direction, distance and propensity to migrate between species (Welcomme 1985; Lucas and Baras 2001).

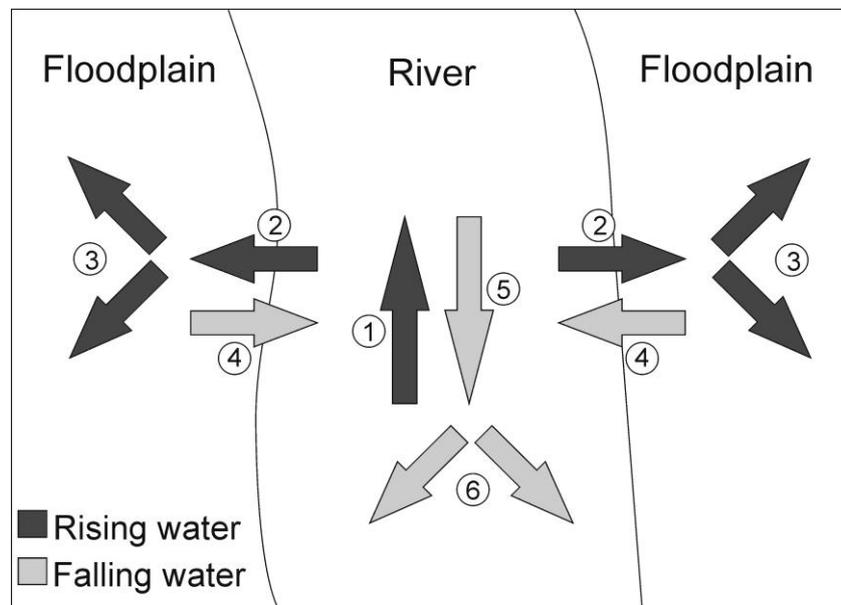


Figure 2.1. Welcomme's (1985) six phases in the distribution of fish in floodplain rivers: 1) longitudinal, usually upstream; 2) lateral, onto floodplain; 3) dispersal on floodplain; 4) lateral, towards main channel; 5) longitudinal, usually downstream; 6) dispersal in river.

Welcomme (1975, 1985) noted that lateral migration onto the floodplains of many African rivers followed a relatively consistent, ordered sequence of species. Among the first migrants are catfish of the genera *Clarias* and *Schilbe* in search of suitable spawning habitat (Williams 1971; Hickley and Bailey 1987; Merron and Mann 1995). Small cyprinids of the genus *Enteromius* are also among the first to colonise the floodplain (Williams 1971; van der Waal 1996; Hocutt and Johnson 2001). These are closely followed by juvenile tilapiine cichlids, and later by *Serranochromis* spp. (Williams 1971; van der Waal 1996). Alestids and mormyrids appear to migrate onto the floodplain later (Hocutt and Johnson 2001). Once on the floodplain, fishes disperse to potentially more favourable areas of richer resources, or with reduced competition or predation (Bell 1991; Lucas and Baras 2001). Dispersal, also referred to as exploratory migratory behaviour, involves the movement of individuals away from a central concentration, and differs from migration, which usually takes place between specific habitats, and often results in aggregations for spawning or feeding (Lucas and Baras 2001; Brönmark *et al.* 2014).

Dispersing fishes play a major role in repopulating and colonising residual floodplain pools and lakes that are subject to heavy cropping by humans and birds in the dry season, and may even dry up (Welcomme 1985). Dispersal, whether into empty habitats or between established communities, has a significant influence on community composition (Holyoak *et al.* 2005). The dispersal of fishes across an inundated floodplain, and strandings in pools as the floodwaters recede, has largely been described as a stochastic process (Lowe-McConnell 1987; Goulding *et al.* 1988; Chapman and Chapman 1993; Saint-Paul *et al.* 2000). Vellend *et al.* (2014), however, argue that dispersal is not strictly stochastic or deterministic. The degree of predictability of community composition can be influenced by two factors. First, the number of individuals of all species moving between sites (mean across species), and second, the difference in the number of individuals of each species moving between sites (variance among species). High mean dispersal across species and high variance among species should result in predictable patterns of community composition and vice versa (Vellend *et al.* 2014). For floodplain fishes, one would therefore expect a relatively predictable colonising fauna in residual floodplain water bodies, dominated by species with a high reproductive potential, and a high propensity for dispersal.

The aim of this chapter was to examine fish colonisation patterns in Lake Liambezi by: 1) comparing the colonising fish communities in Lake Liambezi with those of the source populations in the Zambezi and Chobe river floodplains, and 2) comparing the colonising fish communities from three separate inundation events of the previously dry lake bed. It was hypothesized that the colonising fish communities would differ from the source populations as a result of interspecific differences in the propensity and ability to undertake extensive lateral migrations. These interspecific differences (variance among species), combined with high mean dispersal across species, should result in predictable colonisation patterns among three separate inundation and colonisation events (i.e. a high degree of determinism).

Materials and methods

Data collection

Having dried up completely in 1985 after five consecutive years without inflow (Grobler and Ferreira 1990), Lake Liambezi was partially inundated, and subsequently dried on several occasions before the beginning of the present continuous period of inundation from 2007 (Mutelo 2013). Schlettwein *et al.* (1991) reported that in March 1989, floodwaters from the Zambezi River backed-up the Chobe River and spilled into the lake, inundating approximately 2 km² before drying 8 months later. Mutelo (2013) used satellite imagery to quantify variation in the area extent of Lake Liambezi between 1984 and 2013. He found that the lake in fact reached a maximum area of 12.8 km² in July 1989. The next inundation event occurred 12 years later in 2001. The lake covered approximately 16 km² at its maximum extent in June 2001, before drying in early 2002. The lake was again flooded, but to a lesser extent in 2003, drying the same year. In 2004, the lake received a more substantial flood, covering nearly 50 km². The lake shrank continuously from June 2004 before eventually drying in early 2006. In 2007, the lake was again inundated, reaching a maximum extent of approximately 65 km² in May of that year, before going on to fill in 2009. The annual flood cycle of the Zambezi River is illustrated in Figure 2.2 for the three years during which the largest inundation events occurred.

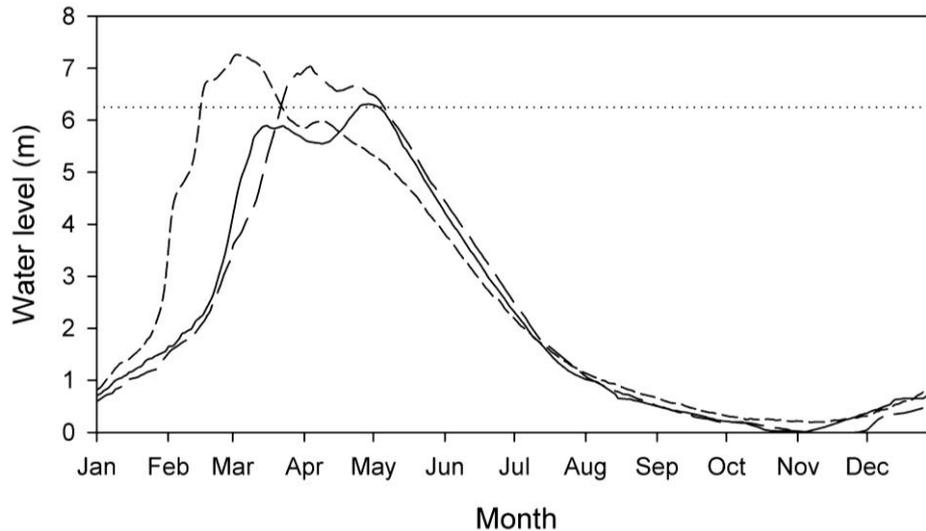


Figure 2.2. The annual flood cycle of the Zambezi River measured at Katima Mulilo during three years that Lake Liambezi was inundated and sampled in 2001 (—), 2004 (— —) and 2007 (— — —), and the theoretical level at which the river overflows into Lake Liambezi (·····).

The data used in this chapter, as well as much of that used in Chapter 3, were collected during the Namibian Ministry of Fisheries and Marine Resources (MFMR) annual monitoring programme. The programme is often subject to financial and logistical constraints, as well as a shortage of scientific expertise. The dataset has some limitations, including small sample sizes, variable timing and effort of collections, and a lack of data on abiotic variables. In the following analyses I attempt to elucidate the patterns in species diversity, composition and abundance associated with the recolonisation of Lake Liambezi, but due to limitations of the dataset, it was not possible to empirically determine the ecological drivers of these patterns.

Sampling of the fish population in Lake Liambezi after inundation was carried out in 2001, 2004 and 2007. In addition, the Zambezi and Chobe river floodplains were sampled at Kalimbeza and Kabula (Figure 1.2), respectively, from where the majority of fish colonising the lake would have originated. The floodplains were sampled during or shortly after the flood peak in 2004 and 2007. Details of the sampling events in each system are summarised in Table 2.1.

Table 2.1. Summary of sampling events on Lake Liambezi and the Zambezi and Chobe floodplains. Asterisks indicate data used in univariate analyses of relative abundance, species richness and diversity, and multivariate analyses of assemblage structure.

System	Year	Month	Gill net nights (<i>n</i>)
Liambezi	2001*	October	5
Liambezi	2004*	July	6
Liambezi	2004	October	6
Liambezi	2004	December	5
Liambezi	2007*	May/June	7
Zambezi	2004*	May	10
Zambezi	2007*	June	9
Chobe	2004*	May	6
Chobe	2007*	June	9

Fish were sampled using standardised multifilament gill nets (110 m × 2.5 m) made up of eleven panels with stretched mesh sizes of 12, 16, 22, 28, 35, 45, 57, 73, 93, 118 and 150 mm. Nets were surface set between 18:00 and 19:00 in the evening and retrieved between 06:00 and 07:00 the following morning. Sampling was concentrated in the eastern half of the lake, between the inflowing Bukalo Channel and Chobe River (Chapter 1, Figure 1.3). Open water and vegetated habitats were sampled. All fish caught were identified to species level according to Skelton (2001), with the assistance of Mr D. Tweddle in keeping abreast of the latest taxonomic revisions and species descriptions now summarised in (Skelton 2016). They were then measured to the nearest mm and weighed to the nearest gram. When one species was particularly numerous in a single mesh, a subsample was taken, where each fish was measured and weighed, and the remainder were counted and weighed collectively. The relative abundance of each species was expressed by catch per unit effort (CPUE), calculated as the mean number or weight of fish per gill net night (fish.net night⁻¹; kg.net night⁻¹).

Data selection and analysis

Two years of gill net data (2004 and 2007) from the source populations of the Zambezi and Chobe river floodplains were analysed. Fish assemblage data were compared for the three replicate first years of inundation (2001, 2004 and 2007). Only data from the first sampling event after inundation in 2004 were used (July 2004), as this was assumed to be most representative of the colonising fish fauna. Gill nets used in 2001 did not include the two smallest mesh sizes 12 and 16 mm. Catches made in these mesh sizes in 2004 and 2007 were therefore excluded for comparison with 2001.

Relative abundance, species richness and diversity

Trends in relative abundance (N) and biomass (W), sample species richness (S), Shannon-Weiner diversity (H') and Pielou's evenness (J') were assessed by univariate statistical analyses performed 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). Analyses were first performed on Euclidean distance measures of untransformed data. Data was tested for homogeneity of variance using permutational analysis of multivariate dispersions (PERMDISP)—based on the mean distance to centroid and performed using 9999 permutations—and square root transformed if heterogeneous. Non-parametric permutational multivariate analyses of variance (PERMANOVA) were then used to test for significant differences among years. Significance values were calculated using the Type III (partial) sums of squares and 9999 unrestricted permutations of the raw data for each analysis. Where significant differences were found between events, post hoc pair-wise comparisons were performed. Statistical significance was set at $\alpha = 0.05$ for all tests.

Assemblage structure

Fish assemblage structure was described by individual species gill net catch per unit effort (CPUE) abundance and biomass data. Multivariate statistical analyses were performed using PRIMER with PERMANOVA. Variation in assemblage structure among years was first visualised using non-metric multidimensional scaling (nMDS) plots. Analyses were performed using Bray-Curtis dissimilarity matrices of abundance and biomass data. Abundance and biomass data were fourth root transformed because of high variability (0 to > 2 500 individuals; 0 to > 14 000 grams), thus reducing the influence of the most abundant species. Multivariate PERMANOVAs were conducted to test for differences in assemblage structure among years. Significance values were calculated as above for univariate analyses. Where significant differences were found between years, post hoc pair-wise comparisons were performed. To ensure significant differences were due to location and not to differences in variability, PERMDISP was used as above, to test for homogeneity of variance among years. Statistical significance for all tests was set at $\alpha = 0.05$.

Differences in assemblage structure among systems and among years were then examined using the constrained canonical analysis of principal coordinates (CAP) procedure. The CAP

procedure initially calculates unconstrained principal coordinate (PCO) axes, then determines how many PCO axes (m) should be chosen, followed by a canonical discriminant analysis (CDA; as the hypotheses concern differences between groups) on the principal coordinates (Anderson and Willis 2003). The CAP procedure provides a statistical estimate of misclassification error using the “leave-one-out” method (Anderson and Willis 2003). Each sample is removed and the CAP analysis performed on the remaining data. The “left out” sample is then classified in the canonical space determined by the other samples. The proportion of samples from each group that are incorrectly classified gives a measure of how distinct groups are in multivariate space. Species responsible for the observed differences between years were investigated by examining the Pearson correlations of species abundance and biomass data with the canonical axes. A correlation of $|r| > 0.5$ was used as an arbitrary cut-off to display species relationships with the canonical axes.

Results

Comparing source populations with colonising populations

Species composition, relative abundance and biomass

The composition of fishes caught using gill nets varied considerably between the Zambezi and Chobe rivers, as well as between years within each system. In total, 36 species were caught in the two river systems in 2004 and 2007 (Table 2.2). Between 15 and 25 species were caught in the Zambezi River, and between 17 and 27 species were caught in the Chobe River each year. In the Zambezi River, *Schilbe intermedius* was most abundant in 2004, while *Brycinus lateralis* dominated in 2007. *Petrocephalus* cf. *okavangensis* was among the top five most abundant species in both years, while *Hydrocynus vittatus* ranked third in 2007. In the Chobe River, *S. intermedius* dominated in both years. *Marcusenius altisambesi* and *B. lateralis* were among the top five most abundant species in both years. *Micralestes acutidens* was very abundant in 2004, but less so in 2007. The species composition of the colonising fishes in Lake Liambezi was more consistent between years. In total, 30 species were captured in 2004 and 2007, with 23 species captured each year. Sixteen species were captured in both years. In 2004, *Enteromius paludinosus* was most abundant, followed by *Enteromius poechii*. The opposite was true for 2007. Together, these two species accounted for 81% and 90% of the fish caught in 2004 and 2007, respectively. *Schilbe intermedius* ranked third in abundance, and *M. altisambesi* fourth for both years.

Table 2.2. Gill net catch composition expressed as percent number (%N) for the Zambezi River, Chobe River and Lake Liambezi from 2004 and 2007, and the life-history strategy of each species: O = opportunistic; P = periodic; E = Equilibrium.

Taxon	Strategy	Zambezi		Chobe		Liambezi	
		2004	2007	2004	2007	2004	2007
Mormyridae							
<i>Cyphomyrus cubangoensis</i>	O	0.3	-	0.7	-	-	-
<i>Marcusenius altisambesi</i>	P	8.4	0.4	9.6	7.7	5.9	0.8
<i>Mormyrus lacerda</i>	P	-	-	-	0.1	<0.1	0.1
<i>Petrocephalus cf. okavangensis</i>	O	9.4	1.3	16.1	0.8	0.6	<0.1
<i>Pollimyrus cf. cuandoensis</i>	O	6.6	0.1	1.1	< 0.1	0.6	<0.1
Cyprinidae							
<i>Enteromius bifrenatus</i>	O	-	-	-	-	0.6	-
<i>Enteromius eutenia</i>	O	-	0.1	-	< 0.1	-	-
<i>Enteromius multilineatus</i>	O	-	-	-	-	<0.1	-
<i>Enteromius paludinosus</i>	O	1.2	-	0.2	< 0.1	28.9	65.2
<i>Enteromius poechii</i>	O	6.5	0.4	1.8	1.5	51.9	24.9
<i>Enteromius radiatus</i>	O	-	-	0.9	0.2	0.6	<0.1
<i>Enteromius unitaeniatus</i>	O	0.1	-	-	-	0.5	<0.1
<i>Labeo cylindricus</i>	O	0.2	-	-	-	0.2	-
<i>Labeo lunatus</i>	P	0.2	0.6	-	0.1	-	<0.1
<i>Opsaridium zambezense</i>	O	0.1	-	-	-	-	-
Alestidae							
<i>Brycinus lateralis</i>	O	10.1	70.9	6.0	39.5	<0.1	<0.1
<i>Hydrocynus vittatus</i>	P	4.6	7.2	4.8	0.1	-	-
<i>Micralestes acutidens</i>	O	6.4	3.3	23.6	0.3	-	-
<i>Rhabdalestes maunensis</i>	O	0.1	-	-	0.2	0.2	0.2
Hepsetidae							
<i>Hepsetus cuvieri</i>	E	0.5	1.0	0.5	1.3	-	<0.1
Schilbeidae							
<i>Schilbe intermedius</i>	P	38.2	13.8	30.0	43.3	9.3	7.6
Clariidae							
<i>Clarias gariepinus</i>	P	0.4	0.3	-	0.3	0.3	0.4
<i>Clarias ngamensis</i>	P	0.1	< 0.1	-	-	-	0.1
<i>Clarias liocephalus</i>	P	-	-	0.2	-	-	-
Mochokidae							
<i>Synodontis nigromaculatus</i>	P	0.3	0.1	-	< 0.1	-	-
<i>Synodontis spp.</i>	P	1.7	0.2	2.8	2.8	0.1	<0.1
Cichlidae							
<i>Hemichromis elongatus</i>	E	0.1	0.1	-	-	-	-
<i>Oreochromis andersonii</i>	E	-	-	-	0.1	-	<0.1
<i>Pharyngochromis acuticeps</i>	E	3.3	0.1	-	0.6	<0.1	-
<i>Pseudocrenilabrus philander</i>	E	-	-	-	0.1	<0.1	<0.1
<i>Sargochromis carlottae</i>	E	-	-	-	< 0.1	-	-
<i>Sargochromis sp. "green bream"</i>	E	0.1	< 0.1	-	-	-	-
<i>Serranochromis altus</i>	E	-	-	-	-	<0.1	-
<i>Serranochromis angusticeps</i>	E	-	-	-	< 0.1	-	-
<i>Serranochromis macrocephalus</i>	E	0.1	-	0.2	0.7	<0.1	<0.1
<i>Serranochromis robustus jallae</i>	E	-	-	-	< 0.1	<0.1	-
<i>Serranochromis thumbergi</i>	E	-	-	-	-	<0.1	-
<i>Coptodon rendalli</i>	E	-	-	-	-	-	<0.1
<i>Tilapia sparrmanii</i>	E	1.2	0.1	0.9	0.2	<0.1	0.25
<i>Tilapia ruweti</i>	E	-	-	-	0.1	-	<0.1
Anabantidae							
<i>Ctenopoma multispine</i>	E	-	-	0.5	-	-	<0.1
Total species		25	19	17	27	23	23

PERMDISP showed that relative abundance and biomass were homogenous among systems (Table 2.3). Relative abundance differed significantly between systems in both 2004 and 2007 (PERMANOVA, Table 2.3), being higher in Lake Liambezi compared to the Zambezi and Chobe Rivers (Figure 2.3). Relative biomass differed between systems in 2004, but not in 2007. In 2004, the relative biomass in the Chobe River was significantly lower than that in Lake Liambezi.

Table 2.3. PERMANOVA and PERMDISP results comparing Euclidean distance measures of untransformed relative abundance and biomass from the Zambezi, Chobe and Lake Liambezi in 2004 and 2007. Significant differences are in bold.

Source	df	PERMANOVA			PERMDISP	
		MS	Pseudo-F	P(perm)	F	P(perm)
2004						
Abundance	2	2.188E6	29.786	<0.001	4.882	0.132
Biomass	2	1.247E8	4.699	0.021	2.363	0.311
2007						
Abundance	2	4.811E6	62.414	<0.001	2.180	0.3509
Biomass	2	6.907E7	3.023	0.072	0.413	0.848

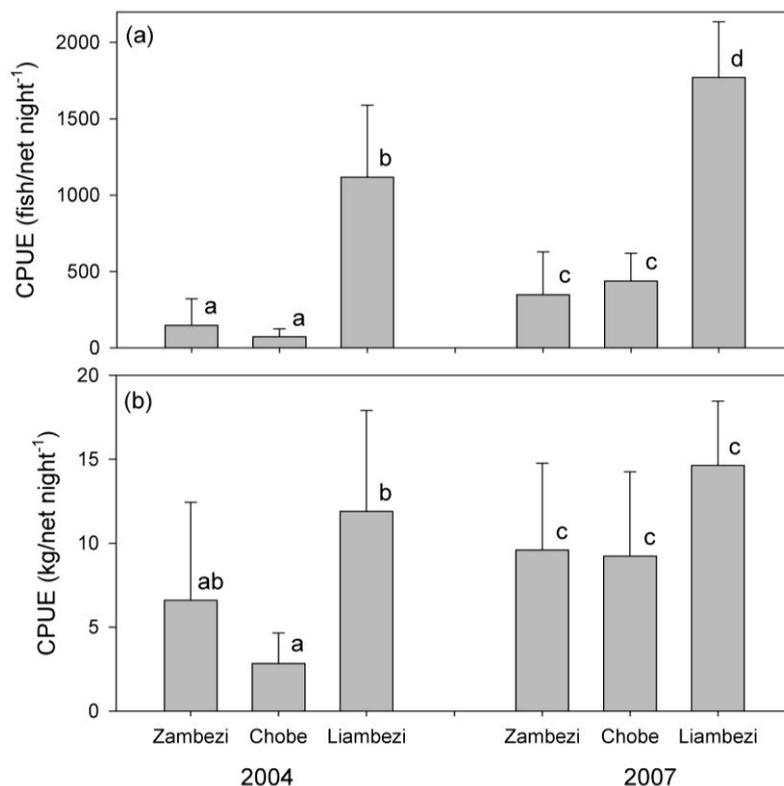


Figure 2.3. Gill net catch per unit effort (CPUE) in (a) numbers and (b) weight from the Zambezi, Chobe and Lake Liambezi. Data from 2004 and 2007 analysed separately. Error bars represent 1 standard deviation. Letters above bars denote pair-wise significant differences (PERMANOVA; $P < 0.05$).

Species richness and diversity

Mean sample species richness differed significantly between systems in 2007 (PERMANOVA, Table 2.4), with the Zambezi River being significantly lower compared to the Chobe River and Lake Liambezi (Figure 2.4), but no differences were seen between systems in 2004. Shannon-Wiener diversity indices did not differ significantly between systems in either 2004 or 2007, despite significant differences in dispersion between systems as indicated by PERMDISP (Table 2.4) after the data were log transformed. Pielou's evenness differed significantly between systems in 2004 and 2007. Some of the observed differences in 2007 may, however, be due to differences in dispersion.

Table 2.4. PERMANOVA and PERMDISP results comparing Euclidean distance measures of sample species richness (SR_s), Shannon-Wiener diversity (H') and Pielou's evenness (J') from the Zambezi, Chobe and Lake Liambezi in 2004 and 2007. Diversity and evenness for 2007 were log transformed to reduce heterogeneity of variance. The remainder of the data were untransformed. Significant differences are in bold.

Source	<i>df</i>	PERMANOVA			PERMDISP	
		MS	Pseudo-F	P(perm)	F	P(perm)
2004						
SR_s	2	35.079	1.955	0.170	1.506	0.258
H'	2	0.145	1.149	0.388	2.662	0.129
J'	2	0.091	12.476	<0.001	0.468	0.668
2007						
SR_s	2	29.374	4.002	0.033	2.828	0.099
H'	2	0.046	2.721	0.092	9.677	<0.001
J'	2	0.021	3.520	0.047	9.418	<0.001

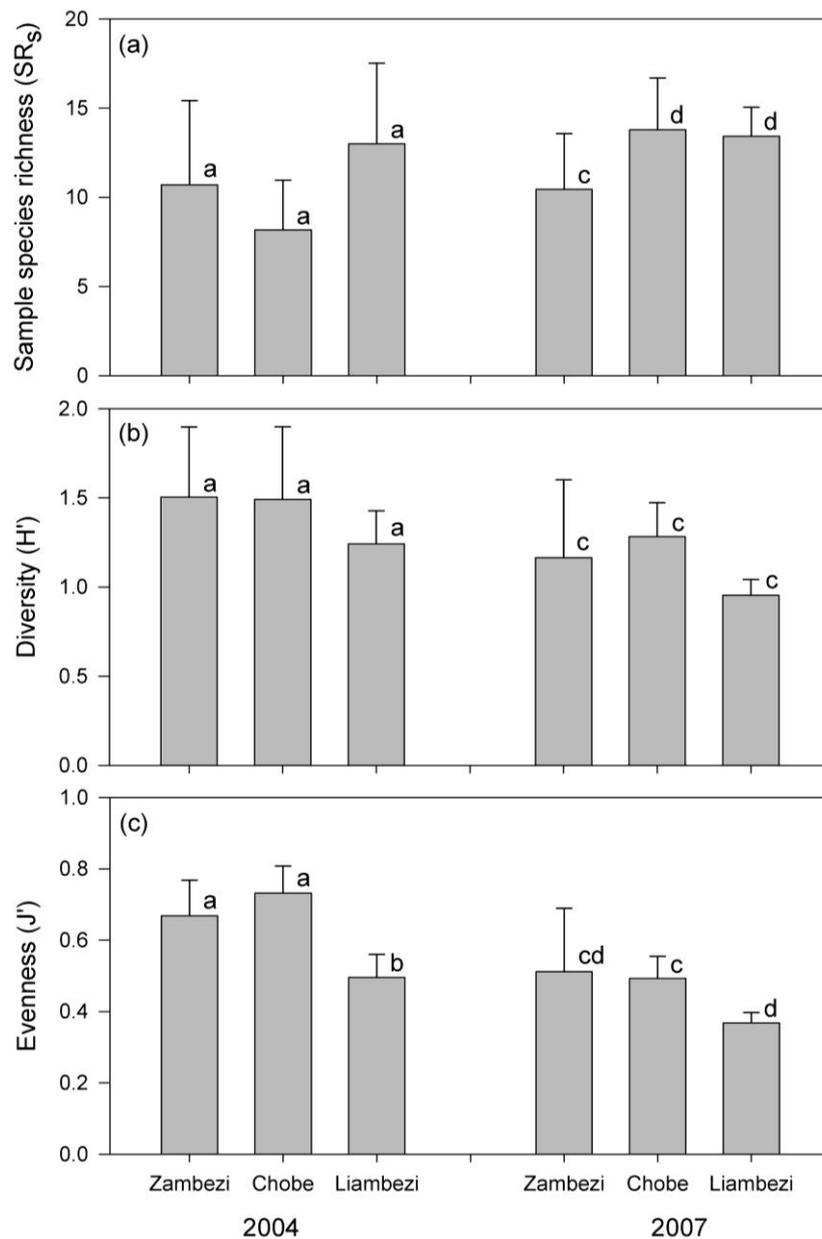


Figure 2.4. Comparison of (a) sample species richness, (b) Shannon-Wiener diversity and (c) Pielou's evenness between the Zambezi River, Chobe River and Lake Liambezi. Data from 2004 and 2007 analysed separately. Error bars represent 1 standard deviation. Letters above bars denote pair-wise significant differences (PERMANOVA; $P < 0.05$).

Assemblage structure

The colonising fish assemblages in Lake Liambezi differed significantly from the source populations in the Zambezi and Chobe rivers in terms of individual species abundance and biomass in both 2004 and 2007 (PERMANOVA, Table 2.5). The Zambezi and Chobe rivers differed significantly from each other in terms of either abundance or biomass in 2007, but not in 2004. Significant differences in dispersion in all four cases (PERMDISP, Table 2.5) may have contributed towards the observed differences. In 2004, variance in abundance

(mean distance to centroid \pm SE) was significantly lower in Lake Liambezi (17.5 ± 1.0) compared to the Chobe (28.3 ± 4.2) and Zambezi (32.3 ± 2.61). Variance in biomass was significantly higher in the Zambezi (32.6 ± 2.2) compared to the Chobe (26.6 ± 4.1) and lake Liambezi (18.6 ± 1.5). In 2007, variance in abundance was significantly lower in Lake Liambezi (11.9 ± 1.1) compared to the Chobe (17.6 ± 1.1) and Zambezi (20.0 ± 0.9). The pattern was the same for variance in biomass, with Lake Liambezi the lowest (12.2 ± 1.0), followed by the Chobe (19.0 ± 1.4) and Zambezi (20.5 ± 1.7).

Table 2.5. PERMANOVA and PERMDISP results on Bray-Curtis dissimilarities of fourth root transformed fish abundance and biomass data comparing fish assemblage structure between two separate inundation events in 2004 and 2007. Significant differences are in bold.

	Source	df	PERMANOVA			PERMDISP	
			MS	Pseudo-F	P(perm)	F	P(perm)
2004							
Abundance	Year	2	7238.5	7.534	<0.001	6.610	0.021
	Residual	19	960.77				
	Total	21					
Biomass	Year	2	7203.6	7.628	<0.001	7.131	0.018
	Residual	19	944.4				
	Total	21					
2007							
Abundance	Year	2	11425	33.138	<0.001	14.92	<0.01
	Residual	19	344.75				
	Total	21					
Biomass	Year	2	10337	26.9	<0.001	8.974	<0.01
	Residual	19	384.27				
	Total	21					

CAP ordinations of the abundance data (Figure 2.5 a, b) confirmed PERMANOVA results, showing that the colonising fish assemblages in Lake Liambezi differed significantly from the source populations in the Zambezi and Chobe rivers in 2004 ($\delta^2 = 0.937$; $P < 0.001$) and 2007 ($\delta^2 = 0.948$; $P < 0.001$). The CAP procedure selected $m = 6$ PCO axes that accounted for 81.8% of the variation in the Bray-Curtis dissimilarity matrix in 2004, and $m = 2$ PCO axes accounting for 100% of the variation in 2007. Allocation success of the leave-one-out procedure was 81.8% in 2004, with the misclassifications occurring between the Zambezi and Chobe rivers. In 2007 the allocation success was 100%. Species contributing to the observed differences in assemblage structure, as given by their correlation with the canonical axes, are illustrated in Figure 2.5 c, d. *Enteromius poechii* and *E. paludinosus*, both more abundant in the lake, contributed the most to the dissimilarity between Lake Liambezi and the Zambezi

and Chobe rivers in 2004 and 2007. *Brycinus lateralis*, which was more abundant in the rivers, contributed significantly to the dissimilarity in 2007.

Results of the CAP ordinations on biomass (Figure 2.6 a, b) were very similar to those for abundance, with significant differences between Lake Liambezi and the Zambezi and Chobe in both 2004 ($\delta^2 = 0.899$; $P < 0.001$) and 2007 ($\delta^2 = 0.939$; $P < 0.001$). The procedure selected $m = 3$ PCO axes in 2004, and $m = 2$ PCO axes in 2007, accounting for 72.7% and 100% of the variation in the Bray-Curtis dissimilarity matrices, respectively. *Clarias gariepinus*, more abundant in the lake, and *H. vittatus*, more abundant in the rivers, were among the most important contributors to the dissimilarity between systems in 2004 (Figure 2.6 c). In 2007, *H. cuvieri* and *B. lateralis*, both more abundant in the rivers, contributed significantly to the dissimilarity between systems (Figure 2.6 d). In Lake Liambezi, the small but numerous cyprinids *E. paludinosus* and *E. poechei*, also contributed a large part towards the dissimilarity between systems in terms of biomass in 2007.

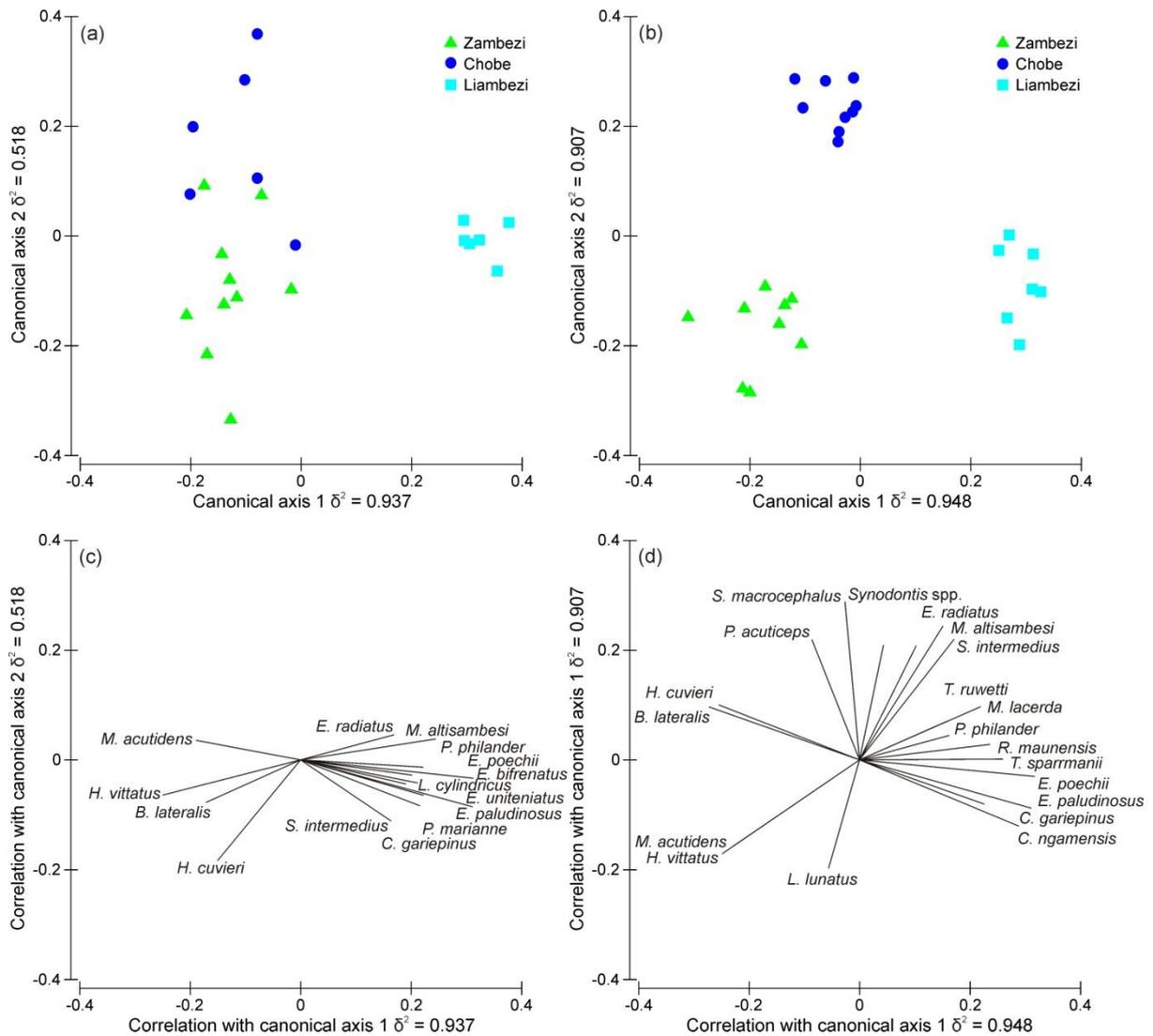


Figure 2.5. Canonical analysis of principal coordinates (CAP) ordination of fourth root transformed fish assemblage abundance data from the Zambezi River, Chobe River and Lake Liambezi for (a) 2004 and (b) 2007, and vectors of species correlations (Pearson; $|r| > 0.5$) with the canonical axes for (c) 2004 and (d) 2007 data.

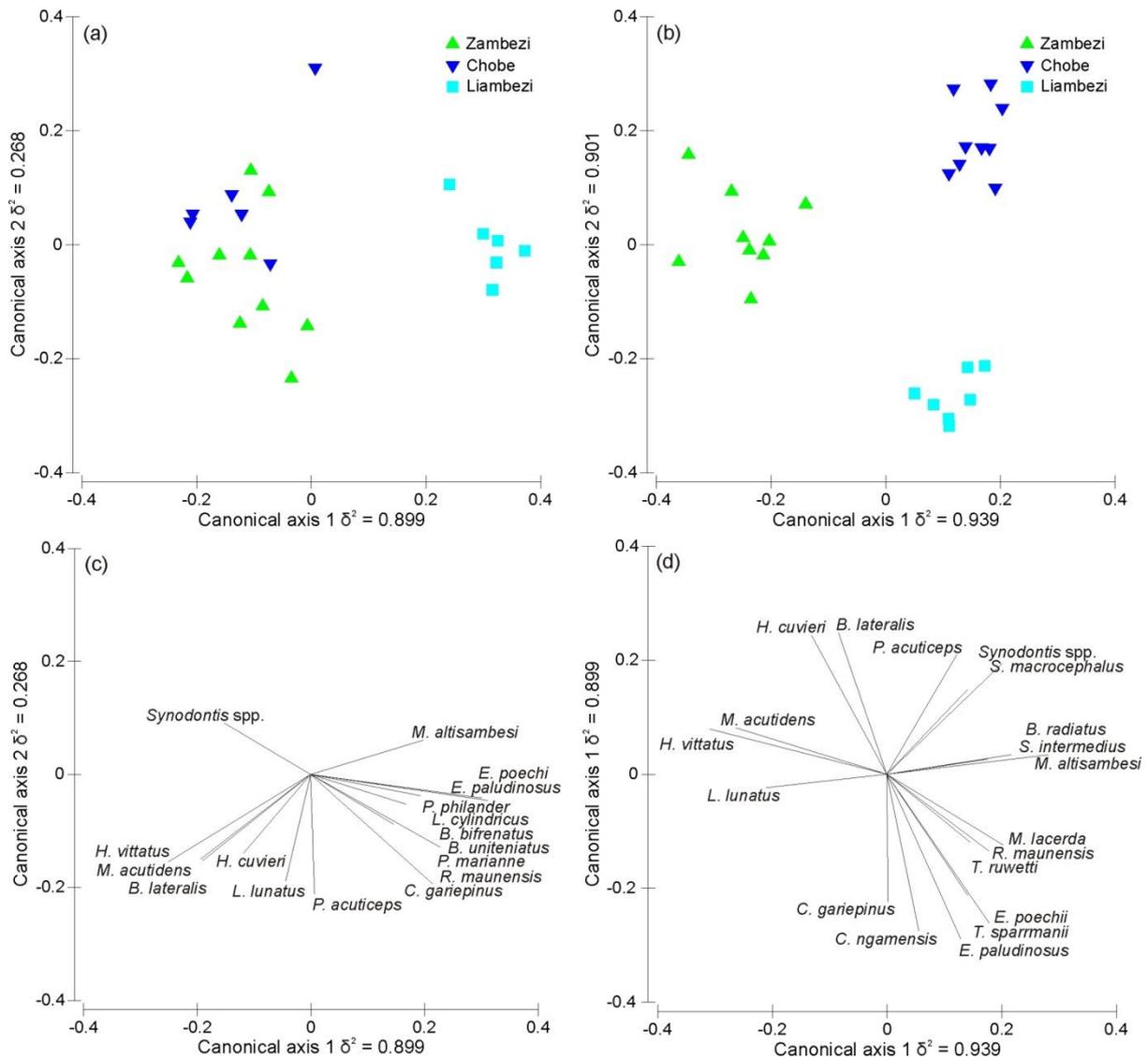


Figure 2.6. Canonical analysis of principal coordinates (CAP) ordination of fourth root transformed fish assemblage biomass data from the Zambezi River, Chobe River and Lake Liambezi for (a) 2004 and (b) 2007, and vectors of species correlations (Pearson; $|r| > 0.5$) with the canonical axes for (c) 2004 and (d) 2007 data.

Comparing colonising populations

Species composition, relative abundance and biomass

In total, 25 species were captured using gill nets across 2001, 2004 and 2007 in mesh sizes 22–150 mm (Table 2.6). Sixteen species were captured in 2001 and 2004, and 18 species in 2007. Of the 25 species captured, 11 were captured across all three years, 4 were captured in two of the three years, and 10 species were captured in only one year. Two cyprinids, *E. paludinosus* and *E. poechii*, accounted for between 63 and 86% of the total catch each year. *Enteromius paludinosus* dominated in 2001 and 2007, while *E. poechii* dominated in 2004. *Brycinus lateralis* was very numerous in 2001, accounting for 22% of the catch, but was

scarce in other years. Four species, namely *E. paludinosus*, *E. poechii*, *S. intermedius* and *M. altisambesi* ranked among the top five in all three years. *Clarias gariepinus* ranked fifth in 2004 and 2007.

Table 2.6. Gill net catch composition from Lake Liambezi after three separate inundation events in 2001, 2004 and 2007, expressed as percent number (%N), and the life-history strategy of each species: O = opportunistic; P = periodic; E = Equilibrium. Excludes catches from 12 and 16 mm mesh sizes from 2004 and 2007.

Taxon	Strategy	2001	2004	2007
Mormyridae				
<i>Marcusenius altisambesi</i>	P	2.7	8.4	1.3
<i>Mormyrus lacerda</i>	P	0.1	< 0.1	0.2
<i>Petrocephalus</i> cf. <i>okavangensis</i>	O	0.2	0.1	-
<i>Pollimyrus</i> cf. <i>cuandoensis</i>	O	0.3	0.6	-
Cyprinidae				
<i>Enteromius paludinosus</i>	O	44.1	10.8	47.6
<i>Enteromius poechii</i>	O	18.8	66.3	38.0
<i>Enteromius radiatus</i>	O	-	-	<0.1
<i>Labeo cylindricus</i>	O	0.6	-	-
Alestidae				
<i>Brycinus lateralis</i>	O	22.3	< 0.1	< 0.1
Hepsetidae				
<i>Hepsetus cuvieri</i>	E	-	-	< 0.1
Schilbeidae				
<i>Schilbe intermedius</i>	P	6.4	12.9	11.2
Clariidae				
<i>Clarias gariepinus</i>	P	0.6	0.5	0.6
<i>Clarias ngamensis</i>	P	< 0.1	-	0.2
Mochokidae				
<i>Synodontis</i> spp.	P	-	-	0.1
Cichlidae				
<i>Oreochromis andersonii</i>	E	1.1	-	< 0.1
<i>Pharyngochromis acuticeps</i>	E	0.4	0.1	-
<i>Pseudocrenilabrus philander</i>	E	0.1	0.1	< 0.1
<i>Serranochromis altus</i>	E	-	< 0.1	-
<i>Serranochromis macrocephalus</i>	E	0.6	0.1	< 0.1
<i>Serranochromis robustus jallae</i>	E	-	< 0.1	-
<i>Serranochromis thumbergi</i>	E	-	< 0.1	-
<i>Coptodon rendalli</i>	E	-	-	< 0.1
<i>Tilapia sparrmanii</i>	E	1.6	0.1	0.4
<i>Tilapia ruweti</i>	E	-	-	0.1
Anabantidae				
<i>Ctenopoma multispine</i>	E	-	-	< 0.1
Total species		16	16	18

Relative abundance and biomass were lowest in 2001, followed by 2004, and highest in 2007 (Figure 2.7). The difference between 2001 and 2007 was significant for abundance, but not for biomass (PERMAOVA, Table 2.7). Variance was homogeneously distributed among years for both abundance and biomass (PERMDISP, Table 2.7).

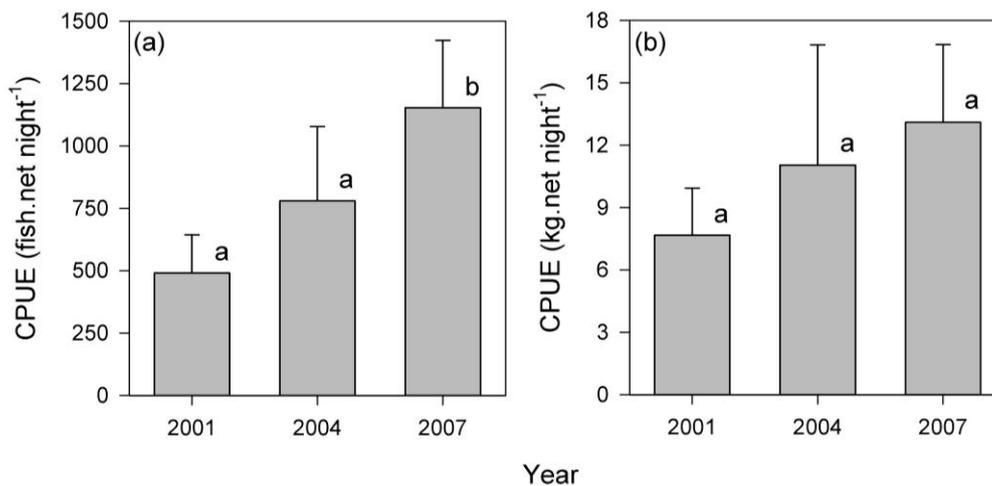


Figure 2.7. Gill net catch per unit effort (CPUE) in (a) numbers and (b) weight after three separate inundation events in 2001, 2004 and 2007. Error bars represent 1 standard deviation. Letters above bars denote pair-wise significant differences (PERMANOVA; $P < 0.05$).

Table 2.7. PERMANOVA and PERMDISP results comparing Euclidean distance measures of untransformed relative abundance and biomass after three separate inundation events in 2001, 2004 and 2007. Significant differences are in bold.

Source	df	PERMANOVA			PERMDISP	
		MS	Pseudo-F	P(perm)	F	P(perm)
Abundance	2	658630	10.142	<0.01	0.333	0.906
Biomass	2	42945000	2.373	0.125	1.153	0.571

Species richness and diversity

Mean sample species richness was lowest in 2004 and highest in 2007 (Figure 2.8), but did not differ significantly among years (PERMANOVA, Table 2.8). Shannon -Wiener diversity did, however, differ significantly among years. Diversity was highest in 2001 and lowest in 2007. Variance was homogeneous among years (PERMDISP, Table 2.8), indicating differences were genuine, and not due to within year dispersion. Pielou's evenness was similarly highest in 2001 and lowest in 2007, but did not differ significantly among years.

Table 2.8. PERMANOVA and PERMDISP results comparing Euclidean distance measures of untransformed sample species richness (SR_s), Shannon-Wiener diversity (H') and Pielou's evenness (J') after three separate inundation events in 2001, 2004 and 2007. Significant differences are in bold.

Source	df	PERMANOVA			PERMDISP	
		MS	Pseudo-F	P(perm)	F	P(perm)
SR_s	2	9.622	2.856	0.096	2.144	0.188
H'	2	0.182	8.808	<0.005	1.951	0.191
J'	2	9.830	2.896	0.088	2.129	0.184

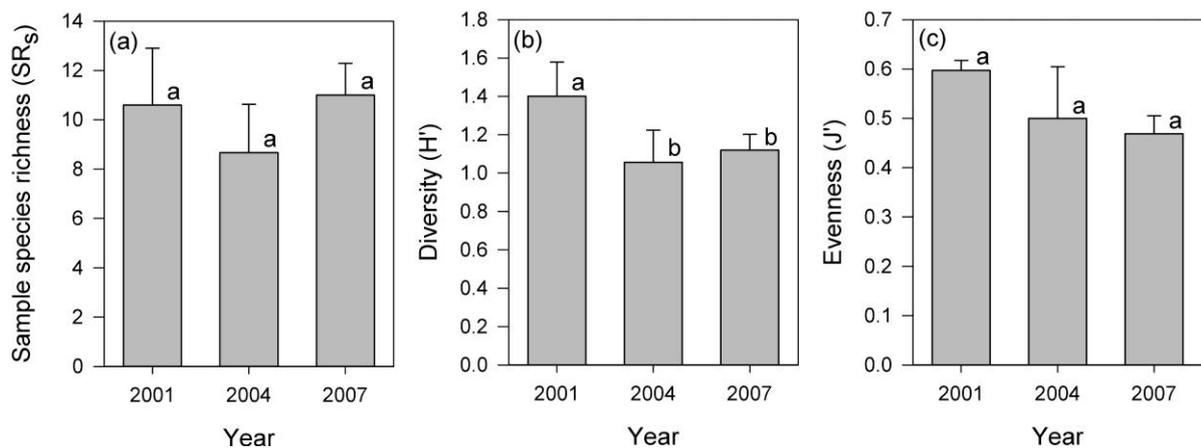


Figure 2.8. Variation in (a) sample species richness, (b) Shannon-Wiener diversity and (c) Pielou's evenness after three separate inundation events in 2001, 2004 and 2007. Error bars represent 1 standard deviation. Letters denote pair-wise significant differences (PERMANOVA; $P < 0.05$).

Assemblage structure

The colonising fish assemblages differed significantly among years by both abundance and biomass (PERMANOVA, Table 2.9). Both were, however, heterogeneously distributed among years (PERMDISP, Table 2.9). Variance in abundance (mean distance to centroid \pm SE) was significantly greater in 2001 (18.5 ± 1.8) compared to 2004 (13.2 ± 1.2) and 2007 (10.5 ± 0.8), while variance in biomass was significantly lower in 2007 (11.3 ± 0.8) compared to 2001 (20.0 ± 3.1) and 2004 (16.7 ± 1.8). The observed differences in assemblage structure among years may be exaggerated by these differences in within-year dispersion.

The CAP ordinations (Figure 2.9 a, b), however, support the PERMANOVA results which showed that the colonising assemblages differed significantly among years in terms of abundance ($\delta^2 = 0.944$; $P < 0.001$) and biomass ($\delta^2 = 0.902$; $P < 0.001$). The CAP procedure selected $m = 2$ PCO axes that accounted for 100% of the variation in both the abundance and biomass Bray-Curtis dissimilarity matrices. Allocation success of the leave-one-out procedure was therefore 100% in each case. Species contributing to the observed differences in assemblage structure, as given by their correlation with the canonical axes, are illustrated in Figure 2.9 c, d.

Table 2.9. PERMANOVA and PERMDISP results on Bray-Curtis dissimilarities of fourth root transformed fish abundance and biomass data comparing fish assemblage structure between three separate inundation events in 2001, 2004 and 2007. Significant differences are in bold.

	Source	df	PERMANOVA			PERMDISP	
			MS	Pseudo-F	P(perm)	F	P(perm)
Abundance	Year	2	2804.1	11.475	<0.001	10.758	<0.005
	Residual	15	244.37				
	Total	17					
Biomass	Year	2	2614.7	8.026	<0.001	5.506	<0.05
	Residual	15	325.81				
	Total	17					

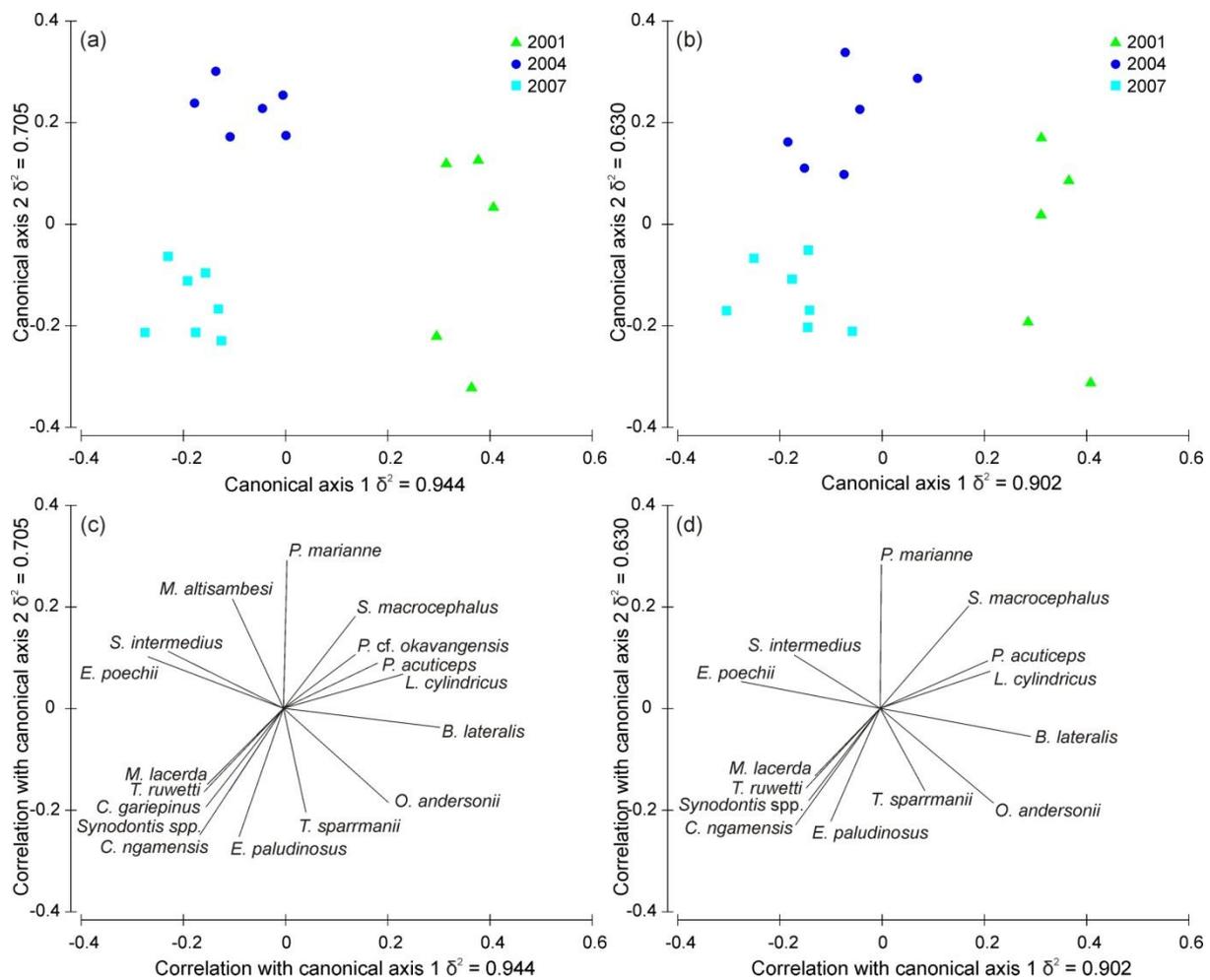


Figure 2.9. Canonical analysis of principal coordinates (CAP) ordination of fourth root transformed fish assemblage (a) abundance and (b) biomass data from three separate inundation events in 2001, 2004 and 2007, and vectors of species correlations (Pearson; $|r| > 0.5$) with the canonical axes for (c) abundance and (d) biomass data.

The CPUE of the twelve species contributing the most to the observed dissimilarity between years in abundance and biomass are illustrated in Figure 2.10. Species whose abundance was

highest in 2001 included the small alestid *B. lateralis*, the cyprinid *Labeo cylindricus* and three cichlids *Pharyngochromis acuticeps*, *Oreochromis andersonii* and *Serranochromis macrocephalus*. *Brycinus lateralis* averaged 109 ± 34 fish and 0.88 ± 0.25 kg.net night⁻¹ in 2001, but was very rare, averaging no more than 4 fish.net night⁻¹ in 2004 and 2007. *Labeo cylindricus* and the three cichlid species mentioned above were far less abundant, all averaging <10 fish.net night⁻¹ in 2001, but were even more scarce in 2004 and, in the case of *L. cylindricus* and *P. acuticeps*, absent from gill net catches in 2007. The mormyrids *M. altisambesi* and *P. cf. cuandoensis* most strongly differentiated 2004 from the other years. However, *M. altisambesi* showed a sharp decline in abundance from 66 ± 8 fish.net night⁻¹ for the first sampling event in July 2004 (used for the CAP ordination) to subsequent events in October (52 ± 11 fish.net night⁻¹) and December (20 ± 4 fish.net night⁻¹) of the same year. *Pollimyrus. cf. cuandoensis* displayed a similar trend, though of a much lower magnitude. Several catfish species including the clariid *C. ngamensis* and mochokid *Synodontis* spp. differentiated 2007 from the other years. Neither of these species were sampled in July 2004, but were quite common, especially the *Synodontis* spp., in October and December 2004. Two small cyprinids *E. paludinosus* and *E. poechii* were important colonisers in all three years, though their abundance varied, ranging from 85 ± 14 to 549 ± 63 fish.net night⁻¹ and 92 ± 25 to 517 ± 104 fish.net night⁻¹, respectively. *Enteromius paludinosus* was most abundant in 2007, and *E. poechii* in 2004. Again though, their abundance varied greatly in 2004, *E. paludinosus* increasing and *E. poechii* decreasing from July to December. The schilbeid catfish *S. intermedius* was very abundant in 2004 (100 ± 27 fish.net night⁻¹) and 2007 (129 ± 14 fish. net night⁻¹), differentiating these years from 2001 (31 ± 13 fish. net night⁻¹).

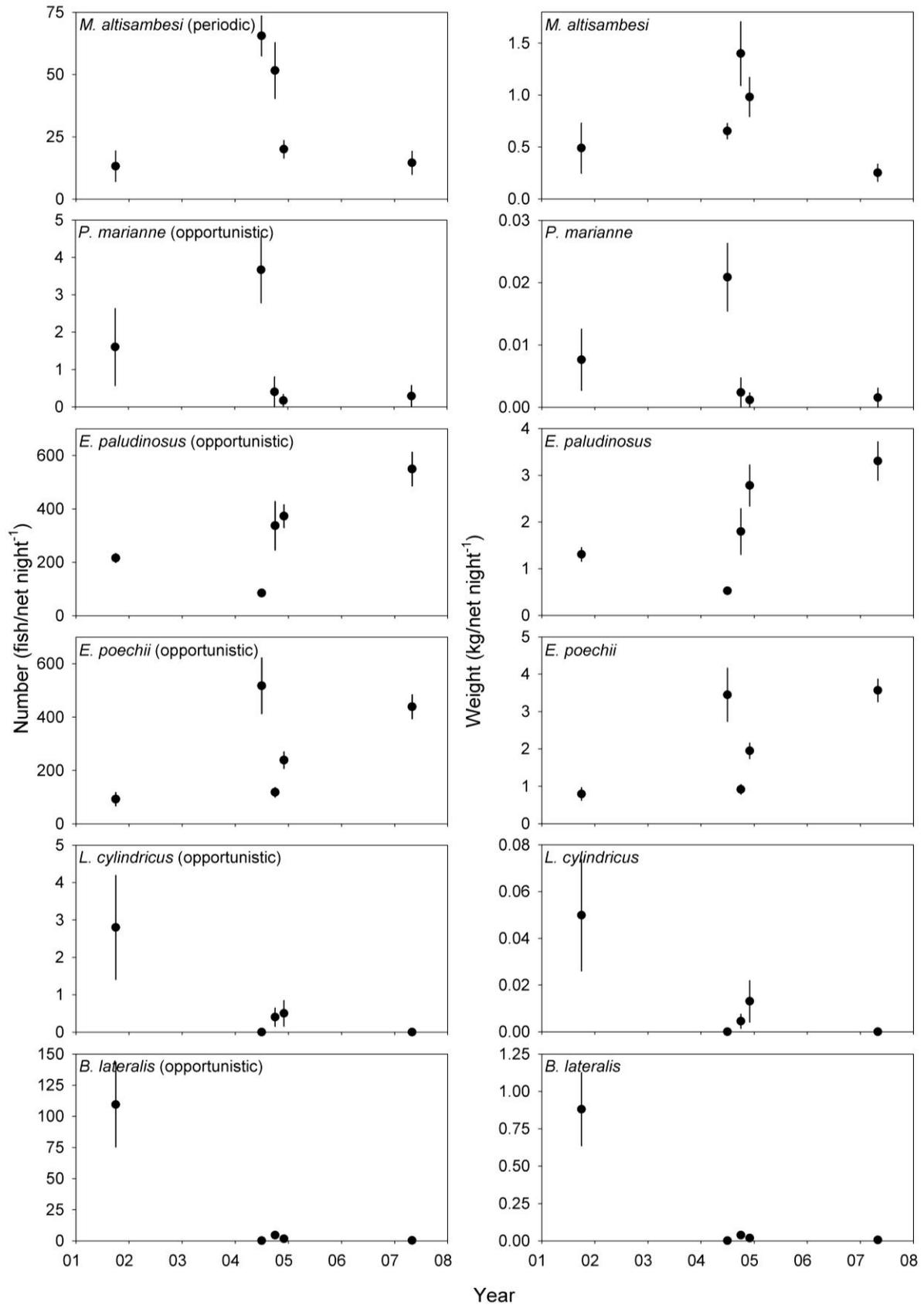


Figure 2.10. Catch per unit effort (CPUE) in number (left column) and weight (right column) of twelve species identified as contributing to differences in colonising assemblage structure among years. Data represent the mean \pm 1 standard error.

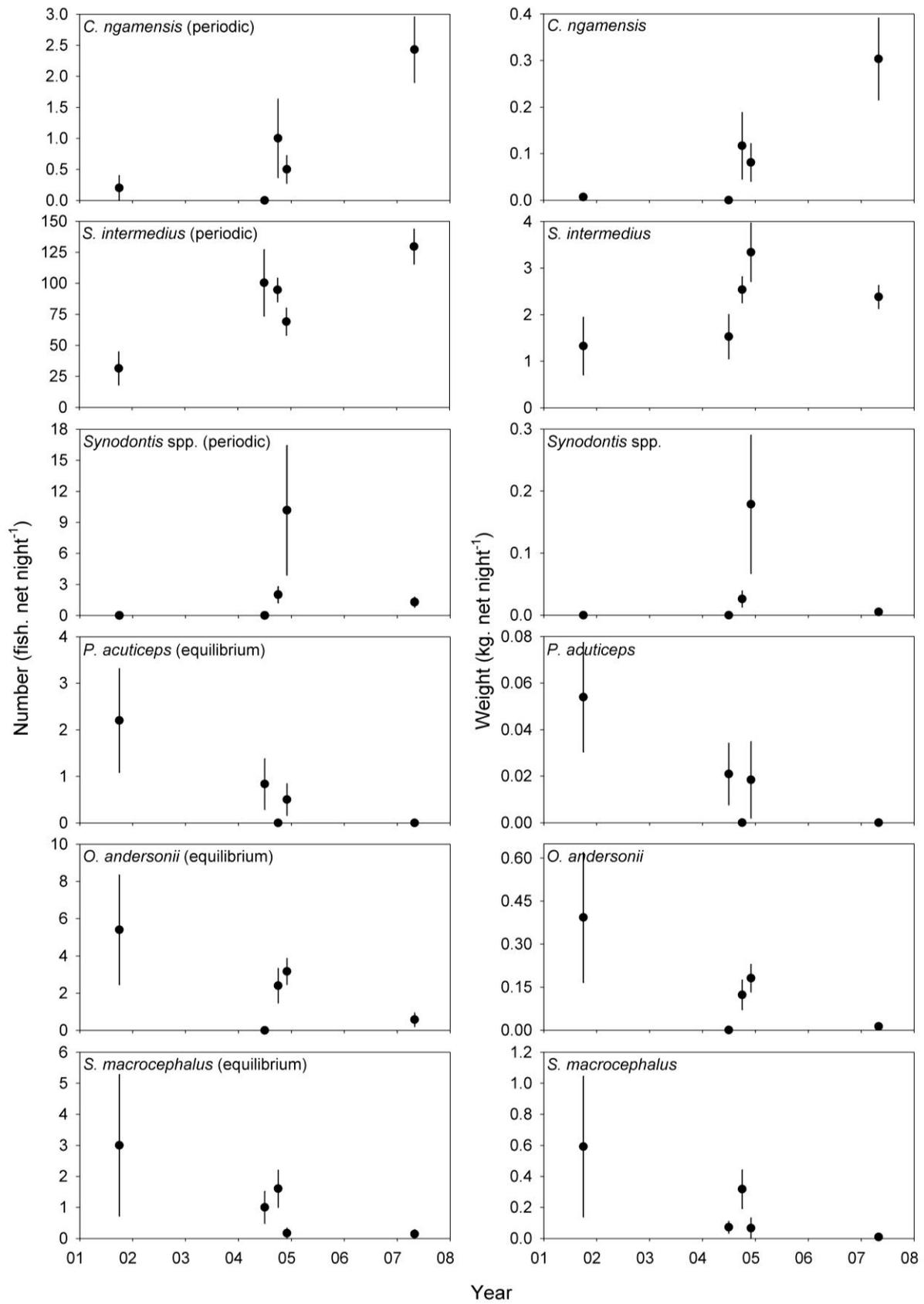


Figure 2.10. Continued.

Discussion

Comparing source populations with colonising populations

In floodplain rivers, the enormously increased volume of water and area of inundation during the annual floods results in the dilution of fishes and consequently lower relative abundances compared to the dry season. Numeric CPUE in the Zambezi and Chobe rivers at peak flood was relatively low as a result. In Lake Liambezi, however, the numeric CPUE was extremely high. This was not a result of receding water levels concentrating the fishes in the lake as the lake was sampled in July 2004, shortly after reaching its peak, and in May 2007 at its peak (Mutelo 2013). The extraordinarily high CPUE suggests that immigration into Lake Liambezi from the floodplains was not a type of stochastic dispersal, but a very active migration. Had the fishes been dispersing away from an area of higher concentration on the floodplains, more comparable relative abundance values would be expected between the rivers and the lake. Furthermore, as the destination of the migrants was unknown, the migration was essentially exploratory in nature, thus differentiating between dispersal and exploratory migratory behaviour (Lucas and Baras 2001). Less pronounced differences in biomass CPUE between the rivers and lake indicates that it was mainly small fish, including small species and juveniles of larger species that undertook the migration.

The diversity of freshwater fish is significantly positively correlated with habitat structural complexity (Willis *et al.* 2005; Arrington and Winemiller 2006). The Zambezi and Chobe rivers are more structurally complex environments than Lake Liambezi, primarily due to variable current velocities, substrates and depth profiles compared to the somewhat uniform lake. Species richness and diversity were therefore expected to be higher in the river systems compared to Lake Liambezi. However, species richness and Shannon-Weiner diversity indices were generally very similar between systems. The apparent similarities between Lake Liambezi and the inflowing floodplain rivers may be partially explained by the differences in relative abundance between the Zambezi, Chobe and Liambezi systems as discussed above. Species richness estimates are sensitive to the number of individuals sampled (Gotelli and Colwell 2001). As the density of fish was so much higher in the lake, the chances of catching any particular species was higher than in the rivers. Pielou's evenness indicated that the fish fauna in the lake was numerically dominated by few species, with numerous rare species. Species relative abundances were more evenly distributed in the Zambezi and Chobe rivers.

Colonising fish communities in Lake Liambezi were distinct from source populations in the Zambezi and Chobe rivers. The dominant colonists, *E. paludinosus* and *E. poechei*, which accounted for the greatest proportion of dissimilarity between systems, were relatively uncommon on the Zambezi and Chobe floodplains. Van der Waal (1996) observed large numbers of *E. paludinosus* caught as floodwaters receded back into permanent water bodies, and regularly caught them in isolated pools distributed across the Zambezi and Chobe floodplains. This suggests that *E. paludinosus* is in fact common on the floodplains, but perhaps prefers shallow, marginal areas. Gill netting was carried out in close proximity to the main channels of each river, potentially accounting for their low abundance. The same may apply for other floodplain specialists such as *Clarias* spp. that are often found at the front of the advancing flood waters (Williams 1971; Hickley and Bailey 1987). *Clarias gariepinus* has also been known to undertake potamodromous spawning migrations from natural and man-made lakes, moving upstream at the very first opportunity that river flow allows (Bowmaker 1973; van der Waal 1996). *Clarias gariepinus* and *C. ngamensis* contributed a large part to the dissimilarity between the lake and rivers, particularly in terms of biomass. Another catfish, *S. intermedius*, dominated gill net catches in the Zambezi and Chobe rivers, but was even more abundant in Lake Liambezi, thus contributing to the dissimilarity between systems. Like *C. gariepinus*, *S. intermedius* is among the first species to move laterally onto the floodplain to spawn (Williams 1971; Merron and Mann 1995). It appears they then disperse in a more traditional manner, i.e. away from a central concentration, unlike *C. gariepinus* and *Enteromius* spp. that follow the advancing flood waters.

The alestids, both large and small species, were important components of the catch in the Zambezi and Chobe rivers. The only species that made up a greater portion of the catch in the lake was *Rhabdalestes maunensis*, which has a preference for floodplain habitats (Skelton *et al.* 1985). *Brycinus lateralis* were scarce in the lake, making up less than 0.1% of the catch, while *H. vittatus* and *M. acutidens* were absent. Many alestids, including *H. vittatus*, undertake potamodromous spawning migrations (Bowmaker 1973; Benech *et al.* 1983). The migrations are thought to allow larvae time to hatch and develop as they drift downstream, before being carried or swimming to appropriate nursery areas (Lucas and Baras 2001). *Brycinus lateralis* is not potamodrometic (Bowmaker 1973), but probably undertakes short lateral migrations onto the floodplain, much like *Brycinus nurse* from the Lake Chad basin (Benech *et al.* 1983). *Micralestes acutidens* prefers riverine habitat, and is seldom found on

the floodplain far from the main channel (Benech *et al.* 1983; Skelton *et al.* 1985; Winemiller 1996a).

Several mormyrids featured prominently among the catches from the Zambezi and Chobe rivers, chief among which was *M. altisambesi*. *Marcusenius altisambesi* made up a greater portion of the catch in the rivers, but was evidently more abundant in the lake. Three cichlid species contributed towards differences in community structure between the rivers and lake and all are small, fairly ubiquitous floodplain species. Two, *Pseudocrenilabrus philander* and *Tilapia sparrmanii*, are among the most abundant species on Upper Zambezi and Kavango river floodplains (Bell-Cross 1971; van der Waal 1996; Winemiller 1996a; Hocutt and Johnson 2001). Both were very scarce in the Zambezi and Chobe rivers, probably because they prefer warm shallow water on the margins of the floodplain. Small cichlids are also not particularly vulnerable to gill nets (van der Waal 1980), so were likely underrepresented in the samples.

Comparing colonising populations

Gill net CPUE in Lake Liambezi after the three separate inundation events did not differ significantly in most cases, but appeared to be influenced by the intensity of the flood in the Zambezi River. The lowest CPUE was recorded in 2001 when an estimated 16 km² was inundated (Mutelo 2013). The CPUE was higher in 2004 when approximately 50 km² was inundated, and higher still in 2007 when 65 km² was inundated (Mutelo 2013). Disparate sampling dates may have been a contributing factor to the differences in CPUE among years. The lake was sampled at its peak in 2007, 1 month after its peak in 2004, and 4 months after its peak in 2001. Environmental conditions may have become increasingly harsh, and predation and fishing pressure more intense with the contraction of the lake, potentially contributing to reduced fish densities. Shannon-Weiner diversity was significantly higher in 2001 compared to 2004 and 2007. *Enteromius paludinosus* and *E. poechii* accounted for a lower proportion of the catch in this low flood year, as is evidenced by the higher evenness value. Species richness was very similar between the three years, as was their composition, with 11 of 25 species sampled across all three years.

The relative abundance rank of the colonising fauna closely resembled the ordered sequence of species that undertake lateral migrations onto the floodplain (Williams 1971; Welcomme 1985; van der Waal 1996; Hocutt and Johnson 2001), with *Enteromius* spp., *Clarias* spp. and

S. intermedius among the most important colonists each year. Despite these similarities, there were significant differences in assemblage structure between years, the most notable of which involved the small alestid *B. lateralis*. *Brycinus lateralis* comprised 22% of the catches in 2001 with a CPUE of 109 fish.net night⁻¹, but less than 0.1% and 0.2–0.3 fish.net night⁻¹ in 2004 and 2007. In the rivers, *B. lateralis* was not particularly abundant in 2004, but was dominant, especially in the Zambezi River, in 2007. Changes in the abundance of *B. lateralis* in the source populations is, therefore, not likely the cause of the disparity among the colonising populations. *Brycinus lateralis* only moves onto the floodplain after the pioneering catfishes and cyprinids (Hocutt and Johnson 2001), and does not appear to disperse as rapidly. The duration of the flood in the Zambezi River in 2001 was longer, and the flood peak later than in 2004 and 2007. The longer period of floodplain inundation in 2001 may have allowed *B. lateralis* time to disperse further from the main channels and permanent backwaters of the rivers, and enabled it to be in a position on the margin of the floodplain from where it could colonise the lake.

Much of the rest of the dissimilarity between years is the result of variation in the relative abundance of the dominant species. *Enteromius poechii* and *S. intermedius*, ranked third and fourth in 2001, but were significantly more abundant in 2004 and 2007. Differences in the relative abundance of *E. paludinosus* accounted for the greatest proportion of dissimilarity between 2004 and 2007. In July 2004 (data used for the multivariate analyses), the CPUE of *E. paludinosus* was 84 fish. net night⁻¹, placing it third in terms of abundance. By December the same year, the CPUE of *E. paludinosus* had risen to 373 fish. net night⁻¹, upping its rank to first as it was in 2007. The increase in abundance was contrary to what was observed for most other small species over the same period, including *E. poechii*, and the reasons for it are unclear. It is possible that *E. paludinosus* was underrepresented in the July sample. Several other, less abundant mormyrids and cichlids contributed towards the dissimilarity between years, but no distinct patterns were discernible. Variations in their abundance may simply be attributable to stochastic dispersal during the flood.

In summary, assemblage structure differed significantly between source populations in the Zambezi and Chobe rivers and the colonising assemblages in Lake Liambezi, implying some degree of determinism, and supporting the first hypothesis that colonising fish communities would differ from the source populations. This may have been a result of interspecific differences in the propensity and ability to undertake extensive lateral migrations. Despite

greater habitat complexity in the Zambezi and Chobe compared to the lake, sample species richness and diversity were generally similar between the three systems. The second hypothesis that colonisation patterns would be similar among years was rejected as assemblage structure differed significantly between colonisation events. There was, however, an element of predictability, in that *E. paludinosus*, *E. poechii*, *S. intermedius* and *M. altisambesi* were ranked among the top five species numerically in all three years, while *C. gariepinus* clinched fifth place in two out of the three years. Chapman and Chapman (1993) observed similarly consistent patterns of species composition in floodplain pools on the Sokoto River, Nigeria, as did Jackson *et al.* (2013) on the Ouémé River in Benin. The relative abundances of the dominant species, however, varied significantly between years, contributing to differences in assemblage structure. These results suggest that interspecific differences in the propensity and ability to undertake extensive lateral migrations contributes to a high degree of determinism in colonising assemblages. Which of the colonising fishes are able to establish and persist in Lake Liambezi following the refilling of the lake in 2009 is the subject of Chapter 3.

CHAPTER 3

Species successions and the development of a lacustrine fish community in Lake Liambezi over an extended period of inundation

Introduction

Patterns in diversity, composition and abundance of ecological communities are influenced by a myriad of factors that Vellend (2010) surmised involve just four distinct kinds of processes: speciation, selection, drift and dispersal. Speciation shapes regional species pools over large temporal and spatial scales. These, in turn, influence local patterns of species richness and diversity on which selection, dispersal and drift act together to shape community dynamics.

Vellend (2010) defines selection as “a deterministic fitness difference between individuals of different species”. Selective processes can be divided into two categories: abiotic and biotic. Undoubtedly, the most important abiotic factor influencing fish communities in shallow, ephemeral lakes such as Lake Liambezi, is the hydrological regime (Dumont 1992; Wantzen *et al.* 2008). Shallow lakes are characterised by marked seasonal fluctuations in water level associated with seasonal rainfall patterns, as well as longer term cycles of several years to several decades, during which endorheic systems may fluctuate between exceptionally high water levels and complete desiccation (Talling 1992).

Life-history strategies strongly influence the rate at which fishes are able to recover from major habitat disturbances such as desiccation. Winemiller (1996b) developed a graphical model that illustrates succession in the relative dominance of alternative life-history strategies in fish communities following a major habitat disturbance (Figure 3.1). The small body size, early maturation and continually high reproductive effort of opportunistic strategists enables them to quickly colonise habitats following major disturbances (Winemiller and Rose 1992). Large bodied, late maturing and highly fecund periodic strategists, which can endure years without good recruitment when environmental conditions are unfavourable, usually produce strong year classes during refilling (e.g. Furse *et al.* 1979). Recruitment success in both opportunistic and periodic strategists is density-dependent, so that once new habitats have

been repopulated, competition and predation can significantly reduce juvenile survival (Winemiller 2005). The abundance of short-lived opportunistic strategists will decline at this stage, while periodic strategists may continue to dominate the fish community despite poor recruitment, due to low adult mortality and high longevity (Winemiller 1996b). If ecological succession proceeds uninterrupted by disturbances, environmental stability and density-dependent recruitment favours equilibrium strategists with low fecundities, large eggs and parental care; traits that limit the potential population growth rate but enhance juvenile survival (Winemiller and Rose 1992; Winemiller 1996b).

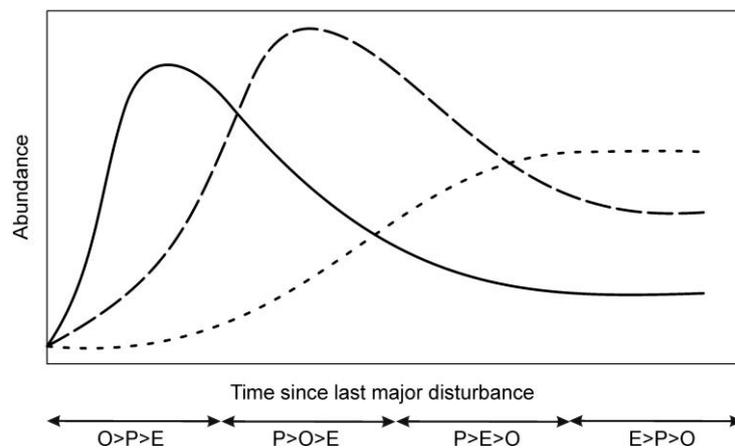


Figure 3.1. Graphical model predicting trends in relative dominance of alternative life-history strategies following major habitat disturbances from Winemiller (1996b). Life-history strategies: O = Opportunistic (—), P = Periodic (— —), E = Equilibrium (— — —).

The relative influence of selective processes on fish assemblage structure in freshwater environments is directly linked to the hydrological regime. Abiotic conditions are generally favourable during high water levels, but deteriorate as water levels recede. In the endorheic lakes Chilwa and Chad, strong winds mix the water column and disturb bottom sediments, resulting in increased turbidity and reduced levels of dissolved oxygen at low water levels (McLachlan 1979; Carmouze *et al.* 1983a). Reduced levels of dissolved oxygen directly affect fish communities by excluding species with a low physiological tolerance to hypoxia (Furse *et al.* 1979; Benech *et al.* 1983; Winemiller 1996a). Water transparency can indirectly affect fish community structure by constraining prey detection and predator avoidance. In neotropical floodplain lakes, catfishes and knifefishes with sensory adaptations to low light dominate assemblages in turbid lakes, while visually oriented cichlids and characins dominate in clear lakes (Rodríguez and Lewis 1997; Tejerina-Garro *et al.* 1998; Lewis *et al.* 2000).

Intense predation by piscivorous fishes and birds can significantly reduce the abundance of prey species (Welcomme 1985; Winemiller 1996a; Jackson *et al.* 2001). This is of particular importance in small habitats such as floodplain pools, where large predatory species which are tolerant of adverse environmental conditions (e.g. *Clarias gariepinus*), may eliminate other fishes (Skelton *et al.* 1982; Winemiller 1996a; Jackson *et al.* 2013). Fishing (effectively predation by humans) may also affect fish communities directly, by reducing the abundance of targeted fish species, and indirectly, by removing top predators that may exert top-down control on lower trophic levels (Craig 1992; Welcomme 1999; Allan *et al.* 2005). In Lake Liambezi, large meshed (76–114 mm) monofilament gill nets are used by fishers to target large cichlid species, especially *Oreochromis andersonii* and *Oreochromis macrochir*, and can remove substantial biomass, for example approximately 27 00 tonnes per annum in 2011/2012 (Peel *et al.* 2015b). This reduction in species biomass is likely to have a significant direct effect on the fish assemblage structure in Lake Liambezi. The effects of interspecific competition on fish community structure in freshwater environments appear to be less important than predation (Jackson *et al.* 2001), and only occurs if the resources shared between species are limited (Craig 1992). Even then, the outcome is usually niche segregation, and not competitive exclusion (Jackson *et al.* 2001). Indeed, van der Waal (1985) noted a high degree of dietary specialisation among the larger fish species of Lake Liambezi, which he interpreted as a means of avoiding competition.

The relative importance of dispersal depends on the frequency and duration of connectivity between habitats (Zeug *et al.* 2005; Miyazono *et al.* 2010). Dispersal between established communities in different environments with divergent selection pressures can strongly influence the importance of local selection and drift (Vellend 2010). Given relatively predictable patterns of dispersal—high mean dispersal across species and high variance among species (Vellend *et al.* 2014; see Chapter 2)—the effect on local selection depends on the relationship between species' dispersal ability and local fitness. A species with high dispersal ability and high local fitness can strongly reinforce local selection. Conversely, a species with high dispersal ability and low local fitness can strongly counter local selection, effectively allowing competitively inferior species to persist via the competition-colonisation trade-off (Tilman 1994).

The aim of this chapter was to describe the temporal succession of fish species in Lake Liambezi over an eight year period of continuous inundation from 2007 to 2014. It was hypothesised that over time, and with greater environmental stability than during filling and drying phases, a diverse colonising fish fauna dominated by opportunistic strategists would be succeeded by a more stable, and less diverse community dominated firstly by periodic strategists, and later by equilibrium strategists according to Winemiller (1996b; Figure 3.1). Factors that may have contributed to the observed changes in fish diversity, composition and abundance are also discussed.

Materials and methods

Data collection

After being inundated in May 2007, Lake Liambezi, while not drying up, gradually reduced in size, until March 2009 when it received a major flood, filling for the first time since the early 1980s (Figure 3.2). The lake received further inflow from the Zambezi River in May 2010, reaching its peak at 370 km² (Mutelo 2013), and again in May 2011. No floodwaters have entered the lake since 2011. The data used in this chapter were collected over an 8 year period from 2007 to 2014. Sampling of the fish population was carried out annually in collaboration with the Ministry of Fisheries and Marine Resources (MFMR) (data available from 2007–2012) during their annual monitoring surveys. I participated in all sampling events from 2010 onward. I carried out more frequent sampling for biological studies in 2010/2011 and 2013/2014. Details of each sampling event are summarised in Table 3.1.

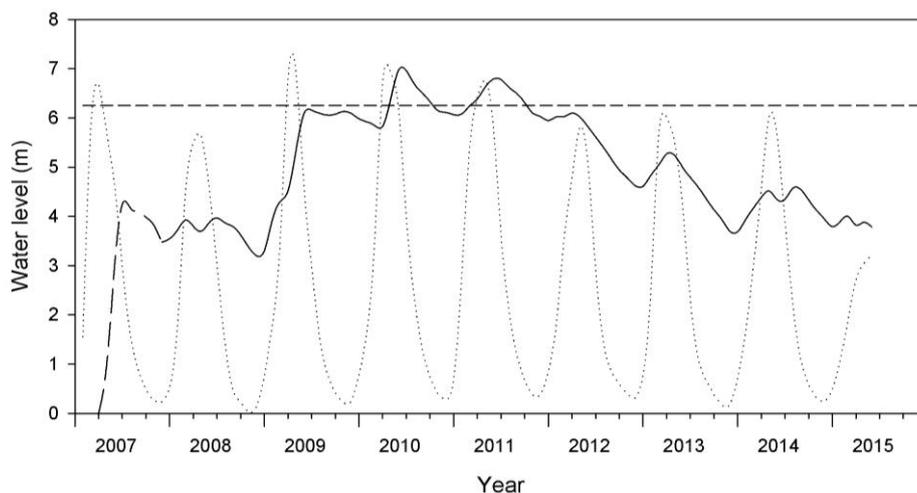


Figure 3.2. Water level of Lake Liambezi (—) since inundation in 2007. The annual flood cycle of the Zambezi River (····), and the level at which the Zambezi River spills into the lake (---) are illustrated to show when the lake received inflow.

Fish were sampled using standardised gill nets as described in Chapter 2. Sampling was concentrated in the eastern half of the lake, around the inflowing Bukalo Channel and Chobe River, and was completed in both open water and vegetated habitats. All fish caught in each mesh size were identified to species level, measured to the nearest mm and weighed to the nearest gram. The relative abundance of each species was expressed as catch per unit effort (CPUE), calculated as the mean number or weight of fish per gill net night (fish.net night⁻¹; kg.net night⁻¹).

Data selection and analysis

Temporal changes in assemblage structure between 2007 and 2014 were assessed using data collected between March and June during the MFMR's annual monitoring surveys, and data collected during biological surveys (events 1, 2, 3, 4, 10, 11, 13, 16; Table 3.1). Data from every sampling event were used to illustrate trends in CPUE of the species identified by multivariate analyses to have contributed to differences in assemblage structure among years.

Table 3.1. Summary of sampling events on Lake Liambezi from 2007 to 2014. Asterisks indicate data used in univariate analyses of relative abundance, species richness and diversity, and multivariate analyses of assemblage structure.

Event number	Year	Month	Gill net nights (n)
1*	2007	May/June	7
2*	2008	June	4
3*	2009	May	5
4*	2010	May	6
5	2010	August	11
6	2010	October	10
7	2010	November/December	8
8	2011	March	10
9	2011	April	6
10*	2011	May	8
11*	2012	May	6
12	2013	February	8
13*	2013	March	8
14	2013	October	5
15	2014	April	10
16*	2014	June	9
17	2014	August	8
18	2014	December	8

Relative abundance, species richness and diversity

Trends in relative abundance (N) and biomass (W), sample species richness (S), Shannon-Weiner diversity (H') and Pielou's evenness (J') were assessed by univariate statistical

analyses performed using the PRIMER package, version 6 with PERMANOVA add on software (Clarke and Gorley 2006; Anderson *et al.* 2008), as described in Chapter 2. Analyses were first performed on a Euclidean distance measure of untransformed data. Data were tested for homogeneity of variance using PERMDISP, and square root transformed if heterogeneous. PERMANOVA were then used to test for significant differences among years.

Assemblage structure

Fish assemblage structure was described by individual species gill net CPUE abundance and biomass data. Multivariate statistical analyses were performed using PRIMER with PERMANOVA as described in Chapter 2. Analyses were performed using Bray-Curtis dissimilarity matrices on fourth root transformed abundance and biomass data. Variation in assemblage structure among years was first visualised using nMDS plots. Multivariate PERMANOVAs were conducted to test for differences in assemblage structure among years. To ensure significant differences were due to location and not to differences in variability, PERMDISP was used to test for homogeneity of variance among years. Differences in assemblage structure among years were then examined using the CAP procedure (see Chapter 2). Species responsible for the observed differences between years were determined by examining the Pearson correlations of fourth root transformed species abundance and biomass data with the canonical axes of the CAP ordination. A correlation of $|r| > 0.5$ was used as an arbitrary cut-off to display species relationships with the canonical axes.

Results

Species composition, relative abundance and biomass

In total, 35 species were captured using gill nets between 2007 and 2014 (Table 3.2). Cichlidae was the most species rich family with 12 species, followed by Cyprinidae with 8 species, and Mormyridae and Alestidae with 4 species each. Gill net catches were dominated numerically by *Enteromius paludinosus* in 2007 and 2008, accounting for 65.0 and 88.0%, respectively. *Enteromius paludinosus* was dominant again in 2009, although the overall distribution of species abundance was more evenly spread and a total of 5 species accounted for 10.0% or more of the catches in 2009. *Rhabdalestes maunensis* was numerically dominant in 2010, accounting for 55.0% of the catch, followed by another alestid, *Brycinus lateralis*, that accounted for 33.0%. *Brycinus lateralis* (Figure 3.3) overwhelmingly dominated catches

from 2011 onwards, making up greater than 80.0% of the catches in all but 2012, when they accounted for 61.0%. *Schilbe intermedius* (Figure 3.3) was the most consistently abundant species, ranking among the top four species in every year.

Table 3.2. Gill net catch composition in Lake Liambezi expressed as percent number (%N) for the continuous period of inundation (2007–2014), and the life-history strategy of each species: O = opportunistic; P = periodic; E = Equilibrium.

Taxon	Strategy	2007	2008	2009	2010	2011	2012	2013	2014
Mormyridae									
<i>Marcusenius altisambesi</i>	P	0.8	-	13.5	0.6	0.6	1.1	0.5	0.1
<i>Mormyrus lacerda</i>	P	0.1	-	-	-	-	-	-	-
<i>Petrocephalus cf. okavangensis</i>	O	0.1	-	0.1	5.2	1.8	3.8	11.7	0.4
<i>Pollimyrus marianne</i>	O	< 0.1	-	0.2	-	-	-	-	-
Cyprinidae									
<i>Enteromius barnardi</i>	O	-	-	-	< 0.1	-	-	0.4	0.1
<i>Enteromius bifrenatus</i>	O	-	-	-	< 0.1	-	-	-	-
<i>Enteromius paludinosus</i>	O	65.2	88.4	22.0	0.7	< 0.1	0.1	-	-
<i>Enteromius poechii</i>	O	24.9	0.9	7.5	0.3	< 0.1	0.2	0.6	0.2
<i>Enteromius radiatus</i>	O	0.1	-	-	0.2	0.1	0.3	0.4	1.5
<i>Enteromius unitaeniatus</i>	O	< 0.1	-	-	< 0.1	-	-	-	0.1
<i>Labeo cylindricus</i>	O	-	-	-	< 0.1	< 0.1	0.1	-	-
<i>Labeo lunatus</i>	P	< 0.1	-	0.1	-	-	-	-	-
Alestidae									
<i>Brycinus lateralis</i>	O	< 0.1	5.6	14.0	33.3	81.0	81.3	60.7	84.5
<i>Hydrocynus vittatus</i>	P	-	-	0.3	0.1	-	-	-	-
<i>Micralestes acutidens</i>	O	-	-	1.5	-	-	-	-	-
<i>Rhabdalestes maunensis</i>	O	0.2	1.2	9.8	55.2	7.2	< 0.1	4.7	5.6
Hepsetidae									
<i>Hepsetus cuvieri</i>	E	< 0.1	-	0.2	0.1	0.2	0.1	0.8	0.5
Schilbeidae									
<i>Schilbe intermedius</i>	P	7.6	3.2	17.4	3.4	6.3	6.9	10.8	2.9
Clariidae									
<i>Clarias gariepinus</i>	P	0.4	0.3	0.2	< 0.1	-	-	< 0.1	0.1
<i>Clarias ngamensis</i>	P	0.1	-	0.1	< 0.1	-	-	< 0.1	-
<i>Clarias theodorae</i>	P	-	-	-	-	-	0.1	-	-
Mochokidae									
<i>Synodontis</i> spp.	P	0.1	0.1	-	0.2	2.1	2.7	1.5	2.0
Cichlidae									
<i>Oreochromis andersonii</i>	E	< 0.1	-	0.2	< 0.1	-	0.1	0.1	-
<i>Oreochromis macrochir</i>	E	-	-	-	-	-	-	0.1	< 0.1
<i>Pharyngochromis acuticeps</i>	E	-	-	-	-	0.2	2.3	1.6	1.6
<i>Pseudocrenilabrus philander</i>	E	< 0.1	0.4	2.6	0.3	< 0.1	-	0.1	-
<i>Sargochromis carlottae</i>	E	-	-	-	< 0.1	-	-	0.1	-
<i>Sargochromis</i> sp. “green bream”	E	-	-	0.1	< 0.1	-	-	0.3	0.1
<i>Serranochromis angusticeps</i>	E	-	-	-	-	-	-	< 0.1	-
<i>Serranochromis macrocephalus</i>	E	< 0.1	-	-	< 0.1	0.1	0.2	0.4	0.1
<i>Serranochromis robustus jallae</i>	E	-	-	-	-	-	-	< 0.1	-
<i>Coptodon rendalli</i>	E	< 0.1	-	0.2	< 0.1	-	-	0.1	-
<i>Tilapia sparrmanii</i>	E	0.3	-	10.0	0.4	0.2	0.8	5.1	0.2
<i>Tilapia ruweti</i>	E	< 0.1	-	0.2	-	-	-	-	-
Anabantidae									
<i>Ctenopoma multispine</i>	E	< 0.1	-	-	-	-	-	-	-
Total species		23	8	20	24	15	16	23	17



Figure 3.3. Dominant species in Lake Liambezi after filling. (a) *Brycinus lateralis* and (b) *Schilbe intermedius*.

Untransformed relative abundance data was heterogeneous, and was therefore square root transformed to ensure homogeneity of variance across years (PERMDISP, Table 3.3). Relative abundance and biomass differed significantly among years (PERMANOVA, Table 3.3). Temporal variation in CPUE across years was considerable, exhibiting an almost sinusoidal pattern (Figure 3.4). Relative abundance and biomass were very high in 2007, the year of inundation. There was a substantial decline in CPUE in 2008 as the water level receded, and a further decline in abundance when the lake refilled in 2009. The CPUE increased very rapidly to 2010, after which it again declined in 2011 and 2012. A significant rise in biomass was seen in 2013, which was again followed by a slight decline to 2014.

Table 3.3. PERMANOVA and PERMDISP results comparing Euclidean distance measures of square root transformed (to ensure homogeneity of variance) relative abundance and untransformed relative biomass from 2007–2014. Significant differences are in bold.

Source	df	PERMANOVA			PERMDISP	
		MS	Pseudo-F	P(perm)	F	P(perm)
Abundance	7	803.43	29.156	<0.001	1.502	0.300
Biomass	7	1.574E8	10.02	<0.001	2.550	0.113

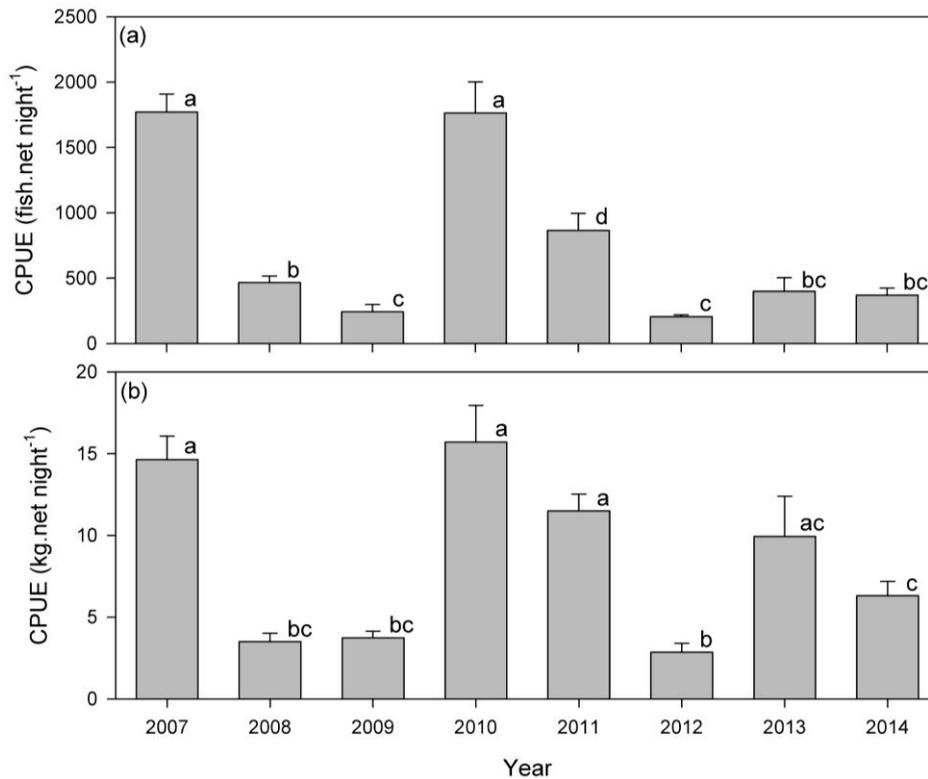


Figure 3.4. Gill net catch per unit effort (CPUE) in (a) numbers and (b) weight over the continuous period of inundation from 2007–2014. Letters denote pair-wise significant differences (PERMANOVA; $P < 0.05$).

Species richness and diversity

Species richness, abundance and diversity all differed significantly among years (PERMANOVA, Table 3.4). Species richness peaks were observed in 2007 after the first inundation, in 2010 after two consecutive years of flooding, and again in 2013 (Figure 3.5). Shannon-Weiner diversity and Pielou's evenness were both significantly higher in 2009, the year of refilling, than in any other year. A smaller peak in both diversity and evenness was observed in 2013.

Table 3.4. PERMANOVA and PERMDISP results comparing Euclidean distance measures of untransformed sample species richness (SR_s), Shannon-Wiener diversity (H') and Pielou's evenness (J') over the continuous period of inundation from 2007–2014. Significant differences are in bold.

Source	df	PERMANOVA			PERMDISP	
		MS	Pseudo-F	P(perm)	F	P(perm)
SR_s	7	46.227	9.219	< 0.001	2.298	0.093
H'	7	0.930	9.058	< 0.001	1.694	0.229
J'	7	0.148	10.539	< 0.001	2.718	0.054

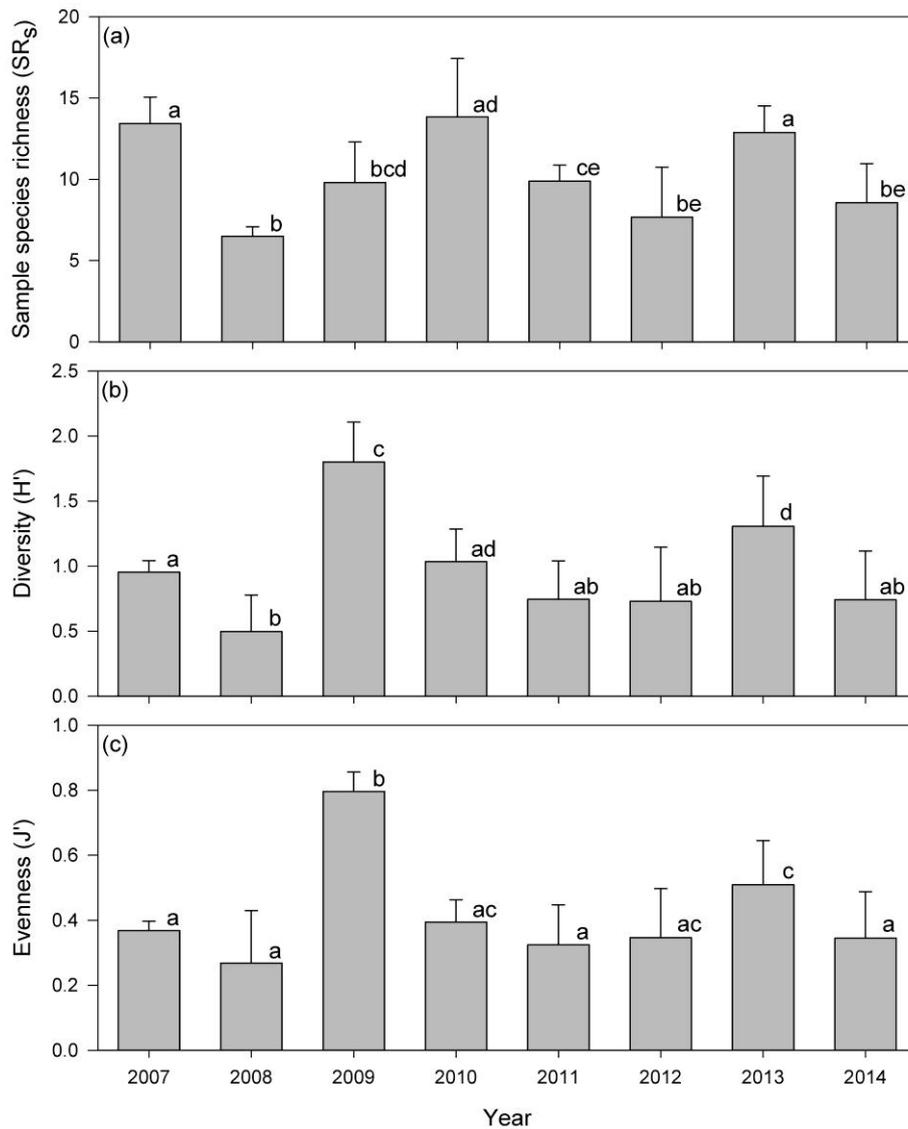


Figure 3.5. Variation in (a) sample species richness, (b) Shannon-Wiener diversity and (c) Pielou's evenness over the continuous period of inundation from 2007–2014. Letters denote pair-wise significant differences (PERMANOVA; $P < 0.05$).

Assemblage structure

Fish assemblage structure differed significantly among years in terms of both individual species abundance and biomass (PERMANOVA, Table 3.5). Post hoc pair-wise comparisons revealed significant differences between each year for abundance and biomass. However, both the abundance and biomass data were heterogeneously distributed among years (PERMDISP, Table 3.5), indicating that some of the observed differences may have been due to within-year dispersion. The CAP ordinations (Figure 3.6a, b), however, support the PERMANOVA results, showing that the fish assemblage structure differs significantly among years in terms of abundance ($\delta^2 = 0.968$; $P < 0.001$) and biomass ($\delta^2 = 0.960$; $P <$

0.001). The CAP procedure selected $m = 7$ PCO axes that accounted for 88.7%, and $m = 8$ PCO axes that accounted for 86.8% of the variation in the abundance and biomass Bray-Curtis dissimilarity matrices, respectively. The greatest changes in assemblage structure took place over the first four years after inundation (2007–2011), after which the fish assemblage structure appeared to stabilise. The leave-one-out allocation success was highest for 2007–2011, though 2012–2014 were still very distinct from each other (Table 3.6). Species contributing to the observed differences in assemblage structure, as given by their correlation with the canonical axes, are illustrated in Figure 3.6c, d.

Table 3.5. PERMANOVA and PERMDISP results on Bray-Curtis dissimilarities of fourth root transformed fish abundance and biomass data comparing fish assemblage structure over the continuous period of inundation from 2007–2014. Significant differences are in bold.

	Source	PERMANOVA				PERMDISP	
		<i>df</i>	MS	Pseudo-F	P(perm)	F	P(perm)
Abundance	Year	7	6701.6	13.886	<0.001	3.999	<0.05
	Residual	45	482.62				
	Total	52					
Biomass	Year	7	6229.7	10.927	<0.001	4.515	<0.05
	Residual	45	570.1				
	Total	52					

Table 3.6. Leave-one-out allocation success of abundance and biomass samples from the canonical analysis of principal coordinates (CAP) procedure.

	Original year	Classified year								Samples	% Correct
		07	08	09	10	11	12	13	14		
Abundance	07	7								7	100
	08		4							4	100
	09			4					1	5	80
	10				6					6	100
	11					8				8	100
	12					2	4			6	67
	13					2		6		8	75
	14						1		8	9	89
Biomass	07	7								7	100
	08		4							4	100
	09			4					1	5	80
	10				6					6	100
	11					7	1			8	88
	12					2	4			6	67
	13							8		8	100
	14					1	1	1	6	9	67

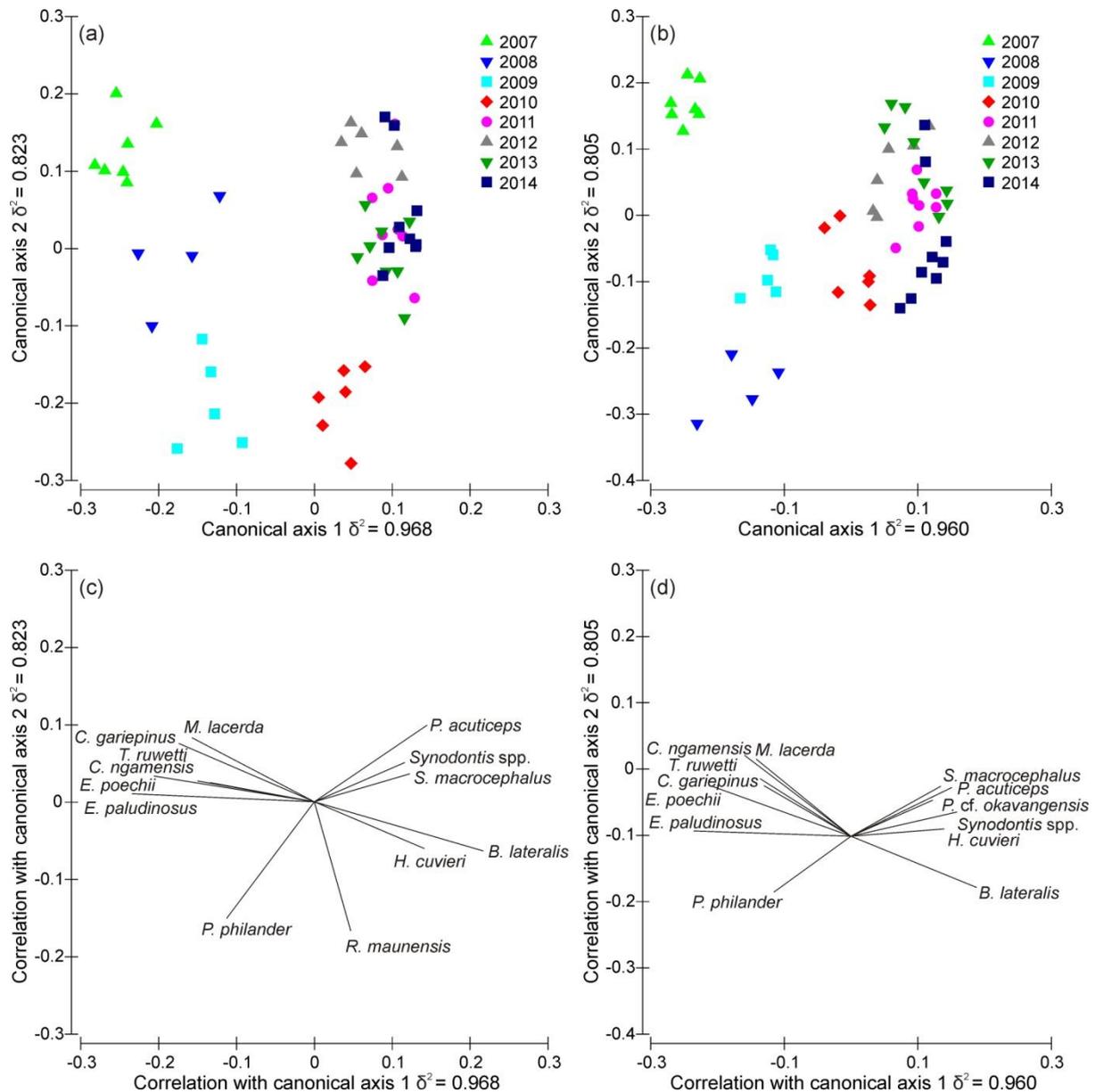


Figure 3.6. Canonical analysis of principal coordinates (CAP) ordination of fourth root transformed fish assemblage (a) abundance and (b) biomass data for the continuous period of inundation from 2007–2014, and vectors of species correlations (Pearson; $|r| > 0.5$) with the canonical axes for (c) abundance and (d) biomass data.

The CPUE of the twelve species contributing the most to the observed dissimilarity between years in abundance and biomass are illustrated in Figure 3.7. The fish assemblage in 2007 was primarily distinguished from subsequent years by the presence of four species, two cyprinids *E. paludinosus* and *Enteromius poechii*, and two clariids *C. gariepinus* and *Clarias ngamensis*. *Enteromius paludinosus* was exceptionally abundant in 2007, averaging 1155 ± 99 fish and 4.8 ± 0.5 kg.net night⁻¹. *Enteromius poechii* was much less abundant, but still a major component of the fish assemblage. Both species experienced a steep decline in

abundance in 2008, and *E. paludinosus* a further decline when the lake filled in 2009. *Enteromius paludinosus* disappeared from the assemblage after 2012, and while *E. poechii* persisted until 2014, it was very scarce. The two clariid species followed a similar initial pattern to the cyprinids, though at a lower magnitude. Both *C. gariepinus* and *C. ngamensis* increased in abundance again following flooding in 2009 and 2010, but did not reach the same abundance and biomass as observed in 2007. While both species continued to decline in abundance, the biomass of *C. gariepinus* remained somewhat stable up to 2014, owing to the few very large individuals remaining in the lake. The small cichlid *Pseudocrenilabrus philander* distinguishes 2009 from other years. *Pseudocrenilabrus philander* increased rapidly in abundance from 2008, peaked in 2009 at 6.4 ± 2.1 fish.net night⁻¹, then declined equally rapidly in 2010. Two small alestids rapidly rose to prominence after the lake refilled. First, *R. maunensis* increased from 24 ± 12 fish.net night⁻¹ in 2009 to 974 ± 187 fish.net night⁻¹ in 2010. This was again followed by an equally rapid decline within the same year as the slightly larger *B. lateralis* began to dominate. *Brycinus lateralis* was most abundant in 2010 and 2011, reaching 743 ± 82 fish.net night⁻¹, then declined to roughly half that, but remained the most abundant species in the assemblage up to 2014. *Serranochromis macrocephalus* and *Synodontis* spp. each peaked in abundance in 2011, then declined steadily while larger fish maintained their relative biomass. *Hepsetus cuvieri* followed a similar pattern, but peaked later, in 2013. *Pharyngochromis acuticeps* increased steadily in abundance from 2010 onward while maintaining a relatively stable biomass. The relative abundance of the mormyrid *Petrocephalus* cf. *okavangensis* was highest shortly after refilling in 2010 (91 ± 33 fish.net night⁻¹), declined rapidly to near zero in 2011, and then experienced a small resurgence in 2013 (47 ± 36 fish.net night⁻¹), helping to distinguish it from other years.

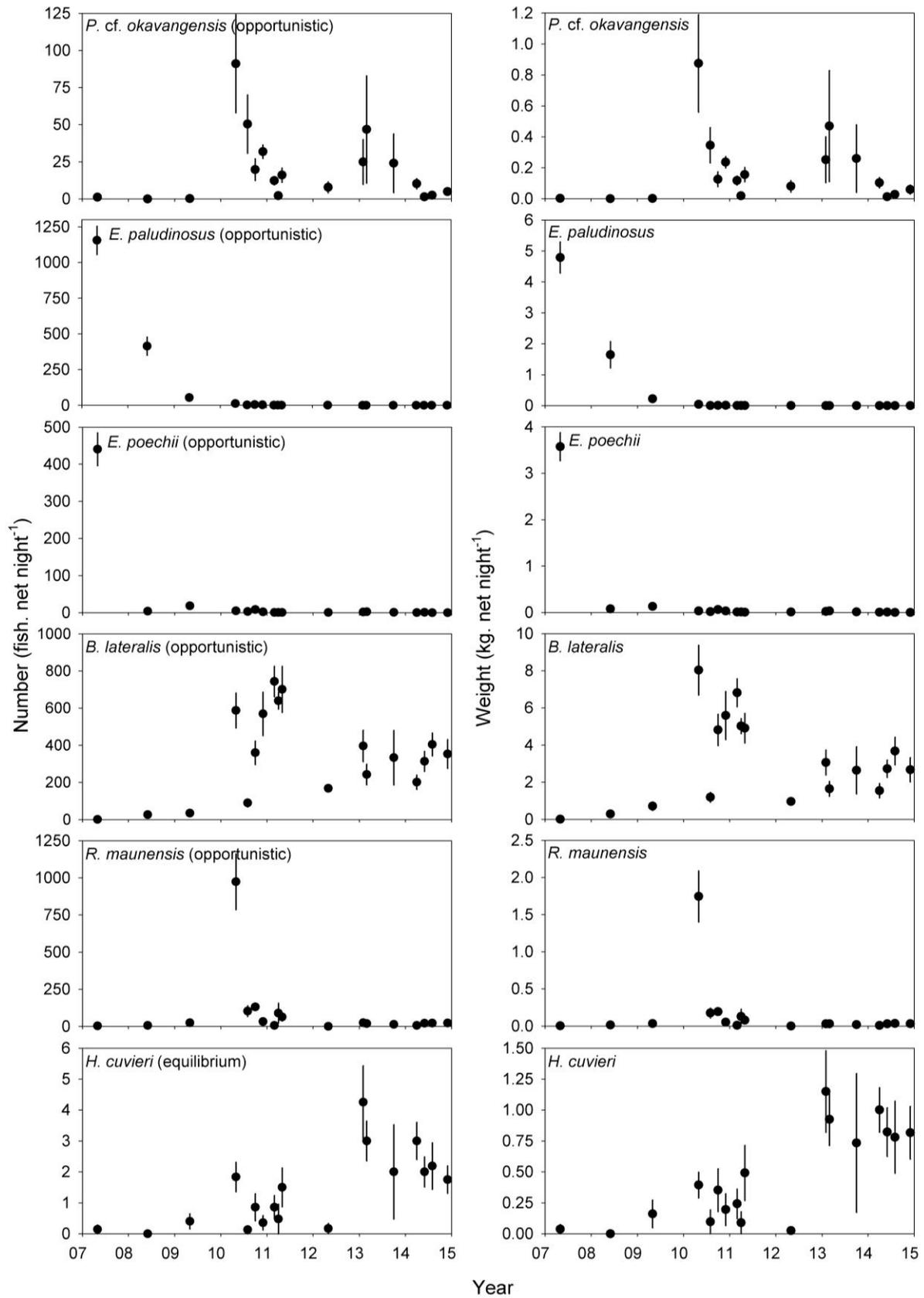


Figure 3.7. Trends in catch per unit effort (CPUE) in number (left column) and weight (right column) of twelve species identified as contributing to differences in assemblage structure among years. Data represent the mean \pm standard error.

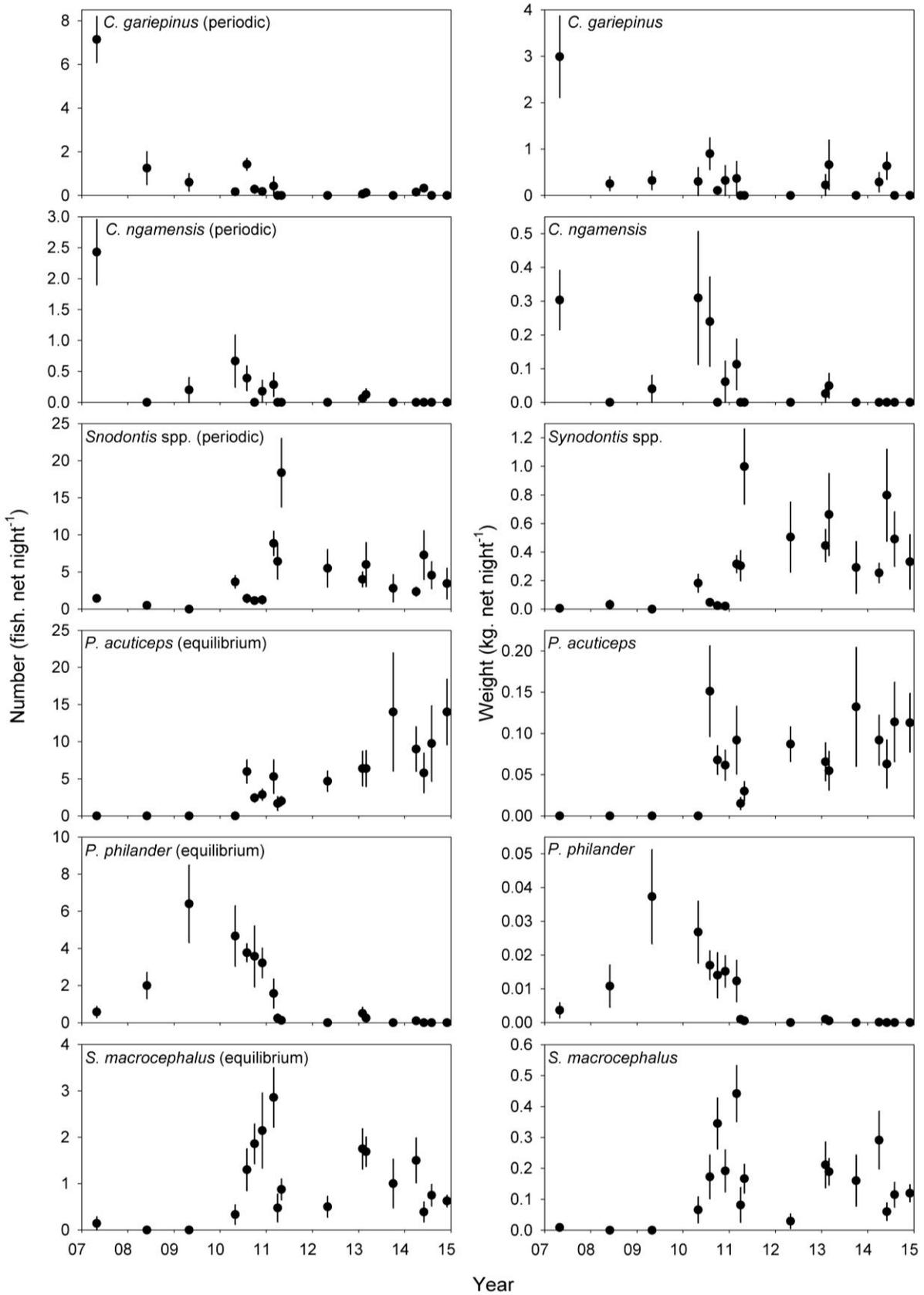


Figure 3.7. Continued.

Trends in the relative dominance of alternative life-history traits are illustrated in Figure 3.8. Opportunistic species dominated the fish community numerically throughout the study period, contributing the least in 2009 when the lake filled (Figure 3.8a). Opportunistic species dominated the colonising fish community in terms of biomass too (Figure 3.8b). They contributed less than periodic species when the lake filled in 2009, but underwent rapid population growth over the following year, accounting for nearly 70% of the biomass in 2010. Opportunistic species experienced a significant decline in biomass between 2010 and 2013, such that periodic strategists assumed the greatest contribution to gill net catches, but recovered once more in 2014. Equilibrium species contributed least to gill net catches almost throughout the study, succeeding opportunistic species in terms of biomass only very briefly in 2013. The gradual rise in importance of equilibrium species is, however, discernible.

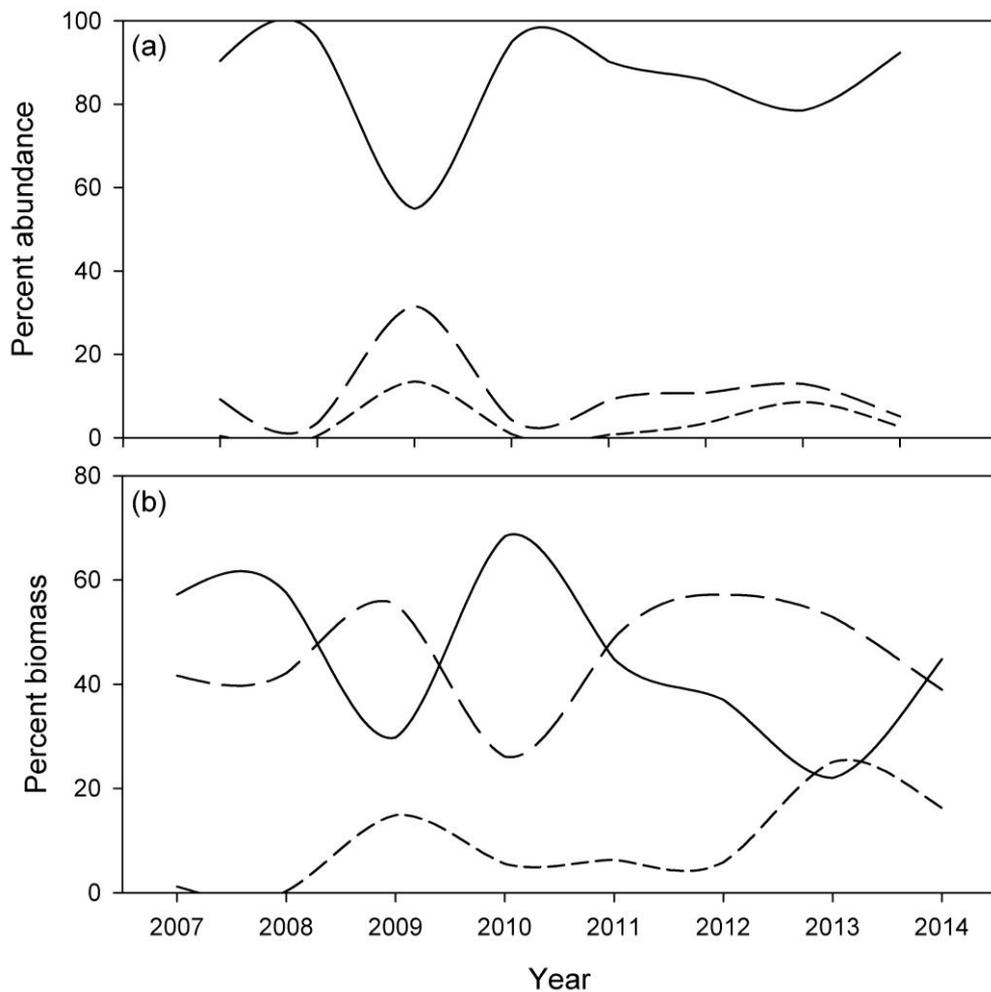


Figure 3.8. Trends in (a) relative abundance and (b) relative biomass in gill net catches of alternative life-history strategies in the fish community of Lake Liambezi over an eight year period of continuous inundation. Life-history strategies: Opportunistic (—); Periodic (— —); Equilibrium (— — —).

Discussion

The fish assemblage of Lake Liambezi underwent significant changes over the period of inundation (2007–2014), from a colonising assemblage dominated by floodplain specialists, to a lacustrine assemblage dominated by fishes that are adapted to more stable environments. The assemblage succession may have been driven by environmental filtering (species adaptations to the hydrological regime and hypoxia), dispersal from the inflowing floodplain rivers, biotic interactions (predation and competition) and human influences (fishing).

Colonising assemblage

The overall relative abundance of fish declined sharply in the year after inundation, despite fish being concentrated by a reduction in lake surface area, from approximately 65 km² in May 2007 to 10 km² in April 2008 (Mutelo 2013). Species richness and diversity also fell; fifteen species captured in 2007 were not recorded a year later. All of these were relatively uncommon though, each making up less than 1% of the total catch by number in 2007. Of the eight species that were recorded in 2007 and 2008, the majority decreased significantly in relative abundance. Increasingly harsh environmental conditions, predation and fishing pressure may all have contributed to the high levels of mortality, as observed in other shallow lakes (Furse *et al.* 1979; Skelton *et al.* 1982; Benech *et al.* 1983), while the lack of suitable spawning habitat and nursery areas for flood-dependent spawners may have resulted in the recruitment failure of these species (Bruton and Jackson 1983).

The dominant colonising cyprinids *E. paludinosus* and *E. poechei* in particular experienced major declines in Lake Liambezi. In Lake Chilwa, Malawi, mass mortalities of *E. paludinosus*, among other species, were recorded in October 1966 during a major lake recession (Furse *et al.* 1979). The cause was hypoxia; fine sediment with a high affinity for oxygen was stirred into suspension from the shallow lake bed by strong winds and wave action, resulting in oxygen depletion. Similar mass mortalities have been observed in Lake Chad (Benech *et al.* 1983). In 1973 the north basin of Lake Chad was isolated from the south, transforming it into a closed basin. When the water level dropped below a critical threshold of 2 metres in 1974, sediments from the lake bed could be lifted into suspension by strong winds, increasing turbidity and nutrient levels, and encouraging phytoplankton growth. Dense phytoplankton blooms caused nocturnal oxygen depletion by respiration, and resulted in

several mass mortalities (Benech *et al.* 1976). Although no direct observations of mass mortalities were made at Lake Liambezi in 2007, a similar scenario of oxygen depletion may have occurred as the lake gradually receded, and winds stirred up nutrient rich sediment and organic matter with a high affinity for oxygen from the lake bed (Seaman *et al.* 1978).

Conditions of aquatic hypoxia select for fishes that possess respiratory adaptations that allow them to cope with such conditions, as well as species with low oxygen requirements. In the north basin of Lake Chad, the air breathing *Polypterus senegalus* became increasingly important as the lake receded (Benech *et al.* 1983). Several *Oreochromis* spp. and mochokid catfishes also grew in importance despite considerable mass mortalities, as they were better able to resist oxygen depletion than many other species. In the south-eastern archipelago of Lake Chad, where oxygen depletion occurred as a result of the decomposition of recently flooded organic matter, *P. senegalus* was again important, as were several *Clarias* spp., and *Brevimyrus nigeri*, the only mormyrid documented to breath air (Benech and Lek 1981; Moritz and Linsenmair 2007). Merron (1988) sampled the fish fauna of Lake Liambezi in 1985, shortly before it dried the same year. The assemblage was dominated by larger fish species, including the air breathing *C. gariepinus*, and the cichlids *O. macrochir*, *O. andersonii*, *Serranochromis angusticeps* and *Coptodon rendalli*. *Clarias gariepinus* also dominated the fish communities of the ephemeral lakes Chilwa, Ngami and Mweru-Wantipa during drying phases (Furse *et al.* 1979; Skelton *et al.* 1982; Jackson 1989).

Large predators such as *C. gariepinus* have the potential to significantly influence assemblage structure. In the Okavango Delta, Botswana, *Clarias* undertake feeding migrations upriver in the dry season (Merron 1993). Their preferred prey items in the Okavango are the mormyrids *Marcusenius altisambesi* and *P. cf. okavangensis*, both of which occurred in Lake Liambezi in 2007. Intense predation by *C. gariepinus* may have contributed to the decline in abundance of the mormyrids as they were not caught in 2008. Visually oriented predators such as *S. macrocephalus* and *H. cuvieri* that prey primarily on small barbs and cichlids (Winemiller 1991; Winemiller and Kelso-Winemiller 1994) were scarce, and would have been negatively influenced by the likely high turbidity levels in 2008 (Rodríguez and Lewis 1997; Tejerina-Garro *et al.* 1998). In general though, the influence of predation by fishes on the fish assemblage structure in Lake Liambezi between 2007 and 2008 was probably low, as the fish community was dominated by small species, and the predator with the greatest potential to influence assemblage structure, *C. gariepinus*, declined

in abundance. The most likely cause of their decline was fishing pressure. Local fishers use baited longlines to target catfish, and large meshed gill nets and seine nets to target cichlids. Fishing mortality may have contributed significantly to the decline in abundance of species in these two groups as the lake receded and fish became increasingly concentrated and easier to catch.

The only species that increased appreciably in terms of relative abundance between 2007 and 2008 was *B. lateralis*, which was not harvested by the fishery. *Brycinus lateralis* may have been able to better withstand the low dissolved oxygen levels that are likely to have occurred by performing aquatic surface respiration, similar to some related neotropical characins (Winemiller 1989a). However, no information on the physiological tolerances or adaptive responses of *B. lateralis* to aquatic hypoxia is currently available.

Assemblage succession

When the lake filled in 2009 the fish assemblage did not revert back to a state similar to that in 2007, but continued to evolve. The cyprinids *E. paludinosus* and *E. poechii* that were so dominant during previous colonisation events (see Chapter 2) made up a much smaller portion of the catch in 2009. Five species, each from a different family, contributed greater than 10% to the catch numerically. These included *E. paludinosus*, *S. intermedius*, *B. lateralis*, *M. altisambesi* and *Tilapia sarrmanii*. Shannon-Wiener diversity and Pielou's evenness were significantly higher in 2009 because of the more even abundance distribution of individual taxa. The overall relative abundance of fishes was much lower than in 2007 and previous colonisation events (Chapter 2). This was likely due to differences in the extent of flooding; the lake covered only 65 km² in 2007 compared to 300 km² in 2009 (Mutelo 2013). The fishes that had managed to survive since inundation in 2007 would likely have had little influence on the assemblage structure after the lake filled. Many may even have emigrated from the lake, against the inflowing floodwaters, because of the high densities and unfavourable environmental conditions they had been subject to before flooding (Louca *et al.* 2009).

Differences in assemblage structure between 2009 and previous colonisation events were probably due to differences in the magnitude and duration of the flood in the Zambezi River. The flood in 2009 was much larger than in previous years, where the maximum lake area inundated never exceeded 65 km². The duration of inflow during the "low flood" years would

have been much shorter than in 2009. The dominant colonisers (*E. paludinosus*, *E. poechii*, *S. intermedius*, *M. altisambesi* and *C. gariepinus*) would have rushed into the lake during this short window of opportunity before the floodwaters ceased flowing into the lake. Other, less prolific colonisers with a lower dispersal ability would not have had a chance to migrate into the lake in significant numbers before the floods abated. In 2009, the dominant colonisers would have again rushed into the lake at the front of the advancing floodwaters, after which their numbers probably declined. As the floodwaters continued to flow into the lake, alestids, mormyrids and cichlids would have followed the early colonisers until they too had entered the lake in significant numbers and the floodwaters subsided.

Environmental conditions in the lake after filling were likely more stable compared to previous years due to higher inflows and more stable water levels, and several species were able to take advantage of this. Two small alestids in particular experienced explosive population growth, and came to dominate the fish assemblage in 2010. *Rhabdalestes maunensis* increased in abundance by 40 times between May 2009 and May 2010. Not far behind was the slightly larger *B. lateralis*, which increased by over 17 times in the same period. The short generation time and prolonged high reproductive effort of these small species—typical of opportunistic life history strategists (Winemiller and Rose 1992)—enabled them to quickly colonise the open waters of the lake shortly after *E. paludinosus* and *E. poechii* had declined. There is no evidence to suggest that the alestids were prevented from increasing earlier due to competition for food with the colonising cyprinids. The small mormyrid *P. cf. okavangensis* also increased significantly in abundance between 2009 and 2010. On account of the rapid population growth of these three species, overall CPUE in 2010 was very high and on a par with that in 2007. Species richness was also high as a result of repeated introductions of riverine fishes from the Zambezi and Chobe in 2009 and 2010. Shannon-Wiener diversity and Pielou's evenness were, however, lower than in 2009, primarily due to the dominance of the alestids.

The dominance of *R. maunensis* was brief; in just three months their numbers crashed to one tenth of what they were at their peak in May 2010. *Brycinus lateralis*, however, continued to increase in abundance, and came to dominate the fish community numerically in 2011. Larger, later-maturing equilibrium strategists including the predatory *S. macrocephalus* and *H. cuvieri*, also increased in abundance, though far more gradually than *B. lateralis*. The large tilapia cichlids *O. andersonii*, *O. macrochir* and *C. rendalli*, although poorly

represented in experimental gill net catches, also increased in abundance over 2010 and 2011, as is evidenced by the rapid development of the fishery that went on to yield approximately 2 700 tonnes in 2011/2012 (Peel *et al.* 2015b).

The migration of fishes into the lake from the Zambezi and Chobe floodplains during the 2010 and 2011 floods did not appear to significantly influence assemblage structure. The size of the established fish community in the lake may have far outweighed the number of immigrants from the floodplains, possibly accounting for the fact that the dispersing fishes had little impact on local selection processes (Vellend *et al.* 2014). *Schilbe intermedius* appeared to benefit most from the floods in 2010 and 2011 as their numbers peaked then, although this did not contribute significantly to differences in assemblage structure between years as they were always an important component of the fish community. Several small cyprinids were able to colonise the lake in 2010, but were unable to establish or persist, and had disappeared by 2011. *Enteromius paludinosus* continued to decline in abundance in 2010 and 2011 despite the chance of recruitment from the rivers during the floods. *Brycinus lateralis* and *R. maunensis* now dominated the open water niche that *E. paludinosus* occupied before the lake filled.

Assemblage maturity

Although assemblage structure differed significantly among years between 2011 and 2014, the most significant changes had already taken place. There was a general decline in the abundance of almost all species after 2011 as the water level dropped, and carrying capacity is likely to have fallen. The spike in species richness in 2013 was a result of unusually good catches in the larger gill net mesh sizes of several less common cichlid species. This occurred during a brief period of reduced commercial fishing effort due to a step up in law enforcement, and does not reflect an actual increase in diversity in the lake. The numerical rank abundance of the most important species was fairly consistent between 2011 and 2014, with *B. lateralis* most abundant, followed by *S. intermedius*, *P. cf. okavangensis*, *R. maunensis*, *Synodontis* spp. and *Pharyngochromis acuticeps*. Fluctuations in the relative abundance of these species, especially *P. cf. okavangensis* and *R. maunensis* will have contributed towards the dissimilarity in assemblage structure between years. Overall, the assemblage structure between 2011 and 2014 was very similar to that observed by van der Waal (1980) between 1973 and 1976, with one notable difference. *Brycinus lateralis* accounted for between 60 and 85% of the gill net catches in 2011–2014, averaging 413

fish.net night⁻¹. In the 1970s, *B. lateralis* averaged only 12.1 fish.50 m net night⁻¹ in the appropriate 25 mm gill net mesh size, comprising only 6.7% of the catch (van der Waal 1980). This may be due, in part, to the higher levels of predation by more abundant predatory fishes in the 1970s (van der Waal 1980), but may also be an indication that *B. lateralis* will decline in abundance over the coming years, even if the lake remains inundated.

In summary, the fish assemblage of Lake Liambezi underwent a succession, from a colonising assemblage dominated by floodplain specialists, to a relatively stable lacustrine assemblage. The succession did not follow the pattern predicted by Winemiller (1996b), where opportunistic strategists dominate the fish assemblage during colonisation, but are soon succeeded by periodic strategists, which are eventually succeeded by equilibrium strategists in the absence of further disturbances. Instead, the evolution of the fish community was characterised by three distinct phases. The first phase involved the inundation and colonisation of the lake in 2007, followed by its decline up until the floods that filled the lake in 2009. During this phase the lake was colonised by fishes from the Zambezi and Chobe floodplains that were composed predominantly of *E. paludinosus* and *E. poechnii*, *S. intermedius*, *M. altisambesi* and *C. garipepinus*, specialists at colonising newly flooded environments. Following inundation, the water level declined, concentrating fishes in an increasingly harsh environment that resulted in high mortality from both abiotic drivers and fishing. The filling of the lake in the March 2009 floods marked the beginning of the second, successional phase. The main coloniser *E. paludinosus* saw a significant decline in abundance, despite the possibility of external recruitment from the neighbouring floodplains. *Rhabdalestes maunensis* underwent explosive population growth between 2009 and 2010, but crashed equally rapidly the same year. *Brycinus lateralis* surpassed its smaller relative, and went on to dominate the fish community. This marked the beginning of the third phase, in 2011, as the fish community began to approach a more stable state. Larger, slower growing species increased steadily in abundance, highlighted by the development of the fishery, based primarily on large tilapiine cichlids. From 2011 to 2014 the fish community was dominated by *B. lateralis* and *S. intermedius*. The following chapter examines the life-history characteristics of eight common fish species in Lake Liambezi, and evaluates their establishment success against life-history theory in an effort to understand the drivers behind species successions.

CHAPTER 4

An evaluation of the life-history strategies and establishment success of eight common fish species in Lake Liambezi

Introduction

Life-history theory has become a useful tool in understanding the patterns and drivers of fish population dynamics in freshwater environments (King *et al.* 2003; Agostinho *et al.* 2004; Bailly *et al.* 2008; Zeug and Winemiller 2008b; Miyazono *et al.* 2010; Mims and Olden 2012, 2013). Based on observed patterns of life-history variation in fishes, Winemiller (1989) and Winemiller and Rose (1992) identified three life-history strategies (opportunistic, periodic and equilibrium) as endpoints of a triangular continuum resulting from trade-offs between generation time, fecundity and juvenile survivorship (Figure 4.1). Opportunistic strategists are generally small bodied, early maturing species, which produce numerous small clutches of eggs over an extended spawning season. They have a high intrinsic rate of population increase, enabling them to rapidly repopulate habitats following disturbances. As a result, they are typically associated with unstable environments that experience frequent and intense disturbances. Periodic strategists are typically characterised by a larger body size, delayed maturation, high fecundity, a short, often synchronous spawning season and low investment per offspring. Periodic strategists are well adapted to seasonal environments that experience predictable patterns of flooding and drawdown. Equilibrium strategists generally include small to medium bodied species with intermediate times to maturity, low batch fecundity, numerous spawning bouts per season, and high investment per offspring in the form of parental care. Equilibrium strategists are adapted to stable environments in which resources may be limiting and recruitment is density-dependent.

Lake Liambezi was colonised by at least 23 fish species, representing a diverse range of life-history traits, when it was partially inundated in 2007 (see Chapter 2). Most of these species declined significantly in abundance, or even disappeared from the fish community before the lake filled in 2009 (see Chapter 3). Twenty species were sampled in the lake after it filled in 2009, with five species, each from a different family, accounting for 10% or more of the gill net catches (see Chapter 3). These included *Enteromius paludinosus*, *Schilbe intermedius*, *Brycinus lateralis*, *Marcusenius altisambesi* and *Tilapia sparrmanii*. Over the following two

years the fish assemblage underwent significant changes that included a decline in the abundance of *E. paludinosus* and *M. altisambesi*, a rapid increase in the abundance of *B. lateralis*, and the development of a highly productive fishery for large tilapiine cichlids including *Oreochromis andersonii* and *Oreochromis macrochir* (Peel *et al.* 2015b). The fish assemblage began to stabilise in 2011 as a lacustrine fish assemblage emerged. From 2011 to 2014 the fish assemblage was dominated by *B. lateralis* and *S. intermedius*, while the large tilapiine cichlids continued to support a productive fishery.

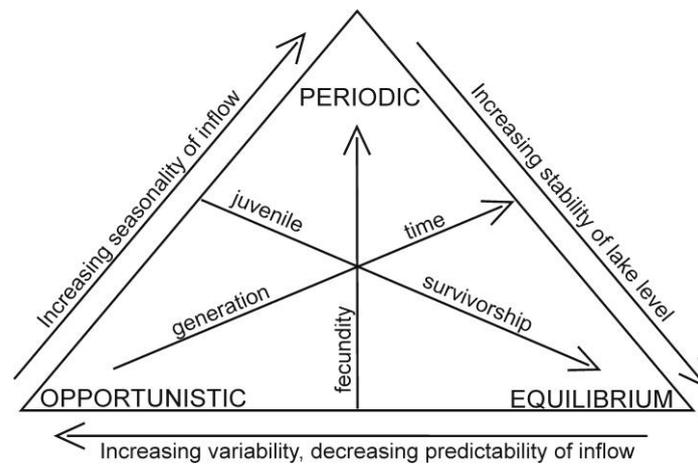


Figure 4.1. Life-history continuum model conceptualised by Winemiller and Rose (1992) summarising the fundamental trade-offs between generation time, fecundity and juvenile survivorship that define the endpoint strategies, and the predicted relationships between hydrological conditions and life-history strategies in Lake Liambezi (adapted from Winemiller 2005).

The aim of this chapter was to assess the life-history strategies of eight common fish species in Lake Liambezi, and evaluate their establishment success against life-history theory and the hypothesised response of fishes with divergent strategies to various hydrological conditions. It was hypothesised that 1) equilibrium strategists would be favoured by the relatively stable hydrological conditions that have prevailed in Lake Liambezi since it filled in 2009; 2) long lived periodic strategists may be able to persist for extended periods in the absence of regular flooding and suitable spawning conditions; and 3) opportunistic strategists would be poorly adapted to the stable hydrological conditions. To test these hypotheses, age and growth, reproductive seasonality and maturity were assessed for each species, and discussed in relation to the hydrological regime and development of the lacustrine fish community in Lake Liambezi (see Chapter 3).

Candidate species

The eight species chosen for detailed biological study represent important components of the lake's ichthyofauna (see Chapters 2 and 3 and Figure 4.2). These include *B. lateralis*, which has dominated the fish community since the lake refilled in 2009; *S. intermedius*, an important component of the fish community since inundation in 2007; *Clarias gariepinus*, a prominent coloniser and important fishery species; *Hepsetus cuvieri* and *Serranochromis macrocephalus*, which are among the most important predators in the lake, and three tilapiine cichlids, *O. andersonii*, *O. macrochir* and *Coptodon rendalli*, that together comprise 60% of the 2 700 t yr⁻¹ commercial gillnet fishery landings (Peel *et al.* 2015b). A short review of the distribution and biology of the eight species follows.

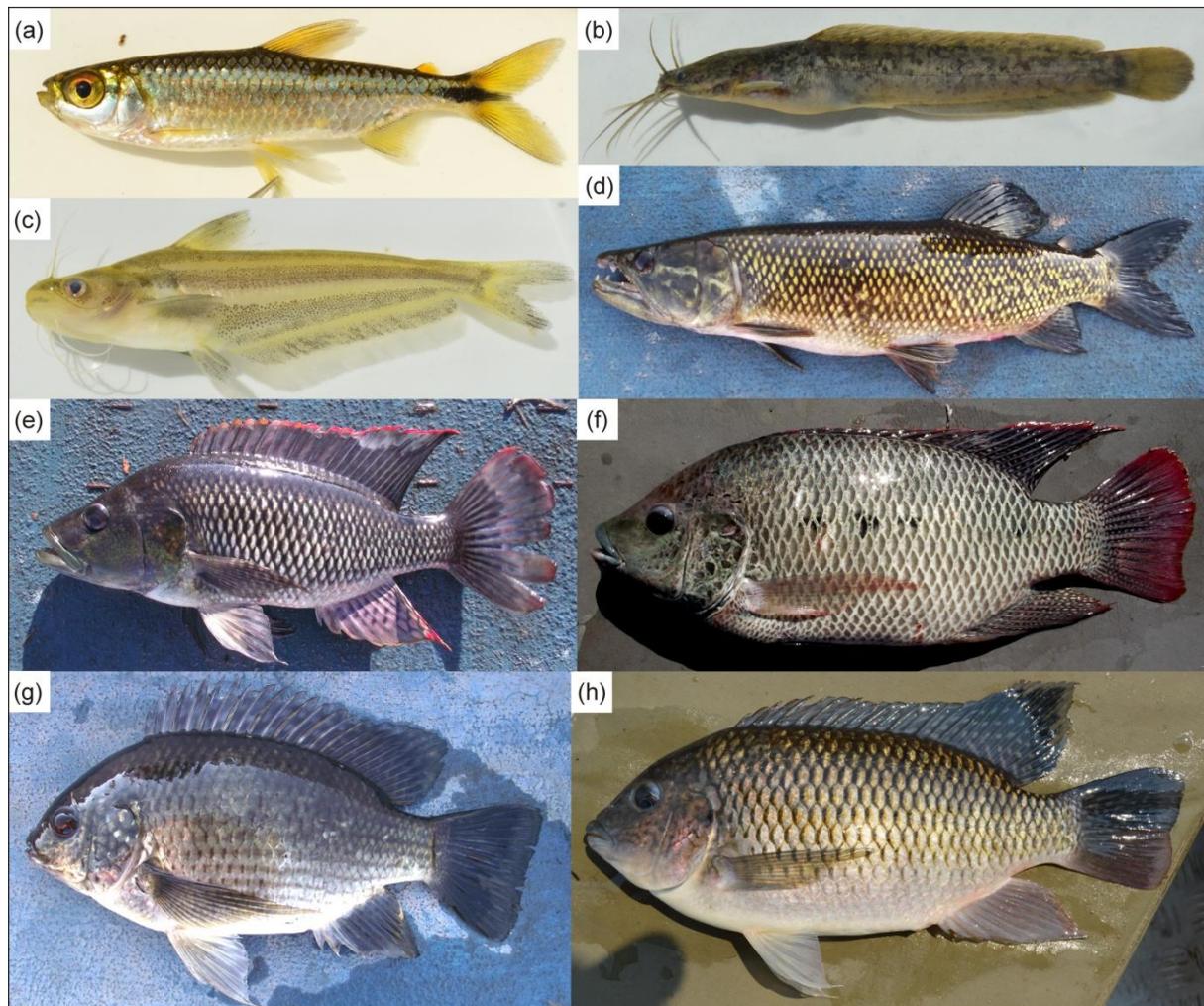


Figure 4.2. Eight common fish species in Lake Liambezi selected for detailed biological research because of their ecological and fishery importance. (a) *Brycinus lateralis*, (b) *Clarias gariepinus* (photo: D. Tweddle), (c) *Schilbe intermedius*, (d) *Hepsetus cuvieri*, (e) *Serranochromis macrocephalus*, (f) *Oreochromis andersonii*, (g) *Oreochromis macrochir*, (h) *Coptodon rendalli*.

Brycinus lateralis

Brycinus lateralis is a small alestid, widely distributed in the Upper and Middle Zambezi, Kavango, Kafue and Cunene rivers. It is also found in the upper reaches of the southern Congo drainage, including the Luapula, Lualaba and Kasai rivers, as well as the east coast Ruvuma, Buzi and St Lucia drainages (Skelton 2001). *Brycinus lateralis* shoals in well-vegetated, still or slow flowing waters such as eddies, backwaters and floodplain lagoons, where they feed on a wide variety of insects, crustaceans, small fish and plant material (Hay 1995; Booth and McKinlay 2001). The age and growth of *B. lateralis* has been investigated using scales by Balon (1971) and Hay (1995). *Brycinus lateralis* grow up to 140 mm FL, reaching 5 years of age in the Kavango River (Hay 1995). They mature at approximately 57 mm FL in the Okavango Delta (Booth and McKinlay 2001), and breed multiple times over a protracted summer spawning season that is independent of the hydrological regime (van der Waal 1985; Booth and McKinlay 2001). Females have a maximum batch fecundity of over 5 000 eggs (Hay 1995), which they lay on submerged aquatic vegetation (Balon 1971).

Clarias gariepinus

Clarias gariepinus is the most widely distributed fish in Africa, with a natural range extending from the Nile River in Egypt to the Orange River in South Africa (Skelton 2001). It is a large, hardy catfish, possessing an accessory air-breathing organ that allows it to tolerate harsh environmental conditions, and even desiccation (van der Waal 1998). It lives in a wide variety of habitats, but prefers backwaters and lagoons associated with large floodplain rivers (Willoughby and Tweddle 1978). *Clarias gariepinus* is a very adaptable predator, feeding on a wide variety of fish, crabs, insects, plant material and detritus (Willoughby and Tweddle 1978; Bruton 1979b; van der Waal 1985; Merron 1993; Winemiller and Kelso-Winemiller 1996). A large amount of research has been conducted on the life-history of *C. gariepinus*, owing to its wide distribution and importance to fisheries. *Clarias gariepinus* are capable of reaching over 1 500 mm (Bruton 1976) and living to 25 years of age (Wartenberg *et al.* 2013). They typically mature at between 300 and 400 mm TL and at 2 to 3 years of age (Willoughby and Tweddle 1978; Bruton 1979a; van der Waal 1985; Merron 1991; Richardson *et al.* 2009). *Clarias gariepinus* often undertake spawning migrations in response to rising floodwaters at the beginning of the summer rainy season (Holl 1968; Bruton 1979a; Clay 1979). The timing of spawning may vary in different localities, and between years in the same locality, as a result of variation in rainfall and flooding patterns (Holl 1968). Large females may lay over 150 000 eggs, which they scatter

onto newly flooded terrestrial grasses (Willoughby and Tweddle 1978; Bruton 1979a; Clay 1979).

Schilbe intermedius

Schilbe intermedius is a medium sized catfish, distributed from the Nile River to the Phongolo River in South Africa (Skelton 2001). It prefers well vegetated still or slow flowing waters, and feeds mostly on small fish, insects and crustaceans (van der Waal 1985; Merron and Mann 1995; Winemiller and Kelso-Winemiller 1996). The age and growth of *S. intermedius* has been investigated using otoliths in two impoundments in southern Africa by Hecht (1980) and Booth and Khumalo (2010), and using vertebrae and pectoral spines by Balon *et al.* (1974) in Lake Kariba and van der Waal (1985) in Lake Liambezi, respectively. *Schilbe intermedius* may reach 330 mm FL (van der Waal 1985) and live to 8 years of age (Booth and Khumalo 2010). They mature anywhere between 110 and 193 mm FL (Hecht 1980; van der Waal 1985; Hay 1995; Merron and Mann 1995; Booth and Khumalo 2010), at approximately 2 years of age (Hecht 1980; Booth and Khumalo 2010). They have a single, short summer spawning season during which fish migrate laterally onto shallow, newly inundated floodplains (Merron and Mann 1995). Females lay up to 100 000 eggs onto flooded vegetation (van der Waal 1985; Hay 1995; Merron and Mann 1995).

Hepsetus cuvieri

Hepsetus cuvieri is found in the west coast Quanza and Cunene rivers, the Upper Zambezi, Kavango and Kafue rivers, and the Luapula and upper Kasai tributaries of the Congo River (Zengeya *et al.* 2011). This species prefers still, well-vegetated backwaters, lagoons and floodplain habitats where it ambushes small fishes (van der Waal 1985; Merron 1991; Winemiller and Kelso-Winemiller 1994). The age and growth of *H. cuvieri* has been studied using scales by van der Waal (1985) in Lake Liambezi and Winemiller and Kelso-Winemiller (1994) in the Upper Zambezi River. *Hepsetus cuvieri* reach 470 mm FL and live to 5 years of age (van der Waal 1985). They mature at 160 mm FL in the Okavango Delta (Merron *et al.* 1990) and 270 mm FL in Lake Liambezi (van der Waal 1985). *Hepsetus cuvieri* breed multiple times over an extended summer spawning season, building foam nests among dense emergent vegetation which are guarded by both parents (Merron *et al.* 1990). Females have an average batch fecundity of approximately 2 600 eggs (Merron *et al.* 1990).

Serranochromis macrocephalus

Serranochromis macrocephalus is found in the Upper and Middle Zambezi, Kavango, Kafue and Cunene rivers, as well as the upper reaches of the Congo's southern tributaries (Skelton 2001). This species prefers backwater and floodplain lagoon habitats and feeds on a variety of fishes including mormyrids, cichlids, cyprinids and alestids (van der Waal 1985; Winemiller 1991). *Serranochromis macrocephalus* reach 425 mm TL in the Upper Zambezi (Winemiller 1991), and live to 8 years in Lake Liambezi (van der Waal 1985). Both sexes mature between 150 mm and 200 mm TL, corresponding to 2 years of age (van der Waal 1985; Winemiller 1991). *Serranochromis macrocephalus* are female mouth-brooders that breed multiple times over an extended summer spawning season (van der Waal 1985). Females have a maximum batch fecundity of approximately 800 eggs (Winemiller 1991).

Oreochromis andersonii

Oreochromis andersonii is a large tilapiine cichlid found in the Upper Zambezi, Kavango, Kafue and Cunene rivers (Skelton 2001). It prefers still backwaters and floodplain lagoons, though larger individuals often inhabit slow flowing areas of large river channels (Winemiller and Kelso-Winemiller 2003). *Oreochromis andersonii* feed primarily on vegetative detritus and algae, but also consume crustaceans and insect larvae (van der Waal 1985; Winemiller and Kelso-Winemiller 2003). *Oreochromis andersonii* have been aged using scales by van der Waal (1985), Dudley (1974, 1979) and Kapetsky (1974), and otoliths by Booth *et al.* (1995) and Peel *et al.* (In review, Appendix 1). *Oreochromis andersonii* can reach 530 mm and 14 years of age, and mature at approximately 250 mm TL and 1–2 years of age (Peel *et al.* In review). *Oreochromis andersonii* breed multiple times over an extended summer spawning season (Dudley 1974; van der Waal 1985; Merron 1991). Males build saucer shaped nests on sandy substrates in which spawning takes place (van der Waal 1985; Merron 1991) Females then mouth-brood up to 3 500 eggs and larvae for a month (Merron 1991).

Oreochromis macrochir

Oreochromis macrochir is distributed throughout the Upper Zambezi, Kavango, Kafue and Cunene rivers, as well as the Upper Kasai River, Chambeshi River and Lake Bangweulu (Skelton 2001). It favours still backwater and floodplain lagoon habitats and feeds on detritus and algae (van der Waal 1985; Winemiller and Kelso-Winemiller 2003). *Oreochromis macrochir* has been aged using both scales and otoliths in conjunction with *O. andersonii*. *Oreochromis macrochir* grow up to 440 mm TL, can reach 15 years of age, and mature at

between 200 and 250 mm TL, corresponding to 1–3 years of age (Peel *et al.* In review). They breed multiple times over an extended summer spawning season (Dudley 1974; van der Waal 1985). Males build nests similar to those of *O. andersonii*, and females mouth-brood up to 1 000 eggs and larvae (van der Waal 1985).

Coptodon rendalli

Coptodon rendalli is widely distributed in southern Africa, from the west coast Quanza and Cunene, across to the Zambezi River and southern tributaries of the Congo, lakes Tanganyika and Malawi, and east coast rivers south to the Phongolo (Skelton 2001). They inhabit a wide variety of habitats including backwaters, lagoons and the margins of large river channels, feeding primarily on aquatic macrophytes (van der Waal 1985; Winemiller and Kelso-Winemiller 2003). *Coptodon rendalli* have been aged using scales (Balon *et al.* 1974; Dudley 1974; Kapetsky 1974; van der Waal 1985) and otoliths (Weyl and Hecht 1998; Peel *et al.* In review). *Coptodon rendalli* grow up to 390 mm TL and 16 years of age (Weyl and Hecht 1998; Peel *et al.* In review). They generally mature at 200–220 mm TL which corresponds to between 1 and 4 years of age depending upon growth rates (Peel *et al.* In review). Breeding pairs clear vegetation and excavate nests with tunnel-like brood chambers (van der Waal 1985), and up to 6 000 eggs are deposited into the brood chambers and guarded by both parents (Kenmuir 1973; Batchelor 1978; van der Waal 1985).

Materials and methods

Data collection

Two biological research programmes have been carried out on Lake Liambezi since its refilling. The first took place between August 2010 and September 2011, and focused on three tilapia cichlid species, *O. andersonii*, *O. macrochir* and *C. rendalli*, and formed part of my MSc thesis (Peel 2012). This information has been included in this chapter as it contributes significantly towards understanding the life-history strategies employed by different species in Lake Liambezi. Supplementary data on the three tilapia cichlid species, as well as on *S. macrocephalus*, also sampled during the first research programme, were collected during a second programme that extended from February 2013 to December 2014. Four additional species, *B. lateralis*, *C. gariepinus*, *S. intermedius* and *H. cuvieri*, representative of other life-history strategies, were also sampled in the second programme.

A total of 13 field surveys were carried out, six during the first programme, and seven during the second. Biological samples were collected in each survey using experimental multifilament gillnets (described in Chapter 2), and monofilament gillnets, and fish were additionally purchased from local fishermen. *Clarias gariepinus* were also targeted using baited 80 m longlines rigged with 20 evenly spaced 9/0 circle hooks on one metre snoods. Fish were measured to the nearest mm fork length (FL) (*B. lateralis*, *S. intermedius* and *H. cuvieri*) or total length (TL) (*C. gariepinus*, *S. macrocephalus*, *O. andersonii*, *O. macrochir* and *C. rendalli*) depending on species morphology, and weighed to the nearest gram. Fish were then dissected to determine sex and the gonads were visually assigned one of five stages of maturity (1 = juvenile, 2 = resting, 3 = developing, 4 = ripe, 5 = spent) according to criteria developed by Nikolsky (1963) that have been refined for *C. gariepinus* by Clay (1979) and for *C. rendalli* and other cichlids by Weyl and Hecht (1998). Otoliths were then removed and stored for ageing.

Otolith preparation and interpretation

Brycinus lateralis and *H. cuvieri* were aged using asteriscus otoliths that were read whole, immersed in methyl-salicylate, and viewed under transmitted white light at 40 × and 20×magnification, respectively. *Clarias gariepinus*, *S. intermedius*, *S. macrocephalus*, *O. andersonii*, *O. macrochir* and *C. rendalli* were aged using sagittal otoliths that were set in clear polyester resin, and sectioned transversely through the nucleus using a double-bladed diamond-edged saw at a thickness of 0.3 mm for the catfishes, and 0.4 mm for the cichlids. Sections were mounted on slides using DPX mounting agent, and viewed under transmitted white light at 20 × magnification.

For all species, the number of growth zones—visible as alternating hyaline and opaque bands—was determined by counting the number of opaque zones from the nucleus to the margin of the otolith (Figure 4.3). All otoliths were read twice by independent readers, without prior knowledge of the date of capture or the length of the fish. If the two readings were the same, the count was accepted. If the readings differed, a third was taken by the primary reader, and if two readings were the same the count was accepted. If the three counts differed at most by two growth zones (e.g. 2, 3, 4), the median estimate was accepted, otherwise the otolith was considered unreadable and excluded from the analysis (Campana 2001). As a single growth zone is deposited annually in the otoliths of all eight species in the

study region (Bokhutlo *et al.* 2015; Peel *et al.* 2016; Taylor *et al.* 2016) growth zones were considered annuli and were used to estimate the age of fish.

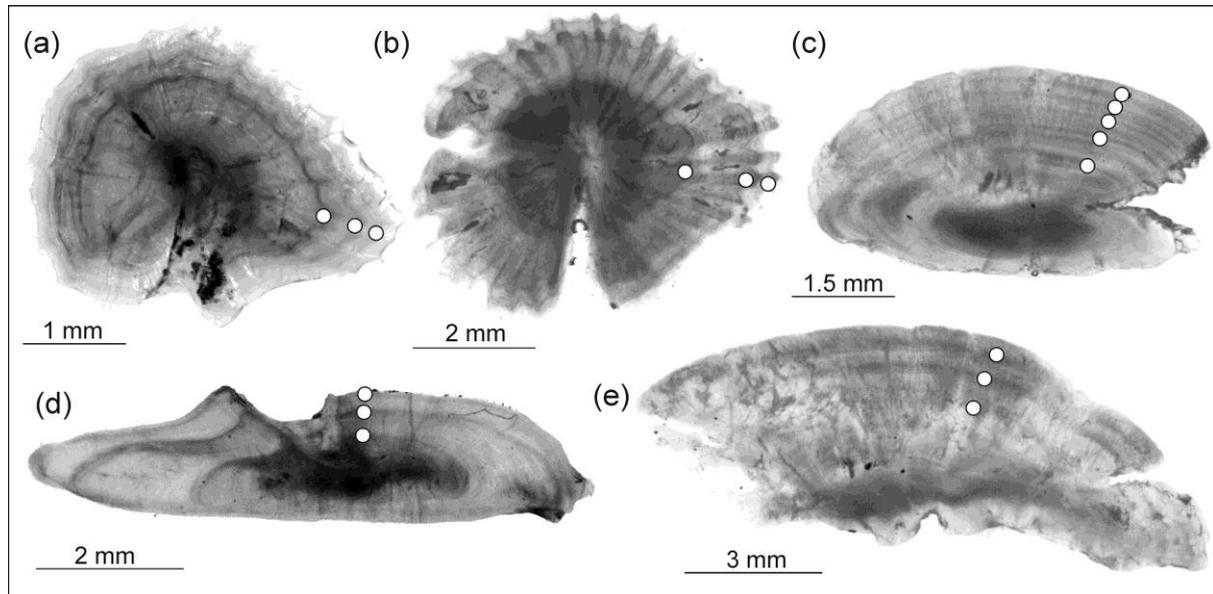


Figure 4.3. Photomicrographs showing annuli (marked by white dots) on whole asteriscus otoliths of (a) *Brycinus lateralis* and (b) *Hepsetus cuvieri*, and sectioned sagittal otoliths of (c) *Schilbe intermedius*, (d) *Serranochromis macrocephalus* and (e) *Clarias gariepinus*, read under transmitted white light.

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

$$APE_j = \frac{1}{R} \sum_{i=1}^R \frac{(X_{ij} - X_j)}{X_j} \times 100,$$

where R is the number of times fish j has been aged, X_{ij} is the i th age determination of the j th fish and X_j is the mean age estimate of the j th fish. APE was averaged across all fish to give an index of average percent error. The CV between age estimates was calculated as:

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

and was also averaged across all fish to give an average CV.

Growth

Age adjustment was carried out to avoid false year class identification and improve the accuracy of observed growth zone counts (Ballagh *et al.* 2011; Winker *et al.* 2011). Monthly age estimates were adjusted according to the month of capture, the month of birth (taken as the median month of the spawning season for those species with an extended season), and the month of annulus deposition on the otolith edge, summarised for each species in Table 4.1.

For fish aged < 1 year caught between the birth date and annulus deposition date, the number of months between birth and capture were added, i.e. a fish born in December and caught in June was 0.5 years. For fish aged < 1 year caught between the annulus deposition date and birth date, the number of months between annuli deposition and capture were added, i.e. a fish born in December and caught in November with annulus deposition in October was 0.08 years.

For fish aged ≥ 1 year with a translucent otolith margin caught between the birth date and annulus deposition date, the number of months between birth and capture were added as before. For fish with an opaque otolith margin caught between the birth date and annulus deposition date, the number of months between capture and birth were subtracted, i.e. a fish with two annuli born in December and caught in September with annulus deposition in October was 1.75 years. For fish caught between the annulus deposition date and birth date, the number of months between capture and birth was subtracted regardless of the state of the otolith edge. No adjustment was made for fish caught during the month of birth.

Table 4.1. The assigned month of birth (from Figure 4.5) and month of annuli deposition (Bokhutlo *et al.* 2015; Peel *et al.* 2016; Taylor *et al.* 2016) used for age adjustment for eight fish species from Lake Liambezi.

Species	Month of birth	Month of annuli deposition
<i>Brycinus lateralis</i>	January	September
<i>Schilbe intermedius</i>	March	October
<i>Clarias gariepinus</i>	March	October
<i>Hepsetus cuvieri</i>	January	October
<i>Serranochromis macrocephalus</i>	December	November
<i>Oreochromis andersonii</i>	December	November
<i>Oreochromis macrochir</i>	December	November
<i>Coptodon rendalli</i>	December	November

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

$$L_t = L_\infty (1 - e^{-K(t-t_0)}),$$

where L_∞ is the predicted asymptotic length, K is the Brody growth coefficient, and t_0 is the theoretical age at zero length (Ricker, 1975). Model parameters were estimated by minimising the negated normal log-likelihood function of the form:

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

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

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

where L_i is the observed length at age, \hat{L}_i is the predicted length-at-age and n is the total number of observations. Parameter variability was estimated using parametric bootstrap resampling (Efron 1981) with 1000 iterations. The percentile method (Buckland 1984) was used to estimate 95% confidence intervals from the resulting bootstrap vectors. Likelihood ratio tests (LRT) were used to test the null hypothesis that growth was equal between sexes with a significance level of $P \leq 0.05$. The growth performance index (Pauly and Munro 1984) was calculated as:

$$\phi' = 2 \log L_\infty + \log K,$$

where L_∞ is the predicted asymptotic length in cm and K the Brody growth coefficient. All calculations were performed in Microsoft Excel.

Reproduction and maturity

Temporal patterns in reproductive seasonality were assessed by plotting the proportion of fish of a given reproductive stage per sampling month. Samples collected during the peak

spawning season of each species were used to determine the mean length (Lm_{50}) and age (tm_{50}) at 50% maturity. Fish were considered mature if they had gonads in the developing, ripe or spent stages. Length-at-maturity was expressed as the proportion of mature fish per size class (L). Lm_{50} was estimated by fitting these data to a two-parameter logistic model of the form:

$$P_L = (1 + e^{-(L-Lm_{50})/\delta_L})^{-1},$$

where P_L is the predicted proportion of mature fish in length class L and δ_L is the steepness parameter of the logistic ogive. Model parameters were estimated by minimising the negated binomial log-likelihood function:

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

where \hat{P}_i is the expected proportion of mature fish in length class i , n_i is the number of individuals and m_i is the number of those individuals that are mature. The null hypothesis that Lm_{50} was equal between sexes was tested using a likelihood ratio test with a significance level of $P \leq 0.05$.

Age-at-50% maturity was calculated from length-at-maturity by reformulating the von Bertalanffy growth equation according to Booth and Weyl (2004) and Winker *et al.* (2012):

$$tm_{50} = t_0 - \frac{1}{K} \ln\left(1 - \frac{Lm_{50}}{L_\infty}\right)$$

The steepness parameter of the logistic ogive for age t , δ_t , was then calculated according to Winker *et al.* (2012) as:

$$\delta_t = \frac{1}{2K \ln(3)} \ln\left(\frac{L_\infty - Lm_{50}}{L_\infty - Lm_{50} - \delta_L \ln(3)}\right)$$

The parameters tm_{50} and δ_t were then used to calculate the proportion of mature fish per age class using the same logistic model used to calculate the proportion of mature fish per size class. All calculations were performed in Microsoft Excel.

Life-history strategies

A principal coordinates (PC) analysis was performed using the PRIMER package, version 6, to validate which of the three endpoint strategies of the Winemiller and Rose (1992) life-history model each study species represented. The analysis was performed on the following seven life-history characteristics: 1) L_{∞} , derived from the female von Bertalanffy growth models; 2) ϕ' , derived from female von Bertalanffy growth models; 3) Lm_{50} , derived from sex-aggregated logistic ogive; 4) duration of spawning season (in months), derived from analysis of reproductive seasonality; 5) relative fecundity of mature female fish caught during the spawning season (relationships between fecundity and length or weight were derived from the literature (Table 4.2)); 6) parental care, from literature; 7) flood dependence for spawning; from literature. Fecundity, Lm_{50} and L_{∞} were log transformed to help achieve multivariate normality. The data were then normalised because each variable was measured using different units (e.g. mm, counts and years). The input data are presented in Table 4.3.

Table 4.2. The relationships between fecundity (F) and length (L) or weight (W) for the eight study species, and the source of the relationship or the source of data used to predict the relationship.

Species	Relationship	Source
<i>B. lateralis</i>	$F=172W(g)^{1.005}$	Hay (1995)
<i>C. gariepinus</i>	$F=0.04L(cm)^{3.39}$	Clay (1979)
<i>S. intermedius</i>	$F=2.56L(cm)^{2.845}$	Merron and Mann (1995)
<i>H. cuvieri</i>	$F=4.074L(mm)^{1.087}$	Merron <i>et al.</i> (1990)
<i>S. macrocephalus</i>	$F=0.001L(mm)^{2.402}$	Winemiller (1991)
<i>O. andersonii</i>	$F=0.001L(mm)^{2.496}$	Merron (1991)
<i>O. macrochir</i>	$F=3.138L(mm)^{0.908}$	van der Waal (1985)
<i>C. rendalli</i>	$F=5.6105L(mm)^{1.279}$	Batchelor (1978)

Table 4.3. Input data for the principal coordinates (PC) analysis used to validate which endpoint strategy of the Winemiller and Rose (1992) model each study species represented. L_{∞} = female predicted asymptotic length; ϕ' = female growth performance; Lm_{50} = mean length-at-50% maturity; SS = length of the spawning season; PC = parental care; FD = flood dependence (1 = yes, 0 = no).

Species	L_{∞}	ϕ'	Lm_{50}	SS (months)	Fecundity	PC	FD
<i>B. lateralis</i>	117	1.85	63	5	1 883	0	0
<i>C. gariepinus</i>	1012	3.68	452	1	157 606	0	1
<i>S. intermedius</i>	260	2.6	159	1	17 073	0	1
<i>H. cuvieri</i>	379	3.11	316	4	2 298	1	0
<i>S. macrocephalus</i>	244	2.87	193	8	481	1	0
<i>O. andersonii</i>	268	2.91	254	6	957	1	0
<i>O. macrochir</i>	254	2.84	221	6	438	1	0
<i>C. rendalli</i>	244	2.98	212	6	5 973	1	0

Results

Ageing precision

Precision between otolith age estimates (Table 4.4) was high for *B. lateralis* and *H. cuvieri* aged, for the first time, using whole asteriscus otoliths. No otoliths were rejected for either species. Of the eight study species, *C. gariepinus* had the greatest proportion of otoliths rejected (8.33%), and displayed relatively poor precision, with a particularly high CV (23%) indicating greater absolute deviation from the mean age. Precision was high for *S. intermedius*, though six (1.75%) otoliths were rejected as unreadable. Precision estimates for the four cichlid species were variable; *C. rendalli* and *O. macrochir* displayed relatively good precision, while that of *S. macrocephalus* and *O. andersonii* was poor. Despite this, no otoliths were rejected for either *S. macrocephalus* or *O. andersonii*. Greater error for these two species was associated with difficulty in interpreting the first annulus in younger fish (< 2 years old).

Table 4.4. Average percent error (APE) and coefficient of variation (CV) of otolith growth zone counts, and the number of otoliths rejected as unreadable for eight fish species from Lake Liambezi.

Species	APE	CV	Sample size (<i>n</i>)	Rejected (<i>n</i>)
<i>Brycinus lateralis</i>	2.30	4.97	334	0
<i>Clarias gariepinus</i>	8.49	23.00	96	8
<i>Schilbe intermedius</i>	4.15	8.45	343	6
<i>Hepsetus cuvieri</i>	6.83	13.23	176	0
<i>Serranochromis macrocephalus</i>	11.54	21.44	199	0
<i>Oreochromis andersonii</i>	13.81	15.73	398	0
<i>Oreochromis macrochir</i>	7.98	10.57	270	0
<i>Coptodon rendalli</i>	5.88	7.18	291	0

Growth

Von Bertalanffy growth curves fitted to sex-aggregated observed length-at-age data for the eight study species are presented in Figure 4.4. The maximum ages reached by *B. lateralis* were 5+ years for males and 6+ years for females. The largest male and female fish sampled were 115 and 131 mm FL, respectively. Growth curves differed significantly between males and females (LRT, $P < 0.01$), with males having a greater predicted L_{∞} and females a faster growth rate (K). The growth performance index ϕ' was 1.85 for females and 1.66 for males.

The oldest *Clarias gariepinus* sampled was 15+ years. In total, nine fish aged > 10 years were sampled. These fish were, however, excluded from the analysis because they were born before the lake was inundated in 2007, and would have immigrated into the lake as adult fish from the Zambezi, Chobe or Kwando rivers. Excluding these fish, the oldest male and female *C. gariepinus* sampled were 6+ years. The largest male and female fish sampled were 1180 and 1125 mm TL, respectively. Because no small *C. gariepinus* (< 400 mm TL) were sampled, the von Bertalanffy growth model had to be reduced to two parameters to enable modelling, by setting t_0 to zero. Growth rates were highly variable for both sexes. Male and female growth parameters differed significantly (LRT, $P < 0.05$), with males having a slightly faster growth rate (K) and a greater predicted L_{∞} . The growth performance index ϕ' was 3.79 for males and 3.68 for females.

Schilbe intermedius reached maximum ages of 4+ years for males and 5+ years for females. The largest male and female fish sampled were 231 and 273 mm FL, respectively. Growth rates were highly variable for both sexes. Large 95% confidence intervals around t_0 are a result of a lack of small fish in the sample. Growth curves differed significantly between sexes (LRT, $P < 0.001$), with female fish having a greater predicted L_{∞} . The growth performance index ϕ' , 2.60 for females and 2.56 for males, was similar.

Hepsetus cuvieri reached maximum ages of 4+ years for males and 3+ years for females. The largest male and female fish sampled were 365 and 436 mm FL, respectively. Initial growth rates were very rapid, with fish reaching L_{∞} before two years of age. Growth parameters differed significantly between males and females (LRT, $P < 0.001$), with females reaching a

greater L_{∞} . The growth performance index ϕ' was higher for females (3.11) than for males (3.07).

Male and female *S. macrocephalus* reached maximum ages of 4+ years. The largest male and female fish sampled were 302 and 280 mm TL, respectively. Both sexes grew rapidly, attaining L_{∞} before 2 years. Growth did not differ significantly between males and females (LRT, $P = 0.18$). The growth performance index ϕ' was 2.87 for females and 2.83 for males.

Male *O. andersonii* reached a maximum age of 5+ years, and females 4+ years. The largest male and female fish sampled were 410 and 320 mm TL, respectively. Growth curves differed significantly between sexes (LRT, $P < 0.001$). Females attained a much smaller L_{∞} at an early age, while male fish continued to grow rapidly up to their maximum observed size and age, but did not attain their predicted L_{∞} . The growth performance index ϕ' was higher for females (2.91) than for males (2.74).

Oreochromis macrochir reached maximum ages of 4+ years for males and 3+ years for females. The largest male and female fish sampled were 315 and 295 mm TL, respectively. Growth curves differed significantly between sexes (LRT, $P < 0.001$), with males reaching a greater predicted L_{∞} . The growth performance index ϕ' was, however, identical (2.84).

Male *C. rendalli* reached 3+ years of age, and females 4+ years. The largest male and female fish sampled were 350 and 300 mm TL, respectively. Growth curves differed significantly between sexes (LRT, $P < 0.001$), with males having a slightly faster growth rate (K) and reaching a greater predicted L_{∞} . The growth performance index ϕ' was 3.10 for males and 2.98 for females.

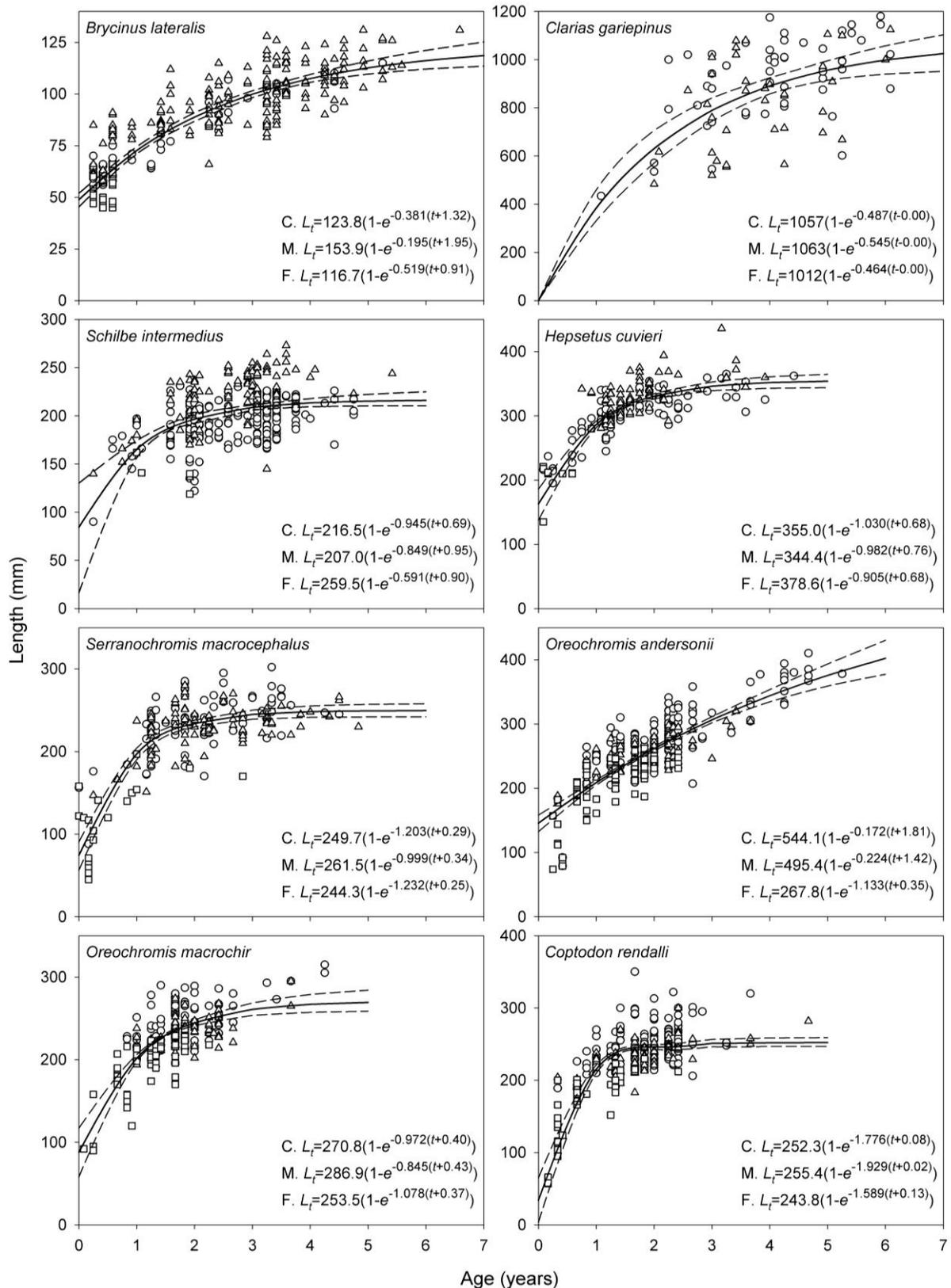


Figure 4.4. Von Bertalanffy growth curves (—) and 95% bootstrap confidence intervals (---) fitted to combined sex observed length-at-age for eight fish species from Lake Liambezi. Growth equations are given for combined sexes (C.), males (M.) and females (F.). □ = juveniles; ○ = males; △ = females.

Reproduction and maturity

The sex ratios and χ^2 test statistics of all eight study species are presented in Table 4.5. The adult population of *B. lateralis* was female dominated, and significantly different from unity. The smallest adult size classes (60–70 mm FL) were, however, male dominated, but by 75 mm FL females were dominant. *Schilbe intermedius* was male dominated overall, and significantly different from unity. *Oreochromis andersonii*, *O. macrochir* and *C. rendalli* were all male dominated and significantly different from unity. The sex ratios of *C. gariepinus*, *H. cuvieri* and *S. macrocephalus* did not differ significantly from unity.

Table 4.5. Sex ratios and χ^2 test statistics for the eight study species from Lake Liambezi.

Species	<i>n</i>	Sex ratio (male:female)	χ^2	<i>P</i>
<i>Brycinus lateralis</i>	364	1:2.5	68.58	< 0.001
<i>Clarias gariepinus</i>	108	1.1:1	0.33	0.564
<i>Schilbe intermedius</i>	361	2.0:1	37.92	< 0.001
<i>Hepsetus cuvieri</i>	166	1.2:1	1.54	0.214
<i>Serranochromis macrocephalus</i>	182	1:1.1	0.20	0.657
<i>Oreochromis andersonii</i>	287	2.1:1	36.97	< 0.001
<i>Oreochromis macrochir</i>	208	1.4:1	4.92	< 0.05
<i>Coptodon rendalli</i>	252	1.7:1	16.25	< 0.001

The reproductive seasonality of the eight study species is illustrated in Figure 4.5. *Brycinus lateralis* with active gonads (developing, ripe or spent stages) were sampled year round. The highest proportion of fish of a resting stage were sampled during the cooler winter months of June and August. The first ripe individuals were sampled in October, and the first spent fish in December. Spawning continued throughout the summer months with the last spent fish sampled in April, and the last ripe fish sampled in June.

Clarias gariepinus and *S. intermedius* displayed relatively short spawning seasons. Over 95% of both species were of a resting stage in June. The proportion of fish with developing gonads began to increase in August. The first ripe *C. gariepinus* were observed in October. In December over 50% of *S. intermedius* were classed as ripe. A small proportion of spent *S. intermedius* were observed in February, but spawning in both species appeared to peak in March–April, with nearly 55% of *C. gariepinus* classed as spent in April.

Hepsetus cuvieri displayed a relatively short spawning season. In April, all *H. cuvieri* sampled had resting gonads. The proportion of fish with developing gonads increased over

winter, peaking in summer during October (58%). The first developing, ripe and spent fish were all caught in December. No ripe fish were sampled after December. Spent fish were observed in February and March.

Serranochromis macrocephalus with active gonads were sampled year round. The lowest proportion of reproductively active fish (33%) was observed in April, at the end of summer. Even as winter set in, the proportion of fish with developing gonads increased in June. The first ripe and spent fish were sampled in August, as soon as water temperatures began to increase again. No spent fish were observed in October, but a high proportion (44%) were ripe. By December, that proportion had turned into spent fish. Reproductive activity continued through the rest of summer, coming to an end in April.

Oreochromis andersonii, *O. macrochir* and *C. rendalli* displayed similar patterns of spawning seasonality. The majority (> 70%) of fish sampled in August were categorised as resting. In October, most had transitioned to the developing stage, while a small proportion of each species had ripe gonads in October. The first spent individuals of each species were sampled in December. Spawning appeared to continue up until March in all three species, after which very few ripe fish were observed.

The sex-aggregated lengths-at-50% maturity of the eight study species are presented in Figure 4.6. Length-at-maturity was also calculated separately for each sex for seven of the study species. LRTs indicated that length-at-maturity did not differ significantly between sexes for these seven species (Table 4.6). For *C. gariepinus*, the sample size was not sufficient to calculate sex-specific length-at-maturity. Age-at-maturity, and the predicted proportion of mature fish per age class are presented in Table 4.7. Age-at-50% maturity ranged from 0.53 years for *B. lateralis* to 1.84 years for *O. andersonii*. Most species reached tm_{50} at between 1.0 and 1.5 years of age.

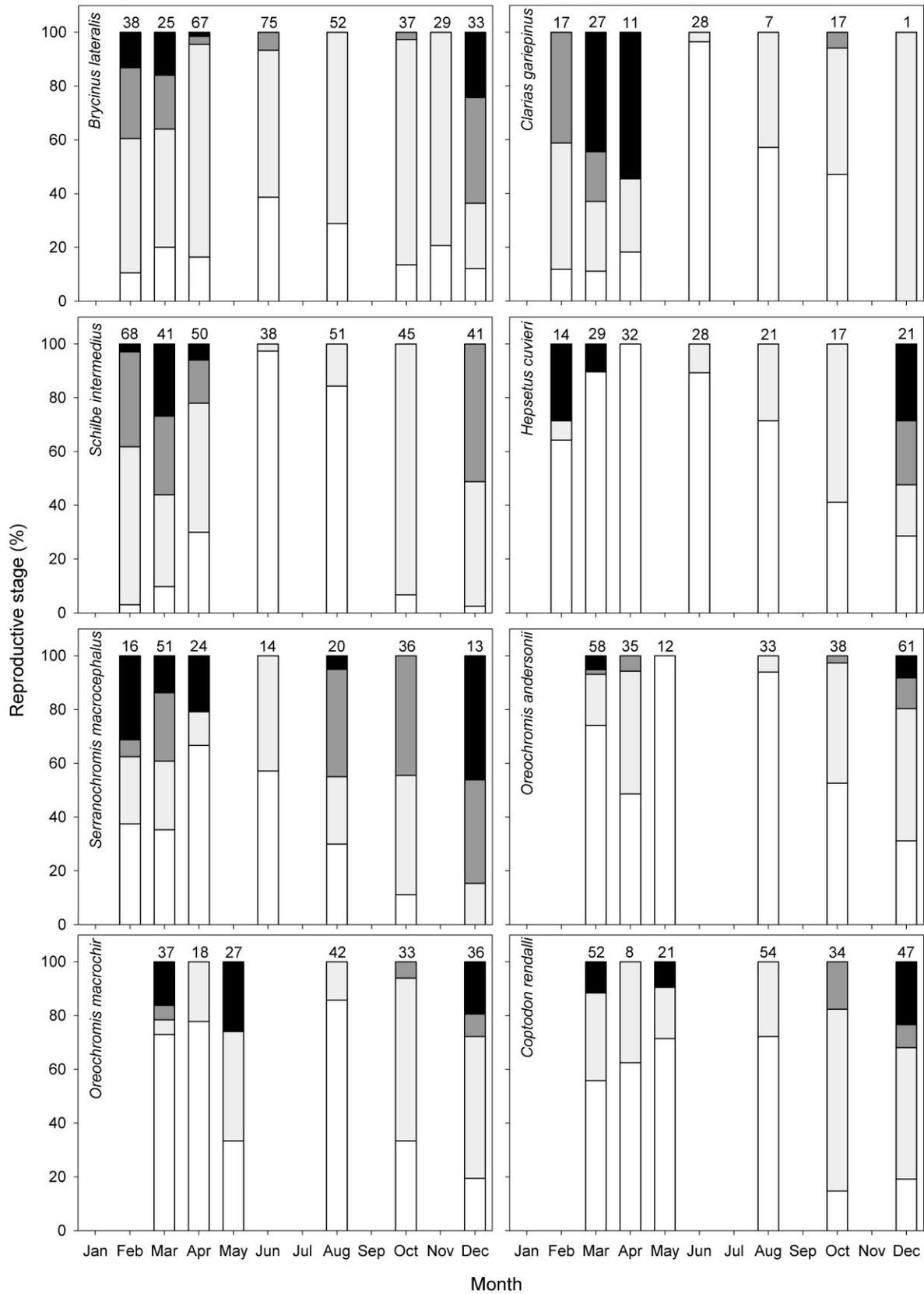


Figure 4.5. Reproductive seasonality of eight fish species from Lake Liambezi. Reproductive stages: Resting Developing Ripe Spent. Numbers above bars denote sample sizes.

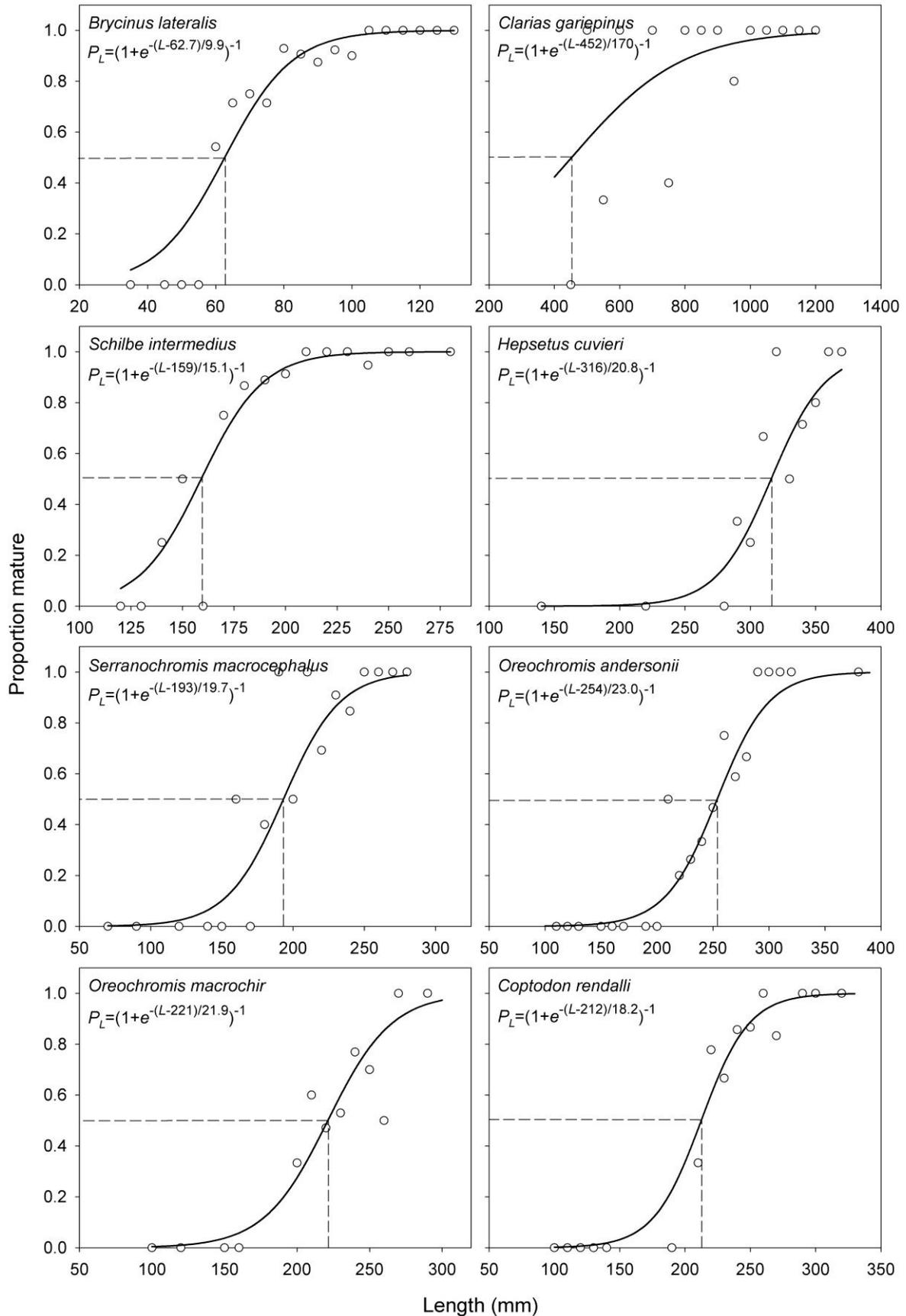


Figure 4.6. Length-at-50% maturity (- -) of eight fish species from Lake Liambezi, estimated by fitting a logistic ogive (—) to the observed proportion of mature fish per length class (○).

Table 4.6. Likelihood ratio test comparisons of male and female length-at-50% maturity.

Species	d.f.	χ^2	<i>P</i>
<i>Brycinus lateralis</i>	2	0.60	0.741
<i>Clarias gariepinus</i>	2	-	-
<i>Schilbe intermedius</i>	2	0.33	0.848
<i>Hepsetus cuvieri</i>	2	1.29	0.525
<i>Serranochromis macrocephalus</i>	2	2.21	0.331
<i>Oreochromis andersonii</i>	2	5.35	0.069
<i>Oreochromis macrochir</i>	2	0.69	0.707
<i>Coptodon rendalli</i>	2	0.94	0.625

Table 4.7. Age-at-50% maturity (tm_{50}), the rate of maturation (δ_t), and the predicted proportion of mature fish per age class of eight fish species from Lake Liambezi.

Species	tm_{50}	δ_t	Age class (years)			
			1	2	3	4
<i>Brycinus lateralis</i>	0.5	0.32	0.81	0.99	1.00	1.00
<i>Clarias gariepinus</i>	1.1	0.40	0.41	0.90	0.99	1.00
<i>Schilbe intermedius</i>	0.7	0.19	0.82	1.00	1.00	1.00
<i>Hepsetus cuvieri</i>	1.5	0.38	0.23	0.80	0.98	1.00
<i>Serranochromis macrocephalus</i>	0.9	0.20	0.57	1.00	1.00	1.00
<i>Oreochromis andersonii</i>	1.8	0.47	0.14	0.58	0.92	0.99
<i>Oreochromis macrochir</i>	1.3	0.32	0.25	0.89	0.99	1.00
<i>Coptodon rendalli</i>	1.1	0.18	0.30	0.99	1.00	1.00

Evidence of reproductive activity is not necessarily indicative of recruitment success, which is well illustrated for two species, *S. intermedius* and *B. lateralis*, for which ample length frequency data are available from experimental gillnet catches (Figure 4.7). Successful recruitment is illustrated by high numbers of juvenile fish. Juvenile *S. intermedius* were abundant in 2007, 2009 and 2010 when flooding occurred. Recruitment in 2011 appeared poor, despite flooding. From 2010 onward, the modal length frequency of *S. intermedius* can be seen increasing steadily each year in the absence of recruitment. *Brycinus lateralis* were not among the most abundant colonisers in 2007, but showed successful recruitment every year thereafter, independent of flooding, as they came to dominate the fish community (Chapter 3).

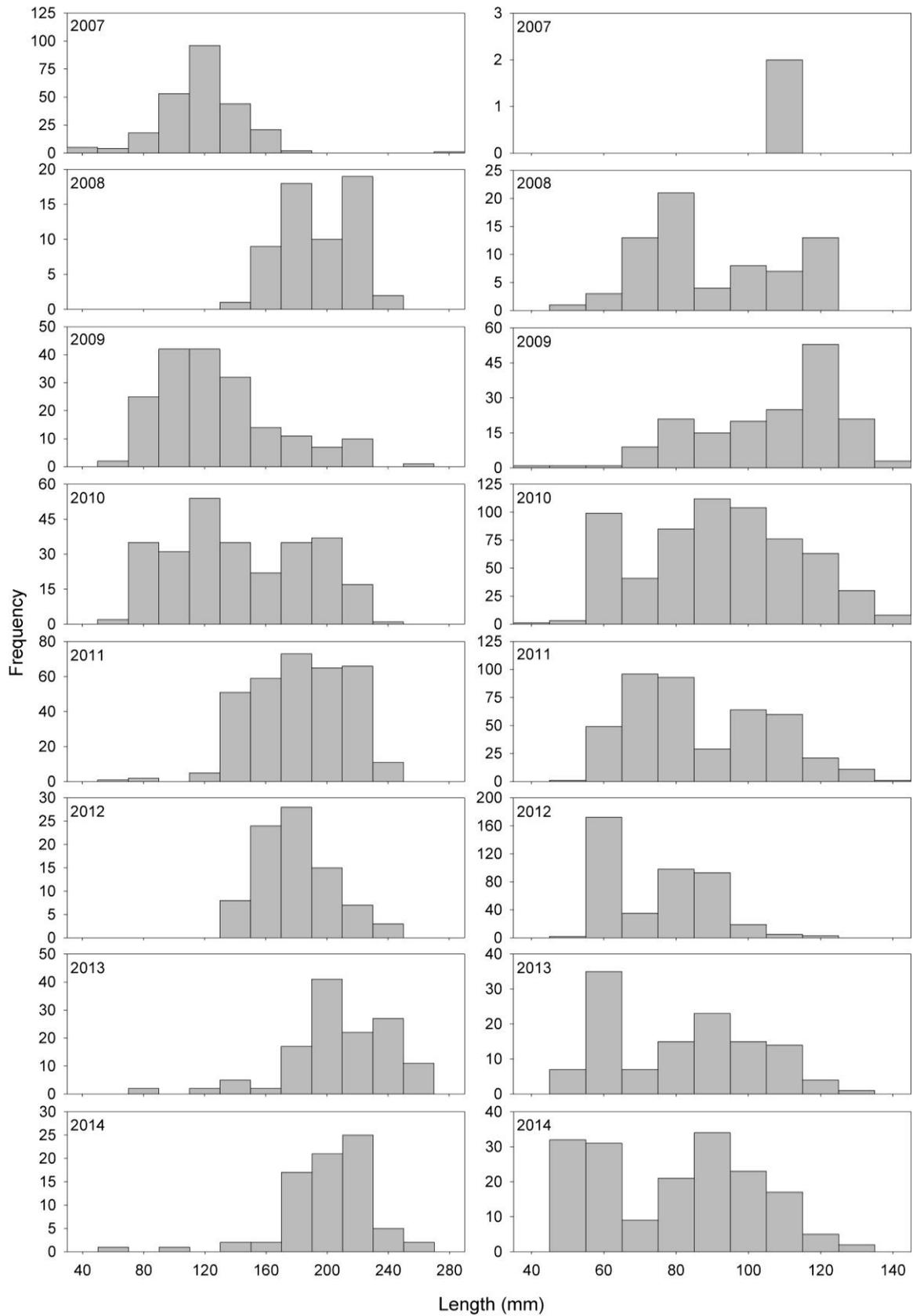


Figure 4.7. Length-frequency histograms of *Schilbe intermedius* (left column) and *Brycinus lateralis* (right column) sampled using experimental gillnets between March and June each year, from 2007 to 2014.

Life-history strategies

The PC ordination produced two axes that explained 91.5% of the variation in the life-history traits used for eight study species (Figure 4.8). The ordination generally supports previous classification of the study species. The periodic strategists *S. intermedius* and *C. gariepinus*, were differentiated from the opportunistic and equilibrium strategists on axis one by their high fecundity, short spawning season and dependence on flooding for successful reproduction. The five equilibrium strategists *H. cuvieri*, *S. macrocephalus*, *O. andersonii*, *O. macrochir* and *C. rendalli* were further separated from *S. intermedius* and *C. gariepinus* on axis one by parental care. Axis two differentiated *B. lateralis*, the only opportunistic strategist, from the equilibrium species and *C. gariepinus* by its small size, lower growth performance, small size at maturity and lack of parental care.

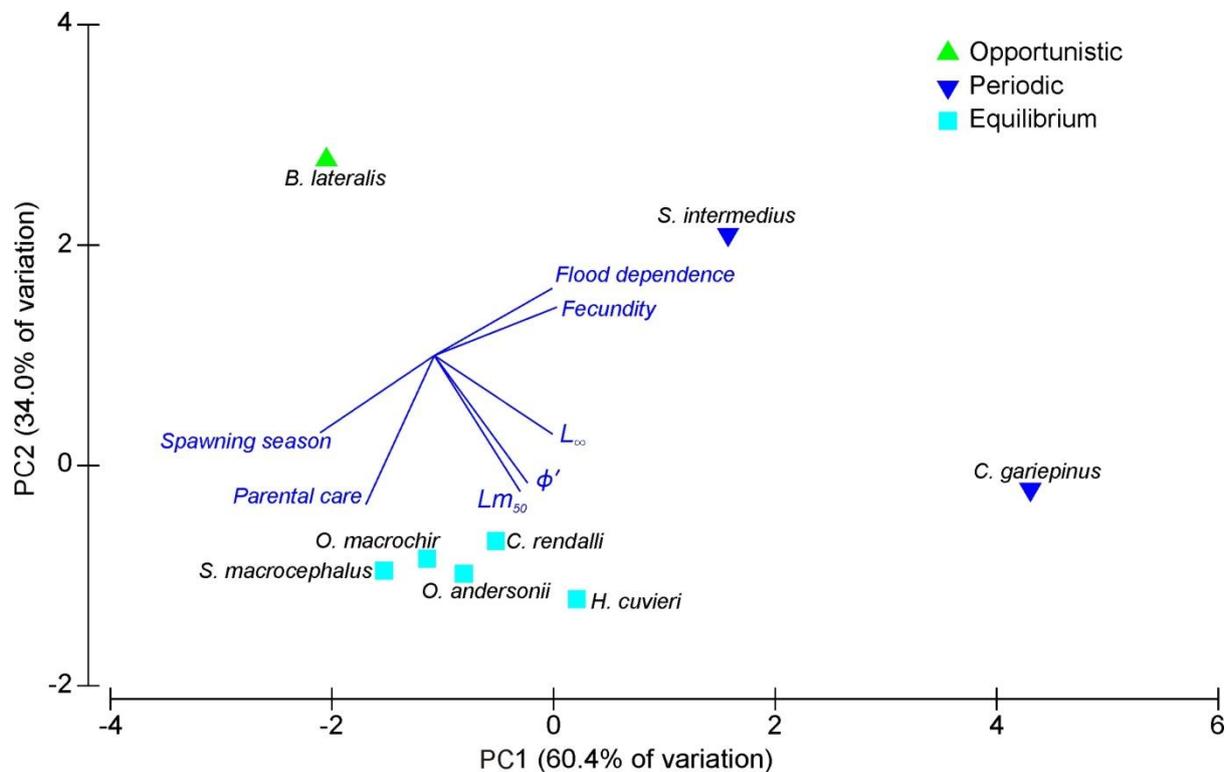


Figure 4.8. Principal component (PC) ordination of the life-history traits of eight species from Lake Liambezi. Vectors of the life-history variables on which the ordination was based are shown. L_{∞} = predicted asymptotic length; Lm_{50} = mean length-at-50% maturity;.

Discussion

The aim of this chapter was to assess the life-history strategies of eight common fish species in Lake Liambezi, and evaluate their establishment success against life-history theory and the hypothesised response of fishes with divergent strategies to various hydrological conditions.

Despite the hydrological stability of Lake Liambezi after filling favouring equilibrium strategists, species representative of all three of Winemiller and Rose's (1992) endpoint strategies were able to persist, and in many cases thrive in the lake. Key aspects of their life-history strategies that enabled them to succeed in the stable lake environment are discussed and compared to species with similar life-history strategies that were unable to establish in Lake Liambezi.

Opportunistic strategists

Brycinus lateralis is small, fast growing, early maturing, and has an extended spawning season—typical of species exhibiting an opportunistic life-history strategy (Winemiller and Rose 1992). They are surprisingly long lived in Lake Liambezi, with males and females reaching 5+ and 6+ years, respectively. This is greater than estimates for this species from Lake Kariba (3+ years) (Balon 1971), but similar to those from the Kavango River (5+ years) (Hay 1995). Female *B. lateralis* grew significantly faster, and to a larger size than male fish, as observed in the Kavango River system (Hay 1995; Booth and McKinlay 2001). The sex ratio in Lake Liambezi was significantly skewed towards females, especially in larger size classes, similar to that in the Kavango River system (Hay 1995; Booth and McKinlay 2001) and Lake Kariba (Balon 1971). The length-at-50% maturity (62 mm FL) did not differ between sexes, and was slightly larger than in the Okavango Delta (57 mm FL) (Booth and McKinlay 2001). Fish reached maturity after only half a year, and spawned throughout the summer months from October to April, as was found in the Kavango River system (Hay 1995; Booth and McKinlay 2001). These traits allowed *B. lateralis* to quickly repopulate the open water habitat after *E. paludinosus* and *E. poecheii* had declined (see Chapter 3). What seems to have enabled *B. lateralis* to thrive in a stable lentic environment where the colonising cyprinids failed, is their ability to breed independently of the flood regime.

Balon (1971) credited *B. lateralis*' ability to breed independently of flooding with enabling it to colonise Lake Kariba in the Middle Zambezi River—where it was scarce before the dam was constructed—and replace its indigenous congener *Brycinus imberi*. *Brycinus imberi* spawned on newly flooded terrestrial grass, which was in plentiful supply during the early filling phase of the lake. Once the lake reached the operating level for hydroelectric power generation in 1963, the water level was reduced for safety reasons at the beginning of each rainy season by opening the flood gates, thus depriving *B. imberi* of its spawning habitat. Balon (1971) suggested that *B. lateralis* originating from the Upper Zambezi River, or from

smaller tributaries of the Middle Zambezi (Bowmaker *et al.* 1978), entered the lake, and were able to spawn on the abundant submerged and free floating aquatic vegetation regardless of the water level. *Brycinus lateralis* quickly colonised the inshore environment after *B. imberi* had disappeared, making up 59% of the catch numerically between 1968 and 1970 (Balon 1973). Further evidence in support of *B. lateralis* ability to breed independently of flooding comes from the Okavango Delta where, fish inhabiting the northern riverine floodplain and southern drainage rivers have identical spawning seasons, despite flooding in the drainage rivers lagging four months behind that of the riverine floodplain (Booth and McKinlay 2001). As a result, *B. lateralis* is able to dominate the open waters of the ephemeral Lake Ngami at the south-western tip of the Okavango Delta, which has an irregular and unpredictable flood regime, similar to that of Lake Liambezi (Bruton 1980).

In the ephemeral Lake Chilwa, where *E. paludinosus* dominates the fish fauna well after each initial filling phase, they undertake spawning migrations to marginal swamps and inflowing rivers at the beginning of the rainy season (Furse *et al.* 1979; Macuiane *et al.* 2009). In Lake Rukwa, *B. imberi* is extremely abundant in both littoral and open water habitats (Ricardo 1938), though little is known of its reproductive habits. Successful reproduction of *E. paludinosus* and *B. imberi* is, in both cases, probably facilitated by the timely rise in lake levels with the onset of the rains. Lakes Liambezi and Ngami are not fed by small affluent rivers like Chilwa and Rukwa, but receive inflow on an irregular and unpredictable basis from much larger floodplain rivers, the timing of which does not often coincide with fish spawning seasons. However, during periods of high rainfall, Lake Liambezi is fed by several temporary streams that drain the surrounding woodland. Floodplain dependent spawners including *E. paludinosus*, *E. poechii* and *Enteromius bifrenatus* migrate up these swollen streams in search of suitable spawning habitat in rain filled pans up to 8 km from the lake (van der Waal 1996; Tweddle *et al.* 2014). The frequency, scale and duration of these events may not be sufficient for these species to maintain large populations in the lake in the absence of flooding.

Periodic strategists

Periodic strategists are typically large, long lived, late maturing and highly fecund animals (Winemiller and Rose 1992). *Clarias gariiepinus* exemplifies this strategy in Lake Liambezi, reaching 1 220 mm TL in length and, having migrated into the lake as an adult fish, 15+ years of age. The largest and oldest fish which were potentially spawned in Lake Liambezi

were 1 180 mm TL, and 6+ years. *Clarias gariepinus* is generally fast growing, but displays considerable individual variation in growth rates (van der Waal 1998; Bokhutlo *et al.* 2015). In dynamic and heterogeneous environments such as the Okavango Delta, this has been attributed to variable environmental conditions (e.g. prey abundance) to which individuals may be exposed during different phases of the hydrological regime (Bokhutlo *et al.* 2015). Environmental factors are unlikely to have contributed significantly towards variable growth rates in Lake Liambezi, as all fishes will have been exposed to similar conditions in the relatively stable and homogeneous system. Inherent differences in feeding behaviour and growth efficiency are more likely to be responsible for the observed variation in Lake Liambezi (Martins *et al.* 2005). Van der Waal (1998) suggested that these inherent differences are maintained by differential mortality rates among large, fast growing fish, which thrive during wetter periods, and small, slow growing fish, which are better able to survive during harsh, dry periods.

Male *C. gariepinus* grew significantly faster, and to a larger size than females in Lake Liambezi, consistent with observations from the Shire River (Willoughby and Tweddle 1978), Lake Sibaya (Bruton and Allanson 1980) and Darlington Dam (Wartenberg *et al.* 2013). The growth performance of *C. gariepinus* in Lake Liambezi was higher than for any other population studied, likely owing to the high productivity in the recently flooded lake (Scholz *et al.* 2002; Potts *et al.* 2008). The sex-aggregated length-at-50% maturity in Lake Liambezi (452 mm TL) was much larger than in the Shire River (305 mm TL) (Willoughby and Tweddle 1978), Lake Sibaya (335 mm TL) (Bruton 1979a) and Okavango Delta (265 mm TL) (Merron 1991), possibly a result of the higher growth rates in Lake Liambezi. In the Shire River and Lake Sibaya, *C. gariepinus* matured after 2 years (Willoughby and Tweddle 1978; Bruton 1979a), so that despite maturing at a larger size in Lake Liambezi, fish matured much earlier, after little more than 1 year. The timing of the spawning season of *C. gariepinus* varies considerably across its wide distribution, as well as between years in the same localities, and is closely related to flooding (Bruton 1979a; Merron 1991). In Lake Liambezi, the spawning season was short, occurring between February and April during the peak of the rainy season.

Schilbe intermedius is considerably smaller, and shorter lived compared to *C. gariepinus*, but represents the periodic strategy by virtue of its high fecundity, low investment per offspring and short spawning season (van der Waal 1985; Hay 1995; Merron and Mann 1995). The

ages attained by *S. intermedius* in Lake Liambezi are comparable to those of other populations in the region (Balon *et al.* 1974; Hay 1995), as well as previous estimates from Lake Liambezi (van der Waal 1985). The species is sexually dimorphic, with females attaining larger sizes than males (Hecht 1980; Merron and Mann 1995). Though few juvenile fish were sampled, the initial growth rate appeared rapid in both sexes, but slowed considerably after the first year when maturity was reached. The sex ratio of *S. intermedius* in Lake Liambezi was significantly skewed towards males, whereas most other studied populations have been female dominated (Hecht 1980; van der Waal 1985; Hay 1995; Merron and Mann 1995). It is difficult to postulate as to why this may be the case. One potentially contributing factor is that larger female fish are more susceptible to being caught as by-catch in commercial gillnets of 76 and 89 mm mesh size used to target larger cichlids. Length-at-50% maturity was attained at 159 mm FL, identical to van der Waal's (1985) estimate from the lake in the past. Merron and Mann (1995) found that males matured at a smaller size (143 mm FL) than females (173 mm FL) in the Okavango Delta. *Schilbe intermedius* matured considerably earlier in Lake Liambezi, at less than 1 year of age, compared to 2 years in the Luphephe-Nwanedzi and Mnjoli dams in South Africa and Swaziland, respectively (Hecht 1980; Booth and Khumalo 2010). The spawning season of *S. intermedius* in Lake Liambezi was, like that of *C. gariepinus*, short, occurring between February and April. Recruitment, however, was only successful during years of flooding.

Both *C. gariepinus* and *S. intermedius* are dependent on flooding for successful reproduction. In floodplain environments, they migrate laterally onto newly inundated floodplains, laying their eggs on flooded grasses and sedges (Bruton 1979a; Clay 1979; Hickey and Bailey 1987; Merron and Mann 1995). In man-made impoundments, *C. gariepinus* sometimes display potamodrometic behaviour, migrating up inflowing streams and rivers to spawn at the very first opportunity (Holl 1968), as Bowmaker (1973) noted, 'leaping with some abandon' over rocky obstacles to their migration. In the natural lakes Chilwa and Sibaya, *C. gariepinus* forego potamodrometic migrations, and breed at the margins of the lakes in newly flooded terrestrial grasses (Bruton 1979a; Furse *et al.* 1979). Van der Waal (1996) observed *C. gariepinus* migrations out of Lake Liambezi, up temporary streams that drain the surrounding woodland. He collected fertilized eggs from flooded grass in shallow pans, and later observed juveniles moving back to Lake Liambezi as the water subsided.

Recruitment failure in the absence of suitable spawning conditions associated with flooding is not uncommon. *Clarias gariepinus* and *S. intermedius* are able to overcome years of poor recruitment by means of the ‘storage effect’ (Warner and Chesson 1985). The longevity of both species, and *C. gariepinus* in particular, allows them to endure periods of unfavourable recruitment conditions. When favourable recruitment conditions return they produce strong year classes, which are then able to survive over numerous potential reproductive periods (see Chapters 2 and 3). When species are highly fecund, as in *C. gariepinus* and *S. intermedius*, even few individuals are capable of producing strong year classes (Warner and Chesson 1985). This is particularly evident in *C. gariepinus* that, in Lake Chilwa, were forced to seek refuge in peripheral swamps when the lake dried in 1968. The lake refilled the following year and *C. gariepinus* quickly recovered, with an estimated fisheries yield of 3 000 t the same year, equivalent to those in the pre-drying period (Furse *et al.* 1979).

Equilibrium strategists

Equilibrium strategists, defined by their low batch fecundity, large eggs, parental care and extended spawning season, are best suited to stable, lentic environments (Winemiller and Rose 1992; Mims and Olden 2012). Five of the larger, more important (to the fishery) species in Lake Liambezi were studied in detail. No species is more important to the fishery in Lake Liambezi than *O. andersonii*, which contributes 43% to the annual fishery yield of 2 700 t (Peel *et al.* 2015b). The oldest male and female fish sampled in the recently filled lake were 5+ and 4+ years, respectively. This is comparable to ages reached by *O. andersonii* in the heavily fished Upper Zambezi River (Peel *et al.* In review) In protected or lightly exploited populations in the Kavango and Kwando rivers they can attain ages exceeding 15 years (Booth *et al.* 1995; Peel *et al.* In review). Males grew to a significantly larger size, as in other populations (Peel *et al.* In review), but females had a higher growth performance. As noted by van der Waal (1985) *O. andersonii* grew rapidly in Lake Liambezi, but did not attain sizes as large as in the Upper Zambezi or Kavango rivers (> 500 mm TL) (Peel *et al.* In review). Fish attained 50% maturity at 254 mm TL, comparable to Upper Zambezi, Kavango and Kwando river populations (Peel *et al.* In review), but much larger than in the Okavango Delta (187 mm TL) (Merron 1991). *Oreochromis andersonii* matured at 1.8 years, later than all other study species in Lake Liambezi. Their extended summer spawning season (December–March) was consistent with that of other populations in the region (Dudley 1974; van der Waal 1985; Merron 1991).

Oreochromis macrochir attained 4+ years of age in the recently filled Lake Liambezi. In more permanent water bodies and under protection from fishing, *O. macrochir* can reach up to 15+ years (Peel *et al.* In review). Males grew to a larger size than females, but growth performance was identical. The growth performance of *O. macrochir* in Lake Liambezi was higher than that in other populations in the region (Peel *et al.* In review). Fish attained 50% maturity at 221 mm TL, comparable to the Kavango and Kwando river populations, but smaller than in the Zambezi River (254 mm TL) (Peel *et al.* In review). The age-at-50% maturity of *O. macrochir* in Lake Liambezi was 1.3 years. The extended summer spawning season (October–March) was, again, broadly comparable with that of other populations (Dudley 1974; van der Waal 1985).

Coptodon rendalli reached 4+ years of age in the recently refilled lake, compared to 13+ years in the Kwando River and 16+ years in Lake Chicamba, Mozambique (Weyl and Hecht 1998). As observed by Dudley (1974) on the Kafue Floodplain, males grew faster and to a larger size than females. The growth performance of *C. rendalli* in Lake Liambezi was higher than in any other population in the region (Peel *et al.* In review). Length-at-50% maturity was attained at 212 mm TL, comparable to most other populations in the region (Peel *et al.* In review), but significantly larger than the 140 mm TL observed by van der Waal (1985) in Lake Liambezi during the previous inundation period. It is not clear why *C. rendalli* would have matured so much smaller in the past, since water levels in the lake at the time were relatively high, and environmental conditions favourable (Seaman *et al.* 1978). *Coptodon rendalli* reached 50% maturity at 1.1 years in Lake Liambezi, and spawned in summer, from October to March.

Serranochromis macrocephalus was the most abundant predatory cichlid in Lake Liambezi during this (see Chapter 3) and previous studies (van der Waal 1985). They attained 4+ years in Lake Liambezi, comparable with estimates from the Barotse Floodplains of the Upper Zambezi River (Duerre 1969; Winemiller 1991), where they attained 5 + years. Van der Waal (1985) recorded a maximum of 8+ years in Lake Liambezi when it was previously inundated. Both sexes grew rapidly, reaching maturity at 193 mm TL—somewhat larger than the 150 mm TL reported by van der Waal (1985)—and 0.9 years of age. *Serranochromis macrocephalus* had the longest spawning season of any species observed in this study, spanning at least 9 months, from August to April. This is longer than van der Waal (1985)

observed for this species in the lake, but similar to what he found for *Serranochromis angusticeps* (July–April).

Hepsetus cuvieri was relatively short lived, with male and female fish reaching 4+ and 3+ years, respectively, similar to previous estimates from the Upper Zambezi (Winemiller and Kelso-Winemiller 1994) and Lake Liambezi (van der Waal 1985) obtained using scales. Early growth rates were very rapid, with both sexes attaining L_{∞} before two years of age. Length-at-50% maturity in Lake Liambezi was attained at 316 mm FL for the present study, compared to 270 mm FL by van der Waal (1985). Both are significantly larger than estimates from the Okavango Delta, where males matured at 161 mm FL and females at 183 mm FL (Merron *et al.* 1990). The differences are most likely a result of *H. cuvieri* growing faster in Lake Liambezi compared to the Okavango Delta, although no growth estimates are available for the latter population. If growth rates are comparable between populations, differences in length at maturity may result from differences in age at maturity. Age-at-50% maturity was estimated at 1.5 years in Lake Liambezi. No other estimates of age at maturity are available for comparison. Spawning took place in summer, from November to February. This is comparable in length to the spawning season of *H. cuvieri* in the seasonal parts of the Okavango Delta, but much shorter than in the perennially flooded areas of the delta, where fish spawn for nine months, from September through to May (Merron 1991).

The above five equilibrium strategists underwent a more gradual population rise compared to the opportunistic and periodic strategists, but it was by no means slow (Chapter 3). After the lake filled in March/April 2009, the gillnet fishery yielded primarily large periodic strategists *C. gariiepinus* and *C. ngamensis* (D. Tweddle, personal communication) that were among the most prolific colonisers (Chapter 2). By November 2010, less than two years after filling, tilapiine cichlids dominated the fishery (Peel *et al.* 2015b). This is similar to observations from Lake Chilwa where, following desiccation in 1968, *Oreochromis shirianus chilwae* took three years to recover to pre-drying levels (Furse *et al.* 1979). So despite their low fecundity, equilibrium strategists have the potential to achieve fairly rapid population growth.

Tilapiine cichlids are renowned for having flexible reproductive traits which vary in response to abiotic and biotic conditions (Fryer and Iles 1972; Trewavas 1983; Merron 1991; James and Bruton 1992; Kolding 1993; Brummett 1995; Duponchelle and Panfili 1998;

Duponchelle *et al.* 2000). In large, stable environments where adult mortality is low, fish mature at a larger size and produce fewer, larger eggs, maximising each individual offspring's chances of survival. In smaller, less stable environments where mortality rates are higher, fish mature at a smaller size and produce many small eggs, increasing the population growth potential and enhancing the species ability to recolonise habitats following major disturbances. Environmental conditions in Lake Liambezi are evidently no more unstable than in the Upper Zambezi, Kwando and Kavango rivers, since the tilapiine cichlids in the lake mature at similar sizes to those in the rivers (Peel *et al.* In review). They do, however, mature at earlier ages, as fish in the lake grow faster and attain sizes at which maturity is reached earlier than other populations (Peel *et al.* In review). This has resulted in reduced generation times of tilapiine cichlids in the lake, and indirectly contributed to increased population growth potential without making the trade-offs between egg size, fecundity and juvenile survivorship.

Another factor that would have facilitated rapid population growth is the fact that equilibrium strategists are able to breed multiple times over an extended spawning season. Kenmuir (1973) found that *C. rendalli*, held in an aquarium at Lake Kariba, continued to breed for as long as the water temperature remained above 20 °C, producing eight broods at almost monthly intervals. With an average batch fecundity of approximately 6 000 eggs (Kenmuir 1973; Batchelor 1978), this represents greater reproductive potential than some periodic strategists, such as *S. intermedius* (Hay 1995; Merron and Mann 1995). In Lake Liambezi, water temperatures remained above 20 °C for nearly 10 months in 2013/2014, yet only *S. macrocephalus* appeared to breed for this long.

Linking life-history to establishment success

The opportunistic *B. lateralis* and the five equilibrium species studied have been able to thrive in Lake Liambezi by effectively decoupling their life cycles from the hydrological regime. All have extended summer breeding seasons during which they have multiple spawning events. *Brycinus lateralis* matured early, helping to maximise its intrinsic rate of population growth and rapidly colonise the open waters of Lake Liambezi. The CPUE of *B. lateralis* fell sharply after the last flood in 2011, but since 2013 has remained stable, at approximately half of the peak value (see Chapter 3). *Brycinus lateralis* continued to show strong recruitment in the absence of flooding, and remained the dominant species throughout

the lake up to the last sampling event in December 2014 (see Chapter 3). The equilibrium strategists, especially *O. andersonii*, have been the mainstay of a highly productive fishery since the latter half of 2010 (Peel *et al.* 2015b). They are expected to exhibit stable population dynamics over time as a result of their adaptations towards density-dependent recruitment and lower intrinsic rate of population growth (Winemiller 2005). Since reaching their respective peaks in abundance in 2011 and 2013, *S. macrocephalus* and *H. cuvieri* have been relatively stable (see Chapter 3). Trends in the relative abundance of the tilapiine cichlids are, however, difficult to elucidate as a result of their low abundance in experimental gillnet catches, and the lack of fishery statistics collected after 2012. The periodic *C. gariepinus* and *S. intermedius* have been able to withstand several years of poor recruitment in the absence of flooding. The high CPUE of *S. intermedius* has remained fairly stable since refilling (see Chapter 3) because it is not targeted by the fishery. The CPUE of *C. gariepinus* fell considerably after inundation in 2007 as a result of fishing pressure, and has remained low since (see Chapter 3). Despite a reduction in the population of *C. gariepinus*, both periodic species have the potential to produce strong year classes as a result of their high fecundity if/when flooding does occur. The following chapter examines the food web structure and trophic dynamics of the fish community in Lake Liambezi in order to determine what sources of primary production support the fish community, how the different species interact, and what influence these interactions may have had on assemblage succession.

CHAPTER 5

Food web structure and trophic dynamics of a mature lacustrine fish community in Lake Liambezi

Introduction

Food webs depict networks of trophic interactions between consumers and resources, and the pathways by which energy flows through ecosystems (Paine 1980). Understanding food web dynamics is a fundamental aspect of community ecology, as food web dynamics interact with life-history and environmental factors to influence patterns of community dynamics (Winemiller 1996b). Stable isotopes, especially those of carbon and nitrogen, are widely used in food web studies. The ratio of carbon isotopes ($\delta^{13}\text{C} = {}^{12}\text{C}/{}^{13}\text{C}$) changes little between trophic levels (0–1.5‰) and can, therefore, be used to evaluate the sources of carbon supporting consumers (DeNiro and Epstein 1978; Peterson and Fry 1987). The ratio of nitrogen isotopes ($\delta^{15}\text{N} = {}^{15}\text{N}/{}^{14}\text{N}$) increases by as much as 3–4‰ per trophic transfer, and can be used to differentiate between species at various trophic levels (DeNiro and Epstein 1981; Minagawa and Wada 1984).

The main advantages of stable isotope analysis over other techniques, such as stomach contents analysis, are that estimates of trophic position are based on assimilated, not just ingested food, as well as providing a long-term average trophic position (Hobson and Welch 1992; Vander Zanden *et al.* 1997; Post 2002). Comparatively, the analyses of stomach contents only provides a snapshot of trophic positions at the time of sampling, and large sample sizes, especially for piscivores which often have empty stomachs, and omnivores with broad, and highly variable diets, are required to adequately describe species trophic positions (Arrington *et al.* 2002; Winemiller *et al.* 2007). Despite the advantages of stable isotopes, stomach contents analysis is still considered a valuable complementary technique (Vander Zanden and Vadeboncoeur 2002; Layman *et al.* 2005; Winemiller *et al.* 2007; Blanchette *et al.* 2014). It provides greater taxonomic resolution than stable isotope analysis, and information on the size of prey consumed, which is an important step towards understanding the functional role of species in an ecosystem (Jackson 1961; Lévêque 1995; Montaña *et al.* 2011).

Lake Liambezi supports extensive areas of aquatic macrophytes (Seaman *et al.* 1978; Peel *et al.* 2015b). Vast, fragmented stands of the emergent reeds *Phragmites australis* and *Typha capensis* provide shelter from wind and wave action, enabling the submerged macrophytes *Lagarosiphon ilicifolius* and *Najas horrida* to flourish in shallower areas. Seaman *et al.* (1978) hypothesised that these macrophytes acted as a ‘nutrient sponge’, limiting the availability of nutrients to microalgae in the open lake, resulting in low algal growth potential. Seaman *et al.* (1978) and van der Waal (1985) thus considered macrophytes to be the most important primary producers supporting invertebrates and fishes in Lake Liambezi, a view widely held at the time (Howard-Williams and Junk 1976; Soares *et al.* 1986; Bayley 1989). Since the direct consumption of macrophytes is rare among the Upper Zambezi ichthyofauna (van der Waal 1985; Winemiller 2004), Seaman *et al.* (1978) concluded that macrophytes must enter the food web mainly as detritus. Studies employing stable isotopes have since revealed that, despite being major primary producers in floodplain ecosystems, macrophytes, with some exceptions (e.g. Hoeinghaus *et al.* 2007; Zeug and Winemiller 2008a), generally contribute relatively little to aquatic food webs (Hamilton *et al.* 1992; Bunn and Boon 1993; Forsberg *et al.* 1993; Thorp and Delong 1994; Thorp *et al.* 1998; Lewis *et al.* 2001). These studies indicated that phytoplankton and periphyton, which usually constitute a small fraction of the potentially available carbon in floodplain ecosystems, are the principal carbon sources supporting invertebrates and fishes (Winemiller 2004; Douglas *et al.* 2005).

Fish communities in tropical floodplain ecosystems are highly diverse, but are usually dominated in terms of biomass by relatively few species (Winemiller 2004). These species represent a small subset of the total trophic pathways, but account for the majority of energy moving through the food web (Winemiller 1990). Dominant primary consumers in Lake Liambezi include the detritivorous tilapiine cichlids (van der Waal 1985; Peel *et al.* 2015b). These, in turn, are important prey for large piscivores such as *Clarias gariepinus* and *Hepsetus cuvieri* (van der Waal 1985; Winemiller and Kelso-Winemiller 1996). Short food chains such as this facilitate the efficient transfer of energy from microalgae to fishes (Lauzanne 1983), enabling tropical floodplain ecosystems to support high fish biomass on a small portion of the potentially available carbon (Lewis *et al.* 2001). High levels of omnivory (feeding at more than one trophic level) among tropical freshwater fishes also contributes to short food chains (Winemiller 1990; Jepsen and Winemiller 2002; Douglas *et al.* 2005; Blanchette *et al.* 2014). Omnivory is considered to be an adaptation to temporal and spatial variations in resource availability driven by strong seasonal hydrology (Lowe-McConnell

1987; Goulding *et al.* 1988; Winemiller 1990). While dietary specialisation is evident in some fishes in Lake Liambezi (e.g. mormyrids and serranochromine cichlids), omnivory is still prevalent, particularly among the various clariid, synodontid and schilbeid catfishes (van der Waal 1985).

The aims of this chapter was to 1) examine which primary production sources support consumer biomass in Lake Liambezi, 2) describe the trophic structure of the fish community and, 3) assess the trophic interactions among fish species, and discuss their potential influences in shaping the lacustrine fish community that emerged in 2011 (see Chapter 3). Stomach contents analysis and stable isotope analysis were used to test the following hypotheses: 1) algal primary production would support a higher proportion of consumer biomass than aquatic macrophytes, 2) the food chain would be short, since a large component of the fish fauna comprises detritivorous and herbivorous cichlids that may be consumed directly by top predators and, 3) trophic interactions among species may have played an important part in species successions described in Chapter 3.

Materials and methods

Stomach content analysis

Analyses of stomach contents were conducted on four of the most abundant large piscivorous fish species in Lake Liambezi, viz. *Schilbe intermedius*, *C. gariepinus*, *Hepsetus cuvieri* and *Serranochromis macrocephalus*, that could have influenced food web structure via predation, and one small zooplanktivorous species, *Brycinus lateralis*, which was a major component of the Lake Liambezi fish fauna (see Chapter 3). Fish were collected using experimental multifilament gill nets (see Chapter 2) and baited longlines (see Chapter 4). Samples of each of the four large piscivorous species were collected on five occasions between October 2013 and December 2014, and their stomach contents were examined in the field. *Brycinus lateralis* were sampled in February 2013, and preserved whole in the field in 10% buffered formalin. Stomach contents of *B. lateralis* were later examined under a dissecting microscope in the laboratory. Stomach contents were identified to the lowest practical taxonomic level, counted and weighed to the nearest 0.1 gram after blotting dry. For *B. lateralis*, an indirect volumetric assessment of each food category was used (Booth and McKinlay 2001), because food items could not be weighed with sufficient precision.

Dietary composition of the five study species was assessed by calculating the index of relative importance (IRI; Pinkas *et al.* 1971) of each prey item, as:

$$IRI = (\%N + \%W) \times \%FO,$$

where %*N* and %*W* are the number and weight of each prey item as a percentage of all prey, and %*FO* is the number of stomachs containing a specific prey item as a percentage of all sampled stomachs. For *B. lateralis* %*V*, the volume of each prey item as a percentage of all prey, was used in place of %*W*. The IRI for each prey item was then expressed as a percentage of the sum of IRI values for all prey items (%IRI).

Stable isotope analysis

Stable isotope samples were collected during August 2011 and August 2012. Limited sampling of basal resources and fishes was carried out in August 2014 to investigate an apparent dietary shift in several fish species between years. Fishes and their potential food sources were collected from across Lake Liambezi, including littoral areas, vegetated habitats and the open lake. Fish were sampled using experimental multifilament gill nets, longlines, by D-netting, electric fishing, and were also purchased from local fishers. For most fishes, tissue samples were taken from white muscle above the lateral line, with all scales and skin removed. For very small (<30 mm) fish species (e.g. *Micropanchax* spp), the whole body was used after removing the head, intestines and scales. Aquatic insects were sampled using a hand-held scoop net, and the whole body, often of multiple individuals of the same species, was used for each sample. Zooplankton was collected using a Bongo net (500 µm mesh) towed on the surface at night. Detritus was sampled using a cone dredge and aquatic macrophytes were handpicked. Phytoplankton associated with particulate organic matter (POM) was sampled by filtering between 0.5 and 2.0 L surface water, depending on water clarity, through 0.45 µm pre-combusted (at 500 °C for 4 hours) glass fibre filters (Advantec).

All samples were oven dried in the field at 50 °C for 24–48 hours. In the laboratory, dried samples were ground to a homogenous powder with a pestle and mortar, and weighed into tin capsules. Samples were analysed using a Europa Scientific 20-20 IRMS linked to an ANCA SL Prep Unit at IsoEnvironmental cc, South African Institute for Aquatic Biodiversity,

Grahamstown, South Africa. Isotope values are expressed in delta notation according to the formula:

$$\delta X = \left(R_{\text{sample}} / R_{\text{standard}} - 1 \right) \times 1000,$$

where X is the element and R is the ratio of the heavy over the light isotope. The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were reported as parts per thousand (‰) relative to Vienna Pee Dee Belemnite and atmospheric nitrogen standards, respectively. Each 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-CH6 and IAEA-N1). Analytical precision for the 2011 samples was ± 0.07 for $\delta^{13}\text{C}$ and ± 0.12 for $\delta^{15}\text{N}$, and for the 2012 samples was ± 0.08 for $\delta^{13}\text{C}$ and ± 0.12 for $\delta^{15}\text{N}$.

Lipids are depleted in ^{13}C relative to other tissues (DeNiro and Epstein 1977; McConnaughey and McRoy 1979). As a result, variations in lipid content between individuals and between species can significantly influence $\delta^{13}\text{C}$ values, and potentially lead to misinterpretations of food web structure (Sweeting *et al.* 2006; Post *et al.* 2007). To account for variations in lipid content in fish samples, mathematical normalisation was performed for samples with a carbon to nitrogen ratio (C:N) > 4 using the (McConnaughey and McRoy 1979) model:

$$L = \frac{93}{1 + (0.246 \times \text{C} : \text{N} - 0.775)^{-1}}$$

$$\delta^{13}\text{C}' = \delta^{13}\text{C} + D \times \left(I + \frac{3.9}{1 + 287/L} \right),$$

where L is the lipid content of the sample, $\delta^{13}\text{C}'$ is the lipid-normalised value of the sample, D is the isotopic difference between protein and lipid, and I is a constant. The parameters D and I were assigned values of 4.46 and 0, respectively, based on calculations from lipid extracted samples of 18 common fish species from the Kavango River by Taylor (2016).

Food web structure

The food web structure of Lake Liambezi was first assessed qualitatively using $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ biplots. The isotope data collected in 2011 and 2012 were assessed separately, as both datasets had strengths and weaknesses. Fish, zooplankton and detritus were more extensively sampled in 2011, and aquatic invertebrates and plants were better sampled in 2012. Organisms were grouped into trophospecies (Yodzis and Winemiller 1999) for graphical illustration, as plotting individual species would have made the visual interpretation of food web structure difficult. Resources were grouped into broad functional groups, and fishes were grouped according to a combination of taxonomic and feeding guilds. The qualitative assessment of food web structure was based on the assumption that trophic enrichment for $\delta^{13}\text{C}$ was 1.5‰ per trophic level (Sweeting *et al.* 2007b), and for $\delta^{15}\text{N}$ was 3.2‰ per trophic level (Sweeting *et al.* 2007a).

Variation in the isotope values ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of basal resources sampled in both years were assessed by multivariate statistical analyses performed using the PRIMER package, version 6 with PERMANOVA add on software (Clarke and Gorley 2006; Anderson *et al.* 2008). Analyses were performed on Euclidean distance measures of untransformed data. PERMANOVA were used to test for significant differences between years. Significance values were calculated using the Type III (partial) sums of squares and 9999 unrestricted permutations of the raw data for each analysis. Where significant differences were found between years, *post hoc* pair-wise PERMANOVAs were performed. Statistical significance was set at $\alpha = 0.05$ for all tests. Important consumer species that showed large variation in $\delta^{13}\text{C}$ between 2011 and 2012 were also tested for significant differences using univariate PERMANOVAs as described above. Here, the additional data collected in 2014 were used to determine whether the differences in $\delta^{13}\text{C}$ values of the tilapiine cichlids between years represented a permanent dietary shift, or simply inter-annual dietary variation.

Community metrics

The trophic structure of the fish community was then compared between 2011 and 2012 using six quantitative isotope metrics (Layman *et al.* 2007; Jackson *et al.* 2011). These included nitrogen range (NR), which provides a measure of trophic length; carbon range (CR), which gives an indication of the diversity of basal resources utilised; mean distance to centroid (CD), which provides a measure of trophic diversity; mean nearest neighbour

distance (MNND), which estimates the density and clustering of species within the community; standard deviation of the nearest neighbour distance (SDNND), which gives a measure of the evenness of species packing in biplot space; and the sample size corrected standard ellipse area (SEA_c). The SEA_c provides a bivariate measure of the mean core isotopic niche of a community, encompassing approximately 40% of the data. The degree of SEA_c overlap between communities was calculated to give a quantitative measure of dietary similarity (Jackson *et al.* 2012). Only fish species collected in both years with a sample size ≥ 3 were included in the analyses. All metrics were calculated using the Stable Isotope Bayesian Ellipses in R (SIBER; Jackson *et al.* 2011) package in the R statistical computing programme (R Core Team, 2013), and bootstrapped ($n = 10000$) to allow comparisons between 2011 and 2012 datasets that differed in sample size.

Trophic structure and species interactions

The trophic structure of the fish community sampled in 2011 was examined in more detail by calculating the SEA_c of each taxonomic/feeding group, and the % of SEA_c overlap between groups. The SEA_c and % overlap of individual species within important consumer groups were then calculated to elucidate interspecific trophic interactions, and explore their potential role in shaping the lacustrine fish community. The groups of species examined included the alestids, which have been a dominant component of the fish fauna in the lake since it filled, the tilapiine cichlids on which the fishery is based, generalist predators that include the highly abundant *S. intermedius*, and piscivores which may influence community food web structure.

Results

Stomach contents analysis

In total, 63 stomachs were examined from *C. gariepinus* (434–1220 mm TL), 125 from *H. cuvieri* (195–386 mm FL) and 74 from *S. macrocephalus* (120–302 mm TL). A significant proportion of these were empty; 75% for *C. gariepinus*, 72% for *H. cuvieri* and 81% for *S. macrocephalus*. *Clarias gariepinus* and *H. cuvieri* ate exclusively fish, while *S. macrocephalus* also ate aquatic insects (Table 5.1). Cichlidae were the only fish identified in the stomachs of *C. gariepinus*. In addition to cichlids, alestids were among the prey of *H. cuvieri* and *S. macrocephalus*. Cichlidae constituted the bulk of *H. cuvieri* prey, while alestids were more important to *S. macrocephalus*. The most frequently identified cichlid

prey species were *Tilapia sparrmanii* and *Pharyngochromis acuticeps*. Larger *Oreochromis* spp. also contributed notably to the diet of *C. gariepinus*.

Table 5.1. Stomach contents of *Clarias gariepinus* (n = 16), *Hepsetus cuvieri* (n = 35) and *Serranochromis macrocephalus* (n = 14) by % number (%N), % volume (%W) and % frequency of occurrence (%FO), and the % index of relative importance (%IRI) of each prey category.

Species and prey category		%N	%W	%FO	%IRI
<i>Clarias gariepinus</i>					
Fish	Fish remains	23.53	8.27	6.35	5.50
	Cichlidae	76.47	91.73	20.63	94.50
<i>Hepsetus cuvieri</i>					
Fish	Fish remains	26.32	8.22	8.00	7.91
	Cichlidae	71.05	89.66	20.00	91.98
	Alestidae	2.63	2.12	0.80	0.11
<i>Serranochromis macrocephalus</i>					
Fish	Fish remains	35.29	30.00	8.11	40.48
	Cichlidae	17.65	13.79	4.05	9.75
	Alestidae	41.18	53.45	6.76	48.88
Aquatic invertebrates	Insect remains	5.88	2.76	1.35	0.89

Of the 241 *S. intermedius* (90–273 mm FL) stomachs examined, 43% were empty. A diverse range of prey were recorded from stomachs that did contain food, including fish, aquatic and terrestrial invertebrates, insect eggs and detritus (Table 5.2). Fish, in particular cichlids, were the most important food source for *S. intermedius* in Lake Liambezi. The most commonly identified cichlid species were *T. sparrmanii* and *P. acuticeps*. Of the aquatic invertebrates, Ephemeroptera were the only order to contribute significantly to the diet of *S. intermedius*.

The stomach contents of 39 *B. lateralis* (24–127 mm FL) were examined, of which 23% were empty. Identifiable stomach contents included fish, aquatic invertebrates, insect eggs and plant matter (Table 5.3). A large portion of the aquatic invertebrate prey were masticated, and could not be identified further. Diptera larvae, primarily *Chaobrus* spp., were the most important prey item identified, accounting for nearly half of the diet of *B. lateralis*.

Planktonic crustacea and fish had similar contributions, followed by insect eggs.

Table 5.2. Stomach contents of *Schilbe intermedius* (n = 137) by % number (%N), % weight (%W) and % frequency of occurrence (%FO), and the % index of relative importance (%IRI) of each prey category.

Prey category		%N	%W	%FO	%IRI
Fish	Fish remains	9.73	10.45	15.35	12.54
	Cichlidae	13.57	69.36	19.09	64.08
	Alestidae	1.36	10.83	2.07	1.02
Aquatic invertebrates	Cyprinodontidae	0.45	0.24	0.41	0.01
	Insect remains	8.60	1.89	15.77	6.69
	Ephemeroptera	36.20	4.83	7.47	12.41
	Trichoptera	0.23	0.03	0.41	0.00
	Coleoptera	0.23	0.00	0.41	0.00
	Hemiptera	0.23	0.00	0.41	0.00
	Odonata	0.90	0.24	1.66	0.08
	Diptera	19.68	0.86	3.32	2.76
	Decapoda	1.13	0.37	1.24	0.08
	Gastropoda	0.23	0.02	0.41	0.00
	Terrestrial invertebrates	Lepidoptera	0.23	0.07	0.41
Orthoptera		0.90	0.29	1.66	0.08
Araneae		0.23	0.03	0.41	0.00
Insect eggs		5.66	0.17	0.83	0.20
Detritus		0.45	0.31	0.83	0.03

Table 5.3. Stomach contents of *Brycinus lateralis* (n = 30) by % number (%N), % volume (%V) and % frequency of occurrence (%FO), and the % index of relative importance (%IRI) of each prey category.

Prey category		%N	%V	%FO	%IRI
Fish	Fish remains	4.19	20.05	20.51	7.88
Aquatic invertebrates	Insect remains	9.95	27.11	46.15	27.09
	Ephemeroptera	2.62	4.33	7.69	0.85
	Trichoptera	2.09	4.10	7.69	0.75
	Odonata	0.52	1.67	2.56	0.09
	Diptera	53.93	18.73	41.03	47.22
	Crustacea	18.85	0.75	25.64	7.96
	Insect eggs		4.71	12.99	23.08
Plant matter		1.05	4.93	5.13	0.49
Unidentified		2.09	5.33	10.26	1.21

Stable isotope analysis

Food web structure

In 2011, 424 samples were collected for stable isotope analysis, comprised of 3 basal carbon sources, 4 general invertebrate groups and 30 fish species (Tables 5.4 and 5.5). In 2012, 318 samples were collected, comprising 4 basal carbon sources, 3 general invertebrate groups and 26 fish species. The $\delta^{13}\text{C}$ values of basal resources ranged between -33 and -9‰ in 2011, and between -32 and -13 ‰ in 2012 (Table 5.4; Figure 5.1). POM had the lowest $\delta^{13}\text{C}$ of all basal

resources, averaging approximately -30‰ in both years. The $\delta^{13}\text{C}$ of emergent plants and filamentous algae, both of which were only collected in 2012, were slightly higher, with average values of -26 and -23‰, respectively. Submerged plants had average $\delta^{13}\text{C}$ values of -21 and -20‰ in 2011 and 2012, respectively. Detritus, which was only collected in 2011, had the highest average $\delta^{13}\text{C}$ value of -18‰. The $\delta^{15}\text{N}$ values of different basal resources sampled in 2011 were similar (3–4‰). However, in 2012 plants and algae had much lower $\delta^{15}\text{N}$ values than POM. This discrepancy is most likely a result of the high natural variability in $\delta^{15}\text{N}$ values of plants. Indeed, the isotope values of submerged plants did not differ significantly between 2011 and 2012 (PERMANOVA; *Pseudo-F* = 2.04, *P* = 0.145). The isotope values of POM were also consistent between years (PERMANOVA; *Pseudo-F* = 3.51, *P* = 0.053).

Table 5.4. Carbon and nitrogen stable isotope values (mean \pm standard deviation) of invertebrates and basal resources sampled in Lake Liambezi in 2011 and 2012.

Groups	2011			2012		
	<i>n</i>	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	<i>n</i>	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$
Invertebrates						
Aquatic insects	10	-28.32 \pm 3.62	6.14 \pm 2.79	24	-26.67 \pm 2.40	5.95 \pm 1.30
Decapods	10	23.96 \pm 0.94	7.22 \pm 0.63	5	-25.43 \pm 0.62	5.79 \pm 0.21
Herbivorous zooplankton	3	-30.75 \pm 0.97	6.08 \pm 0.81	-	-	-
Predatory zooplankton	9	-30.16 \pm 1.35	10.05 \pm 0.68	2	-29.66 \pm 0.08	9.89 \pm 0.03
Basal resources						
POM	17	-30.71 \pm 1.63	4.02 \pm 0.54	16	-29.62 \pm 1.42	4.16 \pm 0.87
Detritus	30	-17.68 \pm 4.09	3.25 \pm 1.14	-	-	-
Filamentous algae	-	-	-	3	-23.20 \pm 1.52	1.63 \pm 0.43
Emergent plants	-	-	-	15	-25.72 \pm 1.28	2.46 \pm 2.92
Submerged plants	7	-21.47 \pm 5.76	3.00 \pm 2.82	25	-19.54 \pm 3.62	0.93 \pm 1.82

Consumer $\delta^{13}\text{C}$ values were between those of POM (-30‰) and submerged plants (-20‰) in both 2011 and 2012 (Table 5.4 and 5.5; Figure 5.1). Four groups of primary consumers can be identified in Figure 5.1, that likely represent three different pathways by which energy from basal resources is assimilated into the food web. Herbivorous zooplankton had the lowest $\delta^{13}\text{C}$ of all consumers. Their position in isotopic space suggests that their diets consist exclusively of POM. Aquatic insects also had low, but more variable $\delta^{13}\text{C}$ values, indicating that while this diverse group relies primarily on POM, they also assimilate carbon from a range of other basal resources. The aquatic insect group consists mainly of benthic insects, so the POM they consume will have settled out of the water column, possibly in the form of planktonic detritus. The third group of primary consumers is the tilapiine cichlids. In 2011, these fish had a higher $\delta^{13}\text{C}$ value than other consumers, which may indicate that a greater

portion of their carbon was derived from aquatic plants and detritus compared to other consumers. Aquatic plants are unlikely to contribute significantly to consumer carbon directly, since only *Coptodon rendalli* feed extensively on macrophytes. They may, however, contribute in the form of detritus. Based on their positioning in the isotopic biplots (Figure 5.1) detritus in Lake Liambezi is most likely to be primarily derived from submerged plants.

The average $\delta^{13}\text{C}$ of tilapiine cichlids was 3‰ lower in 2012 compared to 2011, possibly indicating a shift to a more POM based diet. Further sampling of the tilapiine cichlids was carried out in 2014 to establish whether the shift to a lower $\delta^{13}\text{C}$ diet was permanent. Eleven samples were collected for each of four species (*Oreochromis andersonii*, *Oreochromis macrochir*, *C. rendalli* and *T. sparrmanii*). $\delta^{13}\text{C}$ values differed significantly between the three years for *C. rendalli* (PERMANOVA; *Pseudo-F* = 8.48, *P* = 0.001) and *T. sparrmanii* (PERMANOVA; *Pseudo-F* = 4.69, *P* = 0.015). For both species, post hoc pair-wise comparisons revealed that $\delta^{13}\text{C}$ was significantly lower in 2012 compared to 2011 and 2014. $\delta^{13}\text{C}$ values did not differ significantly between years for *O. andersonii* (PERMANOVA; *Pseudo-F* = 1.53, *P* = 0.233) or *O. macrochir* (PERMANOVA; *Pseudo-F* = 2.33, *P* = 0.113). The differences in $\delta^{13}\text{C}$ between 2011 and 2012 were likely the result of inter-annual dietary variation, and probably did not represent a permanent diet shift in the tilapiine cichlids. Two other groups of fishes showed changes in trophic position between years. Cyprinids showed a decrease in $\delta^{13}\text{C}$, and topminnows an increase in $\delta^{13}\text{C}$ and decrease in $\delta^{15}\text{N}$ between 2011 and 2012. The changes were not investigated further because both groups are minor components of the fish community, and are unlikely to significantly alter major pathways of energy flow through the food web. The trophic structure of the remainder of the fish community appeared to be very similar between years. Community-wide stable isotope metrics were used to quantitatively assess the similarity between years.

Table 5.5. Carbon and nitrogen stable isotope values (mean \pm standard deviation) of fish species sampled in Lake Liambezi in 2011 and 2012, and the taxonomic/feeding group to which species were assigned for broad food web analysis.

Species	2011			2012			Group
	<i>n</i>	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	<i>n</i>	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	
Fish							
<i>Brycinus lateralis</i>	28	-26.71 \pm 1.40	9.82 \pm 0.85	32	-27.89 \pm 2.20	9.81 \pm 0.98	Alestids
<i>Rhabdalestes maunensis</i>	21	-27.97 \pm 0.93	9.89 \pm 0.41	10	-26.15 \pm 1.31	9.64 \pm 0.62	Alestids
<i>Enteromius barnardi</i>	1	-29.16	8.71	-	-	-	Cyprinids
<i>Enteromius bifrenatus</i>	3	-21.66 \pm 1.19	7.36 \pm 0.37	7	-31.31 \pm 0.99	9.11 \pm 0.88	Cyprinids
<i>Enteromius haasianus</i>	6	-24.45 \pm 0.84	8.26 \pm 0.39	-	-	-	Cyprinids
<i>Enteromius poechii</i>	8	-23.14 \pm 2.96	8.25 \pm 0.81	2	-27.10 \pm 0.70	8.36 \pm 0.03	Cyprinids
<i>Enteromius radiatus</i>	21	-25.55 \pm 2.01	8.38 \pm 0.56	11	-26.32 \pm 0.46	8.50 \pm 0.89	Cyprinids
<i>Enteromius unitaeniatus</i>	9	-27.07 \pm 0.80	9.04 \pm 0.36	-	-	-	Cyprinids
<i>Coptostomobarbus wittei</i>	3	-26.85 \pm 2.21	9.90 \pm 0.55	-	-	-	Cyprinids
<i>Labeo cylindricus</i>	1	-24.27	7.78	1	-24.54	8.03	Cyprinids
<i>Pharyngochromis acuticeps</i>	21	-26.94 \pm 2.02	8.46 \pm 0.76	16	-27.60 \pm 2.28	8.92 \pm 1.17	Benthic cichlids
<i>Pseudocrenilabrus philander</i>	17	-24.00 \pm 2.41	9.42 \pm 0.73	5	-23.89 \pm 1.05	8.54 \pm 0.79	Benthic cichlids
<i>Sargochromis</i> sp. "green bream"	20	-24.68 \pm 2.12	8.30 \pm 0.69	1	-23.93	8.82	Benthic cichlids
<i>Sargochromis carlottae</i>	-	-	-	3	-25.37 \pm 2.62	9.47 \pm 1.66	Benthic cichlids
<i>Schilbe intermedius</i>	25	-25.26 \pm 2.24	8.95 \pm 1.04	29	-26.08 \pm 1.82	9.50 \pm 0.83	Generalist predators
<i>Clarias ngamensis</i>	11	-24.46 \pm 2.20	8.92 \pm 0.46	1	-24.23	9.80	Generalist predators
<i>Clarias theodora</i>	1	-22.93	10.55	-	-	-	Generalist predators
<i>Synodontis</i> spp.	17	-27.84 \pm 2.01	9.25 \pm 0.88	3	-26.81 \pm 0.36	10.30 \pm 0.51	Generalist predators
<i>Marcusenius altisambesi</i>	13	-25.67 \pm 2.27	7.51 \pm 0.76	2	-27.74 \pm 3.52	7.70 \pm 0.21	Mormyrids
<i>Petrocephalus</i> cf. <i>okavangensis</i>	7	-26.08 \pm 1.01	9.11 \pm 0.55	6	-25.59 \pm 1.74	8.93 \pm 0.40	Mormyrids
<i>Mormyrus lacerda</i>	1	-30.63	9.30	-	-	-	Mormyrids
<i>Cyphomyrus cubangoensis</i>	-	-	-	1	-26.00	9.20	Mormyrids
<i>Serranochromis macrocephalus</i>	16	-25.49 \pm 2.21	10.35 \pm 0.78	10	-25.56 \pm 2.12	10.48 \pm 1.33	Piscivores
<i>Serranochromis robustus jallae</i>	3	-20.57 \pm 0.65	9.37 \pm 0.41	1	-21.59	9.37	Piscivores
<i>Hepsetus cuvieri</i>	11	-23.69 \pm 1.99	9.91 \pm 0.80	10	-24.61 \pm 3.19	10.36 \pm 1.32	Piscivores
<i>Clarias gariepinus</i>	5	-24.74 \pm 2.36	9.88 \pm 0.46	7	24.33 \pm 1.62	10.04 \pm 0.73	Piscivores
<i>Oreochromis andersonii</i>	10	-26.14 \pm 4.09	6.34 \pm 0.88	20	-27.90 \pm 1.97	7.73 \pm 1.41	Tilapiine cichlids
<i>Oreochromis macrochir</i>	12	-22.46 \pm 1.89	5.38 \pm 0.68	14	-24.49 \pm 2.76	5.15 \pm 0.90	Tilapiine cichlids
<i>Coptodon rendalli</i>	18	-21.92 \pm 3.86	7.12 \pm 0.98	8	-25.75 \pm 2.47	6.70 \pm 1.14	Tilapiine cichlids
<i>Tilapia sparrmanii</i>	16	-24.55 \pm 1.78	7.60 \pm 1.38	18	-26.95 \pm 3.44	7.54 \pm 1.35	Tilapiine cichlids
<i>Tilapia ruweti</i>	2	-21.74 \pm 1.08	8.18 \pm 1.17	-	-	-	Tilapiine cichlids
<i>Micropanchax johnstoni</i>	11	-26.20 \pm 2.11	9.78 \pm 0.50	6	-23.92 \pm 1.00	8.34 \pm 0.53	Topminnows
<i>Micropanchax hutereaui</i>	-	-	-	4	-22.06 \pm 0.72	8.31 \pm 0.38	Topminnows

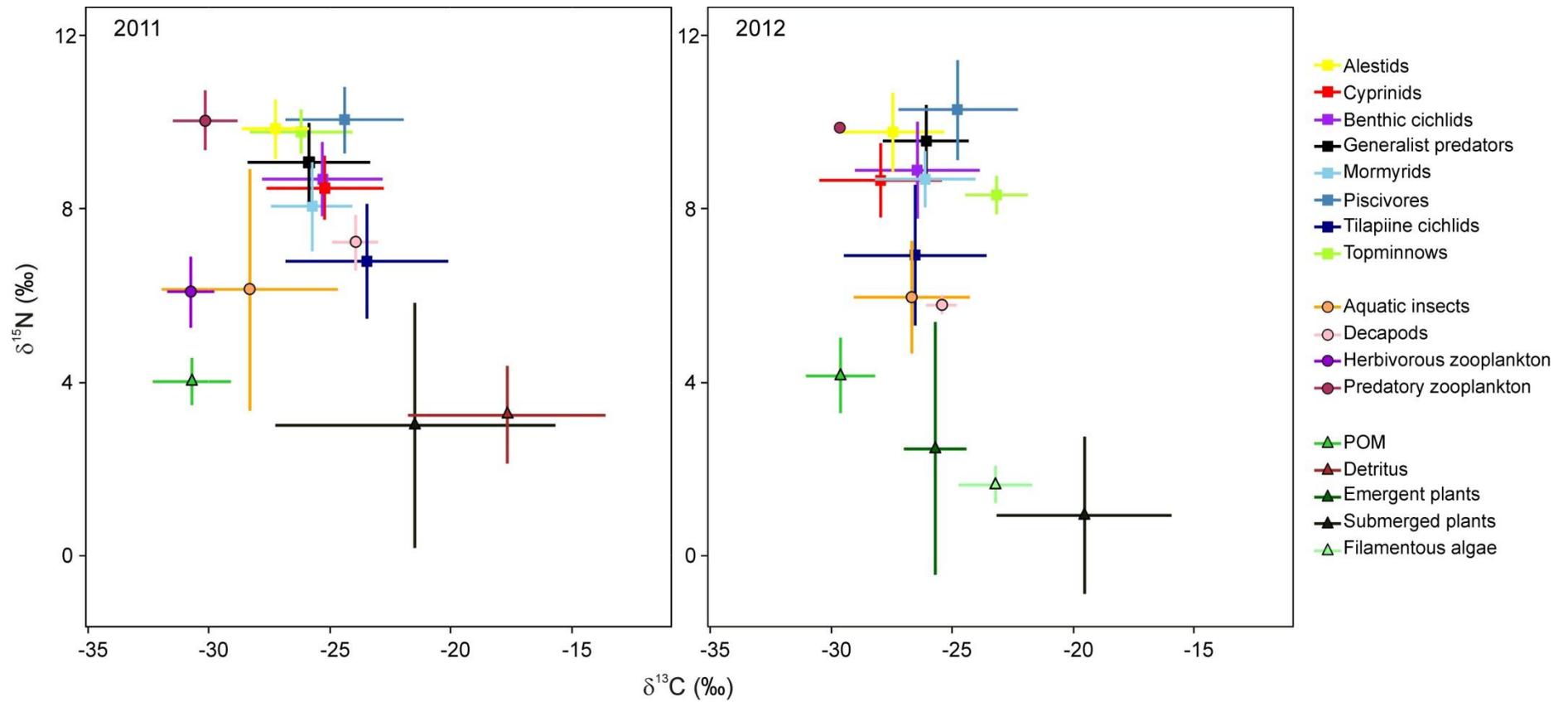


Figure 5.1. Stable $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ isotopic bi-plots of fish groups and their potential food sources from Lake Liambezi in 2011 and 2012. Data points represent the mean, and error bars the standard deviation for each group.

Community metrics

The NR and CR of the fish community in 2012 were higher than in 2011 (Table 5.6), suggesting that both the trophic length and range of basal resources used by the fish community in 2012 was greater. However, the average degree of trophic diversity, measured by the CD, was similar between years. Lower MNND and SDNND in 2011 indicate greater density and evenness of species packing in bi-plot space. For each metric, the difference between years was relatively small, and the overlap of 95% confidence intervals was substantial. The core isotopic niche area (SEA_c) of the whole fish community (Figure 5.2) was slightly larger in 2012 compared to 2011, corroborating results of the other metrics. The degree of overlap between years was also significant. The 2011 SEA_c overlapped with the 2012 SEA_c by 68.3%. The 2012 SEA_c overlapped with the 2011 SEA_c by an even greater 76.8%. Overall, the trophic structure of the fish communities sampled in 2011 and 2012 were therefore very similar. However, the inter-annual variations in trophic positions of the tilapiine cichlids, cyprinids and topminnows precluded the combination of both datasets. As a result, further analyses on the fish community were based only on isotope data collected in 2011, as this was the more comprehensive of fish datasets.

Table 5.6. Stable isotope community metrics (mean with 95% CI in parentheses) comparing the trophic structure of fish communities sampled from Lake Liambezi in 2011 and 2012. NR = $\delta^{15}\text{N}$ range; CR = $\delta^{13}\text{C}$ range; CD = mean distance to centroid; MNND = mean nearest neighbour distance; SDNND = standard deviation of nearest neighbour distance; SEA_c = core isotopic niche area of the community (‰^2).

Metric	2011	2012
NR	5.03 (4.43–5.66)	5.67 (4.84–6.74)
CR	6.95 (5.59–8.89)	7.95 (6.72–9.49)
CD	2.12 (1.88–2.38)	2.05 (1.83–2.28)
MNND	0.87 (0.67–1.08)	0.98 (0.80–1.18)
SDNND	0.54 (0.33–0.79)	0.79 (0.53–1.06)
SEA_c	11.93	13.42
Sample size (<i>n</i>)	259	212

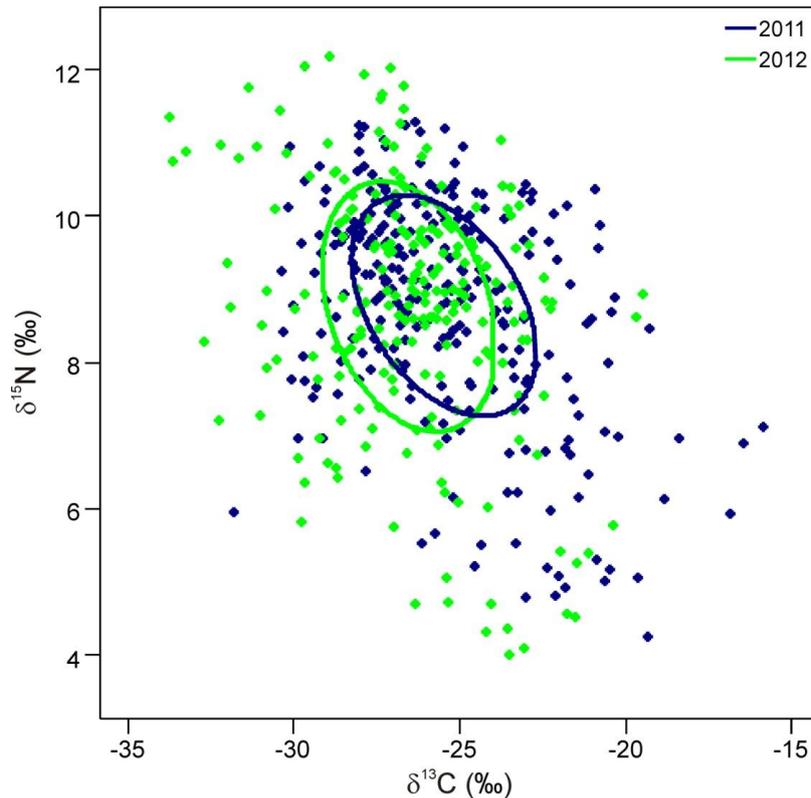


Figure 5.2. The core isotopic niche areas (SEAc) of the whole fish communities in Lake Liambezi in 2011 and 2012.

Trophic structure and species interactions

The SEAc of each group in the fish community are illustrated in Figure 5.3, and the SEAc size and percentage overlap between groups is presented in Table 5.7. Tilapiine cichlids occupied the lowest trophic position in the fish community, and did not show much SEAc overlap with other groups, indicating that they are the only primary consumers in the fish community. Their SEAc was large, suggesting a greater degree of trophic diversity compared to other groups. At the next trophic level there was considerable overlap in isotopic space between cyprinids, benthic cichlids, mormyrids and generalist predators, all of which had similar size SEAc. These four groups were most likely primarily dependent upon aquatic insects for their food resources. Alestids and topminnows occupied a slightly higher trophic level, with considerable SEAc overlap between the two groups. Alestids had the smallest SEAc of any group, indicative of dietary specialisation. Their elevated trophic position and relatively low $\delta^{13}\text{C}$ reflects a diet composed of both herbivorous and predatory zooplankton. Piscivores occupied the highest trophic level in Lake Liambezi, and overlapped relatively little with other groups. The trophic positions of individual fish species within important consumer groups were examined further to elucidate interspecific trophic interactions, and the potential role they may have played in community succession prior to 2011 (see Chapter 4).

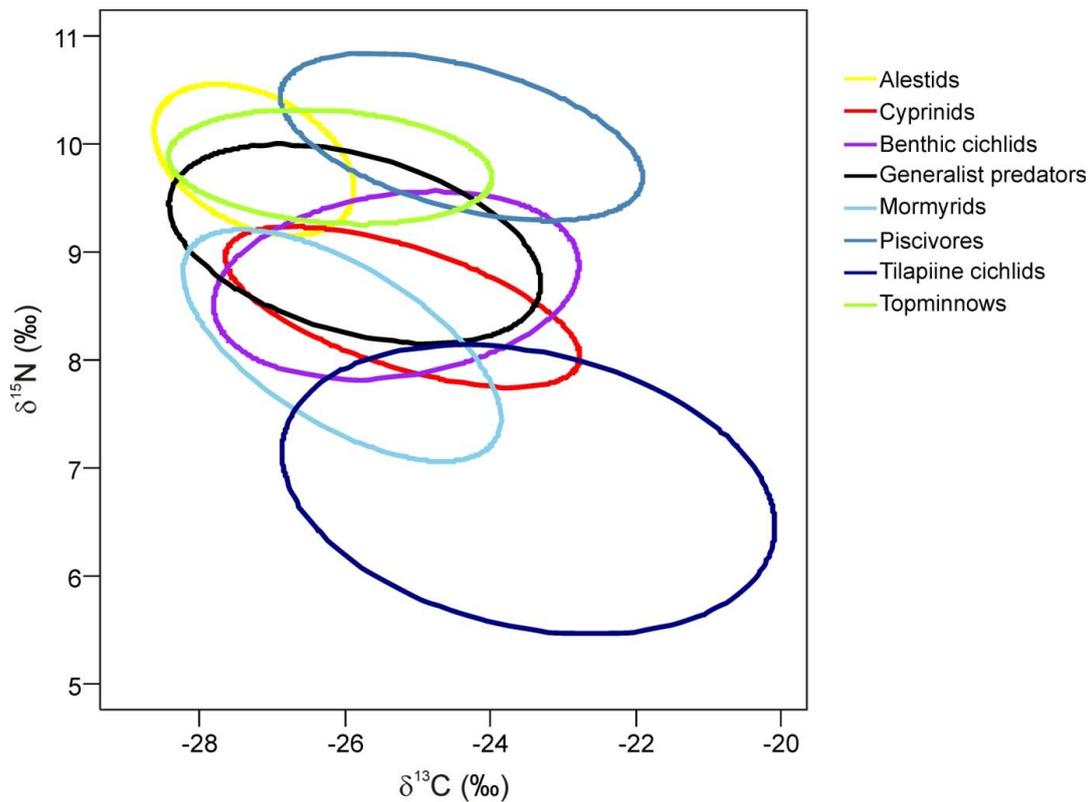


Figure 5.3. The core isotopic niche areas (SEAc) of fish groups in Lake Liambezi in 2011.

Table 5.7. The core isotopic niche area (SEAc) and percent overlap between fish groups in Lake Liambezi in 2011. Columns indicate the group niche area being overlapped, e.g. 82.5 % of the cyprinids niche is overlapped by benthic cichlids, while 55.1% of the benthic cichlids niche is overlapped by Cyprinids. Alest. = Alestids, Cypr. = Cyprinids, B. cich. = Benthic cichlids, G. pred. = Generalist predators, Mormy. = Mormyrids, Pesci. = Piscivores, T. cich. = Tilapiine cichlids, Topm. = Topminnows.

	SEAc	Alest.	Cypr.	B. cich.	G. pred.	Mormy.	Pesci.	T. cich.	Topm.
Alest.	2.80		1.2	2.3	23.1	0.0	3.2	0.0	53.8
Cypr.	4.47	1.9		55.1	45.5	41.9	0.0	5.6	0.0
B. cich.	6.69	5.6	82.5		66.4	54.7	4.7	2.8	13.0
G. pred.	6.78	56.0	69.0	67.2		34.1	8.2	0.0	55.7
Mormy.	5.71	0.1	53.6	46.7	28.8		0.0	15.7	0.0
Pesci.	5.31	6.0	0.0	3.7	6.4	0.0		0.0	40.2
T. cich.	13.77	0.0	17.3	5.9	0.0	37.8	0.0		0.0
Topm.	3.64	70.0	0.0	7.1	29.9	0.0	27.5	0.0	

The trophic level of the alestids *B. lateralis* and *Rhabdalestes maunensis* was similar to that of the piscivores in Lake Liambezi. *Brycinus lateralis*, the larger of the two alestids, had a SEAc of 3.36‰². *Rhabdalestes maunensis* had a significantly smaller SEAc of 1.24‰²,

48.9% of which was overlapped by *B. lateralis* (Figure 5.4). In contrast, only 18.1% of the core niche of *B. lateralis* was overlapped by *R. maunensis*.

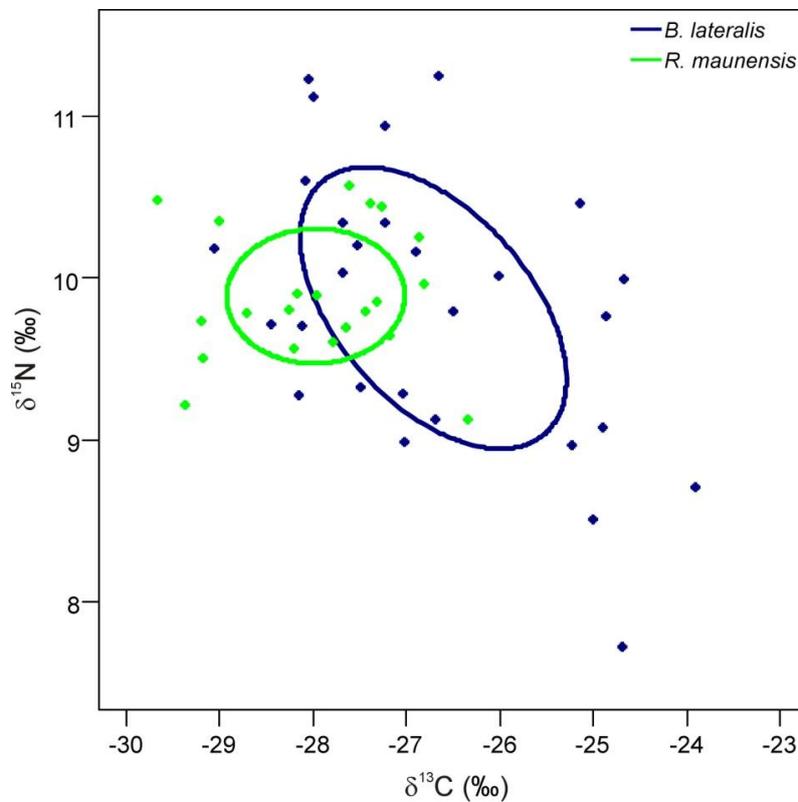


Figure 5.4. The core isotopic niche areas (SEAc) of alestid species in Lake Liambezi in 2011.

Of the four tilapiine cichlids, *O. macrochir* had the smallest SEAc and lowest trophic position (Figure 5.5), indicating this species was a highly specialised primary consumer. The much larger isotopic niche of *O. andersonii* overlapped with that of *O. macrochir* by approximately one third (Table 5.8). *Oreochromis andersonii* generally had a lower $\delta^{13}\text{C}$ and higher $\delta^{15}\text{N}$ than *O. macrochir*. *Coptodon rendalli* had the largest SEAc of the four species, perhaps reflective of the extremely variable isotope values of submerged plants. *Coptodon rendalli* occupied a higher trophic level than both *Oreochromis* spp., and did not overlap with either. It did, however, overlap with *T. sparrmanii*. *Tilapia sparrmanii* had a slightly smaller SEAc, and had a lower $\delta^{13}\text{C}$ than *C. rendalli*. The SEAc of *T. sparrmanii* was laterally compressed in shape, suggesting that the species feeds on a narrow range of basal resources, but exhibits large variation in trophic level.

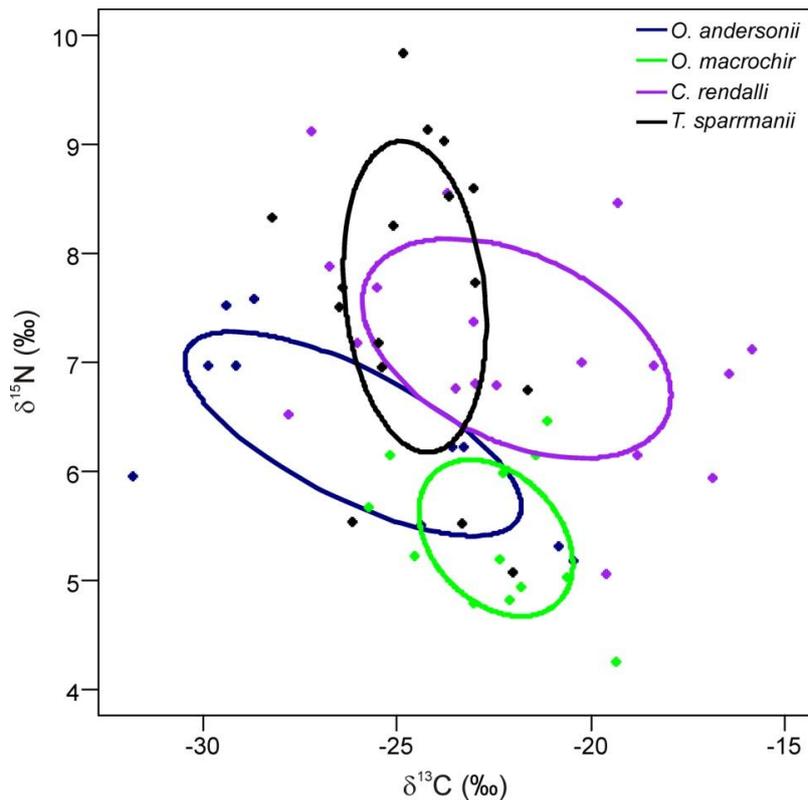


Figure 5.5. The core isotopic niche areas (SEAc) of four tilapiine cichlid species in Lake Liambezi in 2011.

Table 5.8. The core isotopic niche area (SEAc) and percent overlap between tilapiine cichlid species in Lake Liambezi in 2011.

	SEAc	<i>O. andersonii</i>	<i>O. macrochir</i>	<i>C. rendalli</i>	<i>T. sparrmanii</i>
<i>O. andersonii</i>	8.9		35.7	0.1	12.0
<i>O. macrochir</i>	4.2	16.9		0.0	0.0
<i>C. rendalli</i>	11.4	0.1	0.0		49.6
<i>T. sparrmanii</i>	8.1	10.9	0.0	35.3	

The core niche areas of piscivores and generalist predators were examined together. The two most abundant generalist predators, *S. intermedius* and *Clarias ngamensis* occupied a lower trophic level than the top piscivores (Figure 5.6). *Schilbe intermedius* had the larger SEAc of the two species, which overlapped considerably with that of *C. ngamensis* (Table 5.9). There was also extensive SEAc overlap among the three piscivores. Half the SEAc of *H. cuvieri*, and two thirds the SEAc of *C. gariepinus* were overlapped by *S. macrocephalus*.

Serranochromis macrocephalus had a similarly large SEAc size to that of *S. intermedius*. The large isotopic niche of *S. macrocephalus* revealed by stable isotope analysis is contrary to the dietary specialisation inferred from stomach contents analysis. However, the smaller SEAc of

H. cuvieri and *C. gariepinus* appear to confirm that they are relatively specialised piscivores. For both *H. cuvieri* and *C. gariepinus*, $\delta^{15}\text{N}$ tended to decrease with increasing $\delta^{13}\text{C}$.

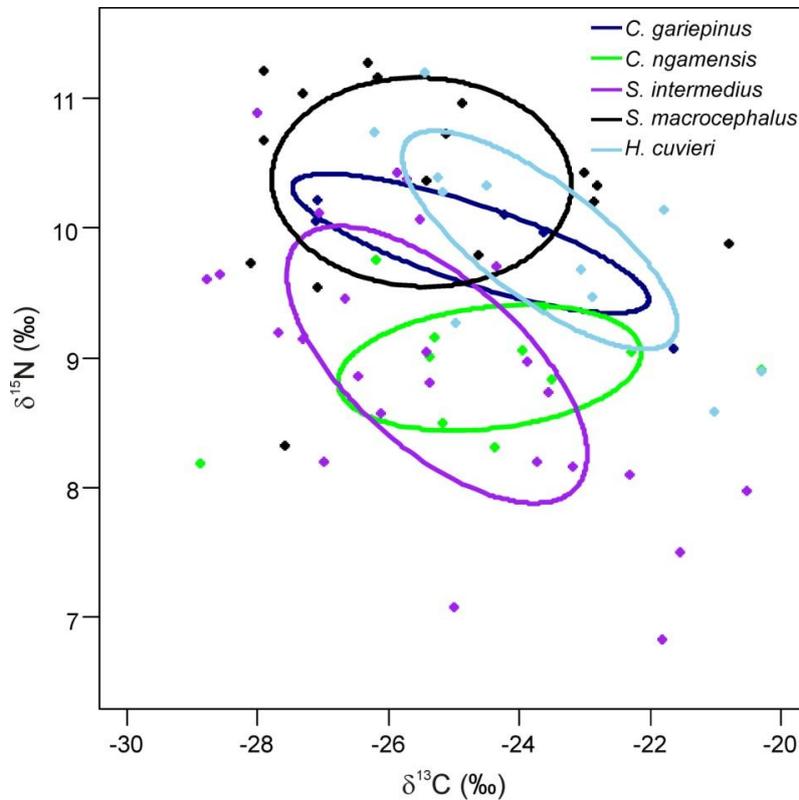


Figure 5.6. The core isotopic niche areas (SEAc) of predatory fish species in Lake Liambezi in 2011.

Table 5.9. The core isotopic niche area (SEAc) and percent overlap between predatory fish species in Lake Liambezi in 2011. *C.gar.* = *Clarias gariepinus*, *C. nga.* = *Clarias ngamensis*, *S. int.* = *Schilbe intermedius*, *S. mac.* = *Serranochromis macrocephalus*, *H. cuv.* = *Hepsetus cuvieri*.

	SEAc	<i>C. gar.</i>	<i>C. nga.</i>	<i>S. int.</i>	<i>S. mac.</i>	<i>H. cuv.</i>
<i>C. gar.</i>	2.73		0.0	3.7	31.7	42.7
<i>C. nga.</i>	3.41	0.1		42.2	0.0	6.1
<i>S. int.</i>	5.83	7.9	72.1		11.6	0.0
<i>S. mac.</i>	5.77	67.0	0.0	11.5		50.3
<i>H. cuv.</i>	3.55	55.7	6.4	0.0	31.0	

Discussion

The aims of this chapter were to determine which primary production sources supported consumer biomass in Lake Liambezi, describe the trophic structure of the fish community, and examine the role of trophic interactions in shaping the lacustrine fish community.

Primary production sources supporting fishes

Stable isotope data indicated that phytoplankton associated with POM was the primary carbon source supporting consumer biomass in Lake Liambezi. Aquatic macrophytes, the most conspicuous source of primary production in the lake, contributed to a significantly lesser degree. These results support isotope studies that highlight the importance of algal carbon in aquatic food webs, even when aquatic macrophytes are the dominant primary producers (Araujo-Lima *et al.* 1986; Bunn and Boon 1993; Forsberg *et al.* 1993; Lewis *et al.* 2001; Herwig *et al.* 2004). Terrestrial C₃ macrophytes can also be important carbon sources for aquatic food webs, particularly when algal growth is light limited (Zeug and Winemiller 2008a; Roach and Winemiller 2015). The probability of a significant contribution of terrestrial carbon in Lake Liambezi, except during the filling phase, was deemed small, due to the large surface area of the lake relative to its circumference, and the fact that the lake is shallow, thus benthic fish are not restricted to nearshore areas that receive greater terrestrial carbon inputs.

Trophic pathways

Carbon from phytoplankton and aquatic macrophytes was assimilated into the food web via three major pathways, one of which was pelagic and two of which were benthic. Phytoplankton was assimilated directly by small, herbivorous zooplankton. During the previous inundation period these were dominated by *Bosmina longirostis* and several rotifer species (Seaman *et al.* 1978). They are preyed upon by larger zooplankton, such as copepods and chaoborid larvae, and small zooplanktivorous fishes that include the alestids *B. lateralis* and *R. maunensis*. Chaoborid and other diptera larvae made up a significant portion of the diet of *B. lateralis*, yet $\delta^{15}\text{N}$ values revealed that they occupied the same trophic level. This may be due to several factors including different tissue turnover rates among species, variable $\delta^{15}\text{N}$ values among sampling periods, and seasonal variation in the abundance of diptera larvae and/or their importance in the diet of *B. lateralis*. *Brycinus lateralis* stomach contents were sampled in February, while isotope samples were collected in August. Greater reliance upon small, herbivorous zooplankton and aquatic insects in August could account for the similar $\delta^{15}\text{N}$ values between predatory zooplankton and zooplanktivorous fish. Marshall and Van der Heiden (1977) noted significant seasonal variation in the diet of *Brycinus imberi* in Lake Chivero, Zimbabwe. Chironomid and chaoborid larvae were extremely abundant in Lake Chivero between January and April, and made up a significant portion of the diet of *B. imberi* during that period. A wide range of other food sources were utilised during the

remainder of the year, including emergent beetle, termite and ant alates, cladocera, plant seeds and grasses. *Brycinus lateralis* from the Okavango Delta, Botswana, display similarly diverse and opportunistic feeding behaviour, consuming a wide variety of insects of different life-history stages, particularly eggs, as well as cladocera, seeds and other plant matter (Booth and McKinlay 2001).

The second major pathway by which basal carbon was assimilated into the food web was via aquatic insects that feed primarily on detritus of planktonic origin. Among the most important aquatic insects in Lake Liambezi are diptera larvae, ephemeroptera, trichoptera and odonata nymphs (Seaman *et al.* 1978). Aquatic insects, in turn, supported numerous fish species, including mormyrids, benthic cichlids, cyprinids, and to a lesser degree, generalist predators. Some of the most specialised insectivorous fishes in Lake Liambezi are the mormyrids *Petrocephalus cf. okavangensis* and *Marcusenius altisambesi*. Both species feed primarily on the dominant aquatic insect groups mentioned above, with *P. cf. okavangensis* consuming proportionally more Ephemeroptera, and *M. altisambesi* more Diptera (van der Waal 1985). Winemiller and Adite (1997) observed a greater dietary differentiation between the two species in the Upper Zambezi River, Zambia, describing *P. cf. okavangensis* as a midwater zooplanktivore, and *M. altisambesi* as a benthic invertivore. The average $\delta^{15}\text{N}$ of *P. cf. okavangensis* was approximately 1.4‰ higher than that of *M. altisambesi*, apparently corroborating Winemiller and Adite's (1997) observations that *P. cf. okavangensis* feed on more predatory zooplankton. The three other mormyrid species sampled in Lake Liambezi, *Mormyrus lacerda*, *Pollimyrus marianne*, and *Cyphomyrus cubangoensis*, were uncommon.

The benthic cichlid group occupied similar isotopic space to that of the mormyrids. The group comprised four species, the small sized *P. acuticeps* and *Pseudocrenilabrus philander*, and medium sized *Sargochromis* sp. “green bream” and *Sargochromis carlottae*. The diets of these cichlids are much more diverse and flexible than those of the mormyrids, with all four species exhibiting some degree of omnivory (van der Waal 1985; Winemiller 1991; Zengeya and Marshall 2007). *Sargochromis* sp. for example, fed primarily on *Nymphaea* spp. seeds and chironomid larvae in Lake Liambezi (van der Waal 1985), grass seeds and aquatic insects in the Upper Zambezi River (Winemiller 1991), and almost exclusively on gastropods in Lake Kariba (Moyo and Fernando 1999). In Lake Liambezi *P. acuticeps* mainly consumes aquatic insects, followed by plant material and detritus (van der Waal 1985). *Pharyngochromis acuticeps* is one of the most numerically abundant cichlid species in Lake Liambezi, and an

important prey species of the top piscivores. It therefore plays an important role in moving energy up the food web.

Cyprinids were among the most prolific colonisers of Lake Liambezi (see Chapters 2), and undoubtedly played a major part in food web dynamics at that time. After the lake filled in 2009, however, all cyprinid species became progressively less abundant (see Chapter 4). Their ecological role will have declined correspondingly, so that when the fish community began to stabilise in 2011 the cyprinids were neither influential consumers nor important prey species. While they shared a large portion of isotopic space with the largely invertivorous benthic cichlids and mormyrids, they are unlikely to have been in direct competition with those species.

The third major pathway by which basal carbon was assimilated into the food web involved the tilapiine cichlids. The tilapiine cichlid group occupied the lowest trophic level of all the fish in Lake Liambezi, indicating that they were largely primary consumers. The group comprised five species, one of which, the floodplain specialist *Tilapia ruweti* was rare, and only sampled in 2011. The remaining four species, *O. andersonii*, *O. macrochir*, *C. rendalli* and *T. sparrmanii* are common and widely distributed throughout the lake. *Coptodon rendalli* is regarded as being a specialised macrophyte feeder. The most important aquatic macrophyte identified in the diet of *C. rendalli* in Lake Liambezi is *L. ilicifolius* (van der Waal 1985). In contrast, *C. rendalli* in the Upper Zambezi River consumed mostly grasses and sedges (Winemiller and Kelso-Winemiller 2003). The disparity is most likely the result of differences in habitat and plant communities, with *L. ilicifolius* dominating in Lake Liambezi (Seaman *et al.* 1978; Peel *et al.* 2015b), and aquatic grasses such as *Vossia cuspidata* being more prevalent on the seasonal floodplains of the Upper Zambezi River (Winemiller and Kelso-Winemiller 2003). The relatively high $\delta^{13}\text{C}$ values ($\approx -22\text{‰}$) of *C. rendalli* in 2011 were in line with that of submerged plants, supporting the dietary observations made by van der Waal (1985). *Coptodon rendalli* exhibited a large $\delta^{13}\text{C}$ range in 2011, from -27.8 to -15.9‰, but rather than being indicative of intraspecific dietary variation (e.g. Gu *et al.* 1997), these values may simply reflect the variation in $\delta^{13}\text{C}$ values of submerged plants, which ranged from -30.3 to -15.6‰. Variation in the $\delta^{15}\text{N}$ values of submerged plants may also account for the relatively high $\delta^{15}\text{N}$ range (4.1‰) of *C. rendalli*.

The isotopic niche of *T. sparrmanii* overlapped with that of *C. rendalli* by approximately one third, supporting previous dietary observations that found *T. sparrmanii* consume a small amount of aquatic macrophytes (van der Waal 1985; Winemiller and Kelso-Winemiller 2003; Zengeya and Marshall 2007). The $\delta^{13}\text{C}$ range of *T. sparrmanii* was, however, half that of *C. rendalli*, indicating they are perhaps more selective in their grazing habits. The average $\delta^{15}\text{N}$ of *T. sparrmanii* (7.6‰) was higher than that of the other tilapiine cichlids, with the exception of *T. ruweti*, and the $\delta^{15}\text{N}$ range was greater than that of any other fish species in 2011. Like *C. rendalli*, this may be in part due to the variation in $\delta^{15}\text{N}$ values of aquatic macrophytes. However, the higher average $\delta^{15}\text{N}$ value suggests that *T. sparrmanii* may be omnivorous, feeding at multiple trophic levels. Van der Waal (1985) recorded a variety of aquatic and terrestrial insects, fish remains and zooplankton in the diet of *T. sparrmanii* in the lake. The level of omnivory probably varies within the population, contributing to the large $\delta^{15}\text{N}$ range of *T. sparrmanii*.

The larger *Oreochromis* species had lower $\delta^{15}\text{N}$ values, and shared little isotopic niche space with *C. rendalli* and *T. sparrmanii*. *Oreochromis andersonii* had a similarly wide $\delta^{13}\text{C}$ range to that of *C. rendalli*, but was on average 4‰ more depleted. *Oreochromis andersonii* with lower $\delta^{13}\text{C}$ values were probably more reliant on algal carbon sources, while those with higher $\delta^{13}\text{C}$ values probably consumed more detritus derived from the abundant aquatic macrophytes. Gu *et al.* (1997) observed similar patterns of diet variation in an alien population of *Oreochromis aureus* from a shallow lake in Florida. In contrast, *O. macrochir* occupied a small isotopic niche, and a lower trophic position than *O. andersonii*. The low levels of dietary overlap revealed by stable isotope analysis supports earlier findings from Lake Liambezi based on stomach contents analysis. Van der Waal (1985) identified algae as the most important food source for *O. andersonii* during the previous inundation period, followed by planktonic crustacea and then detritus. *Oreochromis macrochir* consumed mostly fine amorphous detritus, the origin of which was difficult to identify by microscopic examination (van der Waal 1985). Stable isotope analysis indicated that this was derived primarily from submerged plants. A possible explanation for the difficulty in identifying the detritus as being of plant origin, is that it may be derived from dissolved organic matter (DOM). Plants release soluble organic matter when they begin to decompose, which readily precipitates on any surface, forming amorphous particles lacking in cellular structure (Bowen 1984; Mann 1988). The amorphous material, unlike coarse vegetative detritus, has a very low refractory content and is easily digestible by animals without the aid of microbes (Bowen

1984). In the Upper Zambezi River for example, both species consumed a high proportion of coarse vegetative detritus (Winemiller and Kelso-Winemiller 2003). The dietary importance of this may, however, be overestimated by stomach contents analysis, since coarse detritus is generally of poor nutritional value, and is difficult to assimilate due to its high refractory content (Bowen 1984; Mann 1988).

Integrating trophic pathways

While the three trophic pathways discussed above are by no means discrete (fishes may forage across pelagic and benthic food chains), predators occupying the highest trophic levels fully integrate all the different pathways (Vander Zanden and Vadeboncoeur 2002). The dominant predator in Lake Liambezi in terms of biomass was *S. intermedius* (see Chapter 3). *Schilbe intermedius* was considered a generalist predator because it consumed a wide variety of prey items including fish, aquatic and terrestrial insects, decapods and gastropods. The broad, predominantly fish based diet of *S. intermedius* observed during the present study was consistent with previous dietary observations from Lake Liambezi (van der Waal 1985) and neighbouring floodplain rivers (Merron and Mann 1995; Winemiller and Kelso-Winemiller 1996). The only notable difference is that in Lake Liambezi, *S. intermedius* consumed proportionally more cichlids, whereas cyprinids and mormyrids were more important prey in the floodplain rivers. This reflects differences in fish community composition between the different environments. *Schilbe intermedius* shared a significant amount of isotopic niche space with *C. ngamensis*, which also feeds on a wide variety of fish, insects, molluscs and decapods (Willoughby and Tweddle 1978; van der Waal 1985; Winemiller and Kelso-Winemiller 1996). These two species occupied a lower trophic position than the top predators, overlapping more with benthic cichlids, cyprinids and mormyrids.

Stomach contents analysis of the top predators *C. gariepinus*, *H. cuvieri* and *S. macrocephalus*, revealed very narrow piscivorous diets. *Clarias gariepinus* and *H. cuvieri* apparently fed almost exclusively on cichlids, while *S. macrocephalus* fed predominantly on alestids. The lack of diversity observed in the diets of these three species is almost certainly due to the small sample sizes obtained for each. *Clarias gariepinus* in particular, is known to have a broad omnivorous diet, not dissimilar to that of *C. ngamensis* (Willoughby and Tweddle 1978; Bruton 1979b; van der Waal 1985; Winemiller and Kelso-Winemiller 1996). However, under certain environmental conditions they may specialise on a particular prey. At low water levels in the Okavango Delta, for example, *C. gariepinus* and *C. ngamensis* hunt in

packs, selectively preying upon two mormyrid species, *M. altisambesi* and *P. okavangensis* (Merron 1993). Van der Waal (1985) observed pack hunting behaviour in Lake Liambezi, but did not report on the prey consumed. No such behaviour was observed during the present study, perhaps as a result of the reduced densities of predators brought about by fishing, as Winemiller and Kelso-Winemiller (1996) hypothesised for the Upper Zambezi River. *Hepsetus cuvieri* and *S. macrocephalus* are more specialised piscivores. *Hepsetus cuvieri* feeds predominantly on cichlids, as was the case in this study, but also consumes a variety of other fishes including mormyrids, cyprinids, alestids and poeciliids (van der Waal 1985; Merron 1991; Winemiller and Kelso-Winemiller 1994). In the Upper Zambezi River, *S. macrocephalus* consumed mostly mormyrids, followed by cichlids and cyprinids (Winemiller 1991), while in Lake Liambezi the dominant prey were cichlids followed by alestids (van der Waal 1985).

Both stomach contents and stable isotope analysis revealed a significant level of dietary overlap among the three piscivores. Two factors potentially contributing to this are that: 1) the diversity of prey fishes in Lake Liambezi is lower than in the surrounding floodplain rivers, where greater seasonal variation, habitat diversity and prey diversity engender opportunities for dietary niche segregation; and 2) potential prey are abundant, and predation pressure is low, allowing species to share food resources without having to compete for them. Stable isotope analysis provided strong support for the high contribution of both benthic and tilapiine cichlids to the diets of *C. gariepinus* and *H. cuvieri*, and clearly illustrated how these species integrated the two benthic trophic pathways described above. Individual *C. gariepinus* and *H. cuvieri* with depleted $\delta^{13}\text{C}$ values had high trophic positions, reflecting the greater number of trophic transfers (three) involved in obtaining energy from omnivorous and insectivorous benthic cichlids. Individuals with enriched $\delta^{13}\text{C}$ values had lower trophic positions, as only two trophic transfers were involved in obtaining energy from the detritivorous and herbivorous tilapiine cichlids. Based on this pattern of energy flow, mean food chain length is likely to increase with more intense fishing pressure on the large tilapiine cichlids, as hypothesised by Layman *et al.* (2005).

Serranochromis macrocephalus were, on average, slightly more enriched in $\delta^{15}\text{N}$ and depleted in $\delta^{13}\text{C}$ compared to *C. gariepinus* and *H. cuvieri*, as they fed more evenly across all three trophic pathways. The high contribution of alestids to their diet was not borne out by stable isotope analysis. The average $\delta^{15}\text{N}$ of *S. macrocephalus* was <1‰ higher than that of

B. lateralis. A value somewhat closer to 3.2‰ (Sweeting *et al.* 2007a) would be expected if *B. lateralis* was the dominant prey species. Small cichlid species such as *P. acuticeps* and *T. sparrmanii* with much lower $\delta^{15}\text{N}$ values, likely made up a much higher proportion of the diet of *S. macrocephalus* than indicated by stomach contents analysis. Van der Waal (1985) recorded a dietary contribution of 14% by volume for *B. lateralis*, and 38% for various cichlid species grouped together. These results suggest that *B. lateralis*, the most abundant species in the lake (see Chapter 3), is poorly utilised as a prey resource.

Brycinus lateralis prefers open water habitats in Lake Liambezi where concentrations of zooplankton, their primary food source, are highest (Seaman *et al.* 1978). None of the larger predatory fishes in Lake Liambezi are suitably adapted to exploit prey in this habitat. *Clarias gariepinus* is an adaptable species with a wide range of foraging modes, from filter feeding (Dadebo 2009) to pack hunting (Merron 1993), but they are primarily individual benthic foragers (Bruton 1979b). *Hepsetus cuvieri* is an ambush predator that uses aquatic macrophytes for cover (Winemiller and Kelso-Winemiller 1994), and *S. macrocephalus* is a benthic predator (Winemiller 1991). Lake Liambezi lacks an open water pursuit predator such as *Hydrocynus vittatus* (Jackson 1961), that would be able to efficiently utilise *B. lateralis* and other pelagic species because *H. vittatus* is precluded from establishing in the lake by unfavourable environmental conditions for breeding (van der Waal 1985).

Trophic interactions influencing species abundance

In the absence of effective predation on *B. lateralis*, their population would probably have been regulated by bottom-up or productivity related factors. If food resources were at any time limiting, competition will have occurred between *B. lateralis* and the smaller alestid *R. maunensis*, with which it shared a significant portion of isotopic niche space. *Rhabdalestes maunensis* experienced very rapid population growth after the lake filled in 2009, dominating the fish community numerically in May 2010 (see Chapter 3). In the following three months they experienced a very rapid population decline, while *B. lateralis* continued to increase in abundance at a rapid pace until reaching their peak in early 2011. *Rhabdalestes maunensis* were initially able to the open water habitat thanks to their small size and correspondingly rapid life-history. The larger *B. lateralis* has a slightly slower life-history, but at a certain point may have been able to out-compete *R. maunensis* for the limited food resources, resulting in their population decline. *Rhabdalestes maunensis* were able to persist in the lake at lower numbers, perhaps forced to occupy a less profitable feeding niche in the pelagic

waters. This is the only example from stomach contents and stable isotope analyses of food web dynamics driving species abundance patterns in Lake Liambezi. In the majority of cases, the reverse is true, with species abundance patterns, influenced by a combination of environmental factors, life-history strategies and fishing (see Chapters 3 and 4), driving food web dynamics.

In summary, the investigations into trophic and food web structure supports the hypothesis that phytoplankton production supports a high proportion of consumer biomass in Lake Liambezi. These results add to a large body of evidence highlighting the importance of algal production sources to fishes, even where macrophytes appear to be the dominant source of primary production (Winemiller 2004; Douglas *et al.* 2005). Submerged macrophytes do, however, contribute significantly to the assimilated diets of the tilapiine cichlids, which are the mainstay of the commercial gillnet fishery on Lake Liambezi (Peel *et al.* 2015b). Three major food chains were identified in the lake, and are summarised in Figure 5.7. The phytoplankton based pelagic food chain was longest, involving up to four trophic transfers. The benthic food chain based on detritus of planktonic origin was characterised by high levels of omnivory, and involved up to three trophic transfers. The macrophytic detritus based food chain was shortest, involving just two trophic transfers. Predators fed across all three food chains, but more so on the two benthic food chains. *Brycinus lateralis*, a major component of the phytoplankton based pelagic food chain, appeared poorly utilised as a prey resource. Piscivores present in Lake Liambezi lack the adaptations to pursue *B. lateralis* in open water habitats, resulting in low predation pressure on this species. The abundance of *B. lateralis* was probably regulated by productivity related factors such as intra and interspecific competition for food resources. *Brycinus lateralis* may have out competed the smaller zooplanktivorous *R. maunensis*, resulting in a sharp decline in the abundance of *R. maunensis* in 2010, and their probable displacement to a less profitable feeding niche. The following chapter synthesises the findings from Chapters 2–5 into a chronological description of the patterns of species abundance observed in Lake Liambezi over the study period, and a discussion on the ecological processes that shaped those patterns in abundance.

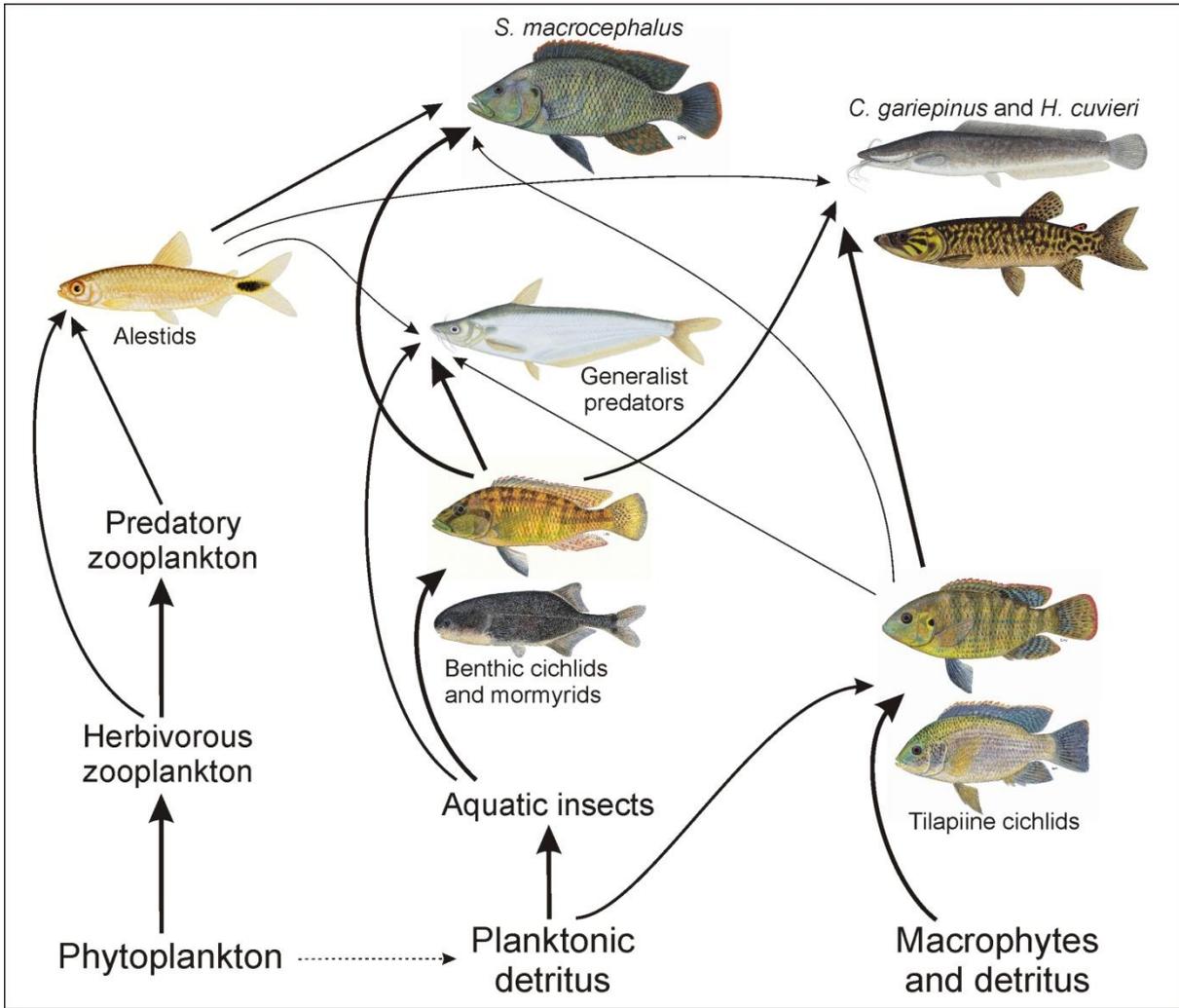


Figure 5.7. Conceptual diagram of the food web in Lake Liambezi, illustrating the flow of energy through three major food chains, and their integration by generalist predators and piscivores in the mature lacustrine fish community. Arrow thickness denotes the relative importance of each trophic transfer.

CHAPTER 6

General discussion

Few ephemeral freshwater lakes in Africa have received scientific attention in the past 35 years despite their importance to human populations. As such, relatively little is known about their ecology, including that of the fishes inhabiting them, and how they respond to periodic and intense disturbances. The aim of this thesis was to contribute toward the understanding of fish colonisation patterns and the drivers of community succession following flooding of a large, shallow ephemeral floodplain lake in southern Africa.

Main findings

Colonisation patterns

After a prolonged period of desiccation through the 1990s, Lake Liambezi received several small floods in the early 2000s during which it was partially inundated, but subsequently dried on each occasion. These short-term flooding-drying cycles provided an ideal opportunity to study fish colonisation patterns, and assess their similarities and differences between years (Chapter 2).

The fish fauna of Lake Liambezi displayed remarkable resilience to drying, with a diverse range of species colonising in large numbers during each flooding event (see Chapter 2). The lake owes its resilience to the fact that it is fed primarily by floodwaters from the Upper Zambezi River, a large, productive and diverse floodplain river (Tweddle 2010). Annually, when the Upper Zambezi River floods, it inundates the Caprivi and Chobe floodplains, covering an area of up to 2 500 km². Numerous fish species migrate laterally onto the floodplains to take advantage of the temporary feeding, spawning and nursery areas they provide (van der Waal 1996). The floodplains teem with juvenile fish in April–May, at the peak of the flood cycle when water begins to overflow, via the Bukalo Channel and Chobe River, into Lake Liambezi. Many of these fish continue their migration from the margins of the floodplain into Lake Liambezi. By the time the floodwaters ceased flowing into Lake Liambezi, the density of fishes in the lake was several times greater than it was on the surrounding floodplains (see Chapter 2). This feature demonstrated that the mainly juvenile fishes entering Lake Liambezi were not simply dispersing in a stochastic manner from areas

of higher concentration on the floodplains, but were undertaking an active exploratory migration in search of new habitats (Lucas and Baras 2001).

The colonising fish communities in Lake Liambezi differed significantly from the source populations on the Zambezi and Chobe river floodplains as a result of interspecific differences in the propensity and ability to undertake extensive lateral migrations (see Chapter 2). The colonising fish communities were dominated by two small cyprinids *Enteromius paludinosus* and *Enteromius poechii*, which were relatively uncommon in deeper parts of the floodplains close to the main channels of the Zambezi and Chobe rivers. The same was true for the large catfishes *Clarias gariepinus* and *Clarias ngamensis* that seem to prefer floodplain margins, often being found at the front of the advancing floodwaters (Williams 1971; Hickley and Bailey 1987). In contrast, the alestids *Hydrocynus vittatus*, *Brycinus lateralis* and *Micralestes acutidens* were far more abundant on the floodplains than they were in the lake. These interspecific differences in dispersal contributed to high levels of variance among species which, when combined with high mean dispersal across species, results in relatively predictable patterns of community composition (Vellend *et al.* 2014).

There was certainly an element of predictability in the colonising fish communities in Lake Liambezi (see Chapter 2). The dominant cyprinids *E. paludinosus* and *E. poechii*, the catfish *Schilbe intermedius*, and mormyrid *Marcusenius altisambesi* ranked among the top five most abundant species in all three colonising fish communities, while *C. gariepinus* ranked fifth in two of the three years. Despite this, however, assemblage structure differed significantly between the three colonisation events. The differences in assemblage structure were attributed primarily to variations in the relative abundance between years of the dominant species mentioned above. Several other less abundant mormyrids and cichlids also contributed towards the dissimilarity between years, but no distinct patterns were discernible. Variations in their abundance may simply have been due to stochastic dispersal during the flood.

Community succession

Lake Liambezi has remained inundated since it was partially flooded in 2007, thanks to exceptionally high floods in 2009, 2010 and 2011 that repeatedly filled the lake, giving those species adapted to the conditions time to flourish in the highly productive new environment. The fish community underwent a succession, from a colonising assemblage dominated by

floodplain specialists, to a lacustrine assemblage dominated by fishes adapted to more stable environments (Figure 6.1).

The colonising assemblage from 2007 underwent dramatic changes in its first year, that included a reduction in the number of species from 23 to 8, and a major decline in their abundance (see Chapter 3), as the lake contracted from 65 km² to just 10 km² (Mutelo 2013). Increasingly harsh environmental conditions, predation and fishing pressure may all have contributed to the high levels of mortality observed in the receding lake. The only species that increased appreciably in terms of relative abundance between 2007 and 2008 was *B. lateralis*, giving an early indication as to the changes to come.

The fishes that had managed to survive since inundation in 2007 would likely have had little influence on the assemblage structure after the lake filled in 2009, as the lake expanded from 10 km² in 2008 to over 300 km². *Enteromius paludinosus* and *E. poechii*, that were so dominant during previous colonisation events, made up a much smaller portion of the catch (see Chapter 3). The abundance distribution of individual taxa was far more even in 2009, with five species from different families (*E. paludinosus*, *S. intermedius*, *B. lateralis*, *M. altisambesi* and *Tilapia sparrmanii*) each contributing more than 10% to the catch numerically. The greater magnitude and duration of the 2009 flood may have given less prolific colonisers, with a lower dispersal ability, the chance to enter the lake in larger numbers before the floodwaters subsided.

After filling in 2009, the vast open waters and pelagic zone of the newly filled lake were largely unpopulated, due to the low abundance of *E. paludinosus* and *E. poechii* that previously occupied this habitat. Two small alestids *Rhabdalestes maunensis* and *B. lateralis*, were quick to colonise this habitat, undergoing explosive population growth between 2009 and 2010 (see Chapter 3). The dominance of *R. maunensis* was, however, brief. Their numbers crashed by 90% in just three months from their peak in May 2010. *Brycinus lateralis* continued to increase rapidly in abundance, and came to dominate the fish community, with 81% of the total catch numerically in May 2011. Larger, later maturing species, including the predatory *Hepsetus cuvieri* and *Serranochromis macrocephalus*, and the tilapias *Oreochromis andersonii*, *Oreochromis macrochir* and *Coptodon rendalli* also increased in abundance over 2010 and 2011, as is evidenced by the rapid development of the fishery (Peel *et al.* 2015b).

There was a general decline in the abundance of almost all species after 2011, possibly indicating the end of the ‘trophic upsurge’ period, and the onset of a ‘trophic depression’ (Lowe-McConnell 1987). While there were large variations in the relative abundance of individual species, the fish community remained largely the same between 2011 and 2014, indicating that it may have reached maturity. *Brycinus lateralis* continued to dominate the fish community numerically, followed by *S. intermedius*, *Petrocephalus* cf. *okavangensis*, *R. maunensis*, *Synodontis* spp. and *Pharyngochromis acuticeps*. Among the most important species in terms of biomass were *B. lateralis*, *S. intermedius*, *Synodontis* spp., *H. cuvieri* and *S. macrocephalus*. Overall, the fish community observed between 2011 and 2014 was very similar to that described by van der Waal (1980) between 1973 and 1976 during a period of relatively high and stable water levels. There was one notable difference, however; *B. lateralis* made up a far greater portion of the catch during the present study than it did during van der Waal's (1980) study. The disparity cannot be fully accounted for by differences in sampling gear, or to higher levels of predation upon *B. lateralis* in the 1970s study. It may be an indication that *B. lateralis* will decline further in abundance in future, even if the lake remains inundated.

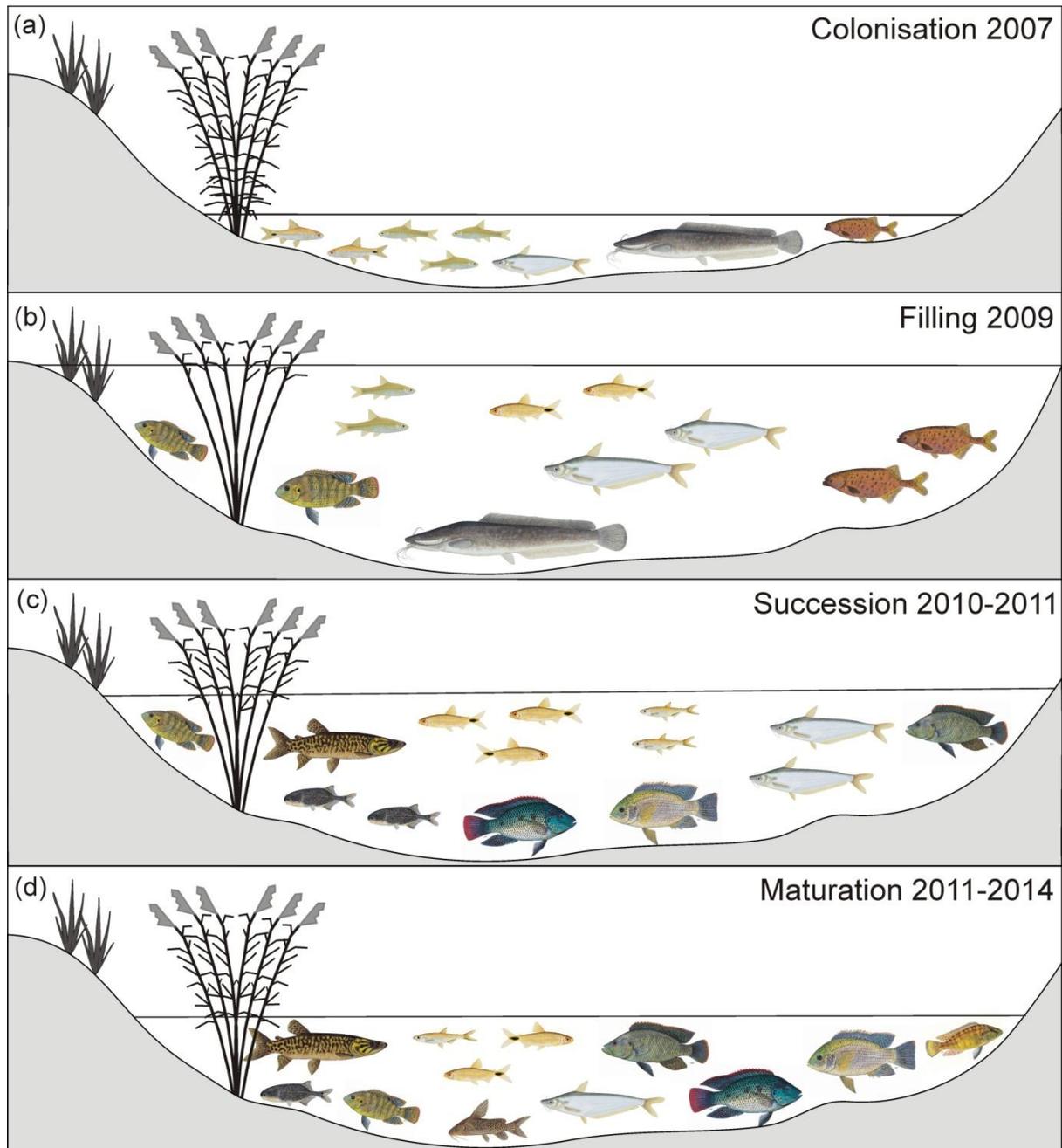


Figure 6.1. Illustration of fish community succession in Lake Liambezi. (a) Colonising community dominated by *Enteromius paludinosus*, *Enteromius poechii*, *Schilbe intermedius*, *Clarias gariepinus* and *Marcusenius altisambesi*; (b) species abundance more evenly distributed after filling, with *Brycinus lateralis* and *Tilapia sparrmanii* among the most abundant species; (c) *Rhabdalestes maunensis*, *B. lateralis* and *Petrocephalus* cf. *okavangensis* undergo rapid population growth in newly filled lake, larger *Oreochromis andersonii*, *Oreochromis macrochir* and predatory *Hepsetus cuvieri* and *Serranochromis macrocephalus* experience slower population growth; (d) species composition remains largely unchanged, general decline in relative abundance of most species after 2011, with the exceptions of *Synodontis* spp. and *Pharyngochromis acuticeps*.

Drivers of succession

In order to understand the drivers behind species successions observed in Lake Liambezi, it was necessary to investigate the life-history strategies of some of the more common fish species, and evaluate their establishment success against life-history theory (Winemiller 1989b; Winemiller and Rose 1992). Life history theory predicts that small bodied opportunistic strategists do well in unstable environments that experience frequent and intense disturbances, such as the short-term flooding-drying cycles experienced by Lake Liambezi in the early 2000s (see Chapter 2). Large bodied periodic strategists are adapted to predictable, seasonal fluctuations in water level, but can generally withstand periods of unfavourable environmental conditions by virtue of their longevity and high fecundity, which enable them to produce strong year classes when favourable conditions do occur (Warner and Chesson 1985). Equilibrium strategists are predicted to thrive in stable environments in which resources may be limiting and recruitment is density-dependent. The relative water level stability in Lake Liambezi following refilling in 2009 was predicted to favour equilibrium strategists, however, species representative of all three of Winemiller and Rose's (1992) endpoint strategies were able to persist, and in many cases, thrive in the lake.

Brycinus lateralis is small, fast growing, early maturing, and has an extended spawning season (see Chapter 4), which is typical of species exhibiting an opportunistic life-history strategy (Winemiller and Rose 1992). Otolith based age estimates revealed that they are surprisingly long lived, reaching 6+ years in Lake Liambezi. *Brycinus lateralis* was able to breed independently of the flood regime in Lake Liambezi, in contrast with the colonising cyprinids *E. paludinosus* and *E. poecheii*, which generally display similar life-history characteristics, but are flood dependent spawners (Furse *et al.* 1979; Macuiane *et al.* 2009). This trait enabled *B. lateralis* to quickly repopulate the open water habitat left vacant by the cyprinids after the lake filled, and to maintain their high abundance as the lake level receded in the absence of flooding. Life-history theory correctly predicted the demise of *E. paludinosus* and *E. poecheii*, but the alestids *B. lateralis* and *R. maunensis* did not conform to the theory, and were able to adapt and thrive in the relatively stable lentic environment.

Clarias gariepinus and *S. intermedius* are periodic strategists (see Chapter 4). *Clarias gariepinus* is large, fast growing and potentially long lived. *Schilbe intermedius* is much smaller, and shorter lived compared to *C. gariepinus*, but represents the periodic strategy by virtue of its high fecundity (van der Waal 1985; Hay 1995; Merron and Mann 1995). *Clarias*

gariiepinus and *S. intermedius* are flood dependent spawners, so despite signs of reproductive activity in non-flood years, recruitment was unsuccessful. Nevertheless, both species have been able to persist, as predicted by life-history theory, because they are relatively long lived, and large adult fish tend to experience low levels of natural mortality. *Clarias gariiepinus* did, however, experience a significant decline in abundance as a result of fishing. This is not necessarily damaging, since even few individuals have the potential to produce strong year classes as a result of their high fecundity if/when floodwaters do reach Lake Liambezi (e.g. Furse *et al.* 1979).

As predicted by life-history theory, equilibrium strategists have been very successful at establishing in Lake Liambezi (see Chapter 3). All five study species (*O. andersonii*, *O. macrochir*, *C. rendalli*, *S. macrocephalus* and *H. cuvieri*) displayed very rapid growth rates when compared to other populations in the region (see Chapter 4). This is most likely due to the high levels of productivity in the recently flooded lake, especially during the early ‘trophic upsurge’ period that appears to have lasted from 2009 to 2011. The result of these rapid growth rates is that the cichlids generally matured at earlier ages, and at similar sizes to neighbouring populations (Peel *et al.* In review). *Hepsetus cuvieri*, in contrast, matured at a much larger size in Lake Liambezi compared to in the Okavango Delta (Merron *et al.* 1990). The ages at which *H. cuvieri* mature in Lake Liambezi and the Okavango Delta are probably similar, although no reliable estimates are available from the Okavango Delta for comparison.

The reduced generation time of cichlids in Lake Liambezi indirectly contributes to increased population growth potential, while maintaining the reproductive traits typically associated with equilibrium strategists, including large egg size, low fecundity, and high juvenile survivorship (Winemiller and Rose 1992). Population growth potential is also enhanced by the cichlids ability to raise multiple broods over an extended summer spawning season (see Chapter 4). These traits enabled the cichlids to quickly establish themselves in Lake Liambezi after filling, and no doubt help them to withstand the high levels of fishing pressure.

As well as life-history, species successions and community structure can be significantly influenced by food web dynamics (Winemiller 1996b). It was therefore essential to gain an understanding of the food web dynamics in Lake Liambezi, including which primary production sources supported consumer biomass, the trophic structure of the fish community, and the trophic interactions among fish species. Using stable isotope analysis, two main

sources of primary production were identified to contribute to consumer biomass (see Chapter 5). The primary source was phytoplankton associated with particulate organic matter (POM). Aquatic macrophytes, the most conspicuous source of primary production in the lake, were thought to contribute to a lesser degree. The findings add to a large body of evidence highlighting the importance of algal production sources to fishes, even where macrophytes are dominant primary producers (Winemiller 2004; Douglas *et al.* 2005).

Three food chains were identified using stable isotope analysis, two of which were based primarily on phytoplankton, and one on macrophytic detritus (see Chapter 5). The phytoplankton based pelagic food chain was longest, involving up to four trophic transfers. Phytoplankton is consumed directly by small herbivorous zooplankton such as *Bosmina longirostis* (Seaman *et al.* 1978), which are preyed upon by larger zooplankton, especially chaoborid larvae. Small zooplanktivorous alestids consume both herbivorous and predatory zooplankton. The second phytoplankton based food chain was benthic, and was supported primarily by planktonic detritus. The food chain was characterised by high levels of omnivory, and involved up to three trophic transfers. The dominant primary consumers were aquatic insects, which, in turn, supported numerous fish species including mormyrids, benthic cichlids, cyprinids, and to a lesser degree, generalist predators. The macrophytic detritus based food chain was shortest, involving just two trophic transfers. The main primary consumers were tilapiine cichlids, which were consumed directly by several piscivores.

The top piscivores in Lake Liambezi, *C. gariepinus*, *H. cuvieri* and *S. macrocephalus*, fed across all three food chains, but more so on the two benthic food chains (see Chapter 5). Stomach contents and stable isotope analysis revealed a significant level of dietary overlap among the three piscivores, all of which consumed a high proportion of cichlids, especially *T. sparrmannii* and *P. acuticeps*. Abundant prey and low predation pressure allowed the piscivores to share food resources without having to compete for them. *Brycinus lateralis*, a major component of the phytoplankton based pelagic food chain, appeared underutilised as a prey resource (see Chapter 5). This may be because *C. gariepinus*, *H. cuvieri* and *S. macrocephalus* lack the adaptations necessary to pursue and capture *B. lateralis* in its preferred open water habitat. *Hydrocynus vittatus*, a highly efficient open water pursuit predator (Jackson 1961), is precluded from establishing in the lake by unfavourable environmental conditions for breeding (van der Waal 1985).

In the absence of effective predation on *B. lateralis*, their population is regulated by productivity related factors such as intra and interspecific competition for food resources. *Brycinus lateralis* and *R. maunensis* shared a significant portion of their isotopic space, implying that competition may occur if/when resources are limiting (see Chapter 5). *Brycinus lateralis* appears to have been the competitively superior of the two species, resulting in a rapid decline in the abundance of *R. maunensis* in 2010, while the *B. lateralis* population grew rapidly for another year (see Chapter 3). *Rhabdalestes maunensis* have been able to persist in Lake Liambezi at lower numbers, having been forced to occupy a less profitable ecological niche with lower levels of competition.

Contributions to the ephemeral lake model

The conceptual model developed by Gawne and Scholz (2006) essentially tries to explain patterns in species diversity, composition and abundance of plant and animal communities in response to the flooding-drying cycle. The model identifies five phases that begin and end with a dry lake bed. The first phase begins with flooding, and is characterised by high levels of productivity and low predator densities. These conditions allow consumer communities to increase rapidly in abundance during the second phase. As water levels begin to recede, predators exert top-down pressure on lower trophic levels during the third phase, intensifying with the addition of avian predation in the fourth phase. Environmental conditions eventually become too harsh for aquatic organisms to tolerate, and the lake dries in the fifth phase. Accounting for the various patterns in species diversity, composition and abundance is very difficult considering that ephemeral lakes have very variable hydrological regimes. Flooding-drying cycles naturally vary widely in duration between lakes and within lakes. Gawne and Scholz's (2006) model appears to be based on a relatively long cycle (3–5 years) in which there is sufficient time for predatory fish communities to establish. The model does not explicitly take variation in the duration of the cycle into account, but it can be easily incorporated. Short cycles (1–2 years) may preclude the establishment of large fish communities, so that phases 2 and 3 of the model (population growth and increasing predation pressure) are skipped, and phase 4 (avian predation intensifies and environmental conditions deteriorate) is brought forward. During longer cycles, in which water levels are sustained by repeated flooding, as in Lake Liambezi, phases 2 and 3 may be drawn out over several years.

Patterns in species diversity, composition and abundance of ecological communities are influenced by four kinds of processes: speciation, selection, drift and dispersal (Vellend 2010). Drift is purely stochastic, and is thus very difficult to incorporate into a predictive or deterministic model. Communities in ephemeral lakes are usually based on a subset of the regional species pool, thus speciation, which shapes regional species pools over large temporal and spatial scales, is adequately accounted for in the ephemeral lake model. Dispersal patterns are responsible for determining the composition of the colonising community, and can also strongly influence the community structure of established communities (Vellend *et al.* 2014). As shown in this thesis, fish dispersal and colonisation patterns can be relatively predictable (see Chapter 2). Dispersal should, therefore, be given greater consideration in the ephemeral lake model. Selection refers to deterministic fitness differences between species, and can be divided into abiotic and biotic factors, which interact to influence patterns of community dynamics. The ephemeral lake model places a great deal of importance on abiotic environmental factors associated with water level fluctuations, and on biotic interactions in the form of competition and predation. It does not, however, consider species adaptations to the local environment, such as life-history strategies, and the plasticity of species life-history strategies, which may vary widely among species in the regional pool, and strongly influence their local fitness.

Life-history theory was a fundamental part of this thesis, and was used to explain the majority of the patterns in fish species diversity, composition and abundance in Lake Liambezi. If the regional species pool is well known, life-history theory may help predict dispersal patterns and the composition of the colonising fauna, which is generally dominated by opportunistic, followed by periodic and equilibrium strategists (Winemiller 1996; Chapter 2). It can be used to predict the establishment success of the colonising species in combination with knowledge of the hydrological regime, although there are always likely to be exceptions such as *B. lateralis* (see Chapters 3 and 4). It can also be used to explain differential population growth rates among species (see Chapter 4). Equilibrium strategists, for example, have a lower population growth potential than opportunistic and periodic strategists, but given time and the absence of further disturbances, they will come to dominate under density dependent conditions (Winemiller and Rose 1992; Winemiller 2005). Life-history theory applies to phases 1, 2 and 3 of the conceptual model that are concerned with colonisation, establishment and population growth. Life-history theory would be an invaluable addition to the ephemeral lake model originally developed by Gawne and Scholz (2006).

Conservation and management

Ephemeral lakes such as Lake Liambezi experience regular and extreme disturbances in the form of drying. Drying has serious consequences for populations of aquatic biota, but reinvigorates the system, and sets the stage for recovery (Gawne and Scholz 2006). Healthy systems are generally resilient, and recover quickly from natural disturbances (e.g. this thesis). Anthropogenic stressors, such as alteration of the physical habitat and flow regime, pollution, alien species introductions and overharvesting reduce resilience and the capacity of these systems to recover from natural disturbances (Rapport and Whitford 1999).

Lake Liambezi relies heavily on the health of the Upper Zambezi and Kwando rivers from which it receives water inputs, and from where fishes can recolonise the lake. Any alterations to the flow regime of these rivers may have negative impacts on the magnitude and duration of flooding, and the frequency with which floodwaters reach Lake Liambezi. The Upper Zambezi and Kwando rivers flow through fairly flat terrain, so that dam construction, except in headwater tributaries such as the Kabompo River, is unlikely to be a major threat to Lake Liambezi. Water abstraction for irrigated agriculture and urban use is likely to increase in the future, contributing to reduced river flows, especially in the dry season (Beck and Bernauer 2011), while climate change is likely to have a greater impact on river flows in the wet season. Climate change models predict that, across much of southern Africa, there will be an increase in temperature, and a decrease in precipitation of up to 10% by the end of the 21st century (de Wit and Stankiewicz 2006; Beck and Bernauer 2011). Lake Liambezi is likely to experience more frequent and longer dry cycles, similar to what it experienced throughout the 1990s. Higher temperatures will contribute to increased rates of evapotranspiration, leading to greater seasonal variation in water level and accelerated rates of drying.

Lake Liambezi is now threatened by the introduction of two invasive alien species, the Nile tilapia *Oreochromis niloticus* (Tweddle 2010) and the Australian redclaw crayfish *Cherax quadricarinatus* (Nunes *et al.* 2016). The indigenous *O. andersonii* and *O. macrochir*, which are the primary fishery species in Lake Liambezi, are threatened by competition and hybridization with *O. niloticus*, and are listed as vulnerable by the IUCN (Marshall and Tweddle 2007; Tweddle and Marshall 2007). The major impact of *C. quadricarinatus* in Lake Liambezi would likely be the destruction of aquatic macrophyte populations, which

may significantly alter ecosystem functioning by increasing turbidity, disrupting invertebrate communities, and degrading fish breeding and nursery areas (Nunes *et al.* 2016). *Cherax quadricharinatus* may directly affect fish catches by damaging fish caught in gillnets, resulting in them being discarded, as well as damaging the nets themselves (Tyser 2010).

Fisheries management

Lake Liambezi is a highly dynamic environment that supports equally dynamic and resilient fish populations. Fish populations and fishery potential fluctuate widely in response to hydrological conditions, but this is not formally recognised in national policy and legislation (MFMR 1995, 2003). The fishery is managed for, and based primarily on large, valuable tilapiine cichlids (Peel *et al.* 2015b). Management is achieved by strict regulation of mesh sizes, which prevents the target species from being harvested before they have reached maturity. This strategy favours commercial operations in stable environments as it optimises the economic return of the fishery, and accepts that a less than maximum yield is obtained (Welcomme 1999). While this strategy has been effectively implemented on Lake Liambezi during the present study period (Peel *et al.* 2015b), the fishery still faces some socio-economic issues (Tweddle *et al.* 2015). Local fishers and fish traders were marginalised soon after the development of the cichlid fishery by non-local businessmen, who hired fishers, many of whom were foreign, to fish for them. They processed fish at the lake shore, and marketed the salted and dried fish directly to Zambia and the Democratic Republic of the Congo, to the detriment of the livelihoods and food security of the local communities (Abbott *et al.* 2015; Tweddle *et al.* 2015). Managing the fishery only for large, commercially valuable species may not, therefore, be the most appropriate management strategy for Lake Liambezi, especially since fishery potential is governed by widely fluctuating environmental factors, fish populations are generally dominated by small, resilient species and fishing has no long term impact on fish populations (Kolding and van Zwieten 2014; Kolding *et al.* 2016b).

The optimal management strategy for Lake Liambezi would be a balanced harvesting approach, that exploits a wide range of species and sizes in proportion to their productivity, without impacting on the relative size and species composition of the fish community (Garcia *et al.* 2011; Kolding and van Zwieten 2014). In reality though, this strategy is almost impossible to implement (Froese *et al.* 2015). Claims that balanced harvesting can emerge from fishing decisions by individual fishers in a small scale fishery (Plank *et al.* 2016) do not hold true for Zambezi fisheries, where uncontrolled fishing has led to the collapse of large

cichlid stocks and a decline in yields (Weyl *et al.* 2010; Froese *et al.* 2015; Tweddle *et al.* 2015). Regularly cited examples of balanced harvesting in African freshwater fisheries, such as the Zambian side of Lake Kariba (Kolding and van Zwieten 2014; Kolding *et al.* 2016a), are actually the remnants of previously valuable cichlid fisheries (Froese *et al.* 2015; Tweddle *et al.* 2015). An adaptive management strategy that accounts for the dynamic nature of the fish community in Lake Liambezi would be more appropriate.

The results presented in this thesis provide the basis for the development of an adaptive fishery management strategy, under which fishery regulations may be changed in response to naturally occurring changes in the fish community. For example, fishers could be allowed to use small meshed gill nets to harvest the highly abundant and short lived colonising cyprinids *E. paludinosus* and *E. poechii*, before they naturally disappear from the fish community approximately two years after inundation. By such a time, cichlid populations will have had a chance to grow, and management could then focus on these large, valuable species, in an effort to maximise the economic yield of the fishery as the current management strategy does. Other species with significant fisheries potential, such as *B. lateralis* and *S. intermedius*, could be harvested in addition to the large cichlids, provided that the methods used to harvest them do not negatively impact the cichlid fishery. Peel *et al.* (2015a) found that *B. lateralis* could be efficiently harvested using 25 mm mesh gill nets of 0.5 m deep, surface set in open water, without any juvenile cichlid by-catch. *Schilbe intermedius* were effectively targeted using 50 mm mesh gill nets of 1 m deep, but juvenile cichlids were also regularly caught. On a large scale, this may have been detrimental to the cichlid fishery. A *S. intermedius* fishery would, in any case, be short lived in the absence of regular flooding, since they cannot breed in the Lake.

The adaptive management strategy would rely on regular monitoring of the fish community and fisheries catches in Lake Liambezi by the Namibian Ministry of Fisheries and Marine Resources (MFMR), and require an effective response system to ensure that fishers alter their harvest patterns as and when necessary. This would require strong buy-in from local fishing communities, who should be involved in the development of the management plan from the beginning. Existing community fishery management structures should be strengthened through formal government recognition to guard against the entrance of foreign fishers, who ignore locally agreed rules and regulations (Tweddle *et al.* 2015). As well as sound biological information, the management strategy requires an understanding of how local communities

livelihood strategies are adapted to cope with fluctuating resource availability (Sarch and Allison 2000). Livelihood diversification should be encouraged to enhance people's ability to cope with fluctuations in the fishery, and to prevent fishers from moving to adjacent systems, where fisheries resources are already heavily exploited.

Future research

This thesis contributes significantly toward our knowledge and understanding of fish ecology in ephemeral lakes in Africa, but there is still considerable potential for improving our ability to predict fish community responses to environmental variation in relation to the flooding-drying cycle. Species functional trait-environment relationships are increasingly used to explain observed patterns, and to predict community responses to environmental change (e.g. Pease *et al.* 2012). A considerable amount of knowledge on species traits is required in order to confidently making such predictions. As an example, Winemiller *et al.* (2015) used data for 38 traits associated with five niche dimensions (habitat, life-history, trophic, defence and metabolism) to construct two novel continuous and discrete niche schemes for a tropical fish community in the Venezuelan Llanos comprising 56 common fish species.

Functional traits associated with life-history and trophic ecology were investigated for some of the more common fish species in Lake Liambezi in this thesis. For the majority of species found in Lake Liambezi, and more importantly in the Upper Zambezi and Kwando rivers, there is very little information of this kind available. Future research should in particular focus on small species, for example *E. paludinosus*, *R. maunensis* and *P. cf. okavangensis* that displayed very interesting abundance patterns in Lake Liambezi. Detailed information on species habitat preferences and dispersal patterns during different phases of the hydrological cycle in the large floodplain rivers would contribute greatly to our ability to predict colonisation patterns in Lake Liambezi, but information of this kind is sadly lacking. There is also very little data available on the basic physiology of fish species in the Upper Zambezi region, making it difficult to predict community responses to hypoxia in the drying lake, for example. It is essential to record habitat and water quality variables in conjunction with fish sampling so that the relationship between species abundance and distribution, functional traits and environmental gradients can be examined. The lack of consistent habitat and water quality records precluded their use in this thesis, and is recognised as a major shortcoming. The experimental gill net fleet used in this study also has its limitations. It was designed with

the aim of minimizing species and size selectivity. Nevertheless, species differ in their vulnerability to capture as a result of behavioural and morphological differences, such as the presence of serrated spines. The effectiveness of potentially less destructive and less selective sampling methods, such as boat-based electric fishing, should be explored in future.

Underwater video could potentially be used to quantify fish migration into the lake through the Chobe River, Bukalo and Linyanti channels, where water clarity is typically much higher than in the lake itself.

Lake Liambezi will most likely dry if it does not receive inflow from the Upper Zambezi River in April–May 2017. Monitoring of the fish community by the Namibian Ministry of Fisheries and Marine Resources should continue until such time as the lake is completely dry, so that data is available for a complete flood cycle. If the lake does dry, it may be a long time before the knowledge gained in this thesis may be applied here. It may, however, be applied to Lake Ngami, an ephemeral lake at the tail end of the Okavango Delta, Botswana that is similar in many respects to Lake Liambezi. Direct comparisons may be made between the two lakes as they share very similar fish fauna, have similar hydrological regimes, and are subject to the same kinds of human impacts.

Concluding remarks

The results presented in this thesis illustrate that fish colonisation patterns in Lake Liambezi are non-random, and are influenced primarily by interspecific differences in the propensity and ability to undertake extensive lateral migrations on seasonally inundated floodplains. Species life-history strategies and adaptations to the local environment in Lake Liambezi, with particular regard to the irregular and unpredictable hydrological regime, played an important role in determining species establishment success and population dynamics. Interspecific biotic interactions played a minor role in driving species abundance patterns in Lake Liambezi. For the most part, species abundance patterns, influenced by a combination of environmental factors, life-history strategies and fishing drive food web dynamics.

These results will hopefully contribute to the conservation and optimal utilisation of the fish resources in Lake Liambezi in future, and to other ephemeral lakes in southern Africa such as Lake Ngami. Management strategies need to be adaptive in order to respond to naturally occurring changes in the fish community. Conserving ecosystem functioning and integrity is

paramount to managing for fishery sustainability. Future research should focus on collecting species trait information associated with five niche dimensions: habitat, life-history, trophic ecology, defence and metabolism (Winemiller *et al.* 2015). Species functional trait-environment relationships can be used to predict fish community responses to environmental change associated with water level fluctuations in ephemeral lakes and floodplain rivers alike. This will contribute to the development of proactive management approaches for dealing with the impacts of human induced environmental change and invasive alien species.

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Appendix 1: Peel, R.A., Weyl, O.L.F. and Omoregie, E. (In review) Comparative biology of three large tilapiine cichlid species from the Upper Zambezi and neighbouring floodplain systems, southern Africa. *African Zoology*.

Comparative biology of three large tilapiine cichlid species from the Upper Zambezi and neighbouring floodplain systems, southern Africa

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The tilapiine cichlids *Oreochromis andersonii*, *Oreochromis macrochir* and *Coptodon rendalli* are among the most important artisanal fishery species in the Upper Zambezi and Okavango Ecoregions, southern Africa. They are threatened by overfishing, and life-history information is urgently needed to develop management strategies for their recovery and sustainable use. Age, growth and maturity were assessed for each species in Lake Liambezi and the Kavango, Kwando and Zambezi rivers in Namibia. Analysis of sectioned sagittal otoliths revealed that all three species are relatively long lived, attaining ages in excess of 10 years in protected areas on the Kavango and Kwando rivers. Growth rates differed significantly between populations of each species in the four systems, being fastest in Lake Liambezi and the Zambezi, followed by the Kavango, and were slowest in the Kwando. This is likely due to differences in productivity, which are a result of differing flood regimes in each system. Age-at-maturity differed significantly between populations of each species as a result of differences in growth rates, but length-at-maturity did not differ significantly between populations. The results show that cichlid populations could be managed using similar exploitation rules in each system. Effort regulation, through the use of fish protection areas, may be required to prevent overfishing of slower growing populations, especially those in the Kwando River.

Key words: Age and growth, reproduction and maturity, *Oreochromis andersonii*, *Oreochromis macrochir*, *Coptodon rendalli*

Introduction

Tilapiine cichlids are important components of floodplain fisheries in the Upper Zambezi and neighbouring floodplain rivers and lakes in southern Africa (Tweddle 2010; Peel et al. 2015; Tweddle et al. 2015). Intense fishing pressure in recent years has, however, resulted in the collapse of some Zambezi fisheries, e.g. a 90% decline in large cichlids on the Caprivi floodplain between 2010 and 2012 (Tweddle et al. 2015). As the abundance of cichlids continues to decline, there is a trend towards fishing for smaller, low value species in an attempt to maintain catches (Welcomme 1999; Tweddle et al. 2015). While some purport that this is ecologically more sustainable than harvesting only large species, and equates to a ‘balanced harvest’ (Kolding & van Zwieten 2011, 2014; Garcia et al. 2012), they fail to recognise, among other factors, the economic impact of overfishing (Weyl et al. 2010; Froese et al. 2015; Tweddle et al. 2015). Managers recognise the need for a holistic approach that optimises the economic return to fishers through the management of large, valuable cichlids, while increasing yields to satisfy high demand from a growing human population, by encouraging the exploitation of small, highly resilient but less valuable floodplain species (Welcomme 1999; Tweddle et al. 2015). The development of management strategies that will allow for the recovery of over-exploited cichlid stocks and ensure they are optimally exploited in future requires an understanding of the target species biology and life-history.

The threespot tilapia *Oreochromis andersonii* (Castelnau, 1861), greenhead tilapia *Oreochromis macrochir* (Boulenger, 1912), and redbreast tilapia *Coptodon rendalli* (Boulenger, 1897) comprise the most commercially important species group in the Upper Zambezi and Okavango ecoregions. Historically, these species accounted for up to 75% of artisanal gillnet catches taken from Lake Liambezi and the Upper Zambezi and Kavango rivers in Namibia (van der Waal 1980, 1990, 1991). Despite their importance to artisanal fisheries, little is known about their life-history and population dynamics in Namibia, and how these vary between populations in different river systems.

The age, growth and maturity of the three species has been investigated by van der Waal (1985) in Lake Liambezi, prior to the ephemeral lake drying in 1985, and by Dudley (1974, 1979) and Kapetsky (1974) on the Kafue Floodplain in Zambia. Age estimates in these studies were obtained using scales that have since been shown to underestimate longevity (Hecht 1980; Booth et al. 1995). Sectioned sagittal otoliths are now considered to be the most suitable ageing structure, and have been used to estimate the age and growth of *O. andersonii*

(Booth et al. 1995) and *O. macrochir* (Booth & Merron 1996) from the Okavango Delta, Botswana, and *C. rendalli* from Lake Chicamba, Mozambique (Weyl & Hecht 1998).

Life-history traits such as growth and maturity vary between populations of conspecific cichlids, mainly as a result of differing environmental conditions (James & Bruton 1992; Booth et al. 1995; Booth & Merron 1996; Weyl & Hecht 1998; Bwanika et al. 2007; Russell et al. 2012). Consequently, population specific management regulations may be required for stocks that exhibit different life-history characteristics. The aim of this study was to test the null hypothesis that: growth rates, length and age-at-maturity did not differ between four populations of *O. andersonii*, *O. macrochir* and *C. rendalli* in north-eastern Namibia. The results will be used to guide the development of management strategies that will ensure the recovery and optimal exploitation of these large, valuable cichlids.

Materials and methods

Study area

The study was carried out in the East Kavango and Zambezi regions of northeastern Namibia. Four populations of *O. andersonii*, *O. macrochir* and *C. rendalli* were sampled from Lake Liambezi and the Kavango, Kwando and Upper Zambezi rivers (Figure. 1). Lake Liambezi (17°53'S, 24°17'E 930 m amsl) is a large (300 km²), shallow (mean depth ~2.5 m) ephemeral floodplain lake located on the Namibia–Botswana border. It is fed by floodwaters from the Upper Zambezi and Kwando rivers during years of exceptionally high flooding. The lake dried up in 1985 after several years of low floods in the inflowing rivers (Grobler & Ferreira 1990). It received moderate inflow in 2007, and eventually refilled in 2009. The Kavango River was sampled at Kwetche (18°13'S, 21°45'E; 1000 m amsl), in the Mahango Core Area of Bwabwata National Park. The area is situated at the head of the panhandle of the Okavango Delta. The park extends for 15 km on the western bank and 22 km on the eastern bank. The river is approximately 200 m in width and fringed by floodplains up to 3 km wide, which are inundated from February to May. The Kwando River was sampled at Susuwe (17°44'S, 23°21'E; 968 m amsl) and Nakatwa (18°10'S, 23°25'E; 957 m amsl), in the Susuwe Core Area of Bwabwata National Park and in Mudumu National Park, respectively. At Susuwe, only the western bank of the river is protected while Nakatwa, a series of backwaters, lies wholly within a protected area. The river is approximately 40 m in width and fringed by floodplains up to 3.5 km wide. Flooding is of a lower magnitude and occurs later in the year (July–August) than in the Kavango and Upper Zambezi rivers due to

the reservoir like capacity of large floodplains further upriver. The Zambezi River was sampled at Kalimbeza (17°31'S, 24°32'E; 938 m amsl) on the Caprivi floodplain. The river is approximately 350 m in width, and bordered by floodplains up to 12 km wide that are inundated from March to June.

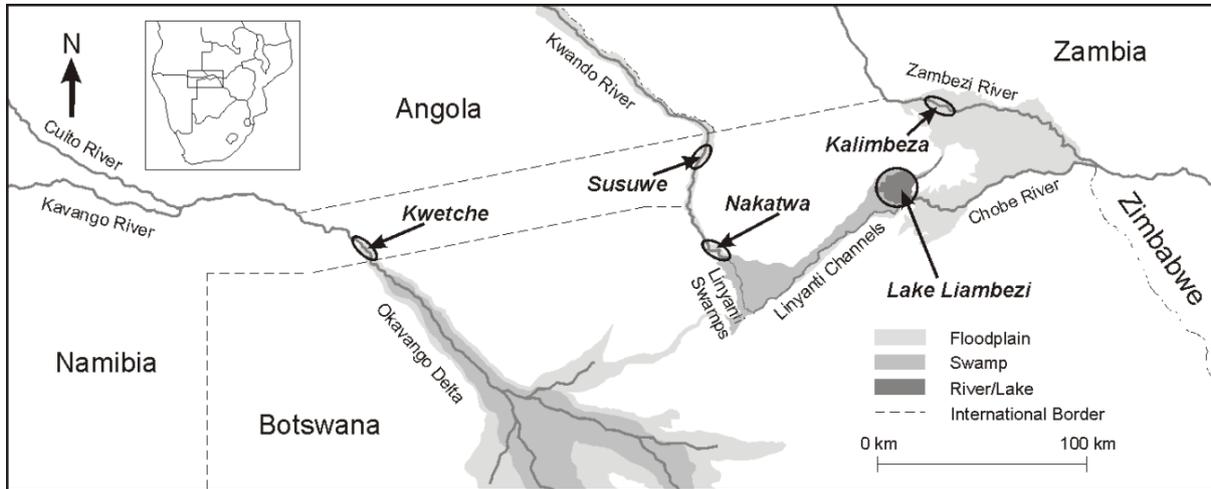


Figure 1: Northeastern Namibia, showing locations of the five sampling areas on Lake Liambezi and the Kavango, Kwando and Zambezi rivers.

Fish sampling

Samples were collected during bimonthly faunal surveys of each system from August 2010 to September 2011, and on an *ad hoc* basis thereafter until August 2014. Fish were collected using gillnets, seine nets, angling, and were additionally purchased from local fishermen. Live fish were sacrificed by concussion followed by destruction of the brain, measured to the nearest mm total length (TL) and weighed to the nearest gram. Fish were then dissected to determine sex, and the stage of maturity was determined macroscopically according to criteria outlined by Weyl & Hecht (1998). Sagittal otoliths were removed and stored for ageing.

Otolith preparation and interpretation

Otoliths were set in clear polyester resin, sectioned transversely through the nucleus at a thickness of 0.4 mm, and mounted on slides using DPX mounting agent. Sections were viewed under transmitted white light at varying magnification (20–40 ×), and the number of growth zones—visible as alternating translucent and opaque zones—was determined by counting the number of opaque zones from the nucleus to the margin of the otolith (Figure.

2.). Peel *et al* (2016) demonstrated that a single growth zone is laid down annually in the otoliths of *O. andersonii*, *O. macrochir* and *C. rendalli* from the four populations sampled in this study. Growth zones were therefore considered annuli, and were used to estimate the age of fish.

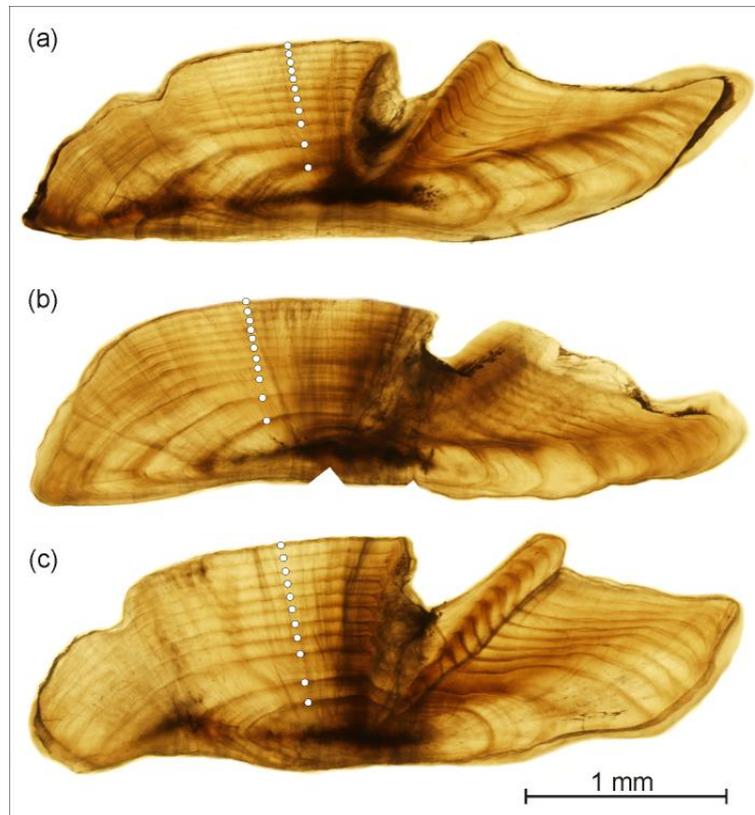


Figure 2: Photomicrographs of sagittal otolith sections viewed using transmitted white light from (a) a 415 mm L_T , 11 year old *Oreochromis andersonii*, (b) a 260 mm L_T , 11 year old *Oreochromis macrochir*, and (c) a 333 mm L_T , 11 year old *Coptodon rendalli* all sampled from the Kwando River. White dots represent annuli.

All otoliths were read twice by independent readers without knowledge of the date of capture or the length of the fish. If the two readings were the same, the count was accepted. If the readings differed a third was taken by the primary reader and if two readings were the same the count was accepted. If the three counts differed at most by two growth zones (e.g. 2, 3, 4), the median estimate was accepted, otherwise the otolith was considered unreadable and excluded from the analysis (Campana 2001). The precision of growth zone counts was assessed using the average percent error (APE) method (Beamish & Fournier, 1981) and by calculating the average coefficient of variation (CV) (Chang, 1982).

Growth

To avoid false year class identification and improve the accuracy of observed growth zone counts, monthly age estimates were back-calculated by assuming that all fish were born during the middle of the extended spawning season in December, and that peak opaque zone detection in the otoliths of all three species was in November (Peel et al. 2016). For fish with a translucent otolith margin that were caught between December, and November the following year, the number of months between birth and capture were added, i.e. a fish with two annuli caught in June was 2.5 years. For fish with an opaque otolith margin caught between December and November, the number of months between capture and birth were subtracted, i.e. a fish with two annuli caught in September was 1.75 years.

Length-at-age data was described by fitting the three-parameter von Bertalanffy growth model of the form: $L_t = L_\infty (1 - \exp(-K(t - t_0)))$, where L_∞ is the predicted asymptotic length, K is the Brody co-efficient (Ricker, 1975) and t_0 is the theoretical age at zero length. Model parameters were estimated by minimising the negated normal log-likelihood function. Parameter variability was estimated using parametric bootstrap resampling (Efron 1982). The percentile method (Buckland 1984) was used to estimate 95% confidence intervals from the resulting bootstrap vectors. Likelihood ratio tests (LRTs) (Cerrato 1990) were used to test the null hypothesis that growth was equal between sexes, and between populations. Growth was compared between sexes and populations using the growth performance index, calculated as: $\phi' = 2 \log L_\infty + \log K$ (Pauly & Munro 1984). Combined sex growth estimates were illustrated despite several instances in which growth differed between sexes, because males and females cannot be managed as separate stocks.

Reproduction

Temporal patterns in reproductive seasonality were assessed by plotting the percent of fish of a given maturity stage per sampling month for each species. The four populations of each species were combined because of a paucity of data from the Kavango and Upper Zambezi rivers during the flooding season, when fish disperse onto the floodplains and become difficult to capture. This was considered acceptable because sampling areas across all four systems had similar latitude, altitude and resulting temperature regimes (Peel et al. 2016).

Samples of each species collected during the peak spawning season (November–January) were used to determine the mean length (L_{m50}) and age (tm_{50}) at-50%-maturity for each population. Fish were considered mature if they had gonads in the developing, ripe or spent stages. Length-at-maturity was expressed as the proportion of mature fish per 10 mm size class (L). L_{m50} was estimated by fitting these data to a two-parameter logistic model of the form: $P_L = (1 + \exp^{-(L-L_{m50})/\delta})^{-1}$, where P_L is the predicted proportion of mature fish in size class L and δ describes the width of the logistic ogive. Using age estimates from sectioned otoliths, tm_{50} was estimated by fitting the same logistic model to the proportion of mature fish per age class. Model parameters were estimated by minimising the negated binomial log-likelihood function. LRTs were used to test the null hypothesis that L_{m50} and tm_{50} were equal between populations.

Results

Age and growth

For all three species, precision estimates between otolith readings were highest from the Kavango and Kwando (Table 1). Precision estimates were also high for *O. andersonii* and *C. rendalli* from the Zambezi and Liambezi, respectively. Precision estimates for *O. andersonii* were lowest in Liambezi, while those of *O. macrochir* and *C. rendalli* were lowest in the Zambezi. No otoliths were rejected. When compared by age class, precision estimates between populations and species were generally similar (Table 1). Precision varied considerably in younger year classes (0 and 1), primarily as a result of differences in sample sizes, and was generally low but comparable between populations and species. Precision in older year classes (2, 3 and 4+) was much higher and comparable between populations and species.

Table 1: Average percent error (APE) and coefficient of variation (CV) between otolith readings of *Oreochromis andersonii*, *Oreochromis macrochir* and *Coptodon rendalli* sampled from Lake Liambezi and the Kavango, Kwando and Zambezi rivers in Namibia (2010–2014).

Species and system	Total		APE by age class									
	APE	CV	0	n	1	n	2	n	3	n	4+	n
<i>O. andersonii</i>												
Liambezi	13.81	15.73	63.64	44	9.33	175	6.37	151	2.14	14	5.12	14
Kavango	1.99	3.90	0.00	1	4.17	24	2.50	61	1.04	18	0.90	59
Kwando	3.20	7.10	–	–	33.33	1	7.62	27	1.78	71	2.30	54
Zambezi	5.49	8.82	0.00	2	9.60	66	4.23	64	4.35	23	0.01	32
<i>O. macrochir</i>												
Liambezi	7.98	10.57	27.78	24	6.48	175	4.42	66	12.96	3	12.12	2
Kavango	4.02	6.94	–	–	12.50	8	3.30	30	0.00	5	1.12	9
Kwando	2.64	6.83	0.00	4	0.00	7	6.22	28	2.49	59	2.21	146
Zambezi	10.38	12.79	80.00	5	10.56	24	3.23	28	0.00	2	1.61	15
<i>C. rendalli</i>												
Liambezi	5.88	7.18	9.30	43	6.87	131	3.60	111	2.67	5	0.00	1
Kavango	4.85	8.63	0.00	2	7.87	17	4.42	42	2.78	6	3.51	8
Kwando	3.23	5.26	29.63	9	18.52	9	5.60	17	1.03	78	1.32	128
Zambezi	6.47	10.04	22.22	6	5.80	46	6.61	34	3.81	7	3.19	15

The maximum number of opaque zone counts (age) for each population of *O. andersonii* were 5, 14, 13 and 6 for Liambezi and the Kavango, Kwando and Zambezi, respectively. Maximum ages for males and females from the Kavango were the same, while males reached 1 year older in Liambezi and the Zambezi, and 2 years older in the Kwando. Von Bertalanffy growth curves fitted to observed length-at-age data are presented in Figure 3. Growth differed significantly between males and females in all four populations (LRTs, d.f. = 3, $P < 0.001$), with males having a greater asymptotic length.

Combined sex growth differed significantly between all four populations of *O. andersonii* (LRTs, d.f. = 3, $P < 0.001$). Initial growth rates were fastest in Liambezi, followed by the Zambezi and Kavango, and slowest in the Kwando. The relatively young Liambezi and Zambezi fish continued to grow rapidly up to their respective maximum sizes of 410 and 505 mm, and did not attain their predicted asymptotic lengths. Kwando and Kavango fish went on to attain asymptotic lengths similar to the maximum size reached by Liambezi and Zambezi river fish, respectively, at approximately 10 years of age in both systems. The growth performance index was highest for the Zambezi population (2.91), followed by the Kavango (2.84), Liambezi (2.71), and the Kwando (2.55).

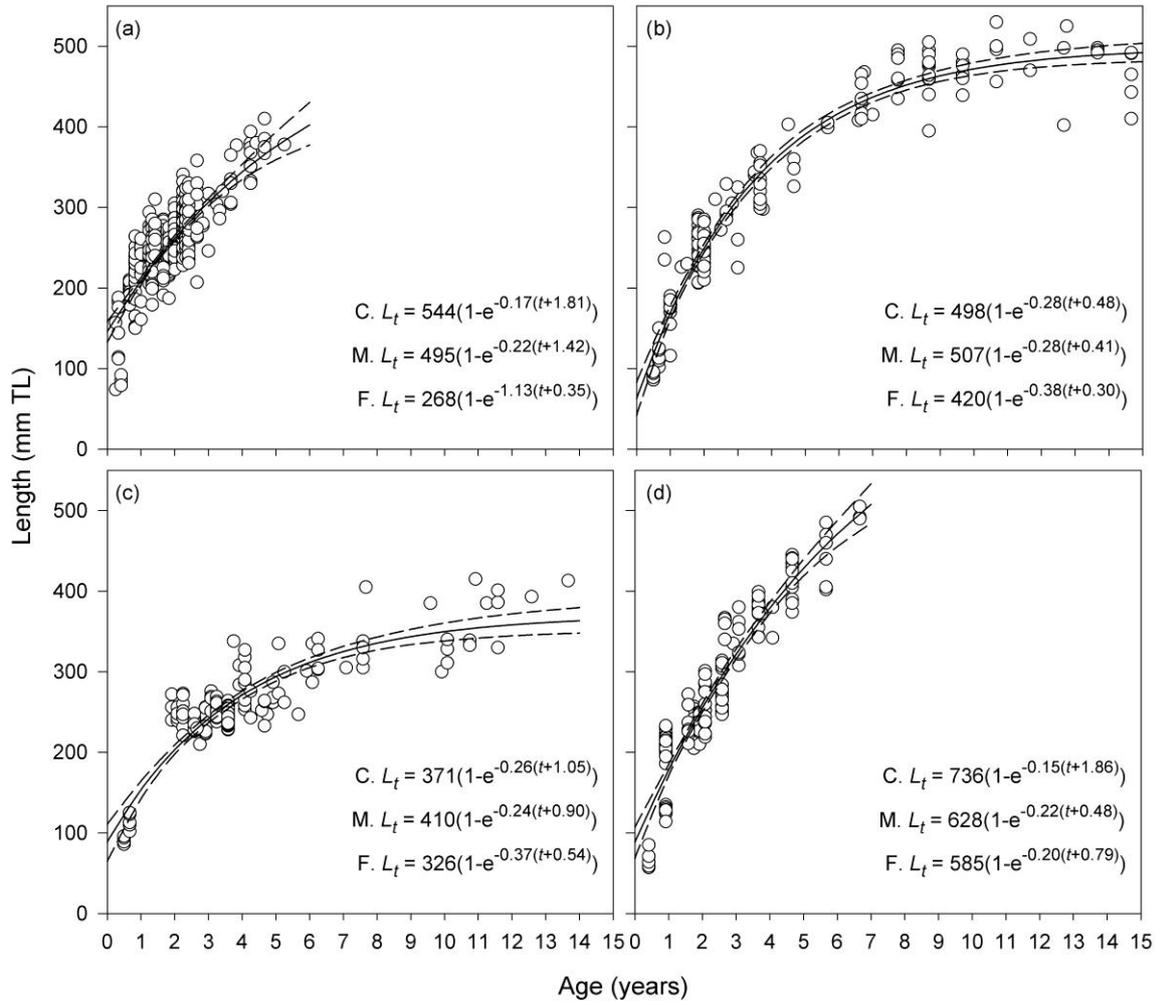


Figure 3: Von Bertalanffy growth curves (—) and 95% bootstrap confidence intervals (---) fitted to combined sex observed length-at-age (○) for *Oreochromis andersonii* from (a) Lake Liambezi, (b) Kavango River, (c) Kwando River and (d) Zambezi River (2010–2014). Growth equations are given for combined sexes (C.), males (M.) and females (F.).

The maximum ages reached by each population of *O. macrochir* were 4, 15, 13 and 11 for Liambezi and the Kavango, Kwando and Zambezi, respectively. Males reached 1 year older than females in Liambezi and the Kwando, and 3 years older in the Zambezi. In the Kavango, however, females reached 5 years older than males. Von Bertalanffy growth curves fitted to observed length-at-age data are presented in Figure. 4. Growth differed significantly between males and females in Liambezi and the Kwando (LRTs, d.f. = 3, $P < 0.001$), with males having a greater asymptotic length, but did not differ in the Kavango and Zambezi (LRTs, d.f. = 3, $P > 0.05$).

Combined sex growth differed significantly between all four populations of *O. macrochir* (LRTs, d.f. = 3, $P < 0.001$). Growth was fastest in Liambezi, followed by the Zambezi and Kavango, and was slowest in the Kwando. The fast growing Liambezi population reached asymptotic length after just three years, and at a similarly small size to the Kwando population which attained asymptotic length much later. The asymptotic length of the Kavango population was intermediate between the two smaller populations and the Zambezi population which was largest. The growth performance index was highest for the Liambezi population (2.85), followed by the Kavango (2.72), and was similar between the Kwando (2.66) and Zambezi (2.65) populations.

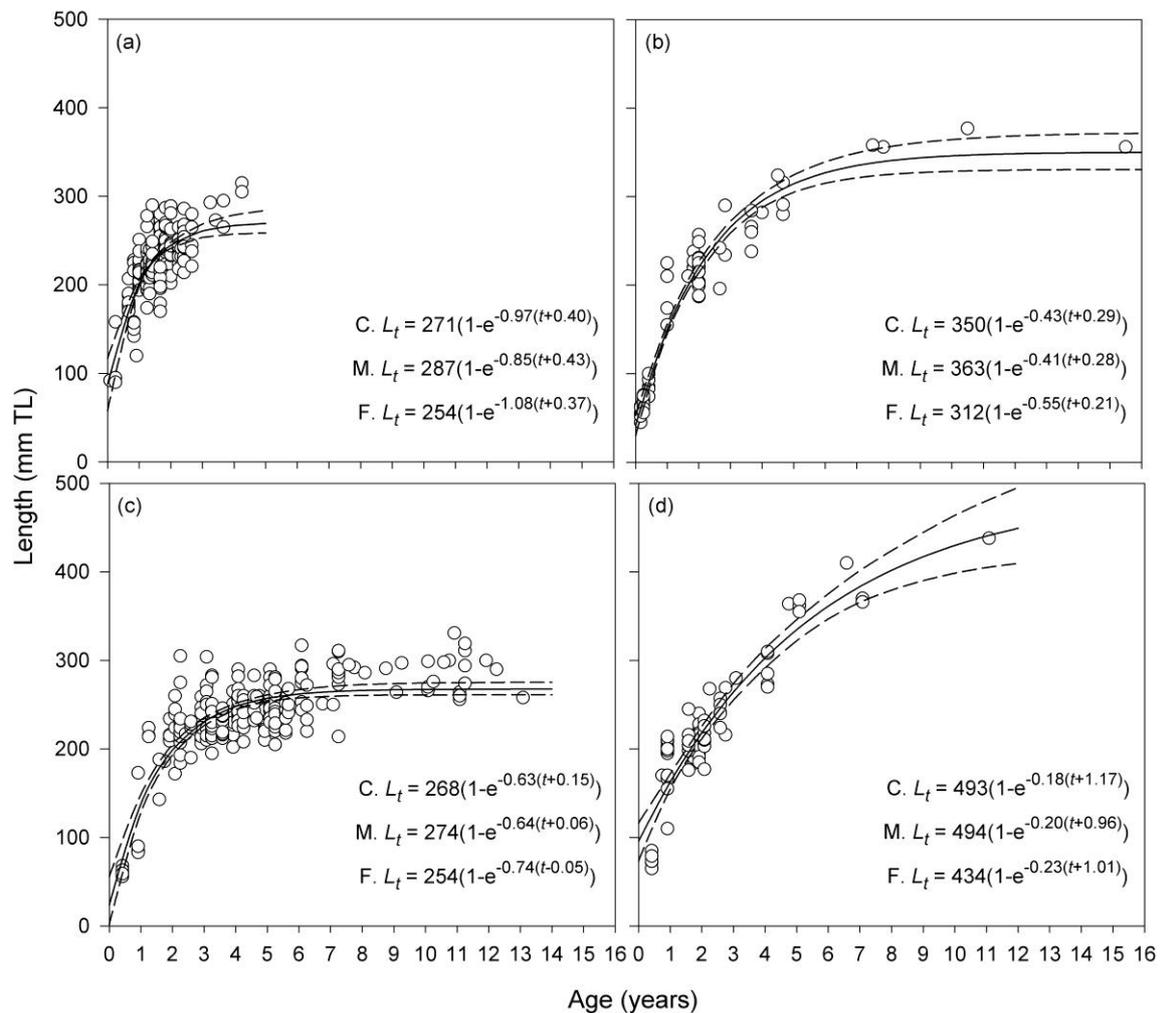


Figure 4: Von Bertalanffy growth curves (—) and 95% bootstrap confidence intervals (---) fitted to combined sex observed length-at-age (○) for *Oreochromis macrochir* from (a) Lake Liambezi, (b) Kavango River, (c) Kwando River and (d) Zambezi River (2010–2014). Growth equations are given for combined sexes (C.), males (M.) and females (F.).

The maximum ages reached by each population of *C. rendalli* were 4, 7, 13 and 7 for Liambezi and the Kavango, Kwando and Zambezi, respectively. Males reached 2 years older than females in the Kavango and Zambezi, and females reached one year older in Liambezi and the Kwando. Von Bertalanffy growth curves fitted to observed length-at-age data are presented in Figure 5. Growth differed significantly between males and females in Liambezi and the Kwando (LRTs, d.f. = 3, $P < 0.001$), with males having a greater asymptotic length, but did not differ in the Kavango and Zambezi (LRTs, d.f. = 3, $P > 0.05$).

Combined sex growth of *C. rendalli* differed significantly between all (LRTs, d.f. = 3, $P < 0.001$) but the Kavango and Zambezi populations (LRTs, d.f. = 3, $P = 0.17$). Growth was fastest in Liambezi, but fish reached asymptotic length earliest, after two years. Kavango and Zambezi populations grew similarly up to 3 years, after which the Kavango population went on to a higher asymptotic length. Growth was slowest in the Kwando River, but fish went on to a relatively large asymptotic length, similar to the Zambezi population. The growth performance index was highest for the Liambezi population (3.05), followed by the Zambezi (2.86), Kavango (2.75) and Kwando (2.55).

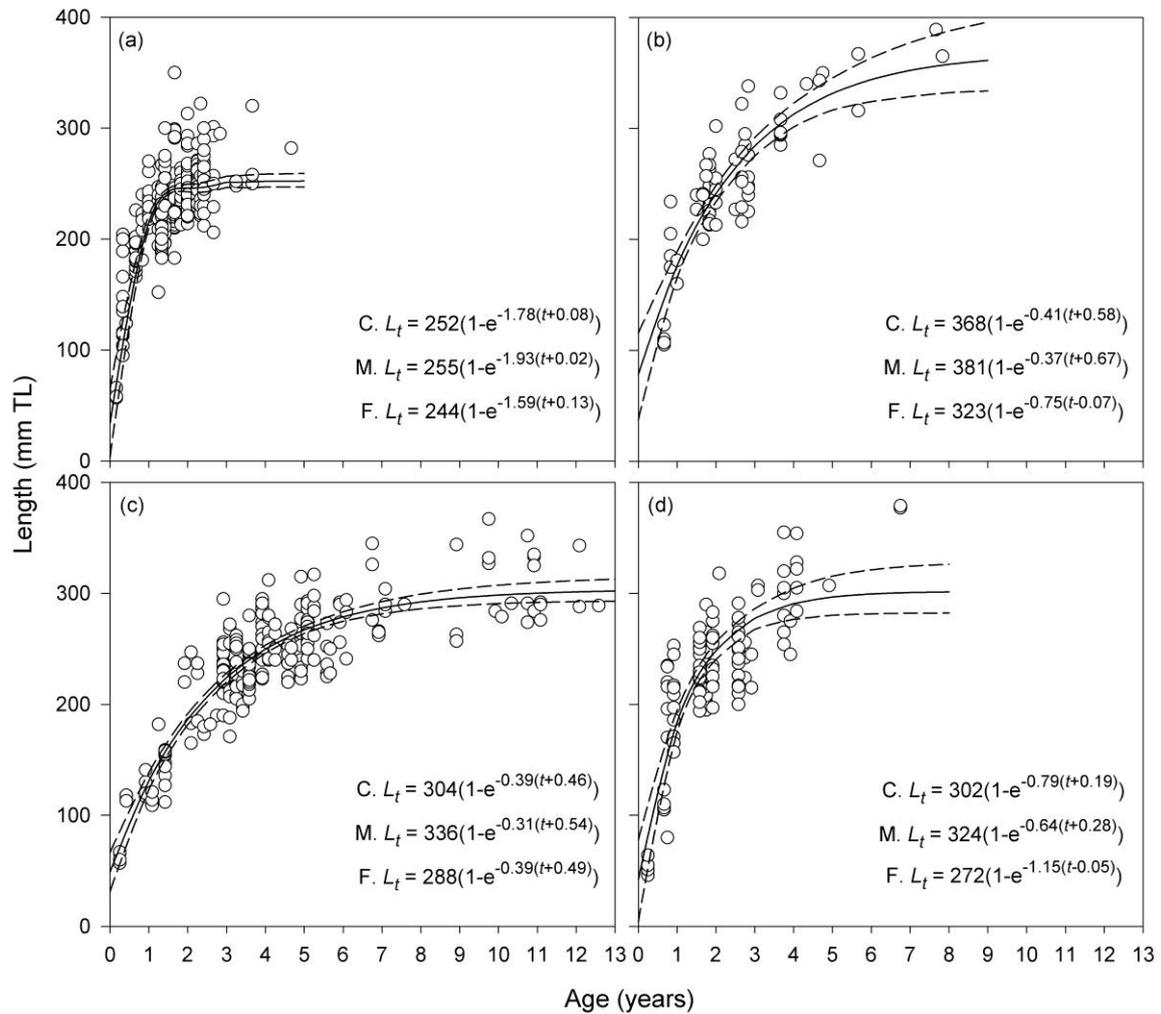


Figure 5: Von Bertalanffy growth curves (—) and 95% bootstrap confidence intervals (---) fitted to combined sex observed length-at-age (○) for *Coptodon rendalli* from (a) Lake Liambezi, (b) Kavango River, (c) Kwando River and (d) Zambezi River (2010–2014). Growth equations are given for combined sexes (C.), males (M.) and females (F.).

Reproduction

The sex ratios of *O. andersonii*, *O. macrochir* and *C. rendalli* are presented in Table 2. The sex ratios of all four populations of *O. andersonii* were male dominated and significantly different from unity in Lake Liambezi and the Kavango River. The sex ratios of *O. macrochir* in Lake Liambezi and the Kavango River were male dominated, and differed significantly from unity. In the Kwando and Zambezi rivers, the sex ratios of *O. macrochir* were very slightly male and female dominated, respectively, but did not differ from unity. The sex ratios of *C. rendalli* were male dominated and significantly different from unity in all four systems.

Table 2: Sex ratios and χ^2 test statistics (d.f. = 1) for four populations of *Oreochromis andersonii*, *Oreochromis macrochir* and *Coptodon rendalli*.

Species	System	<i>n</i>	Sex ratio (male:female)	χ^2	<i>P</i>
<i>O. andersonii</i>	Liambezi	287	2.1:1	36.97	< 0.001
	Kavango	141	4.6:1	58.73	< 0.001
	Kwando	142	1.1:1	0.45	0.50
	Zambezi	141	1.3:1	2.56	0.11
<i>O. macrochir</i>	Liambezi	208	1.4:1	4.92	< 0.05
	Kavango	47	3.3:1	13.30	< 0.001
	Kwando	215	1.1:1	0.38	0.54
	Zambezi	43	1:1	0.02	0.88
<i>C. rendalli</i>	Liambezi	252	1.7:1	16.25	< 0.001
	Kavango	72	2.4:1	12.50	< 0.001
	Kwando	209	1.4:1	6.55	< 0.05
	Zambezi	89	2:1	9.45	< 0.005

The proportion of reproductively active adult female *O. andersonii*, *O. macrochir* and *C. rendalli* indicated that reproductive activity generally extended throughout the austral summer from September to April, following the seasonal water temperature cycle (Figure 6). The lowest proportion of reproductively active fish was observed during the coolest months of June and July. Reproductive activity increased as water temperatures began to rise in August and September, with the majority of fish categorised as having developing gonads. Fish with developing gonads were sampled almost throughout the year, with the highest proportions sampled just prior to and during the first half of the spawning season. The first and highest proportion of ripe *O. andersonii* and *O. macrochir* were sampled in September, and *C. rendalli* in October. Spent *O. andersonii* were sampled from November to March, with the highest proportion sampled in January (33%). Spent *O. macrochir* were sampled over a protracted period, from November through to May, with the highest proportion sampled in December (29%). Spent *C. rendalli* were sampled over the same period as *O. macrochir*, as well as in July, after the spawning season. The highest proportion (52%) were sampled early in the spawning season, in November.

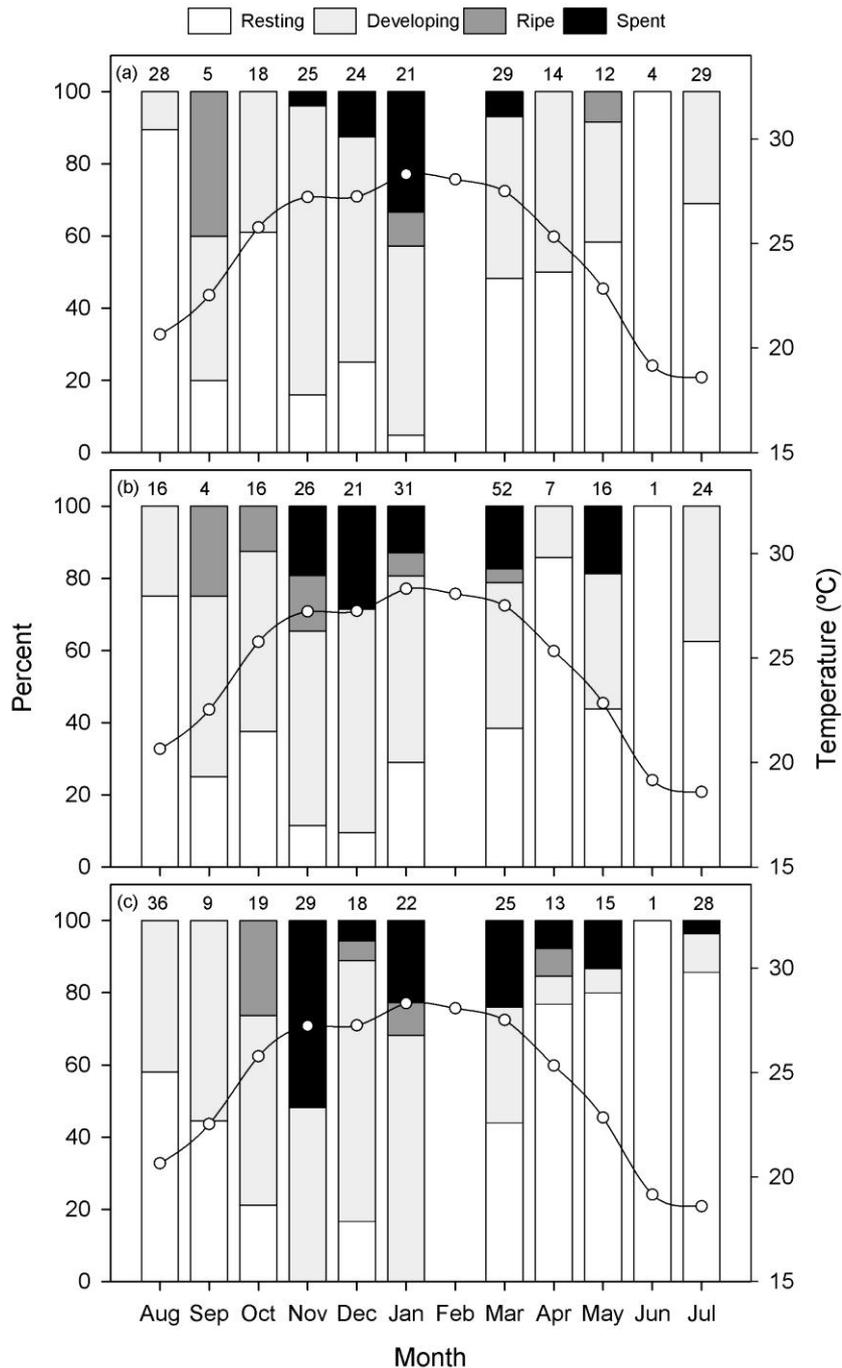


Figure 6: Combined reproductive seasonality of four populations of adult female (a) *Oreochromis andersonii* (b) *Oreochromis macrochir* and (c) *Coptodon rendalli* from Lake Liambezi and the Kavango, Kwando and Zambezi rivers (2010–2011) and mean monthly water temperatures from the four systems. Numbers above bars denote sample sizes.

The lengths-at-50%-maturity (L_{50}) of combined sex *O. andersonii* ranged from 238 mm TL in the Kavango to 254 mm TL in Liambezi (Figure 7), and did not differ significantly between the four populations (LRTs, d.f. = 2, $P > 0.05$). For *O. macrochir*, L_{50} ranged from

199 mm TL in the Kavango to 254 mm TL in the Zambezi (Figure 8). Length-at-maturity differed significantly between the Zambezi and other populations (LRTs, d.f. = 2, $P < 0.05$), with the Zambezi population having a higher Lm_{50} . For *C. rendalli*, Lm_{50} ranged between 195 mm TL in the Kavango River and 214 mm TL in the Zambezi River (Figure 9). Length-at-maturity did not differ significantly between the four populations (LRTs, d.f. = 2, $P > 0.05$).

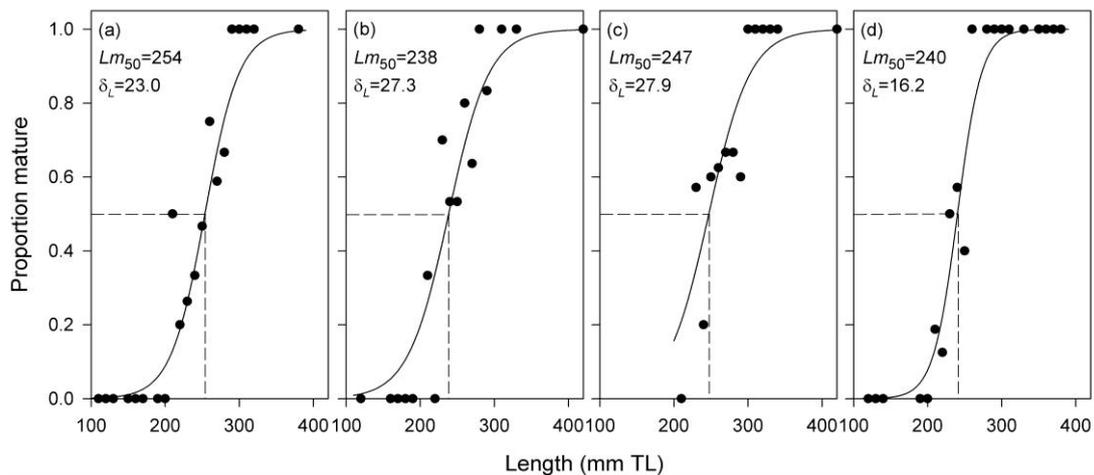


Figure 7: Length at 50% sexual maturity for *Oreochromis andersonii* (combined sexes) from (a) Lake Liambezi ($n = 149$), (b) Kavango River ($n = 81$), (c) Kwando River ($n = 56$) and (d) Zambezi River ($n = 97$) estimated by fitting a logistic ogive (—) to the observed (●) proportion of mature fish per length class.

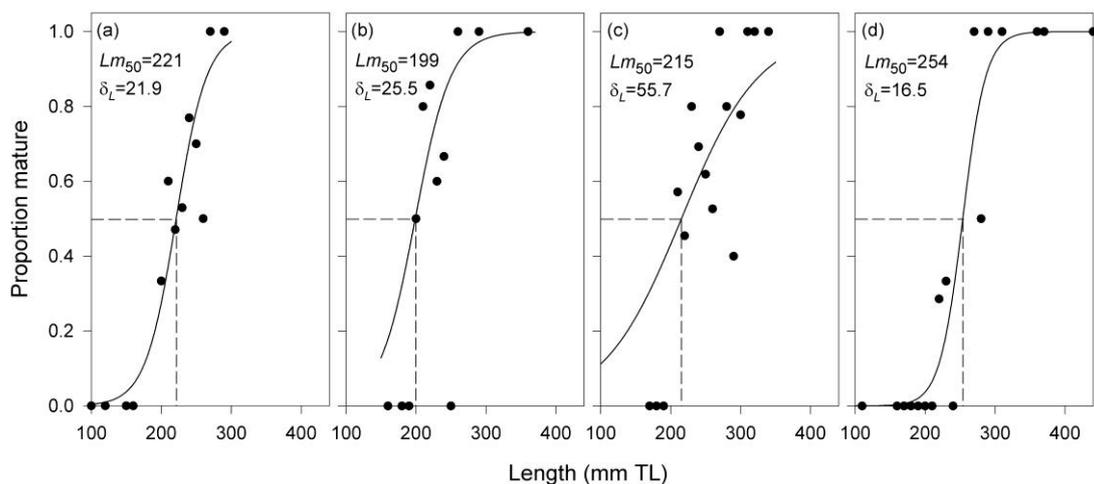


Figure 8: Length at 50% sexual maturity for *Oreochromis macrochir* (combined sexes) from (a) Lake Liambezi ($n = 84$), (b) Kavango River ($n = 38$), (c) Kwando River ($n = 124$) and (d) Zambezi River ($n = 48$) estimated by fitting a logistic ogive (—) to the observed (●) proportion of mature fish per length class.

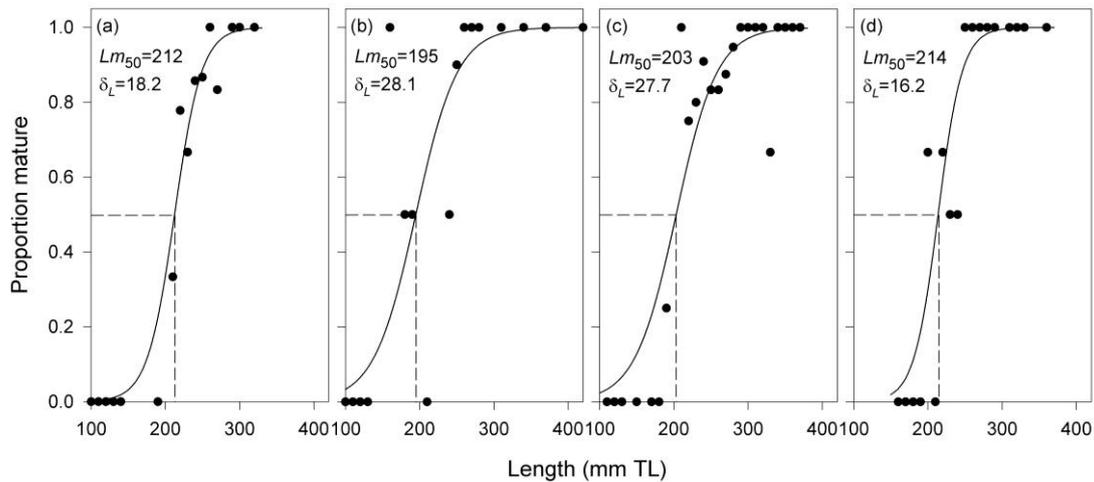


Figure 9: Length at 50% sexual maturity for *Coptodon rendalli* (combined sexes) from (a) Lake Liambezi ($n = 117$), (b) Kavango River ($n = 57$), (c) Kwando River ($n = 147$) and (d) Zambezi River ($n = 36$) estimated by fitting a logistic ogive (—) to the observed (●) proportion of mature fish per length class.

Age-at-50%-maturity (tm_{50}) of combined sex *O. andersonii* ranged from 1.49 years in the Kavango to 2.9 years in the Kwando (Table 3). Age-at-maturity differed significantly between the Kwando and other populations, and between the Zambezi and Kavango (LRTs, d.f. = 2, $P < 0.05$). For *O. macrochir*, tm_{50} ranged from 1.01 years in Liambezi to 2.99 years in the Zambezi. Age-at-maturity for the Zambezi and Kwando populations differed significantly from each other and from the Liambezi and Kavango populations (LRTs, d.f. = 2, $P < 0.05$). For *C. rendalli*, tm_{50} ranged from 1.06 years in Liambezi to 2.53 years in the Kwando. Age-at-maturity differed significantly between the Kwando and the other populations (LRTs, d.f. = 2, $P < 0.05$).

Table 3: Age at 50% sexual maturity (tm_{50}) for four populations of *Oreochromis andersonii*, *Oreochromis macrochir* and *Coptodon rendalli* (sexes combined), and the predicted proportion of mature fish per age class estimated by fitting the observed proportion of mature fish per age class derived from otolith samples to a logistic ogive.

Species	System	<i>n</i>	tm_{50}	δ_t	Age class (years)				
					1	2	3	4	5
<i>O. andersonii</i>	Liambezi	136	1.6	0.72	0.31	0.64	0.88	0.97	
	Kavango	80	1.5	1.44	0.41	0.58	0.74	0.85	0.91
	Kwando	55	2.9	0.81	0.09	0.25	0.53	0.79	0.93
	Zambezi	97	2.0	0.57	0.15	0.49	0.85	0.97	0.99
<i>O. macrochir</i>	Liambezi	82	1.0	0.59	0.48	0.78	0.94	0.98	
	Kavango	38	1.3	0.75	0.18	0.49	0.81	0.95	0.99
	Kwando	122	2.5	2.93	0.37	0.45	0.54	0.62	0.70
	Zambezi	49	3.0	0.56	0.18	0.49	0.81	0.95	0.99
<i>C. rendalli</i>	Liambezi	93	1.1	0.39	0.47	0.91	0.99	0.99	
	Kavango	59	1.1	0.46	0.45	0.87	0.98	0.99	0.99
	Kwando	145	2.5	0.85	0.14	0.34	0.63	0.84	0.94
	Zambezi	37	1.4	0.49	0.32	0.78	0.96	0.99	0.99

Discussion

Age and growth

Oreochromis andersonii, *O. macrochir* and *C. rendalli* have been aged using both scales and otoliths in several previous studies, but no estimates of ageing precision have been published. Precision estimates for the three study species varied considerably between populations, and were highest in the Kavango and Kwando where sampling took place in protected areas, and numerous old fish were captured. Precision was generally lower in the Zambezi and Liambezi where fish populations are heavily exploited, and the majority of fish sampled were young. Interpreting the first annulus was often difficult in young fish (1–2 years), but was easier in older fish (> 2 years). Disparity among precision estimates are likely due to differences in age composition between populations, as precision increases with age (Campana 2001), rather than to differences in otolith readability. Precision estimates obtained in the present study were broadly comparable with other cichlids aged using sectioned sagittal otoliths, including *Oreochromis niloticus* (APE = 5.6%; CV = 7.9%) from Ugandan crater lakes (Bwanika et al. 2007) and *Diplotaxodon limnothrissa* (APE = 10.5%; CV = 7.4%) from Lake Malawi (Kanyerere et al. 2005).

The maximum ages of *O. andersonii*, *O. macrochir* and *C. rendalli* of 14, 15 and 13 years, respectively, were comparable to otolith age estimates of these species elsewhere (Table 4).

Fishes from the ephemeral Lake Liambezi were much younger because the lake was only inundated in 2007 (Peel et al. 2015), while heavy fishing pressure on the Zambezi River will have removed many of the older fish from the population (Tweddle et al. 2015). Males of all three species generally grew to a larger size than females, and reached L_{∞} at a later age, as noted by Dudley (1974) on the Kafue floodplain, Zambia. Where male and female growth did not differ, i.e. for *O. macrochir* and *C. rendalli* in the Kavango and Zambezi, sample sizes were smaller and did not include all age and size classes of each sex, resulting in larger confidence intervals around the fitted von Bertalanffy growth curves.

The growth rates of combined sexes *O. andersonii*, *O. macrochir* and *C. rendalli* varied considerably between populations in the present study, as well as with previous studies. Initial growth rates of all three species in the present study were fastest in Lake Liambezi, probably owing to high levels of productivity in the recently flooded environment (Baldwin & Mitchell 2000). *Oreochromis andersonii* attained more than half, and *O. macrochir* and *C. rendalli* nearly two thirds their maximum observed lengths after one year in the lake. Despite slower initial growth rates, all three species went on to attain much larger sizes in the Zambezi and Kavango. Growth may have been truncated in Liambezi by heavy fishing pressure. However, van der Waal (1985) also noted that, under much lower fishing pressure than during the present study (Peel et al. 2015), *O. andersonii* in Liambezi did not attain sizes as large as those in the Zambezi. Populations from Liambezi and the Kwando attained similar maximum sizes.

Overall, the growth performance of *O. macrochir* and *C. rendalli* were highest in Lake Liambezi, while that of *O. andersonii* was highest in the Zambezi (Table 4). The growth performance of *O. andersonii* and *C. rendalli* were lowest in the Kwando. *Oreochromis macrochir* displayed similarly poor growth performance in the Zambezi and Kwando. The poor growth performance of *O. macrochir* in the Zambezi is in sharp contrast with the other species. It is not clear whether these differences are genuine, or are a result of inadequate sample sizes. The estimated t_0 for *O. macrochir* in the Zambezi is much lower than that of the other populations in this study, resulting in a lower K and consequently poor growth performance. The consistently poor growth performance of the Kwando populations, however, suggests that this small river is much less productive than the Zambezi and Kavango. The Zambezi and Kavango receive large seasonal flood pulses that facilitate the

exchange of carbon and nutrients between the river channel and floodplain, resulting in high levels of productivity (Junk et al. 1989; Bayley 1995). In addition to receiving a smaller flood, flooding in the Kwando usually occurs later, in July–August when water temperatures are at their lowest. Productivity is likely to be lower as a result, and fish may not be able to utilise the food resources on the floodplain as efficiently as they might in the Zambezi and Kavango, where flooding coincides with high water temperatures.

Oreochromis andersonii and *O. macrochir* display similar size and growth characteristics between the Kwando River, Kafue River (Kapetsky 1974) and Okavango Delta (Booth et al. 1995; Booth & Merron 1996). *Coptodon rendalli* also have similar growth characteristics in the Kwando and Kafue (Kapetsky 1974), indicating that the environmental conditions influencing growth are similar between these three systems. *Oreochromis andersonii* and *O. macrochir* grow faster in the Kavango River in Namibia than they do further downstream in the Okavango Delta. This may be attributed to differences in the hydrological regime between the two regions as discussed above for the Kwando River. The growth performance of *O. andersonii* from Lake Liambezi was similar between van der Waal's (1985) study in the 1970s and the present study. In contrast, *O. macrochir* and *C. rendalli* grew much slower in the 1970s when compared to the present study. This is despite the use of scales by van der Waal (1985b) that have been shown to underestimate the age of older fish, and consequently overestimate growth (Hecht 1980; Booth et al. 1995). Lake Liambezi had been inundated for a much longer period (≈ 10 years) when sampled by van der Waal (1985), and the overall productivity may have declined since the initial trophic upsurge period after inundation, resulting in slower growth rates of *O. macrochir* and *C. rendalli*. The growth rates of *O. andersonii* and *C. rendalli* in the Zambezi River are among the highest observed for these species (Table 4).

Reproduction

As equilibrium strategists (Winemiller & Rose 1992), cichlids are well adapted to stable environmental conditions, and are capable of breeding independently of the hydrological regime. Reproductive seasonality is very closely related to temperature (Dudley 1974; van der Waal 1985; Weyl & Hecht 1998). In equatorial environments, where temperatures are high year round, spawning can occur throughout the year, whereas in more temperate environments, spawning is often restricted to a few months of the year (Russell et al. 2012). The spawning season of *O. andersonii*, *O. macrochir* and *C. rendalli* did not differ between

Lake Liambezi and the Kavango, Kwando, and Zambezi rivers, as the four systems had similar latitude, altitude and resulting temperature regimes. Reproductive activity in all three species began in September as water temperatures started to rise, peaked between November and January, and continued up until May, when temperatures dropped below 25 °C. This was consistent with what was previously known about the breeding seasonality of these species from neighbouring systems (Dudley 1974; van der Waal 1985; Merron 1991; Weyl & Hecht 1998).

Cichlids are renowned for having flexible reproductive traits which vary in response to abiotic and biotic conditions (Fryer & Iles 1972; Trewavas 1983; Merron 1991; James & Bruton 1992; Kolding 1993; Brummett 1995; Duponchelle & Panfili 1998; Duponchelle et al. 2000). In large, stable environments where adult mortality is low, fish mature at a larger size and produce fewer, larger eggs, maximising each individual offspring's chances of survival. In smaller, less stable environments where mortality rates are higher, fish mature at a smaller size and produce many small eggs, increasing the population growth potential and enhancing the species resilience to major habitat disturbances such as drought. Length-at-maturity in male *Oreochromis mossambicus* from small reservoirs in South Africa ranged between 110 and 265 mm standard length (James & Bruton 1992). Merron (1991) recorded lengths-at-maturity for *O. andersonii* ranging from 105 to 155 mm SL in perennially and seasonally flooded areas in the Okavango Delta.

In contrast to the high variability in length-at-maturity in the above examples, length-at-maturity of *O. andersonii* and *C. rendalli* did not differ significantly from each other in the four sampling areas (Table 4). For *O. macrochir* it was significantly higher in the Zambezi River compared to that in the Kwando River. These estimates were, however, based on small sample sizes. As lengths-at-maturity of *O. andersonii* and *C. rendalli* did not differ between systems, it can be assumed that the differences for *O. macrochir* are an artefact of the data, although larger sample sizes for these systems are required to substantiate this. The similarities in length-at-maturity between populations observed in this study indicate that the environmental variables influencing length-at-maturity are similar in each system, despite the fact that growth varies considerably.

Lengths-at-maturity of *O. andersonii* in this study were similar to that observed by van der Waal (1985) in Lake Liambezi, and large compared to those observed by Merron (1991) in

the Okavango Delta. Lengths-at-maturity of *O. macrochir* in the Kwando River and Lake Liambezi were similar to that observed by van der Waal (1985) in the lake prior to it drying up, while estimates from the Zambezi River were larger and estimates from the Kavango River were smaller. *Coptodon rendalli* in this study matured at similar sizes to those in Lake Kariba (Kolding et al. 1992) and Lake Chicamba (Weyl & Hecht 1998), but significantly larger than they did in Lake Liambezi (van der Waal 1985). Age-at-maturity, unlike length-at-maturity, differed markedly between populations as a result of variation in growth rates. Age-at-maturity was lowest in Lake Liambezi where the initial growth rates were fastest, and highest in the Kwando River where growth was slowest.

Table 4: Ageing method and measured life-history parameters for *Oreochromis andersonii*, *Oreochromis macrochir* and *Coptodon rendalli* from different locations. t_{max} = maximum observed age; L_{max} = maximum observed length (mm TL); L_{∞} , K and t_0 = von Bertalanffy growth model parameters; ϕ' = growth performance index; L_{m50} = length at 50% maturity; t_{m50} = age at 50% maturity.

Species & Locality	Period	Structure	t_{max}	L_{max}	L_{∞}	K	t_0	ϕ'	L_{m50}	t_{m50}
<i>O. andersonii</i>										
Kafue River ^A	1970	Scales	11	–	497	0.15	-1.34	2.56	–	–
Lake Liambezi ^B	1973–76	Scales	9	430	450	0.31	-1.13	2.79	260	1.7
Okavango Delta ^C	1984–86	Otoliths	13	397	331	0.25	-2.33	2.44	187	1.0
Lake Liambezi ^D	2010–14	Otoliths	5	410	544	0.17	-1.81	2.71	254	1.6
Kavango River ^D	2010–14	Otoliths	14	530	499	0.28	-0.48	2.84	238	1.5
Kwando River ^D	2010–14	Otoliths	13	415	371	0.26	-1.05	2.55	247	2.9
Zambezi River ^D	2010–14	Otoliths	6	505	736	0.15	-0.86	2.91	240	2.0
<i>O. macrochir</i>										
Kafue River ^A	1970	Scales	7	–	308	0.31	-0.52	2.47	–	–
Lake Liambezi ^B	1973–76	Scales	8	390	469	0.20	-1.35	2.64	200	1.4
Okavango Delta ^E	1984–86	Otoliths	11	291	275	0.42	-1.07	2.50	–	–
Lake Liambezi ^D	2010–14	Otoliths	4	315	271	0.97	-0.40	2.85	221	1.0
Kavango River ^D	2010–14	Otoliths	15	377	350	0.43	-0.29	2.72	199	1.3
Kwando River ^D	2010–14	Otoliths	13	331	268	0.63	-0.15	2.66	215	2.5
Zambezi River ^D	2010–14	Otoliths	11	438	493	0.18	-1.17	2.65	254	3.0
<i>C. rendalli</i>										
Lake Kariba ^F	1968–71	Scales	5	336	485	0.15	-0.42	2.53	220	3.7
Kafue River ^A	1970	Scales	8	–	364	0.31	-0.64	2.62	–	–
Lake Liambezi ^B	1973–76	Scales	7	320	393	0.16	-1.88	2.40	140	0.9
Lake Chicamba ^G	1995–96	Otoliths	16	310	239	0.64	-0.91	2.56	212	2.5
Lake Liambezi ^D	2010–14	Otoliths	4	350	252	1.78	-0.08	3.05	212	1.1
Kavango River ^D	2010–14	Otoliths	7	389	368	0.41	-0.58	2.75	195	1.1
Kwando River ^D	2010–14	Otoliths	13	367	304	0.39	-0.46	2.55	203	2.5
Zambezi River ^D	2010–14	Otoliths	7	379	302	0.79	-0.19	2.86	214	1.4

^AKapetsky (1974), ^Bvan der Waal (1985), ^CBooth *et al.* (1995), ^DPresent study, ^EBooth and Merron (1996), ^FBastl (1974), ^GWeyl and Hecht (1998)

In summary, we reject the null hypotheses that growth rates and age-at-maturity do not differ significantly between four populations of *O. andersonii*, *O. macrochir* and *C. rendalli* in north-eastern Namibia. Our data, however, support the null hypothesis that length-at-maturity does not differ significantly between four populations of *O. andersonii* and *C. rendalli*. Differences in length-at-maturity for *O. macrochir* are not believed to be genuine, and are tentatively ascribed to inadequate sample sizes from the Kavango and Zambezi populations.

These results provide the basis for developing a fishery management strategy that will ensure the recovery and optimal exploitation of these large, valuable cichlids. The lack of significant differences in length-at-maturity between populations means that a single minimum mesh size, designed to harvest fish after they have reached maturity, can be set for all four systems. Large differences in growth rates between populations means that the different systems are likely to be able to sustain very different levels of fishing effort. Lake Liambezi and the Zambezi River, where fish grow fastest, are likely to be able to withstand higher fishing effort than the Kavango River, followed by the Kwando River. Fishing effort may therefore have to be regulated, especially in the Kavango and Kwando rivers, to prevent overfishing. This may be achieved through strengthening community ownership of the fish resources, and the establishment of community based fish protection areas (Tweddle et al. 2015).

Acknowledgements

We gratefully acknowledge the Ministry of Fisheries and Marine Resources, Namibia, for granting permission to carry out this research, and for providing technical, logistic and personnel support. This research was funded through the Namibia Nature Foundation by the Integrated Community-Based Ecosystem Management Project, the Nedbank Namibia Go-Green Fund, and the Southern African Scientific Service Centre for Climate Change and Adaptive Land Management. Additional support and funding were received from the NNF/WWF Zambezi/Chobe Fisheries Project, EU/NNF Community Conservation Fisheries in KAZA Project, University of Namibia, National Research Foundation of South Africa (NRF, UID: 77444), the South African institute for Aquatic Biodiversity and Rhodes University.

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