

BIOLOGY AND ECOLOGY OF LARGEMOUTH BASS
***MICROPTERUS SALMOIDES* IN TWO TEMPERATE SOUTH**
AFRICAN IMPOUNDMENTS

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

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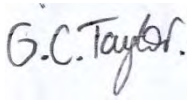
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ABSTRACT

Globally largemouth bass *Micropterus salmoides* is one of the most widely introduced game fish species which has now become invasive in many countries. Well researched in its native North America, there are few studies on this species in its introduced range. This study aims to improve the understanding of the biology and ecology of *M. salmoides* in temperate southern Africa, where it threatens native biota and supports a popular recreational fishery. This aim was addressed by assessing the age, growth, maturity, reproductive seasonality, feeding, mortality and movement, of two *M. salmoides* populations from Wiggleswade (1000 ha, 723 m amsl, 32°35'S; 27°33'E) and Mankazana (35 ha, 66 m amsl, 33°09'S; 26°57'E) Dams in the Eastern Cape of South Africa.

The most suitable structure for ageing *M. salmoides* was determined by comparing the accuracy and precision of otoliths and scales. Scales tended to underestimate the age of fish older than five years. Sectioned sagittal otoliths were the more precise structures for ageing (otoliths CV = 15.8 vs. scales CV = 21.9). The periodicity of growth zone formation was validated as annual for otoliths using both edge analysis (EA), and mark recapture of chemically tagged fish (MRCT). EA indicated one annual peak in the frequency of opaque margins between September and January using a periodic logistic regression and a binomial model linked with a von Mises distribution for circular data. MRCT showed the linear relationship between time at liberty and number of growth zones distal to the fluorescent band was not significantly different from one (slope = 0.89).

Reproduction was similar to that in native and non-native populations with fish reaching age at 50% maturity at ca. two years, and length at 50% maturity at 259-290 mm FL depending on growth rate. Spawning season occurred in the spring months of August to October. The Wiggleswade Dam population reached similar ages (14 yrs) to populations in temperate North America. Growth was described using the von Bertalanffy growth equations of $L_t = 420(1 - e^{-0.33(t+0.21)})$ mm FL in Wiggleswade and $L_t = 641(1 - e^{-0.22(t+0.76)})$ mm FL in Mankazana. Growth performance of both populations, described using the phi prime index, seemed to be correlated with temperature and the Wiggleswade Dam population ($\Phi' = 2.8$) grew similarly to those native temperate North American populations and the non-native populations of Japan and Italy. The Mankazana population had a higher growth

performance ($\Phi' = 2.9$) compared to Wriggleswade and growth was comparable to other non-native African populations. Both populations utilised all available food resources, with the Mankazana population being in better condition than the Wriggleswade population as a result of a more diverse diet, highly abundant food sources throughout the year, and potentially the adoption of a more conservative ambush feeding strategy. The Wriggleswade population, which was utilised by competitive anglers, showed low mortality rates ($Z = 0.43 \text{ yr}^{-1}$), and translocated fish dispersed from the common release site, travelling an average distance of 4 km over the study time of 494 days.

These results indicated that *M. salmoides* are successful in these environments, growing at expected temperature dependant rates, maturing at two years, using all available food groups, and suffering from low mortality. It is therefore likely that they will persist in South Africa and establish where introduced.

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CHAPTER 1: GENERAL INTRODUCTION

Recreational angling is popular worldwide in both freshwater and marine environments (Cooke & Schramm, 2007) with an estimated participation of up to 10.6% of the industrialised world's population (Arlinghaus & Cooke, 2009). Within the last 20 years the popularity and growth of recreational fisheries (Schramm et al., 1991a, b) has resulted in their significant contribution to regional and national economies (Marta et al., 2001; Cooke & Schramm, 2007; Cooke et al., 2009). Although their economic value is difficult to quantify, Canada's recreational fishery's industry was estimated to be worth CAN\$ 4.4 – 7 bil annually as cited by Post et al. (2002), and a trophy largemouth bass fishery in Lake Fork (Texas) generated a total output at a state level of US\$ 9.5 mil (Chen et al., 2003). This increase in both the popularity of this pastime, coupled with its associated socio-economic importance has been found to grow proportionally with industrialisation to a peak, after which society becomes aware of conservation needs (Cowx et al., 2010). Unfortunately in most countries the movement towards conservation comes after the stocking of popular non-native sport fishes (Cambray, 2003; Johnson et al., 2009; McCafferty et al., 2012), which have consequently become a major conservation concern in many of the world's freshwater ecosystems (Cowx & Collares-Pereira, 2002, Cambray, 2003).

Largemouth bass *Micropterus salmoides* (Lacépède 1802) are native to North America where they are an important freshwater angling species (Robbins & MacCrimmon, 1974; Jackson, 2002; Quinn & Paukert, 2009). Because of their popularity with anglers, these piscivorous predators have been introduced into a wide range of recipient habitats in Europe, Asia, South and North America (Robbins & MacCrimmon, 1974; Welcomme, 1988; Lever, 1996) and Africa (de Moor & Bruton, 1988; Weyl & Hecht, 1999; Skelton & Weyl, 2011) (Figure 1.1), and are consequently estimated to be one of the five most introduced fish species globally (Welcomme, 1992). The effective equilibrium life history strategy displayed by this species, characterising a medium sized fish maturing at a moderate age, that achieves high juvenile survivorship as a result of some parental care (Mims et al., 2010), almost guarantees that where introduced they establish successfully. Once established *M. salmoides* are successful predators which prey on a wide range of native biota (Weyl & Hecht, 1999; Weyl & Lewis,

2006; Wasserman et al., 2011), which has been shown to result in decreased native fish abundance (Gratwicke & Marshall, 2001; Ellender et al., 2011) and changes in the structure of invertebrate communities (Weyl et al., 2010). Predation impacts together with interspecific competition (Bacheler et al., 2004; Fine et al., 2011; Saylor et al., 2012) may ultimately lead to changes in ecosystem structure and functioning (Jackson, 2002; Jang et al., 2006; Gozlan et al., 2010) and *M. salmoides* are listed among the 100 world's worst invasive alien species (Lowe et al., 2000).



Figure 1.1: The global distribution of *Micropterus salmoides* with the green area identifying the native range and the orange the non-native range of this species (adapted from Skelton & Weyl, 2011).

Introduced into South Africa in 1928 as a game fish species for recreational angling purposes, *M. salmoides* can now be found in all of the major catchments of southern Africa (de Moor & Bruton, 1988; Skelton & Weyl, 2011), with a preference for slow flowing or static waters such as impoundments (Skelton, 2001; van Rensburg et al., 2011). Commonly referred to as dams in South Africa, impoundments are known as invasion sources as their accessibility encourages continuous propagule pressures through stocking, their young age ensures niche availability and their high incidence of disturbance results in less biotic resistance to invasion (Elton, 1958; de Moor, 1996; Johnson et al., 2008). Since South Africa is a water scarce country, many dams are scattered across the landscape (King et al., 2011), most of which are inhabited by a suite of non-native species including *M. salmoides* (de Moor & Bruton, 1988;

McCafferty et al., 2012). Within these environments *M. salmoides* is commonly utilised in subsistence and recreational fisheries which are of considerable value (McCafferty et al., 2012).

On the other hand South Africa is also regarded as an alien invasion freshwater hotspot (Leprieur et al., 2008), with *M. salmoides* contributing to the host of 21 non-native fish species that have now become established in the country as a result of human activity (van Rensburg et al., 2011). The predation of *M. salmoides* has severely impacted a number of native stream fishes, especially in areas in which no predators occurred previously. For example in the Swartkops River system the Endangered Eastern Cape redbfin minnow *Pseudobarbus afer*, has been restricted to a small stretch of stream above a waterfall, downstream of which the invasion of *M. salmoides* and smallmouth bass *Micropterus dolomieu* has resulted in the extirpation of this endemic native species (Ellender et al., 2011). *Micropterus salmoides* are also keen competitors with native predatory fish such as the Eastern Cape rocky *Sandelia bainsii* (de Moor & Bruton, 1988).

Micropterus salmoides therefore contribute both to the economy of South Africa and its biodiversity crisis and require management because of the threat they pose to indigenous species. Realising the need for management, legislation governing the importation and movement of alien fishes has been proposed under the National Environmental Management: Biodiversity Act (NEM:BA) for alien species (NEM, 2004). This legislation focuses on regulation by area through the exclusion of non-native species from areas of biodiversity concern, and limiting their further spread into areas where they do not occur (NEM, 2004; van Rensburg et al., 2011). Proposed legislation limits the use of invasive fishes to specific areas, which are still under debate, in order to address the trade-off between economic interests such as recreational fishing and aquaculture use, and conservation priorities associated with the threats to native ecosystems (van Rensburg et al., 2011). Under this current management legislation, an understanding of the biology and ecology of *M. salmoides* is important not only for managing fisheries but also for understanding their invasions within southern Africa.

1.1 Thesis outline

The overall aim of this thesis is to contribute to the understanding of the biology and ecology of *M. salmoides* in South Africa. To achieve this aim, the two populations of Wriggleswade and Mankazana Dams in the Eastern Cape of South Africa are assessed. The thesis is structured as follows.

After the general introduction in Chapter 1, Chapter 2 describes the location, physical characteristics, water quality and fish species present within the study sites, and summarises the general sampling methods adopted to attain the samples.

When studying aspects of the biology of a species such as rates of growth and mortality, an accurate and precise estimation of age is required (Beamish & McFarlane, 1987; Campana & Thorrold, 2001). Chapter 3 therefore investigates the precision of ageing scales versus otoliths, in order to determine the most precise structure to age *M. salmoides* in temperate South Africa.

In Chapter 4, growth zone deposition rates are assessed to determine accuracy. This is undertaken using the indirect method of edge analysis in both populations, and directly in Wriggleswade and two farm dams via the mark recapture of chemically tagged fish.

With confidence in the accuracy and precision of the age estimates acquired, the growth, maturity and reproductive seasonality of the populations are assessed in Chapter 5 and compared to those of other native and non-native *M. salmoides* populations.

The feeding ecology of both populations is then explored using gut content analysis in Chapter 6.

To understand the impact of humans on the species the effects of angling are assessed in Chapter 7. Specifically mortality rates and the dispersal of tournament translocated fish are investigated in Wriggleswade Dam.

Finally the general discussion in Chapter 8 explores the success of these two temperate South African non-native *M. salmoides* populations, and the direction that future studies should take to address additional biological and ecological questions.

CHAPTER 2: STUDY AREA AND GENERAL SAMPLING METHODS

In order to assess the biology and ecology of *Micropterus salmoides* within the environment in question, the areas of study must be described. The aims of this chapter are: (1) to describe the two study sites firstly with respect to geographic location, land use and utilisation; (2) to characterise the fish fauna of the ecosystems and to define the physical water parameters; and (3) to outline the general methods used to obtain the samples.

2.1 Study area

This study was carried out on the largemouth bass *Micropterus salmoides* populations of two lentic water bodies in the Eastern Cape Province of South Africa: Wriggleswade and Mankazana Dams¹ (Figure 2.1).

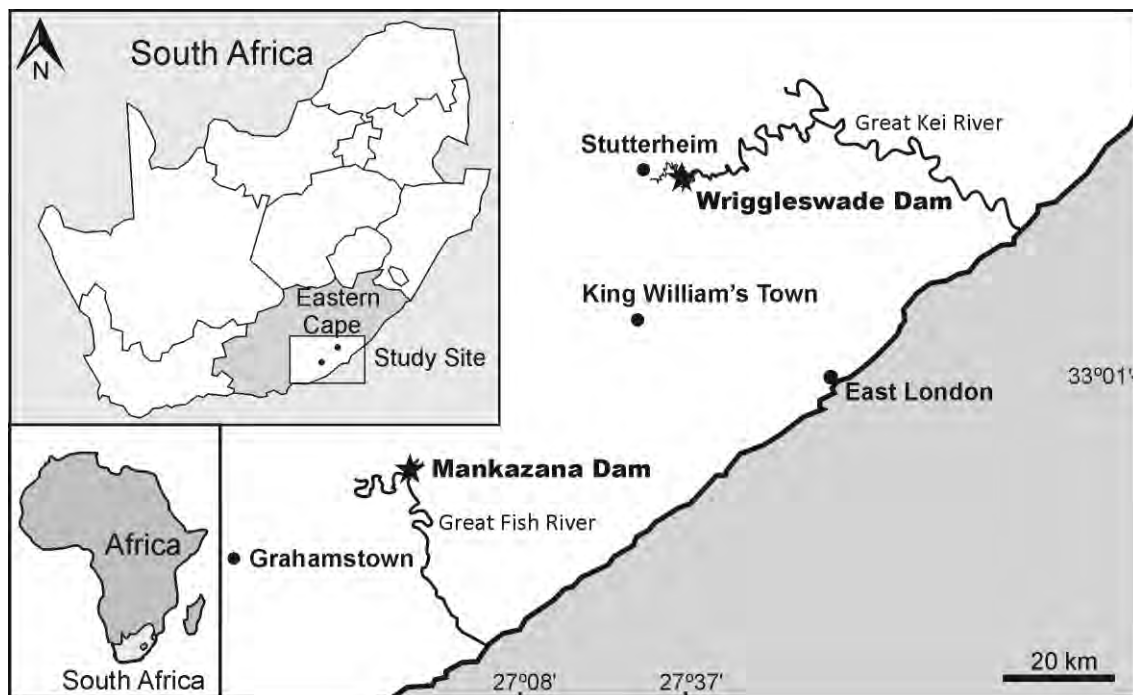


Figure 2.1: The study site of the two dams and their respective river systems located in the Eastern Cape of South Africa.

¹In South Africa and for the purpose of this thesis, the word “dam” will be used to describe an artificially created water body, and is equivalent to the term reservoir or impoundment used elsewhere.

2.1.1 Wriggleswade Dam

Wriggleswade Dam is an impoundment of the Kubusi River on the Great Kei River Catchment constructed in 1991 (Figure 2.2). This dam is fed by the Kubusi and Little Kubusi Rivers which drain the south western section of the Amatola Mountain range northwest of the town of Stutterheim. Situated 20 km outside the town of Stutterheim and 75 km inland of the city of East London (Figure 2.2), Wriggleswade Dam is used as a reserve water storage reservoir for the Buffalo City Metro Municipality, with water being transferred via tunnel, canal and river linkage (Midgley et al., 1994).

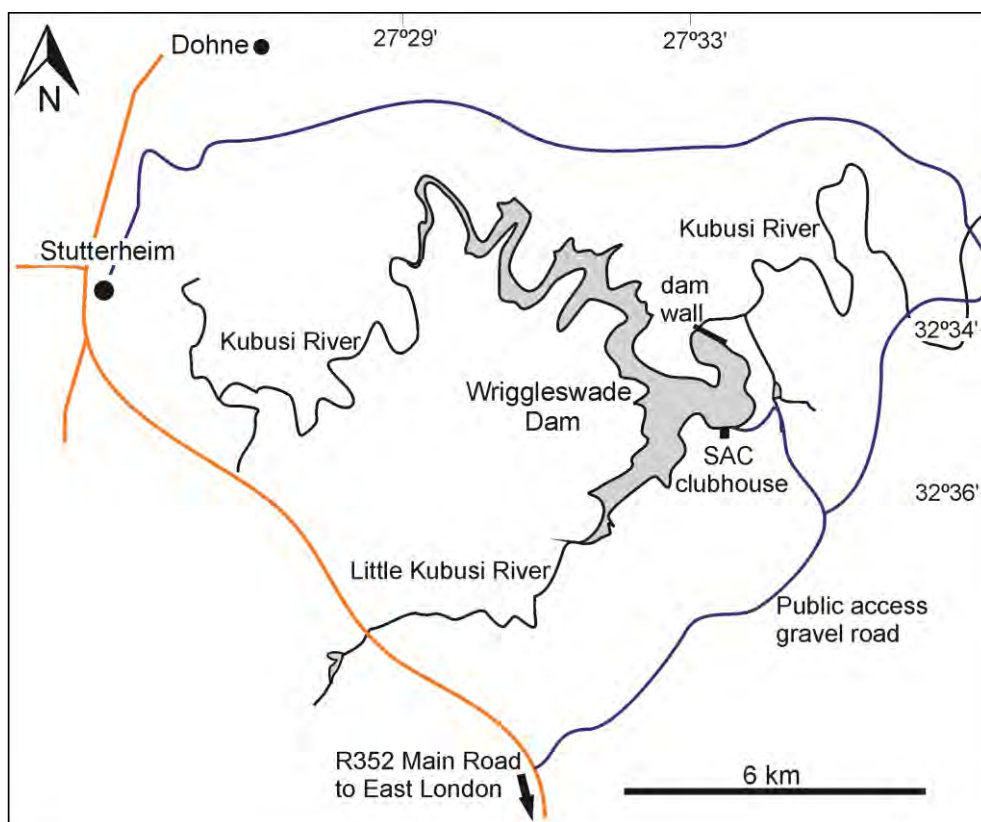


Figure 2.2: Wriggleswade Dam, an impoundment of the Kubusi River on the Great Kei River system in the Eastern Cape of South Africa situated at an altitude of 723 m above mean sea level. The small town of Dohne, situated North West of Wriggleswade Dam, is the location of the weather station from which temperature and precipitation data were used to describe the climate of the area.

Access to the dam is managed by the Stutterheim Aquatics Club (SAC) which leases private Department of Water Affairs land, and there is little subsistence fishing as the dam is surrounded by privately owned farmland and club leased land (Figure 2.3).

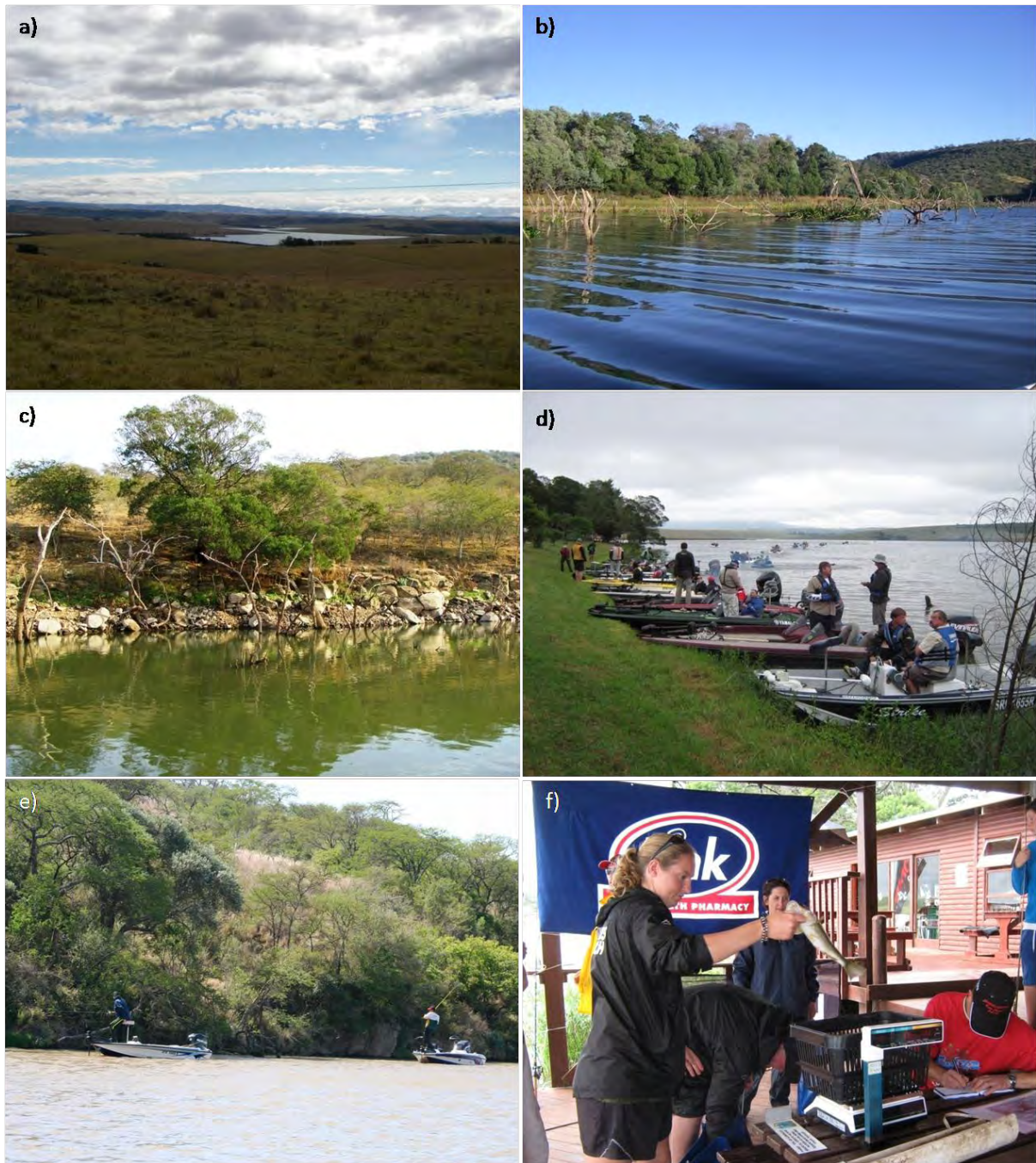


Figure 2.3: (a) Wriggleswade Dam situated amongst privately owned farmland in the Eastern Cape of South Africa. The riparian zone is typically bordered by macrophyte beds, (b) coarse woody habitat or (c) a rocky shoreline. Competitive organised angling events are commonly hosted at the dam, and (d) illustrates the “push off” of such events whereby anglers are released at a defined time in a pre-decided order, from which they travel to their desired spots and (e) fish with the aid of technology such as electric motors and echo-sounders. At the end of the fishing day during tournaments anglers bring their fish to the SAC clubhouse where they (f) weigh them in on an electronic balance.

The dam is a popular competitive bass angling water body on which a number of events both involving monetary prizes (money events) and ranking points (league events) are hosted annually. The league events are run by the national administrative body for organised bass angling, the South African Bass Anglers Association (SABAA), which is comprised of five divisional bodies that cumulatively incorporate most of South Africa's area: Northern division (Limpopo, Gauteng North, Mpumalanga); Southern Division (Gauteng Central, Gauteng South, Northern Free State, North West Northern Region); Western division (Western Province, Boland, Northern Cape); Eastern division (Eastern Cape, Border, and Southern Cape); Kwazulu Natal division (Midlands, South Coastal, North Coastal, Northern Kwazulu Natal) (McCafferty, 2012). These divisions are then split into regional chapters, where eligibility is determined by a minimum number of affiliated SABAA members. Within each chapter or club, membership is subdivided into purchasable junior, silver and gold card categories, which dictate the eligibility of the angler to participate at the varying levels of competitive events. Silver card members may participate in club events, while gold card members are eligible to fish in club, divisional and national events, so allowing them a chance to be awarded Provincial and/or National colours and fish inter-provincially and/or for the South African team.

Three SABAA clubs utilise Wiggleswade Dam on a regular basis during the warmer season (September to April), inter- club divisional tournaments are held biannually to choose a provincial team, and inter-provincial tournaments are held every few years to choose a national team (Table 2.1). In addition to these SABAA associated league events, Wiggleswade Dam hosts the annual Mercury Amatola Bass Classic, which is a big fish “open” competition that attracts many sponsors and competitors. Any angler may compete in this money event, irrespective of any association with SABAA.

Table 2.1: The competitive angling events held annually at Wiggleswade Dam, Eastern Cape, South Africa.

Event	Type	Events annually	Anglers per event
Club	SABAA league	13	30
Divisional	SABAA league	2	40
National	SABAA league	Once every 3 years	50
Classic	Open money	1	200

The divisional and club SABAA events and the classic involve two eight to ten hour days of angling, while the national tournaments are three eight to ten hour days. All SABAA events

have a limit of five fish per day, while the Classic has a three fish limit. All fish to be weighed must be over the minimum size limit of 30 cm total length, and anglers are penalised for “short” fish. The organised bass anglers of South Africa uphold a strict catch and release angler ethic, and fish stored in oxygenated compartments or live-wells may be culled (released) for larger fish throughout the day.

2.1.1.1 Fish fauna

Fish fauna present in the Kubusi River catchment collected before the construction of the dam included a number of native and non-native species (SAIAB, collection records). Native fauna were comprised of two small cyprinids: the chubyhead barb *Barbus anoplus* (SAIAB, 1981: 127614), and the vulnerable (Cambray, 2007) Amatola barb *Barbus amatolicus* (SAIAB, 1981: 127615). Non-native fauna included two extralimital species, the large cyprinid smallmouth yellowfish *Labeobarbus aeneus* (SAIAB, 1985: 132047) native to the Orange-Vaal River system, and the cichlid banded tilapia *Tilapia sparrmanii* (SAIAB, 1985: 132050) native to a number of river systems north of the Orange River and Kwazulu- Natal south coast rivers up to the Zambezi system (Skelton, 2001), and three alien centrarchid species: the spotted bass *Micropterus punctulatus* (SAIAB, 1988: 131189), the largemouth bass *Micropterus salmoides* (SAIAB, 1981: 127630), and the bluegill sunfish *Lepomis macrochirus* (SAIAB, 1988: 132051).

To add to this information, the fish community in Wriggleswade Dam was sampled using gill nets, seine nets, and fyke nets and a backpack electro fisher. Multifilament gillnet fleets comprised panels of netting with stretched mesh sizes of 35, 45, 47, 57, 65, 73, 77, 93, 106, 118, 150 and 153 mm were used. Gillnet fleets were set overnight (between 5-6 pm and 6-7 am), parallel to the shoreline at a depth of approximately 3 m to ensure that all mesh sizes were set in a similar depth. Double ended fyke nets with an 8 m guiding net and a first-ring diameter of 55 cm with a 10 mm mesh size at the cod end were used in conjunction with the gill nets. Fyke nets were set overnight either as individual units or in pairs, parallel to the shoreline at depths of between 1.5 and 2 m. Six to ten gill nets and six fyke nets were set monthly from May to August 2011 and in April 2012. To overcome the limitation of the different species selectivity of each gear, a 1 m seine of 2 mm mesh and a 30 m seine 2 m deep with a mesh of 12 mm in the wings and 8 mm in the cod end was used to sample small

prey species in the littoral zone (<1 m depth) where possible. In Wriggleswade two 30 m seine net pulls and a number of 1 m seine net pulls were conducted in both winter and summer surveys.

All fish sampled were identified to species level. Fish caught in the gill nets were counted, measured to the nearest millimetre fork length (FL) or total length (TL), recorded with respect to mesh size, and weighed per net to get a total weight per species per mesh size. Fish caught in fyke nets, seine nets and by electro fishing were counted and measured.

Relative abundance and catch composition was estimated for gill and fyke net catches. The most important species of the gill net catch composition by number, weight and frequency of occurrence were described using the index of relative importance (IRI)

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

where %N and %W are percentage contributions of each species by number and by weight to the total catch of each dam and %FO is the percentage frequency of occurrence of each species in the total number of net settings (Kolding, 1998). Relative fish abundance was expressed as catch per unit effort (CPUE) as numbers and weight. CPUE is calculated as:

$$CPUE = \frac{C_i}{E_i}$$

where C_i is the catch of species i (in numbers or weight) and E_i is the effort expended to obtain i . CPUE was standardised as number.net night⁻¹ and kg.net night⁻¹ (Kolding, 1998).

Gill net data indicated that in Wriggleswade Dam *M. salmoides* and *L. aeneus* were the most important species, and the large common carp *Cyprinus carpio* caught were important with respect to biomass sampled (Table 2.2). Fyke net data followed similar trends, with an increase in the abundance of African longfin eel *Anguilla mossambicus*, a species susceptible to this gear. The smaller species sampled in seine nets and by electro fishing were the abundant estuarine round herring *Gilchristella aestuaria* followed by juvenile *M. salmoides* in Wriggleswade Dam (Table 2.2).

Results of these surveys combined with angler reports and personal observation of catch are summarised in Table 2.3, and the species present are depicted in Figure 2.4.

Table 2.2: The catch composition, relative abundance and length structure of all the species caught in Wriggleswade Dam using gill, fyke and seine nets. Catch per unit effort (CPUE) is expressed as average $\pm$ SE (N and kg.net night⁻¹).

Gear	Species	FO	%N	% W		CPUE (N/net)		N (net sets)	Length			N (fish)
									Mean	Min	Max	
Gill	<i>M. salmoides</i>	71.6	45.7	19.9	43.7	1.8 $\pm$ 0.2	1.1 $\pm$ 0.2	74	308	169	592	132
	<i>L. aeneus</i>	50.0	39.8	52.4	42.9	1.6 $\pm$ 0.3	2.9 $\pm$ 0.5	74	490	272	625	115
	<i>C. carpio</i>	35.1	13.8	27	13.4	0.5 $\pm$ 0.1	1.5 $\pm$ 0.4	74	432	106	750	40
	<i>A. mossambica</i>	2.7	0.69	0.6	0.03	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	74	686	471	888	2
Fyke	<i>A. mossambica</i>	13.3	33.3			0.2 $\pm$ 0.1		30	692	471	888	5
	<i>C. carpio</i>	10.0	20			0.1 $\pm$ 0.0		30	103	101	104	3
	<i>M. salmoides</i>	13.3	46.7			0.2 $\pm$ 0.1		30	298	242	375	7
Seine	<i>G. aestuaria</i>	100	81.5			18 $\pm$ 5.0		3	43	30	70	53
	<i>G. callidus</i>	33.0	4.6			1 $\pm$ 1.0		3	59	39	75	3
	<i>M. salmoides</i>	33.0	13.8			3 $\pm$ 3.0		3	98	74	136	9

Information on the introduction of species into the dam has been collected mainly through personal communication with long standing fishers and local farmers of the area. These data allowed for the following description of the fish fauna of Wriggleswade Dam.

Northern strain largemouth bass *Micropterus salmoides* and *L. macrochirus* were already present in the Kubusi River Catchment, and moved into Wriggleswade from flooded farm dams up river upon filling in about 1996. Approximately 1000 Florida strain largemouth bass *Micropterus floridanus* fingerlings of about 80 – 100 mm TL were stocked into Wriggleswade Dam in 1995 from the Transvaal (²Anonymous pers. comm.). The results of a genetic study identified the *M. salmoides* population in Wriggleswade Dam as a hybrid strain (Northern strain x Florida strain), of which 67% carried Florida bass genes (Schirrmann, 2011). Smallmouth bass *Micropterus dolomieu* have been stocked on a number of occasions from the Rooikrantz Dam (32°45'11"S, 27°19'29"E) on the adjacent Buffalo River catchment 28 km southwest of Wriggleswade and 20 km northwest of King Williams Town, but appear not to have established. *Cyprinus carpio*, previously established in a number of small farm dams up river from the dam, and were first recorded by fishers in the dam in 1996 (Anonymous, pers. comm.). No record of an introduction of the African sharptooth catfish *Clarias gariepinus* into the dam is known. The estuarine round herring *Gilchristella aestuaria* were supposedly stocked along with the freshwater mullet *Myxus capensis* in the 1990s from the Amalinda Hatchery in East London, which was previously run by the Government Nature Conservation Agency (Anonymous, pers. comm.).

²Introductions are illegal in South Africa and the names of informants have been omitted to protect the source.

Table 2.3: The names and source of the different fish species sampled in Wiggleswade Dam, Eastern Cape, South Africa.

Species	Common name	Native/Translocated/ Non-native	State
Centrarchidae			
<i>Micropterus salmoides</i>	Largemouth bass	Non-native	Established
<i>Micropterus floridanus</i>	Florida bass	Non-native	Established
<i>Micropterus punctulatus</i>	Spotted bass	Non-native	Established
<i>Micropterus dolomieu</i>	Smallmouth bass	Non-native	Not established
<i>Lepomis macrochirus</i>	Bluegill sunfish	Non-native	Not established
Gobiidae			
<i>Glossogobius callidus</i>	River goby	Native	Established
Clupeidae			
<i>Gilchristella aestuaria</i>	Estuarine round herring	Translocated	Established
Anguillidae			
<i>Anguilla mossambica</i>	African longfin eel	Native	Established
Cyprinidae			
<i>Labeobarbus aeneus</i>	Smallmouth yellowfish	Translocated	Established
<i>Cyprinus carpio</i>	Common carp	Non-native	Established
Clariidae			
<i>Clarias gariepinus</i>	African sharptooth catfish	Translocated	Not established
Cichlidae			
<i>Tilapia sparrmanii</i>	Banded tilapia	Translocated	Not established

In addition a number of species that have been stocked into the dam however, have not subsequently been recorded. *Myxus capensis* is one of these species, along with the *Tilapia sparrmanii* which were already present upstream, and were stocked from Rooikrantz Dam. In addition mature Mozambique tilapia *Oreochromis mossambicus*, native to the lower reaches of the system, were stocked in about 2009 from the coastal areas near East London and have not been recorded since (Anonymous, pers. comm.).



Figure 2.4: The fish species recorded in Wriggleswade Dam: a) largemouth bass *Micropterus salmoides*, b) smallmouth bass *Micropterus dolomieu*, c) spotted bass *Micropterus punctulatus*, d) African longfin eel *Anguilla mossambicus*, e) African sharptooth catfish *Clarias gariepinus*, f) common carp *Cyprinus carpio*, g) smallmouth yellowfish *Labeobarbus aeneus*, h) bluegill sunfish *Lepomis macrochirus*, i) river goby *Glossogobius callidus*, j) estuarine round herring *Gilchristella aestuaria*, and k) banded tilapia *Tilapia sparrmanii*. .

2.1.1.2 Physical characteristics

The climate of the area is moderately temperate with winter and summer rainfall. Mean monthly air temperatures at Wriggleswade Dam ranged from 13.2 °C in July to 20.9 °C in February with an annual mean of 16.4 °C (SAWS, 2012), while average surface water temperatures ranged from 10.2 °C in July to 23.3 °C in February with an annual mean of 17.2 °C (Figure 2.5). This area receives both summer and winter rainfall, with peaks in precipitation falling in the southern hemispheres summer months. The total annual rainfall for the Dohne area (Figure 2.2) is between 700 and 900 mm with the peak precipitation months

of January and February receiving an average of between 100 mm and 180 mm (SAWS, 2012).

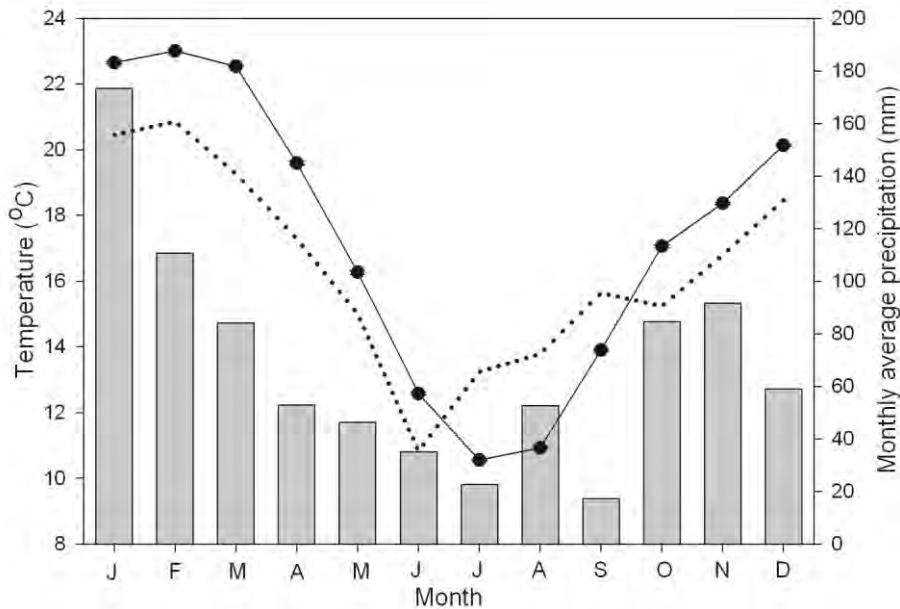


Figure 2.5: Combined mean monthly surface water temperatures (solid line) $\pm$ SE of Wiggleswade Dam, Eastern Cape of South Africa taken from November 2009 to September 2012 recorded using a Hobo temperature logger. Mean monthly air temperature (dotted line) and mean monthly precipitation data (bars) were sourced from the South African Weather Service (SAWS, 2012) station at Dohne (13 km northwest of Wiggleswade) near Stutterheim.

Wiggleswade Dam covers an area of 1000 ha, has a capacity of 91.5 mil m³ of water when full and its level does not fluctuate greatly due to its limited use as a water supply (Figure 2.6) (DWA, 2012). In January 2011 the dam filled from its drought conditions of 60% capacity, and has remained at $\pm 100\%$ capacity since then with floods occurring in January and March 2012 (DWA, 2012).

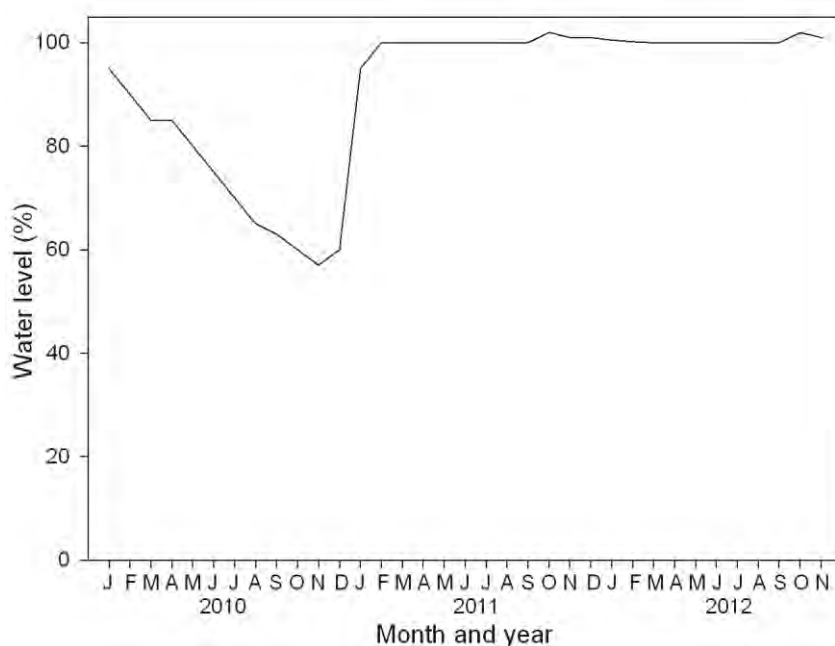


Figure 2.6: The fluctuations in water level from January (J) 2010 until November (N) 2012 of Wiggleswade Dam, Eastern Cape, South Africa (DWA, 2012).

The water quality parameters of pH, total dissolved solids (TDS), conductivity and turbidity were measured for a number of months with results summarised in Table 2.4. Turbidity was the only parameter with considerable variation, ranging from 20 NTUs in summer to 57 NTUs in winter. Conductivity and TDS ranged around 120 μ s and 60 ppm respectively and pH was slightly alkaline at 9.

Table 2.4: The mean, range and standard error (SE) for water quality readings taken during the surveys conducted in the winter months of July – September 2011 and August- September 2012, the autumn months of May – June 2011, and the summer month of March 2012 in Wiggleswade Dam, Eastern Cape. Electrical conductivity (μ s), total dissolved solids: TDS (ppm), pH and temperature ($^{\circ}$ C) were measured using a Hanna HI98129 Combo pH and electrical conductivity meter (HANNA Instruments Inc., Woonsocket, USA). Turbidity (NTU) was measured using a Hanna HI 98703 turbidimeter (HANNA Instruments Inc.).

Parameter	Mean	Range	SE
pH	9	7.9-10.3	0.04
TDS	61	47-66	0.29
conductivity	121	95-261	0.75
Turbidity	44	21-125	1.20

2.1.2 Mankazana Dam

Mankazana is a 35 ha impoundment of a tributary to the Great Fish River 40 km upstream of the river mouth and 10 km South East of Committees Drift at an altitude of 66 m above mean sea level (Figure 2.7). It is located in a rural area near the villages of Ndlambe and KwaNdlambe (Figure 2.8) and land use in the catchment consists of human consumption and subsistence livestock farming (Midgley et al., 1994). The dam is utilised by some subsistence fishers and by recreational anglers.

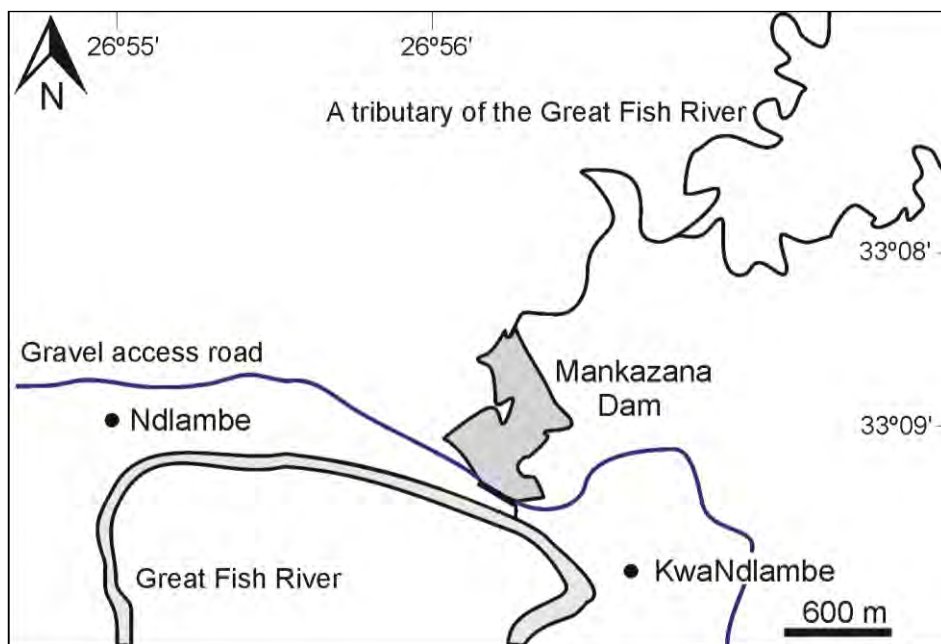


Figure 2.7: Mankazana Dam, an impoundment of a tributary of the Great Fish River, on the Great Fish River catchment in the Eastern Cape of South Africa.

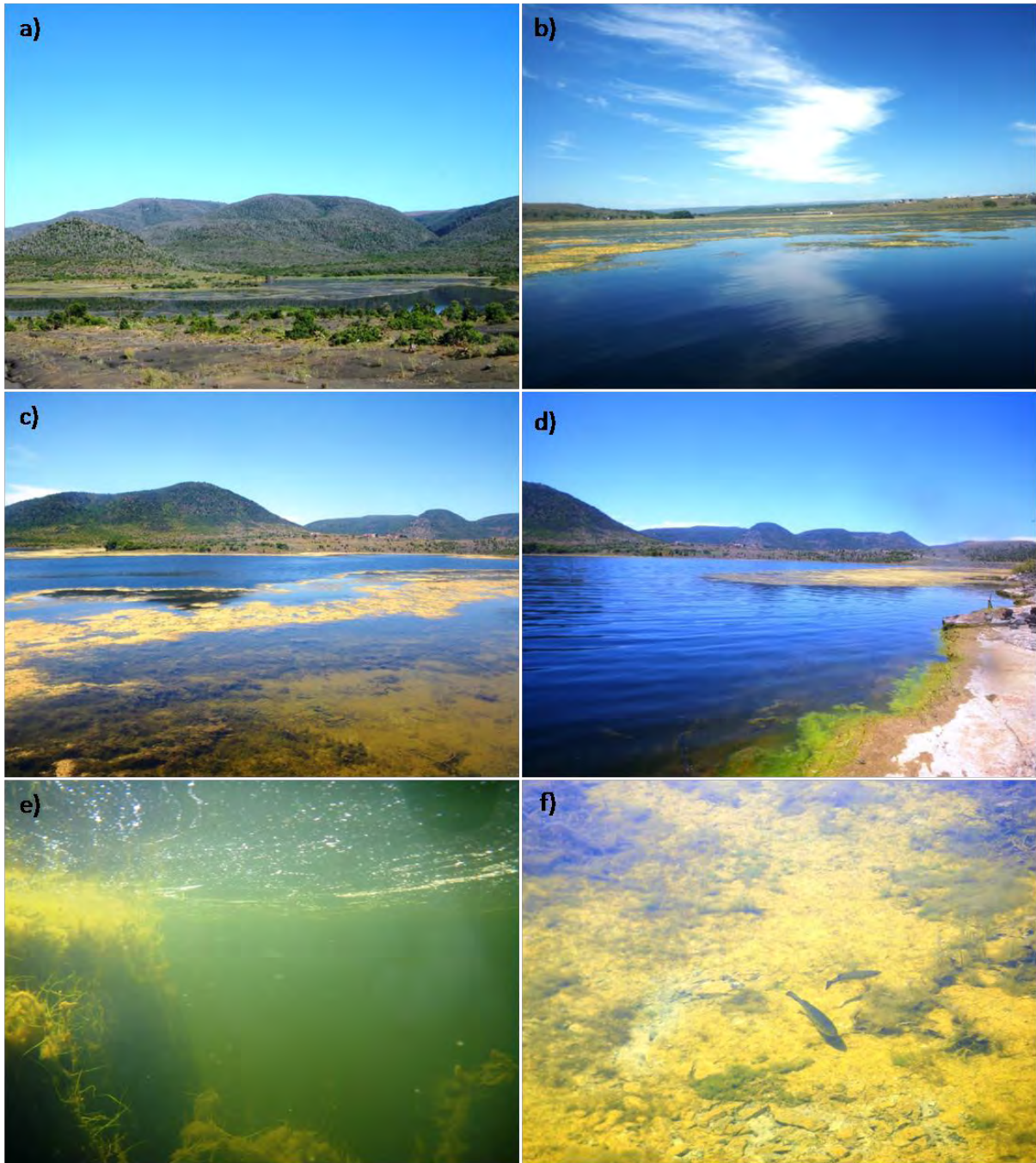


Figure 2.8: Mankazana Dam (a) situated amongst communal land in the Eastern Cape of South Africa. The dam is characterised by (b) extensive macrophyte beds both in deep water and (c) on the riparian zone, in addition to (d) the occasional sharp rocky drop off. The water is clear (e), and (f) on the shallow margins free of macrophytes largemouth bass *Micropterus salmoides* can be seen nesting in pairs in spring.

2.1.2.1 Fish fauna

A number of native and non-native species have been recorded in the Great Fish River downstream of the dam. Native species include the Anguillid eels: African mottled eel *Anguilla bengalensis labiata* (SAIAB, 1996: 54452), *A. mossambica* (SAIAB, 1997: 54694), giant mottled eel *Anguilla marmorata* (SAIAB, 1981: 15060), the Cyprinids: *B. anoplus* (SAIAB, 1997: 54693), moggel *Labeo umbratus* (SAIAB, 2006: 88509), goldie barb *Barbus pallidus* (SAIAB, 2001: 63900), *O. mossambicus* (SAIAB, 1994: 49132), eastern cape rocky *Sandelia bainsii*, an Anabantidae (SAIAB, 2003: 74883) and *G. callidus* (SAIAB, 2003: 74887). Other recorded native species translocated from within southern Africa include *L. aeneus* (SAIAB, 1997: 54692), *C. gariepinus* (SAIAB, 1995: 47174), *T. sparrmanii* (SAIAB, 1981: 15659), and the Austroglanididae rock catfish *Austroglanis sclateri* (SAIAB, 2001: 65400). Non-native species found within the system include the western mosquitofish *Gambusia affinis* (SAIAB, 1997: 54697), *C. carpio* (SAIAB, 1987: 27284), *L. macrochirus* (SAIAB, no date: 128155), and *M. salmoides* (SAIAB, 1983: 128548).

No records were available for any native species present in the catchment as the impounded stream is episodic and only flows after rainfall events. The fish fauna of Mankazana were therefore described after sampling using gill nets, fyke nets, angling and by backpack electro fisher (Table 2.5, Table 2.6) as described for Wriggleswade Dam. Six gill net fleets and two fyke nets were set monthly from July to September 2011 and in April 2012. The presence of dense macrophyte beds on all of the dams margins (Figure 2.8) inhibited the use of seine nets, and backpack electro fishing (SAMUS-725 GN) was used occasionally as an alternative.

Table 2.5: The catch composition, relative abundance and length structure of all the species caught in Mankazana Dam using gill and fyke nets and by electro fishing (EF). Catch per unit effort (CPUE) is expressed as average $\pm$ SE (N and kg.net night⁻¹).

Gear	Species	FO	%N	%	IRI	CPUE	CPUE	N (net sets)	Length			N
				W		(N/net)	(kg/net)		Mean	Min	Max	(fish)
Gill	<i>O. mossambicus</i>	82.1	56.7	46.7	58.4	8.8±1.5	7.6±1.7	28	230	95	423	245
	<i>L. umbratus</i>	67.9	27.4	44	33.3	4.2±1.0	7.2±1.8	28	454	394	502	118
	<i>M. salmoides</i>	50.0	14.1	9.1	8.0	2.1±0.5	1.5±0.4	28	275	134	481	58
	<i>T. sparrmanii</i>	21.4	1.8	0.21	0.3	0.3±0.1	0.0±0.0	28	126	91	195	8
Fyke	<i>A. mossambica</i>	50.0	50			0.5±0.5		2	433			1
	<i>O. mossambicus</i>	50.0	50			0.5±0.5		2	138			1
EF	<i>G. callidus</i>								61			1

The species native to the system were *G. callidus*, *A. mossambicus*, *L. umbratus* which was introduced in an attempt to develop a subsistence fishery, and *O. mossambicus*. *Micropterus salmoides* were introduced into the dam in 2005 (Anonymous pers. comm.) (Figure 2.9).

Table 2.6: The fish species sampled in Mankazana Dam, Eastern Cape, South Africa.

Species name	Common name	Native/Translocated/ Non-native	Source
Centrarchidae			
<i>Micropterus salmoides</i>	Largemouth bass	Non-native	Established
Gobiidae			
<i>Glossogobius callidus</i>	River goby	Native	Established
Cyprinidae			
<i>Labeo umbratus</i>	Moggel	Translocated	Not established
Anguillidae			
<i>Anguilla mossambica</i>	African longfin eel	Native	Established
Cichlidae			
<i>Oreochromis mossambicus</i>	Mozambique tilapia	Translocated	Established
<i>Tilapia sparrmanii</i>	Banded tilapia	Translocated	Established



Figure 2.9: The fish species recorded in Mankazana Dam: a) largemouth bass *Micropterus salmoides*, b) African longfin eel *Anguilla mossambicus*, c) Mozambique tilapia *Oreochromis mossambicus*, d) banded tilapia *Tilapia sparrmanii*, e) river goby *Glossogobius callidus* and f) moggel *Labeo umbratus*.

2.1.2.2 Physical characteristics

The area surrounding Mankazana Dam has a warm temperate climate with a mean annual temperature of 18.7 °C (8.5 °C in winter to 28.0 °C in summer) (SAWS, 2012). Mankazana's average surface water temperatures ranged from 13 °C in July to 26 °C in November. Total annual rainfall fluctuates around 500 mm (Midgley et al., 1994; SAWS, 2012) and falls throughout the year with peaks in January and March (Figure 2.10).

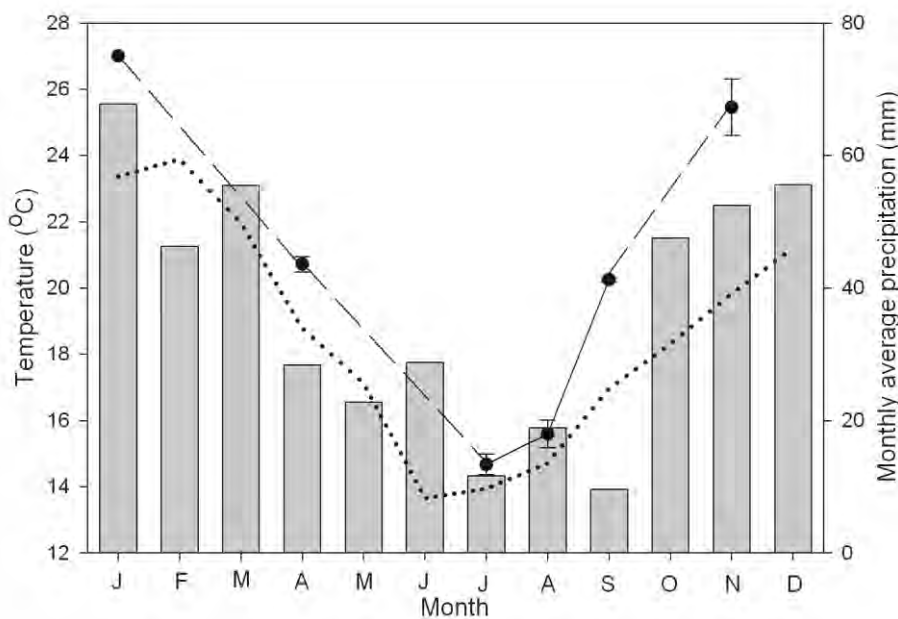


Figure 2.10: Average surface water temperature readings ($\pm$ SE) taken with a Hanna HI98129 Combo meter (black circles) in Mankazana Dam, Eastern Cape of South Africa. Mean monthly air temperature (dotted line) and mean monthly precipitation data (bars) sourced from the South African Weather Service (SAWS, 2012) station in Fort Beaufort (52 km North West of Mankazana at an altitude of 392 m amsl).

The geology of the surrounding catchment is sedimentary rock and the dam is based on clayey loam soils (Midgley et al., 1994). With respect to water quality Mankazana Dam had an alkaline pH, relatively high conductivity and total dissolved solids (TDS) and a low turbidity of on average 10 NTUs (Table 2.7).

Table 2.7: The mean, range and standard error for the water quality readings taken during the surveys conducted in the winter months of 2011 (from July to September), and the spring of 2012 (November) in Mankazana Dam, Eastern Cape. Surface water temperature (°C), pH, total dissolved solids (ppm), conductivity (µs) and turbidity (NTU) were measured using the same equipment as those in Wiggleswade Dam.

Parameter	Mean	Range	SE
pH	10.2	8.5-10.8	0.12
Conductivity	525.2	432-568	6.61
TDS	260.3	205-275	3.93
Turbidity	10.6	2.5-16.6	0.97

2.2 General sampling methods

Micropterus salmoides for biological analysis were sampled monthly from both dams by angling with artificial lures, and in Wiggleswade Dam samples were also obtained from monthly club tournaments where possible. In addition, this target species and the fish communities in both dams were sampled using gill nets, fyke nets, and seine nets and a backpack electro fisher as described previously.

All *M. salmoides* sampled were euthanized by concussion followed by destruction of the brain, measured to the nearest mm FL and TL and weighed to the nearest gram. Fish were then dissected and their sex and reproductive stage of development determined macroscopically using visual staging criteria. The stomach contents were then examined, and sagittal otoliths and scales removed and stored in Eppendorf tubes for ageing. Any specific methodologies applied are described in detail in the relevant chapter.

CHAPTER 3: ARE SCALES SUITABLE STRUCTURES FOR AGEING *MICROPTERUS SALMOIDES* IN SOUTH AFRICA?³

3.1 Introduction

The accurate and precise estimation of age is an important component of biological research on fishes because this forms the basis for determining rates of growth, maturity and mortality (Campana, 2001). In fishes factors which influence metabolic rates (e.g. temperature or spawning) are reflected in the growth of calcified structures such as scales and otoliths and result in the appearance of alternating opaque and hyaline growth zones (Figure 3.1). These growth zones, when counted, are used to estimate age (Weyl & Hecht, 1999; Beamish et al., 2005; Britton & Harper, 2005).

Otoliths are generally considered the most suitable structures for ageing fishes because unlike scales, they grow continuously and are metabolically inert (Campana & Thorrold, 2001). Otoliths do however have the disadvantage that they require the killing and dissection of the fish from which they are collected as well as considerable processing, such as sectioning, before growth zones can be read (Campana & Fowler, 2012). Alternatively, scales have the advantages that they are easily collected, do not require the sacrifice of the fish and can be read without prior processing (Carlander, 1987). Scales are therefore a potentially useful structure for ageing largemouth bass *Micropterus salmoides* populations in situations where non-destructive methods of sampling are required. For example, scales would be useful for ageing populations of *M. salmoides* during ecological studies in small streams, such as the Blindekloof in the Eastern Cape, where invasive *M. salmoides* populations are small (Ellender et al., 2012) and the removal of a sample of fish from the system would alter the fish community and confound the study. In addition the collection of scales during competitive catch and release tournaments would allow scientists to gather information quickly and cheaply with the support of anglers. The use of otoliths for ageing African *M. salmoides* populations has however become standard practice (Weyl & Hecht, 1999; Beamish

³Accepted for publication: Taylor, G.C. & Weyl, O.L.F. (2012). Otoliths versus scales: evaluating the most suitable structure for ageing largemouth bass *Micropterus salmoides* in South Africa. *African Zoology*, 47 (2), 358-362.

et al., 2005; Britton et al., 2010a) and it is therefore necessary that the suitability of scales be evaluated prior to their use as an alternative structure for ageing.

Results from comparative assessments conducted in North America differ between localities. Some studies showed good correlation between otolith and scale based estimates of *M. salmoides* age (e.g. Heidinger & Clodfelter, 1987) while others demonstrated that scales were only useful for the ageing of younger fish (e.g. Besler, 1999; Long & Fisher, 2001; Maceina & Sammons, 2006). As a result of such inconsistencies it is important that the suitability of scales be evaluated on a regional basis. The aim of this chapter was therefore to evaluate the usefulness of scales for ageing *M. salmoides* populations in the Eastern Cape of South Africa by comparing age estimates derived from scales against those from otoliths.

3.2 Materials and methods

For the evaluation, a total of 496 *M. salmoides* were sampled from the two dams. A total of 350 fish were sampled from Wriggleswade Dam and 146 fish were sampled from Mankazana Dam. Of the 350 *M. salmoides* from Wriggleswade (38 – 575 mm fork length FL), 193 were female, 145 were male, and 12 were unsexed juveniles. Of the 146 *M. salmoides* (132 – 490 mm FL) from Mankazana, 80 were female, 64 were male and two were unsexed juveniles. Once the fish was killed the two sagittal otoliths were removed immediately and cleaned. Then an average of three scales were removed from between the lateral line and the first dorsal spine on the left hand side of the body and cleaned.

Otoliths and scales were prepared and read following recommendations by Weyl & Hecht (1999) and Regier (1962). To enhance the visibility of growth zones, otoliths were burnt over a low intensity ethanol flame until they were pale brown; set in clear polyester casting resin; sectioned transversely through the nucleus (thickness 0.3 mm) using a double bladed diamond edge saw and mounted on a glass slide using DPX mountant. Otolith sections were examined under a binocular microscope using transmitted light at variable magnification (10-40×) and pairs of opaque and hyaline growth zones (Figure 3.1) were counted with no

reference to the size of the fish. Scales were cleaned using water and tissue paper, read at the lowest magnification (x10) in order to reduce the bias created by false rings (accessory checks) and other artefacts, and following recommendations made by Regier (1962) annuli were only counted if common to two or more of the scales viewed.

Each sample was read three times (zones were counted twice by one reader with a one-week interval and once by a second reader) without reference to the size of the fish that the otolith or scale was taken from. The mode of these three readings was then adopted for each structure as the estimated age for each fish. If no mode could be calculated, or if one of the samples was considered to be unreadable by one of the readers, then the sample was discarded from further analysis. For African *M. salmoides* populations growth zone deposition rate has been validated as annual for both otoliths (Weyl & Hecht, 1999; Beamish et al., 2005; Chapter 4) and scales (Britton & Harper, 2005) and therefore for this chapter all growth zone counts were assumed to represent the estimated age of the fish in years.

To assess for differences in precision between otoliths and scales an average percentage error (APE) (Beamish & Fournier, 1981) and coefficient of variation (CV) (Campana et al., 1995) were calculated.

Average percent error was calculated using:

$$APE = \frac{1}{N} \sum_{j=1}^N \left[\frac{1}{R} \sum_{i=1}^R \frac{|X_{ij} - X_j|}{X_j} \right]$$

where: N is the number of fish aged, R is the number of times each fish is aged, X_{ij} is the i th age determination of the j th fish, X_j is the average age calculated for the j th fish. This was then multiplied by 100 to become the index of average percent error. The Coefficient of Variation (CV) was calculated as:

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

where CV_j is the age precision estimate for the j th fish. The CV was averaged across all fish to produce a mean CV.

The Bowker (1948) method was used to test the hypothesis that the ages determined by scales show a symmetrical display of error around the otolith age (Hoenig et al., 1995). This method tests the hypothesis that an $m \times m$ contingency table consisting of two classifications of a sample into categories (scale age vs otolith age) is symmetric about the main diagonal. The test statistic is distributed as a chi-square variable with $m(m-1)/2$ degrees of freedom for a table that has no empty cells. The test statistics is

$$\chi^2 = \sum_{i=1}^{m-1} \sum_{j=i+1}^m \frac{(n_{ij} - n_{ji})^2}{n_{ij} + n_{ji}}$$

where n_{ij} = the observed frequency in the i th row and j th column and n_{ji} = the observed frequency in the j th row and i th column.

Lastly, age estimates from otoliths and scales were compared graphically as recommended by Campana et al. (1995) to check for deviations in observed ages between structures.

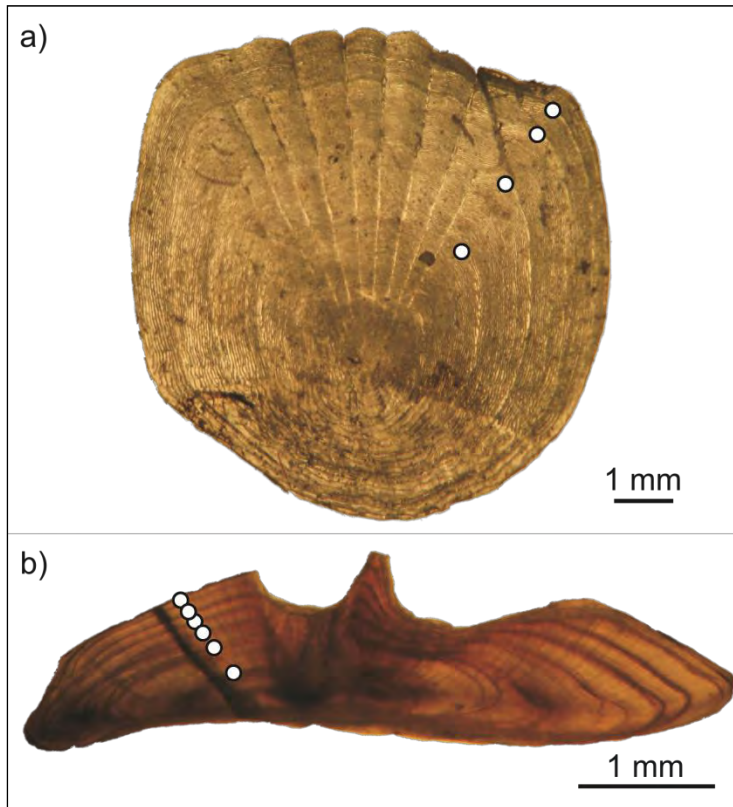


Figure 3.1: The two structures used to age *Micropterus salmoides* from the two dams in the Eastern Cape of South Africa: (a) a scale taken from a four year old female of 359 mm FL and (b) an otolith taken from a six year old female of 368 mm FL.

3.3 Results

In comparison, otoliths were more readable than scales with only 1.4% of otoliths being discarded as unreadable in both dams, while 41.7% and 7.5% of the sample collected from Wiggleswade Dam and Mankazana Dam, respectively, could not be aged using scales. Fish were also assigned older ages using otoliths (13 and four years) than with scales (six and three years) in both localities and otoliths yielded more precise estimates of age as indicated by a lower average percentage error (APE) and coefficient of variation (CV) for the combined sample (Table 3.1). For both structures reading precision tended to be lowest for one year old fish, and increased with age.

Table 3.1: Comparisons of precision of ageing *Micropterus salmoides* using scales (s) versus sagittal otoliths (o) by age group in two dams in the Eastern Cape, South Africa.

Statistic	Total sample	Age							
		0	1	2	3	4	5	6	≥ 7
n_o	489	114	58	109	95	51	18	19	25
IAPE _o	13.61	8.2	23.1	13.6	15.8	14.4	11.7	13.2	8.5
CV _o	15.78	7.5	26.2	16.9	18.7	16.7	14.2	18.2	10.9
n_s	338	130	50	73	52	23	10		
IAPE _s	17.97	4.1	35.2	24.5	24.5	22.8	19.4		
CV _s	21.89	3.8	38.7	30.0	33.9	30.2	27.5		

A Bowker's test (Bowker, 1948) comparing the more precise otolith age estimates versus the scale age estimate showed that growth zone counts were not symmetrically distributed around the agreed ages (otolith age = scale age) of the fish in the Wiggleswade Dam population (H^2 : $\chi^2 = 136$, d.f. = 27, $P < 0.05$). Overall, only 19% of otolith ages agreed with scale ages, 78% of scale ages were lower than the otolith age estimates, and 3% of the scale ages were higher than the otolith age estimates. Scales therefore tended to underestimate age for *M. salmoides* in Wiggleswade Dam where the population included older individuals. In contrast, growth zone counts were symmetrically distributed around the agreed ages of the *M. salmoides* from the Mankazana population (H^2 : $\chi^2 = 13$, d.f. = 7, $P = 0.07$), and 82% of otolith ages agreed with scale ages, 4% of scale ages were lower than the otolith age estimates, and 4.8% of the scale ages were higher than the otolith age estimates. Scales did not underestimate the ages of *M. salmoides* from Mankazana Dam because most fish were younger than four years.

Graphical comparison recommended by Campana et al. (1995) demonstrated that the two structures yielded similar estimates of age until fish were five years old, where after scale based estimates were consistently lower than those obtained from sectioned otoliths (Figure 3.2).

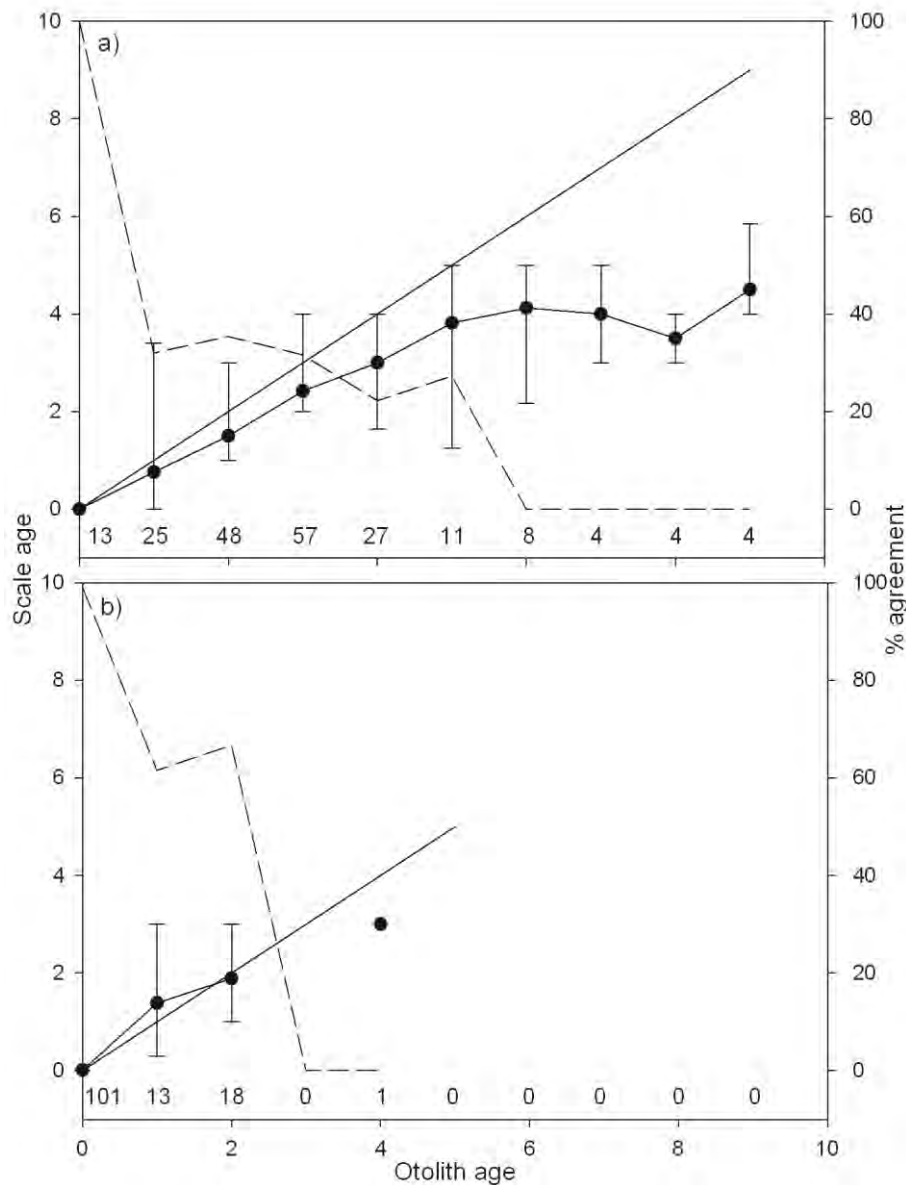


Figure 3.2: Age estimates using scales versus otoliths around the one to one relationship (solid line) and the percentage agreement (dashed line) between the two structures used to age *Micropterus salmoides* from (a) Wriggleswade and (b) Mankazana Dams in the Eastern Cape of South Africa. The 95% confidence intervals are given as error bars for each mean scale age estimated for the respective otolith age, and the sample sizes for each otolith age group are given at the bottom of each graph.

3.4 Discussion

The results are consistent with those studies conducted in North America that found that scales tended to underestimate the age of older individuals (Dietrich, 1953; Maraldo & MacCrimmon, 1979; Besler, 1999; Long & Fisher, 2001; Maceina & Sammons, 2006). The present study therefore demonstrated that scales are not suitable structures for ageing *M. salmoides* because populations may contain fish that are considerably older than five years (e.g. in Wriggleswade Dam fish lived to 13+ years). Accurate and precise age estimates are a fundamental requirement for biological studies. For this reason sectioned sagittal otoliths were used for the rest of this study.

CHAPTER 4: VALIDATION OF ANNULUS FORMATION IN OTOLITHS OF *MICROPTERUS SALMOIDES*⁴

4.1 Introduction

The accurate and precise estimation of age is an important component of fish biology because it forms the basis for an understanding of the rates at which fish grow, mature and die (Campana, 2001). In fishes, age is most commonly estimated by counting alternating opaque and hyaline growth zones on calcified structures such as scales and otoliths (Campana, 2001). Age estimates are available for many largemouth bass *Micropterus salmoides* populations in their native North America (e.g. Maraldo & MacCrimmon, 1979; Beamesderfer & North, 1995; Maceina et al., 2007) but relatively few ageing studies have been conducted in their introduced range (Yodo & Kimura, 1996; Weyl & Hecht, 1999; Lorenzoni et al., 2002; Beamish et al., 2005; Britton & Harper, 2005; Schulz & Leal, 2005). This situation precludes broader analyses of proposed hypotheses such as the attempt to link rapid growth rates of *M. salmoides* in its introduced range to temperature (Helser & Lai, 2004; Neal & Noble, 2006; Britton et al., 2010a). The reasons for the paucity in ageing studies on this globally important species are not clear but may be linked with the costly (in terms of time) but fundamental requirement for validating growth zone deposition rate prior to using growth zone counts directly as estimates of age (Beamish & McFarlane, 1983; Campana, 2001).

Validation is considered a fundamental requirement in ageing because the interplay of environmental (e.g. temperature), behavioural (e.g. feeding, spawning) and biological (calcium metabolism) factors controlling the deposition of growth zones can result in different growth zone deposition rates not only between species in the same locality but also between populations of the same species (Gauldie & Nelson, 1990; Campana, 1999). In a large dam in South Africa for example, growth zone deposition rate was annual for native cyprinids (Winker et al., 2010a; Ellender et al., 2012) but biannual for the non-native common carp *Cyprinus carpio* which differed from the annual deposition rate validated for *C. carpio* populations elsewhere (Winker et al., 2010b). Common methods of validation include

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the indirect method of edge analysis (EA) and direct methods such as the mark-recapture of chemically tagged wild fish (MRCT) (Campana, 2001).

EA is based on the assumption that a growth increment is formed on a yearly cycle, and that the outermost increment state frequency (opaque zone present or absent) should form a yearly sinusoidal cycle when plotted against time (Campana, 2001). EA therefore requires a large sample of hard parts from fish that are ideally collected at monthly intervals. Chemically marking wild fish relies on injecting, immersing, or feeding fish with a fluorescing, calcium-binding chemical such as oxytetracycline hydrochloride (OTC) which is rapidly incorporated into calcified structures at the time of marking and forms a permanent fluorescing band (Campana, 1999). The fish is then released back into the wild and recaptured after some time at liberty. On examination of the calcified structure from the recaptured fish, a permanent mark is visible under ultraviolet light and the growth increments formed distal to this mark can be counted and compared to the time that the fish spent at liberty (Campana, 2001). Both processes are time consuming, preclude the rapid assessment of fish age and require fairly large sample sizes of fish. Possibly because of such constraints, ageing studies on introduced *M. salmoides* populations in Italy (Lorenzoni et al., 2002), Spain (Rodriguez-Sánchez et al., 2009), Puerto Rico (Neal & Noble, 2002), and Portugal (Godinho & Ferreira, 1993) have been undertaken without prior validation. While the assumption made in these studies that growth zone deposition rate is annual may be valid, there has never been a comprehensive regional assessment of growth zone deposition rate for *M. salmoides*.

In this chapter, EA and MRCT are used to test the hypothesis that one opaque and hyaline zone was deposited annually in sagittal otoliths of *M. salmoides* sampled from four temperate South African populations. The results are then compared with those of a comprehensive collection of literature to test the common assumption that growth zone deposition rate in *M. salmoides* otoliths is annual throughout its distribution range.

4.2 Materials and Methods

4.2.1 Study site

Fish were sampled from two small farm dams in addition to the study dams: Wiggleswade and Mankazana in the Eastern Cape Province of South Africa. Growth zone deposition rate was estimated indirectly using edge analysis (EA) from fish sampled from Mankazana and Wiggleswade Dams, and directly by mark-recapture of chemically tagged fish (MRCT) in Wiggleswade Dam and the two farm dams: Dames (33°19'22"S; 26°35'25"E, 6 ha, 500 m amsl) and Howarth (33°24'53"S; 26°20'15"E, 5 ha, 403 m amsl).

4.2.2 Edge analysis

For EA a total of 332 fish (38 to 619 mm FL) were sampled from Wiggleswade Dam and 288 fish (46 to 490 mm FL) were sampled from Mankazana Dam monthly from February 2011 to April 2012. All fish were dissected, and their sagittal otoliths removed and prepared for reading as described in Chapter 3. Growth zones were reflected as alternating opaque and hyaline zones (Figure 4.1) and according to common practise one opaque/hyaline growth zone pair was considered a growth zone and counted. The optical appearance of the edge of the otolith (either opaque or hyaline) was also noted (Figure 4.1). To reduce potential reader bias, each otolith was read three times with at least a one week interval between readings and with no reference between the otolith and the size of fish from which it was obtained.

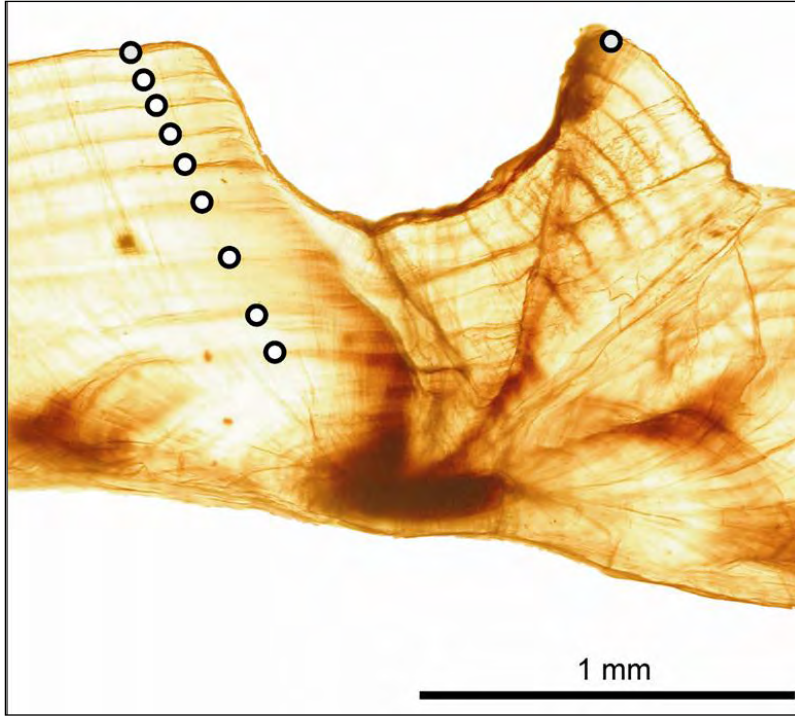


Figure 4.1: An otolith from a nine year old *Micropterus salmoides* from Wiggleswade Dam illustrating the opaque edge (grey outermost circle) and the annual opaque growth zones under reflected light (white circles).

For EA the optical appearance of the otolith edge was categorised as opaque zone present (1) or absent (0) and modelled using two statistical methods. Firstly, as recommended by Winker et al. (2010b), using a periodic logistic regression (Flury & Levri, 1999) of the form:

$$\text{Logit}(\hat{\pi}_i) = \beta_0 + \beta_1 \sin\left(2\pi \left(\frac{MOY_i}{PE}\right)\right) + \beta_2 \cos\left(2\pi \left(\frac{MOY_i}{PE}\right)\right),$$

where *logit* is the link function for the binomial distribution, $\hat{\pi}_i$ is the expected proportion of otoliths with an opaque zone present at the margin for each angular transformed month of any year MOY_i (with January being assigned a value of 1 and December 12). PE is the assumed monthly periodicity of growth zone deposition (12 for an annual cycle) and $\beta_0, \beta_1, \beta_2$ the regression coefficients (Beamish et al., 2005). Regression parameters were estimated by minimizing the binomial negative log-likelihood function of the form:

$$-LL = -\sum_{i=0}^{12} [m_i \ln(\hat{\pi}_i) + (n_i - m_i) \ln(1 - \hat{\pi}_i)],$$

where n_i is the number of otoliths examined per month and m_i represents the number of otoliths with an opaque zone present on the margin. To test the null hypothesis (H_1^0) that growth zone deposition is annual, a likelihood ratio test

$$\chi_k^2 = -2(LL_{reduced} - LL_{full})$$

was conducted, where $LL_{reduced}$ is the log-likelihood for the *reduced* model with the constraint that PE is fixed at 12, LL_{full} is the log-likelihood for the *full* model where PE is estimated, and k is the difference in estimated parameters of the two models. Similarly, the null hypothesis (H_2^0) that growth zone deposition is bimodal was tested where PE was fixed at six.

Secondly, using the method recommended by Okamura & Semba (2009) in which a binomial model is linked with a von Mises distribution for circular data. This distribution takes the characteristics of the EA into account, using the Akaike Information Criterion (AIC) to determine if the periodicity of growth zones is categorised as no cycle, annual or biannual.

For this method a vector $x = (x_1, \dots, x_n)$ is the assumed response variable in which one of the elements x_i equals 1 for an opaque band and 0 for a translucent band. A vector x is linked to a covariate $m = (m_1, \dots, m_n)$, which is the month in which the i th sample was collected. Each $m_i \in \{1, \dots, 12\}$ is linked to the first day of the month $y(m_i)$, which is expressed in radians. Given this notation and using a binomial model, the probability mass function of the observations x given the parameter θ is:

$$P(x|\theta) = \prod_{i=1}^n \left\{ \frac{\gamma}{y(m_i + 1) - y(m_i)} \int_{y(m_i)}^{y(m_i+1)} f(u|\mu, \rho) du \right\}^{x_i} \cdot \left\{ 1 - \frac{\gamma}{y(m_i + 1) - y(m_i)} \int_{y(m_i)}^{y(m_i+1)} f(u|\mu, \rho) du \right\}^{1-x_i}$$

where $\theta = (\gamma, \mu, \rho)$, $y(1)=0$, $y(2)=(31/365) \cdot 2\pi, \dots$, $y(12)=2\pi$, γ is an adjustment parameter to ensure that the probability of the edge type is between 0 and 1, μ is the day (radian) corresponding to the peak of the probability distribution of opaque bands, and ρ is the dispersion parameter in the probability distribution of opaque bands. Note that the model takes differences in monthly sample sizes into consideration. The parameter γ has to satisfy the following constraint:

$$0 \leq \gamma \leq \left[\max \left\{ \frac{1}{y(m_i + 1) - y(m_i)} \int_{y(m_i)}^{y(m_i+1)} f(u|\mu, \rho) du \right\} \right]^{-1}$$

When a growth band pair is formed annually, the density function $f(u|\mu, \rho)$ is simply a von Mises distribution, which is a common statistical distribution for circular data:

$$f(u|\mu, \rho) = \frac{\exp\{\rho \cos(u-\mu)\}}{2\pi I_0(\rho)} \text{ where } 0 \leq \mu < 2\pi, 0 \leq \rho < \infty,$$

$$\text{and } I_0(\rho) = \sum_{i=0}^{\infty} \frac{\rho^{2i}}{2^{2i}(i!)^2}$$

is the modified Bessel function of order zero. The “CircStats” package in the R statistical software (R Development Core Team, 2007) was used for this analysis.

The parameter θ is estimated using the maximum likelihood approach by maximizing the logarithm of the probability mass function equation. The numerical optimization was carried out using the Nelder-Mead or the BFGS method in “optim” of the R statistical software. The AIC was used to estimate the goodness of fit by using the log-likelihood and the number of estimated parameters. The model with the lowest AIC value is preferred because it is estimated to be the closest to the unknown reality that generated the data. Results were displayed using the delta AIC notation whereby the lowest AIC value was subtracted from the other AIC values from that distribution, displaying the lowest AIC value as zero.

4.2.3 Mark-recapture of chemically tagged fish

Fish for MRCT were captured by angling, measured to the nearest mm FL, injected with 60 mg kg⁻¹ fish mass of commercially available oxytetracycline hydrochloride (HiTet 120; Bayer, Leverkusen, Germany), tagged with either a Hallprint (Victor Harbour, South Australia) plastic dart (model PDL) or a T-bar anchor (model TBA-2) tag as described in Chapter 7 and released. Sample size depended on environment. In Howarth Dam a total of 80 fish (200-480 mm FL) were marked between September and November 2004. In Dames Dam a total of 36 fish (200-500 mm FL) were marked during December 2006 and in Wiggleswade Dam 786 fish (213-582 mm FL) were marked and released between May 2011 and January 2012.

Upon recapture, fish were dissected and sagittal otoliths taken and stored in the dark to prevent the degrading effect ultraviolet light has on the fluorescence of the mark formed by OTC on calcified structures (Winker et al., 2010b). Otoliths were processed as described in Chapter 3 with the exception that they were not burnt prior to setting. Sections were viewed under fluorescent (460-490 nm and 510-550 nm) light to determine the position of the fluorescent mark and under transmitted white light to count the number of opaque and hyaline growth zones distal to the fluorescent mark (Figure 4.2). Because one opaque and hyaline growth zone pair represents one growth increment, each was assigned a score of 0.5 such that the sum of the opaque (0.5) and hyaline (0.5) growth zones distal to the fluorescent mark could be plotted against time at liberty. A *t*-test was then used to test the hypothesis that the slope of the regression differed from a 1:1 relationship and the intercept differed from 0.

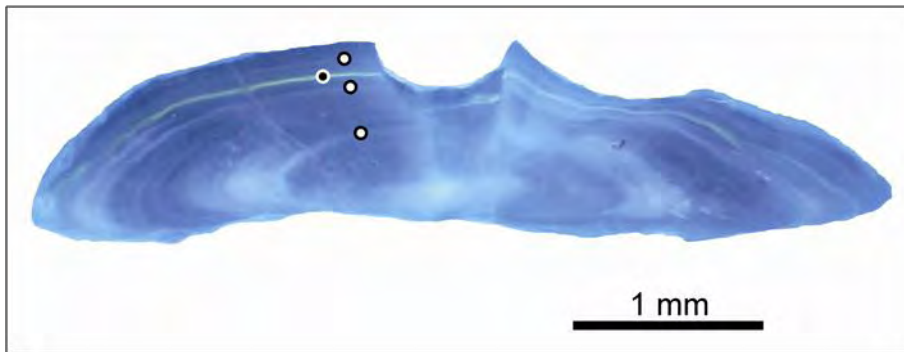


Figure 4.2: The otolith of a three year old *Micropterus salmoides* of 240 mm FL tagged with 60 mg/kg body mass oxytetracycline hydrochloride and released into Dames Dam on 10/12/2006 and recaptured on 15/04/2008. The white circles represent the annual opaque growth zones, and the black circle represents the fluorescent band of OTC under ultraviolet light deposited during tagging.

4.3 Results

4.3.1 Edge analysis

Observed and predicted data for both dams indicated that the highest proportion of otoliths had opaque margins from November to January (Figure 4.3). Periodic regression parameters for samples from Wriggleswade and Mankazana Dams are provided in Table 4.1. Periodic logistic regression analysis failed to reject the null hypothesis that one opaque zone was deposited annually in Wriggleswade ($\chi^2 = 1.55$, d.f. = 3, $P = 0.21$) and Mankazana Dams ($\chi^2 = 3.40$, d.f. = 3, $P = 0.065$) and rejected the alternative hypothesis that growth zone

deposition was bimodal ($\chi^2 = 30.37$, d.f. = 3, $P < 0.05$) ($\chi^2 = 70.57$, d.f. = 3, $P < 0.05$) (Table 4.1).

Table 4.1: Parameter estimates from the periodic logistic analysis predicting the temporal proportion of opaque zone deposition over a one year period for *Micropterus salmoides* in Wiggleswade and Mankazana Dams, Eastern Cape, South Africa. The periodicity (PE) was estimated for the full models and fixed for the unimodal and bimodal models.

Parameter	Wiggleswade			Mankazana		
	Full	Annual	Biannual	Full	Annual	Biannual
β_0	-1.23	-1.88	-1.47	-1.84	-1.33	-0.96
β_1	-1.39	0.01	-0.30	0.16	-1.00	-0.66
β_2	1.29	1.63	0.78	2.36	1.92	0.20
PE	16.15	12	6	10.18	12	6
d.f.	4	3	3	4	3	3
$\ln L$	-145.32	-146.09	-160.50	-127.87	-129.57	-163.15

In addition, the method recommended by Okamura & Semba (2009) showed the lowest AIC values for an annual cycle in Wiggleswade and Mankazana Dams compared to no cycle and the binomial cycle (Table 4.2, Figure 4.3).

Table 4.2: The Akaike Information Criterion characterising the periodicity of growth zone formation as annual (delta AIC values of zero) for the *Micropterus salmoides* populations of Wiggleswade and Mankazana Dams, Eastern Cape, South Africa using both the von Mises and the wrapped Cauchy distributions.

Dam	Distribution	Δ AIC		
		No cycle	Annual	Biannual
Wiggleswade	von Mises	39	0	27
	wrapped Cauchy	41	0	28
Mankazana	von Mises	85	0	50
	wrapped Cauchy	103	0	73

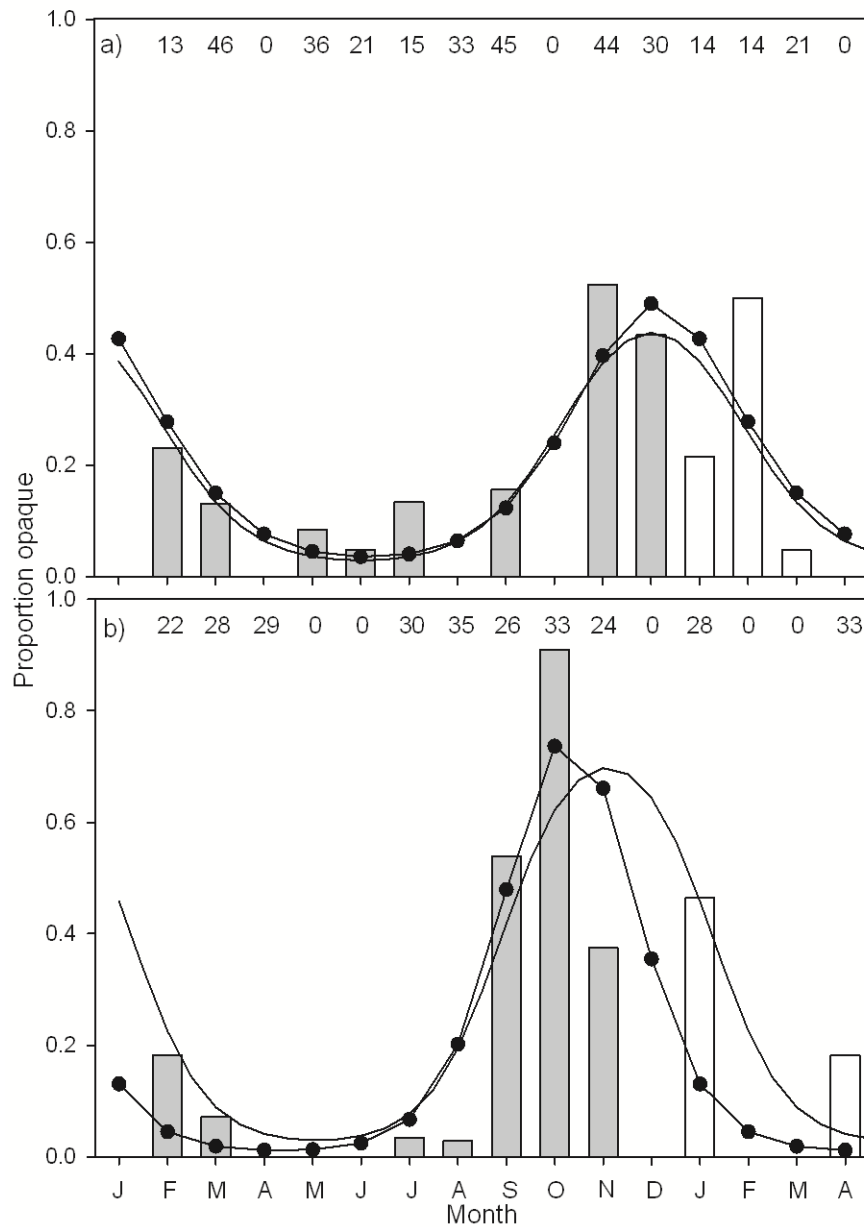


Figure 4.3: Proportion of opaque sagittal otolith margins from *Micropterus salmoides* sampled monthly from (a) Wiggleswade and (b) Mankazana Dams between January 2011 and April 2012, Eastern Cape, South Africa. The solid line represents the predicted binomial periodic regression model while the connected black dots represent the predicted annual von Mises distribution. Observed opaque proportions are given as bars, with the grey bars illustrating the restricted year of data used for the von Mises distribution analysis. The sample sizes per month are given at the top of the bars.

4.3.2 Mark-recapture of chemically tagged fish

Thirty five chemically marked fish were recaptured after time at liberty of between 14 and 503 days (0.04 to 1.38 years) (Table 4.3). All otolith sections had a visible clear fluorescing

band incorporated into them (Figure 4.2). Those fish that were recaptured during or after the opaque zone deposition period predicted from EA had two to 14 growth zones prior to the mark and had one growth zone (an opaque and a hyaline zone) distal to the fluorescent mark (Table 4.3). The slope of the linear relationship between time at liberty (years) and the number of growth zones (linear regression: $F = 51.5$, d.f. = 34, $P = 0.00$) was 0.89. The null hypothesis that the slope of the regression = 1 could not be rejected (t -test, $t = 0.76$, d.f. = 2,33, $P = 0.45$) and the intercept was not significantly different from zero (t -test, $t = 0.88$, d.f. = 2,33, $P = 0.38$) (Figure 4.4). The present study was therefore able to validate the annual deposition of one opaque and one hyaline zone in adult *M. salmoides* aged between two and 14 years and from three different localities (Table 4.3).

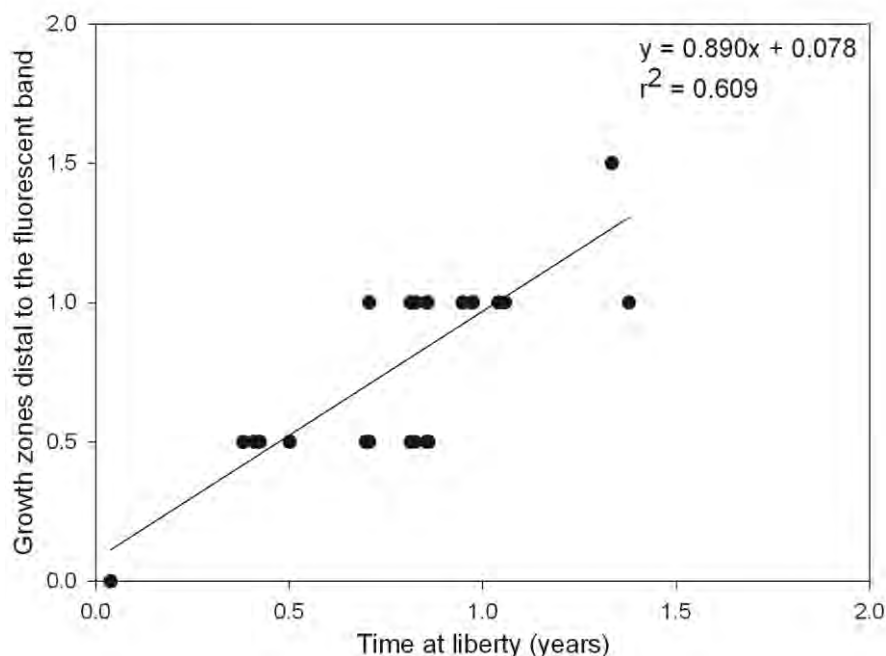


Figure 4.4: The relationship between the number of growth zones distal to the fluorescent band and the time at liberty for the *Micropterus salmoides* recaptured from Howarth, Dames and Wriggleswade Dams, Eastern Cape, South Africa.

Table 4.3: Summary of the *Micropterus salmoides* that were injected with oxytetracycline hydrochloride (OTC) and recaptured after being at liberty in the wild in Howarth, Dames and Wiggleswade Dams. The summary includes the dam, the number of opaque zones that were deposited before OTC injection (B), the number of growth zones (O = opaque (0.5), H = hyaline (0.5)) deposited after OTC injection (A), and the total number of growth zones (Age). The growth (Δ FL) in mm was calculated as the difference between the length at injection FL₁ mm and the length at recapture FL₂ mm. The visual appearance of the otolith edge is presented as either opaque (O) or hyaline (H) (Figure 4.1).

Dam	Date injected	Date re-captured	Time at liberty (days)	FL ₁ (mm)	FL ₂ (mm)	Δ FL (mm)	Sex	Growth zones						
								B	H	O	H	A	Edge	Age
Howarth	2004/11/19	2005/12/10	386	304	327	23	M	3	1	1	-	1	O	4
Dames	2006/12/10	2008/04/10	487	-	240	-	-	2	1	1	1	1.5	H	3.5
Dames	2006/12/10	2007/12/25	380	500	580	80	-	8	1	1	-	1	O	9
Dames	2006/12/20	2007/12/01	346	388	410	22	-	5	1	1	-	1	O	6
Wiggleswade	2011/05/14	2012/03/11	302	401	408	7	M	5	1	1	-	1	O	6
Wiggleswade	2011/05/14	2012/09/28	503	373	374	1	M	5	-	1	1	1	H	6
Wiggleswade	2011/05/15	2011/10/11	149	450	446	-4	F	9	-	1	-	0.5	O	9.5
Wiggleswade	2011/05/15	2012/03/11	301	388	404	16	F	5	1	-	-	0.5	H	5.5
Wiggleswade	2011/05/15	2011/10/11	149	430	430	0	M	9	1	-	-	0.5	H	9.5
Wiggleswade	2011/09/10	2012/03/11	183	355	342	-13	M	4	-	1	-	0.5	O	4.5
Wiggleswade	2011/10/08	2012/09/28	356	335	335	0	F	3	-	1	1	1	H	4
Wiggleswade	2011/10/08	2012/09/28	356	330	336	6	F	3	-	1	1	1	H	4
Wiggleswade	2011/10/08	2012/09/28	356	360	369	9	F	4	-	1	1	1	H	5
Wiggleswade	2011/10/08	2012/03/11	155	378	371	-7	M	6	-	1	-	0.5	O	6.5
Wiggleswade	2011/10/09	2012/09/28	355	410	451	41	F	7	-	1	1	1	H	8
Wiggleswade	2011/10/09	2012/09/27	354	357	358	1	F	3	1	1	-	1	O	4
Wiggleswade	2011/10/09	2012/03/11	154	425	422	-3	M	14	1	-	-	0.5	H	14.5
Wiggleswade	2011/11/19	2012/09/26	312	440	452	12	F	9	1	1	-	1	O	10
Wiggleswade	2011/11/19	2012/09/26	312	424	444	20	F	7	1	-	-	0.5	H	7.5
Wiggleswade	2011/11/19	2012/09/28	314	350	342	-8	F	5	-	1	-	0.5	O	5.5
Wiggleswade	2011/11/19	2012/09/27	313	348	349	1	F	3	-	1	-	0.5	O	3.5

Table 4.3 Continued

Dam	Date injected	Date re-captured	Time at liberty (days)	FL ₁ (mm)	FL ₂ (mm)	Δ FL (mm)	Sex	Growth zones						
								B	H	O	H	A	Edge	Age
Wriggleswade	2011/11/19	2012/09/26	312	385	370	-15	F	6	-	1	1	1	H	7
Wriggleswade	2011/11/19	2012/09/27	313	305	308	3	M	4	-	1	1	1	H	5
Wriggleswade	2011/11/19	2012/09/27	313	415	415	0	F	8	-	1	1	1	H	9
Wriggleswade	2011/11/20	2012/09/27	312	419	425	6	M	4	-	1	1	1	H	5
Wriggleswade	2011/11/20	2011/12/04	14	315	315	0	F	5	-	-	-	0	-	5
Wriggleswade	2011/12/03	2012/09/26	298	299	300	1	M	3	-	1	1	1	H	4
Wriggleswade	2011/12/04	2012/09/26	297	352	352	0	M	6	-	-	1	0.5	H	6.5
Wriggleswade	2011/12/04	2012/09/26	297	336	337	1	F	5	-	1	1	1	H	6
Wriggleswade	2011/12/04	2012/09/27	298	323	326	3	M	4	1	1	-	1	O	5
Wriggleswade	2012/01/14	2012/09/27	257	340	343	3	M	5	-	1		0.5	O	5.5
Wriggleswade	2012/01/14	2012/09/28	258	420	421	1	F	7	-	1	1	1	H	8
Wriggleswade	2012/01/14	2012/09/28	258	390	394	4	M	6	1	-	-	0.5	H	6.5
Wriggleswade	2012/01/15	2012/09/26	255	330	338	8	F	3	1	-	-	0.5	H	3.5
Wriggleswade	2011/09/10	2012/01/27	139	450	468	18	F	9	-	1	-	0.5	O	9.5

4.4 Discussion

This study confirmed the annual deposition of a single opaque/hyaline growth zone pair in four temperate *M. salmoides* populations in Africa using both EA and MRCT methods. While EA is considered a less robust validation method than MRCT because it is dependent on the reader recognising the state of the otolith edge (Campana, 2001), the MRCT results indicate that EA adequately validated growth zone deposition rate in Wriggleswade Dam where both methods were applied. These results are consistent with those recently undertaken on four cyprinids in South Africa where EA and MRCT also provided complimentary results (Winker et al., 2010a, b; Ellender et al., 2012), which supports the annual deposition found using EA, the most commonly applied method of validation in the literature (Table 4.4).

Table 4.4: Summary of studies on the validation of *Micropterus salmoides* growth zone deposition rate in otoliths. Methods of validation are edge analysis (EA), mark recapture of chemically tagged fish (MRCT), length frequency (LF), back-calculation (BC), mark recapture (MR), known age fish (KA) and the counting of daily rings (DR). The period of opaque zone deposition is given in months from 1 (January), to 12 (December).

Location	Coordinates	Method	Period	Max age
South Africa ¹	33°24'S, 26°20'E	EA, MRCT	10-2	14
Mozambique ²	19°08'S, 33°08'E	EA	7-10	5
Zimbabwe ³	17°49'S, 30°32'E	EA	10-2	9
Florida, USA ⁴	28°31'N, 81°23'W	EA	4-6	12
Florida, USA ⁵	28°30'N, 81°44'W	KA, BC	2-7	5
Texas, USA ⁶	30°09'N, 99°20'W	KA, BC		8
Texas, USA ⁷	30°09'N, 99°20'W	KA		16
Japan ⁸	34°36'N, 136°6'E	EA, BC	6-8	7
Illinois, USA ⁹	39°38'N, 89°28'W	EA, KA, BC, MR, DR	5-7	11
Canada ¹⁰	45°04'N, 79°57'W	BC, MR	5-6	7+

¹Current study; ²Weyl & Hecht (1999); ³Beamish et al. (2005); ⁴Crawford et al. (1989); ⁵Hoyer et al. (1985); ⁶Howells et al. (1995); ⁷Buckmeier & Howells (2003); ⁸Yodo & Kimura (1996); ⁹Taubert & Tranquilli (1982); ¹⁰Maraldo & MacCrimmon (1979).

EA indicated that the highest proportion of otoliths with opaque margins was obtained from fish sampled during early summer (November and January in South Africa). This was consistent with EA results from other studies (Table 4.4) and may be a result of a lag between zone deposition and detection. This is because the state of the growth zone formed at the edge

of the otolith only becomes visually discernible after it is deposited. As a result, opaque margins detected in early summer had to have been deposited during a slow growth period sometime previously. This slow growth period is most likely linked to decreased metabolic rates during low winter temperatures (Lemons & Crawshaw, 1985) and energetically costly spring spawning (Cooke et al., 2001). While the influence of each on growth zone deposition is unknown, it is likely that their combination is responsible for growth zone deposition in the otolith.

Annual growth zone deposition in *M. salmoides* sagittal otoliths found in this study was also consistent with findings from validation studies conducted through the present distributional range of this species in an array of climatic conditions ranging from 45°N to 33°S (Table 4.4). This result has also been found by Maceina et al. (2007) in an assessment of the State and Provincial Fisheries Agencies and the ageing literature from North America and Canada. While growth zone deposition rate has not been validated for otoliths from tropical *M. salmoides* populations, Britton & Harper (2005), working on the equatorial Lake Naivasha, used marginal increment analysis and corroboration with length frequency data to validate the annual deposition of growth checks on scales. Since there is evidence that growth zone deposition rates are similar between scales and otoliths (Maraldo & MacCrimmon, 1979), annual growth zone deposition can be inferred. Our data therefore support the hypothesis that a single opaque/hyaline growth zone is deposited on *M. salmoides* otoliths throughout their distributional range and is in support of the assumptions made in non-validated ageing studies conducted on this species elsewhere (Godinho & Ferreira, 1993; Lorenzoni et al., 2002; Neal & Noble, 2002; Rodriguez-Sánchez et al., 2009). Future validation studies should concentrate on the more robust MRCT method which is commonly used to identify the effect of fish stocking (Doe, 2005; Hoffman & Bettoli, 2005) but has not been previously used to validate growth zone deposition rate in *M. salmoides* (Table 4.4).

CHAPTER 5: AGE, GROWTH AND REPRODUCTION OF *MICROPTERUS SALMOIDES* IN TWO TEMPERATE AFRICAN DAMS

5.1 Introduction

Largemouth bass *Micropterus salmoides* are a well-researched species in their native and non-native ranges in North America (Clugston, 1964; Maraldo & MacCrimmon, 1979; Diana & Wahl, 2009; Mims et al., 2010; Gaeta et al., 2011), however there is a paucity of information on their biology and ecology in their introduced range (Azuma & Motomura, 1998; Britton et al., 2010a). Determinations of age, growth and maturity are fundamental in understanding the biology of fishes as they allow for the assessment of establishment success between populations.

In a study on the success of *M. salmoides* in subtropical Lake Chicamba, Weyl & Hecht (1999) for example, used growth performance as an indicator of both the ability of this species to meet nutritional requirements and its adaptation to prevailing environmental conditions. They demonstrated that *M. salmoides* growth performance in this subtropical population was superior to that in many native populations and attributed the fast growth of this species to favourable water temperatures and high prey availability (Weyl & Hecht, 1999). In Lake Chicamba, *M. salmoides* spawned earlier (spring) than native fishes (summer) which allowed juveniles to initially grow in a competitor free environment and then prey on native fish juveniles when these became available later in the year. Working in tropical Lake Naivasha, Britton & Harper (2005) also reported fast growth rates for this species which was later attributed to high annual water temperatures (Britton et al., 2010a). Tropical conditions in that lake resulted in an extended spawning season of eight months (Dadzie & Aloo, 1990). In comparison with the maximum age attainable by this species (24 years: Green & Heidinger, 1994), both the Lake Chicamba and the Lake Naivasha populations were short lived attaining a maximum age of five years. Fast growth and reduced longevity (five years) in the tropical and subtropical *M. salmoides* populations were hypothesised to be as a result of the high bioenergetic cost associated with the extended spawning season (Neal & Noble,

2006). While this hypothesis is consistent with findings from the tropical Lake Naivasha population, there are inconsistencies within subtropical African populations. Lake Chicamba fish were short lived despite having a short (two-month) spawning season and fish from the subtropical Lake Manyame in Zimbabwe attained fairly old ages of nine years (Beamish et al., 2005). Further assessment of such inconsistencies in introduced populations is however constrained by the lack of data from across the climatic range of *M. salmoides* introductions.

This chapter aims to improve the understanding of establishment success of *M. salmoides* by assessing growth, maturity and reproductive seasonality in two *M. salmoides* populations from the temperate region in South Africa. Using the results from these temperate populations, I test whether these populations conform to previously proposed hypotheses on the relationship between temperature and (1) the extent of the spawning season, (2) longevity and (3) growth performance.

5.2 Material and methods

Fish sampled were measured to the nearest mm FL and TL and weighed to the nearest gram. Fish were then sexed, and their reproductive stage determined macroscopically using the visual staging criteria described by Weyl & Hecht (1999) (Table 5.1). The two sagittal otoliths were removed, cleaned and stored dry in labelled Eppendorf tubes.

Table 5.1: Macroscopic criteria used to determine reproductive stages of maturity in male and female *Micropterus salmoides* from Wriggleswade and Mankazana Dams, Eastern Cape of South Africa (Weyl & Hecht, 1999).

Macroscopic stage	Description
1. Juvenile	Gonads not fully formed but present as two small sacs.
2. Resting	Ovary slightly yellowish. Oocytes macroscopically distinguishable. Testis small and opaque.
3. Developing	Ovary enlarged, oocytes readily visible and yellow. Testis broadened, distended and cream, in colour.
4. Ripe	Oocytes of maximum size, yellow, and hydrates. Testis swollen to maximum size.
5. Spent	Ovary partly empty and flaccid with irregular oocyte size. Testis flaccid.

5.2.1 Reproduction

Using fish sampled during the peak spawning season (identified by plotting the proportion of fish at each stage of maturity per sampling month), length at maturity was expressed as the proportion of mature fish in each 20 mm FL size class. The length at 50% maturity (Lm_{50}) was then estimated by fitting these data to a two-parameter logistic model of the form:

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

where $P(L)$ is the percentage of mature fish at FL (mm) and δ_L the width of the logistic ogive. Maximum likelihood estimates of the parameters were obtained by minimising the binomial negative log-likelihood of the form:

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

where $\hat{P}_i$ is the predicted proportion of mature fish in length class i , n_i is the number of individuals sampled and m_i is the number of these individuals that are mature. Likelihood ratio tests were used to test the null hypothesis that Lm_{50} values were equal between sexes and populations. Age at 50% maturity (tm_{50}) was estimated by converting the Lm_{50} value to age using the von Bertalanffy growth parameters.

5.2.2 Age and growth

Otoliths were prepared as described in Chapter 3, and growth zone deposition rate was validated as annual in Chapter 4. Growth zone counts were therefore approximated to age in years. Female, male and grouped sex age and corresponding length data were fitted to the von Bertalanffy growth model of the form:

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

where L_t is the length at age t , L_∞ is the predicted asymptotic length, K is the Brody growth coefficient, and t_0 is the age at zero length (Ricker, 1975). The parameters were estimated by minimising the binomial negative log-likelihood function using:

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

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

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

and $\hat{L}_i$ is the predicted total length-at-age, L_i is the observed length-at-age and n is the total number of observations. The variability of the parameters was estimated using the conditioned parametric bootstrap resampling technique described by Efron (1980).

Due to the young age of the *M. salmoides* population from Mankazana Dam the accuracy of the estimated von Bertalanffy growth parameters is questionable and the average lengths at ages one, two, three and four were assessed using *t*-tests assuming unequal variance, for a more accurate comparison with the population of *M. salmoides* from Wiggleswade Dam.

5.2.3 Intraspecific life history comparison

Available age-derived life history parameters for *M. salmoides* populations across their non-native distribution range were collated from published literature. For ease of comparison between this study and growth studies conducted on other populations of *M. salmoides*, the growth performance index phi prime (Φ) was calculated:

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

where measurements in centimetres FL (Munro & Pauly, 1983) were used. This index accounts for the interaction and dependence of the von Bertalanffy growth parameters L_{∞} and K and allows for comparisons of growth performance across populations (Winker et al., 2010a). All length estimates given in total length (TL mm) and standard length (SL mm) were first converted to fork length (FL mm) using the length–length relationships $FL = 0.955TL - 1.526$ (current study) and $TL = 0.242 + 1.138SL$ (taken from Lorenzoni et al., 2002). Phi prime values were then plotted against annual average air temperatures from either the paper from which the growth parameters were taken, or from the World Weather Online (2011) website to standardise results. To define the native and non-native range relationships between temperature and phi prime index (growth), linear regression analyses were conducted and plotted.

5.3 Results

A total of 578 *M. salmoides* were sampled from Wriggleswade Dam and 287 from Mankazana Dam. In Wriggleswade the sex ratio was 1.13 females: 1 male, while in Mankazana the sex ratio was 1.14 females: 1 male, and neither sex ratios differed significantly from overall unity (Wriggleswade: $\chi^2 = 1.10$, d.f. = 1, $P = 0.29$; Mankazana: $\chi^2 = 0.64$, d.f. = 1, $P = 0.42$).

5.3.1 Spawning season and maturity

The frequency of occurrence of macroscopically staged ripe fish increased from late winter (July) to a maximum in early spring (September) in both populations. The Wriggleswade population appeared to spawn slightly later than the Mankazana population as spent fish were only recorded from this population from November (Figure 5.1). Spawning in the temperate populations therefore occurred between August and October.

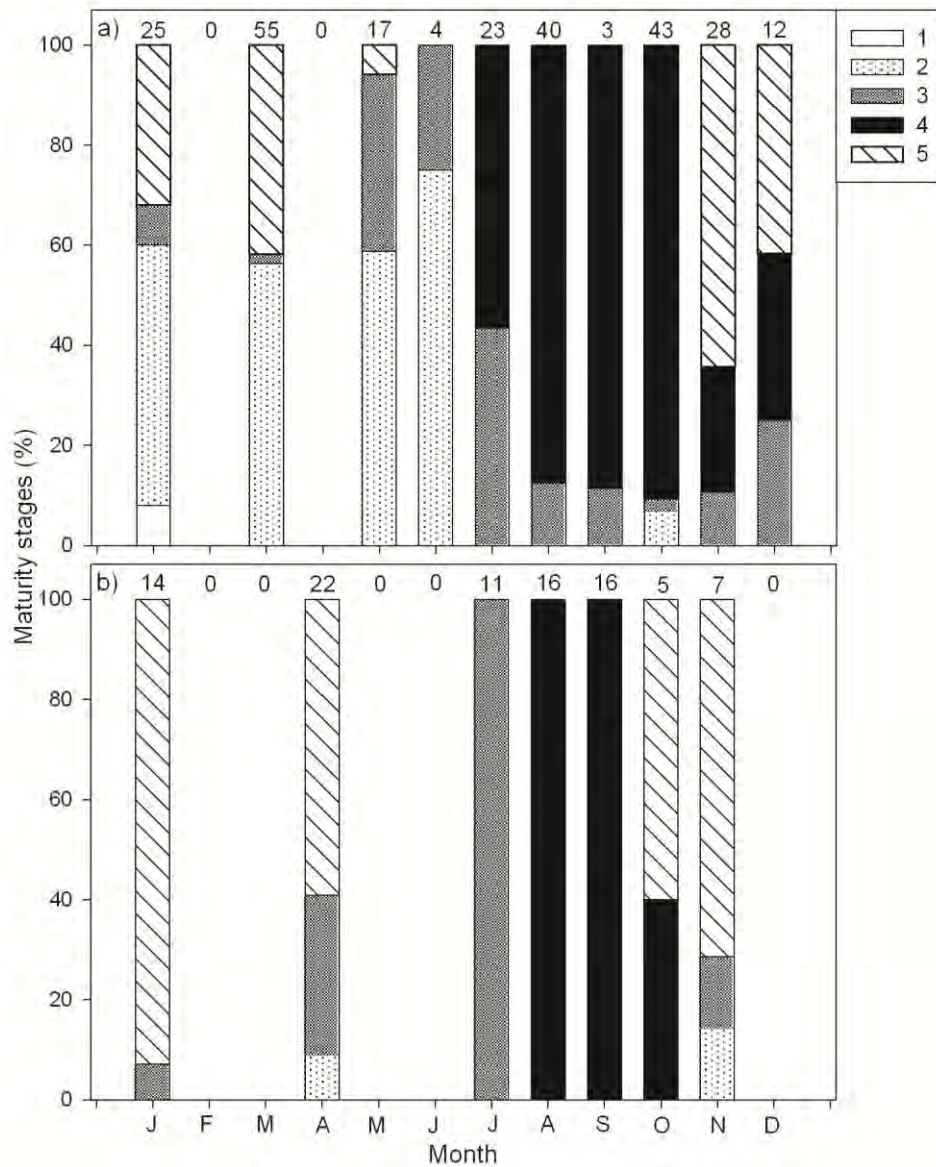


Figure 5.1: The proportion of mature (above the Lm_{50}) *Micropterus salmoides* sampled per month from (a) Wriggleswade and (b) Mankazana Dams in the Eastern Cape of South Africa. The key for the macroscopic staging criteria described in Table 5.1 is given to the right, and sample sizes are given above each bar.

Of 130 *M. salmoides* sampled from Wriggleswade during peak spawning months, 67 were female, 61 were male and two were juveniles for which sex was indistinguishable. In Mankazana 90 individuals were sampled during peak spawning months, of which 48 were female and 42 were male. For both populations male and female Lm_{50} values did not differ significantly (maximum likelihood ratio test; $P > 0.05$), and therefore data were pooled and total Lm_{50} values estimated. Length at maturity (Lm_{50}) was reached at 259 mm FL ($\delta_L = 1.70$ mm) at a calculated age (tm_{50}) of 2.3 years in Wriggleswade and at 290 mm FL ($\delta_L = 1.78$

mm) at a calculated age of 1.8 years in Mankazana. These differences in age at maturity are artefacts since ages were corrected to the estimated peak spawning season (September).

Minimum length at maturity was similar in both populations with the smallest mature fish found to be 215 mm FL in Wriggleswade Dam compared to that of 213 mm FL in Mankazana Dam.

5.3.2 Growth

Of the 578 *M. salmoides* sampled from Wriggleswade, 298 were female, 264 were male, and 16 were juveniles in which the sex could not be distinguished. Of the 287 *M. salmoides* sampled from Mankazana, 149 were female, 131 were male, and seven were juveniles in which the sex could not be distinguished. Age ranged from 0 – 14+ years in Wriggleswade and 0 – 5+ years in Mankazana. The von Bertalanffy growth models parameters are shown in Table 5.2 and the model fitted to the observed length at age data for *M. salmoides* populations in these two dams are shown in Figure 5.2. In Wriggleswade, female growth differed from male growth significantly (likelihood ratio test; $P < 0.05$), while in Mankazana there were no significant differences between sexes (likelihood ratio test; $P > 0.05$). Growth also differed between the two South African populations (likelihood ratio test; $P < 0.05$) with lower asymptotic lengths and slower rates of growth found in Wriggleswade's population.

Table 5.2: Von Bertalanffy growth model parameter estimates [95% C.I.] describing the length at age of *Micropterus salmoides* sampled from Wriggleswade and Mankazana Dams, Eastern Cape, South Africa.

Dam	Parameters	von Bertalanffy growth model		
		Juv. + Females	Juv. + Males	Combined
Wriggleswade	L_{∞}	472 [447, 502]	364 [351, 374]	420 [403, 440]
Mankazana	L_{∞}	598 [472, 1078]	632 [458, 1720]	739 [548, 1712]
Wriggleswade	K	0.27 [0.23, 0.32]	0.45 [0.42, 0.52]	0.33 [0.28, 0.38]
Mankazana	K	0.28 [0.11, 0.47]	0.23 [0.06, 0.45]	0.18 [0.06, 0.31]
Wriggleswade	t_0	-0.29 [-0.55, -0.06]	0.00 [-0.07, 0.17]	-0.22 [-0.47, 0.00]
Mankazana	t_0	-0.52 [-0.94, -0.26]	-0.69 [-1.23, -0.34]	-0.84 [-1.29, -0.53]
Wriggleswade	n	311	278	579
Mankazana	n	158	138	287

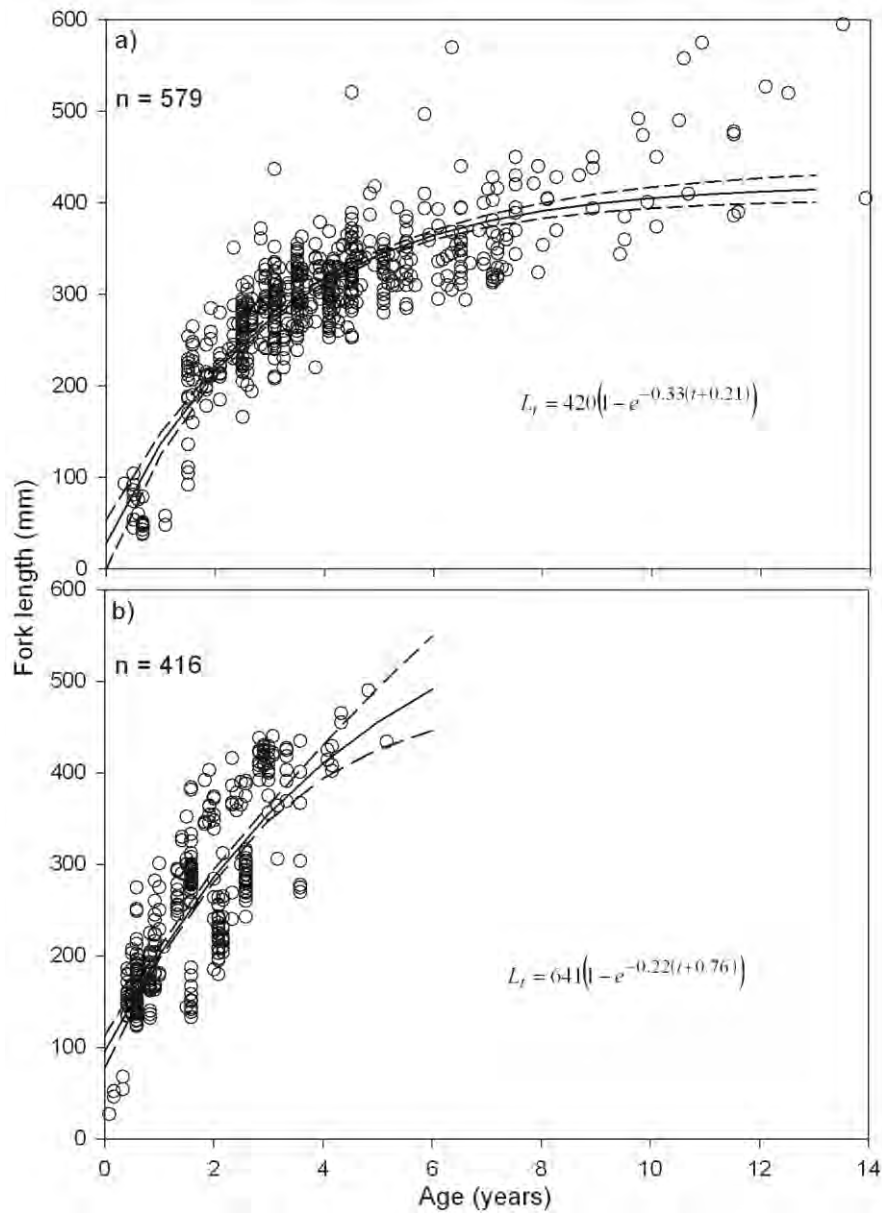


Figure 5.2: Observed individual lengths at age for *Micropterus salmoides* populations from (a) Wriggleswade and (b) Mankazana Dams, Eastern Cape, South Africa. The combined von Bertalanffy growth models are fitted as the solid lines, and the dash lines are the 95% bootstrap confidence intervals.

In addition a comparison of the average lengths at ages one, two, three and four for the *M. salmoides* of Wriggleswade and Mankazana Dams showed that fish from Mankazana Dam were significantly longer at all ages (Table 5.3) compared to those from Wriggleswade Dam.

Table 5.3: A comparison of the average lengths ($\pm$ SE) at ages one, two, three and four for the *Micropterus salmoides* populations of Wiggleswade and Mankazana Dams showing the significant differences ($P < 0.05$) using one tailed t -tests. The ages are given as for example 1+ meaning between the age of one and two years old. The last group 4+ means between the age of four and five years old.

Age	Wiggleswade Fork length (mm)	Mankazana Fork length (mm)	t -test
1+	199.1 $\pm$ 8.3	291.2 $\pm$ 6.1	$t = 8.95$, d.f. = 80, $P = 0.00$
2+	263.6 $\pm$ 3.7	298.8 $\pm$ 8.6	$t = 3.77$, d.f. = 121, $P = 0.00$
3+	295.6 $\pm$ 3.2	399.5 $\pm$ 6.9	$t = 13.73$, d.f. = 30, $P = 0.00$
4+	317.9 $\pm$ 3.3	436 $\pm$ 10.9	$t = 10.32$, d.f. = 8, $P = 0.00$

5.3.3 Life history comparisons

The growth performance for the *M. salmoides* populations of Wiggleswade and Mankazana were calculated as phi primes of 2.80 and 2.99 respectively. These growth performances fit in with the growth of the native range (linear regression: $F = 46.9$, d.f. = 47, $P = 0.00$) and non-native (linear regression: $F = 26.6$, d.f. = 13, $P = 0.00$) populations from the literature, showing a trend of increased phi prime values with annual average air temperature (Figure 5.3).

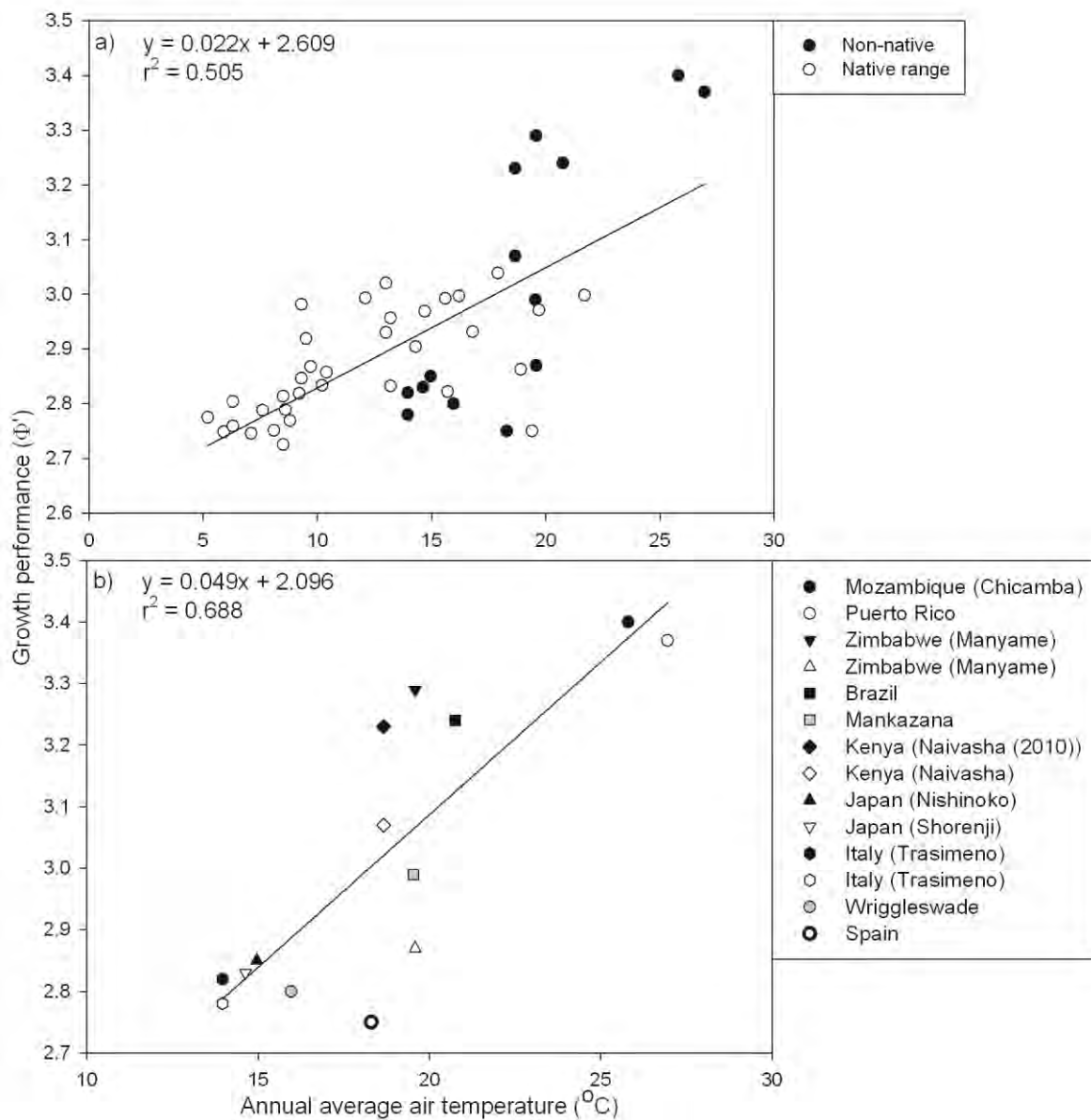


Figure 5.3: The relationships between growth performance (Φ') and annual average air temperature ($^{\circ}\text{C}$) of *Micropterus salmoides* populations from Wriggleswade and Mankazana Dams, Eastern Cape, South Africa, compared to a number of (a) native range (North American) populations (Beamesderfer & North, 1995), and a number of other (b) non-native populations: Wriggleswade and Mankazana (Current study), Lake Chicamba, Mozambique (Weyl & Hecht, 1999), Lucchetti Reservoir, Puerto Rico (Neal, 2003), Primera de Palos' Lake, Spain (Rodriguez-Sanchez et al., 2009), Lake Trasimeno females and males, Italy (Lorenzoni et al., 2002), Lake Naivasha, Kenya (Britton & Harper, 2005), and (Britton et al., 2010a), Lake Manyame females and males, Zimbabwe (Beamish et al., 2005), a lake in southern Brazil (Schulz & Leal, 2005), Lake Shorenji and Lake Nishinoko, Japan (Yodo & Kimura, 1996).

The life history characteristics of the temperate South African *M. salmoides* populations in comparison with data on other non-native populations from the literature are summarised in Table 5.4.

Table 5.4: Maximum observed age ($t_{\max}$) and length ($L_{\max}$), von Bertalanffy growth parameters (mm FL), growth performance (phi prime Φ') (Munro & Pauly, 1983), length at 50% maturity (L_{m50}) and age at 50% maturity (tm_{50}) for *Micropterus salmoides* from different localities. For comparison, total length (TL mm) and standard length (SL mm) were converted to fork length (FL mm) by $FL = 0.955TL - 1.526$ (current study) and $TL = 0.242 + 1.138SL$ (taken from Lorenzoni et al., 2002). F = female, M = male and C = combined data for the different regions.

Region	$t_{\max}$	$L_{\max}$	t_o	K	L_{∞}	Φ'	L_{m50}	tm_{50}
Wriggleswade F ¹	14	595	-0.29	0.27	472	2.78	276	2.7
Wriggleswade M ¹	14	445	0	0.45	364	2.78	265	2.5
Wriggleswade C ¹	14	595	-0.22	0.33	420	2.80	259	2.3
Mankazana F ¹	5	490	-0.52	0.28	598	3.00	296	1.8
Mankazana M ¹	4	465	-0.69	0.23	632	2.96	285	1.7
Mankazana C ¹	5	490	-0.84	0.18	739	2.99	290	1.8
Lake Chicamba, Mozambique F ²	5	-	-	-	-	-	290	0.9
Lake Chicamba, Mozambique M ²	5	-	-	-	-	-	305	0.9
Lake Chicamba, Mozambique C ²	5	540	-0.01	1.17	466	3.40	-	-
Lucchetti Reservoir, Puerto Rico ³	3+		0.21	1.44	404	3.37	264	1
Primera de Palos' Lake, Spain M ⁴	6+	364	-1.04	0.19	549	2.76	-	1
Primera de Palos' Lake, Spain F ⁴	6+	422	-1.05	0.18	559	2.75	-	2
Lake Trasimeno, Italy M ⁵	7	-	0.06	0.42	378	2.78	212	2
Lake Trasimeno, Italy F ⁵	9	-	0.02	0.33	449	2.82	288	3
Lake Bracciano, Italy F ⁶	3+	328	-	-	-	-	208	1+
Lake Bracciano, Italy M ⁶	3+	328	-	-	-	-	219	1+
Lake Naivasha, Kenya F ⁷	4	-	-	-	-	-	288-335	-
Lake Naivasha, Kenya M ⁷	4	-	-	-	-	-	240-287	-
Lake Naivasha, Kenya ⁸	4+	491	-0.01	0.46	508	3.07	-	-
Lake Naivasha, Kenya ⁹	5	527		0.61	531	3.23	-	-
Lake Manyame, Zimbabwe F ¹⁰	9	599		0.66	548	3.30	-	1
Lake Manyame, Zimbabwe M ¹⁰	9	482		0.41	424	2.87	-	1
Lake Manyame, Zimbabwe C ¹⁰	9	599		0.55	442	3.03	-	1
A lake in southern Brazil ¹¹	3	447	0.09	0.99	421	3.24	-	-
Lake Shorenji, Japan ¹²	6	413	-0.07	0.50	372	2.84	-	-
Lake Nishinoko, Japan ¹²	7	469	-0.09	0.46	395	2.85	-	-
North America ¹³	15	686	-0.02	0.20	580	2.86	-	-

¹ Current study, ² Weyl & Hecht, 1999, ³ Neal, 2003, ⁴ Rodriguez-Sanchez et al., 2009, ⁵ Lorenzoni et al., 2002, ⁶ Marinelli et al., 2007, ⁷ Dadzie & Aloo, 1990, ⁸ Britton & Harper, 2005, ⁹ Britton et al., 2010a, ¹⁰ Beamish et al., 2005, ¹¹ Schulz & Leal, 2005, ¹² Yodo & Kimura, 1996, ¹³ Beamesderfer & North, 1995 (average values)

Length at maturity of the temperate South African populations was comparable to the tropical and sub-tropical populations of Lake Naivasha (Dadzie & Aloo, 1990), Lucchetti Reservoir (Neal, 2003; Neal & Noble, 2002), and Lake Chicamba (Weyl & Hecht, 1999), and higher than the Italian populations (Lorenzoni et al., 2002; Marinelli et al., 2007). Fish matured at younger ages in Lake Chicamba (Weyl & Hecht, 1999) and Lake Manyame (Beamish et al., 2005) compared to those from the more temperate South Africa and Italy (Lorenzoni et al., 2002). *Micropterus salmoides* lived longer in the South African dam of Wriggleswade (to 14 years) than in any other non-native populations. Larger maximum lengths (L_{∞}) were reached in the southern African dams of Wriggleswade, Lake Manyame (Beamish et al., 2005) and Lake Chicamba (Weyl & Hecht, 1999), compared to the much smaller asymptotic lengths in populations from Italy (Lorenzoni et al., 2002), Spain (Rodriguez-Sanchez et al., 2009) and Japan (Yodo & Kimura, 1996).

5.4 Discussion

The success of an introduced species is dependent on both its life history characteristics which determine its ability to overcome abiotic conditions (Moyle & Light, 1996), and on the nature of the receiving environment (Elton, 1958). Temperate South Africa has a relatively species poor freshwater environment with few native predators, so making it particularly susceptible to invasion (de Moor, 1996). *Micropterus salmoides* established easily in this environment because of their equilibrium life history strategy described by Mims et al. (2010) which characterises a medium bodied fish that reaches a moderate age at maturity and has low fecundity and high juvenile survivorship, so making this species ideally suited to South African conditions.

Successful reproduction or a high degree of fitness is a key element of fish biology often excelled at by non-native invasive populations (Moyle, 1986). *Micropterus salmoides* is no exception, and reproduce successfully in a wide range of non-native habitats (Dadzie & Aloo, 1990; Weyl & Hecht, 1999; Neal, 2003; Beamish et al., 2005; Marinelli et al., 2007; Rodriguez-Sánchez et al., 2009). In temperate South Africa *M. salmoides* populations reach maturity at an average age and length compared to both native (Swingle & Smith, 1943;

Nieman et al., 1979) and non-native populations (Table 5.4), and spawn in late winter to early spring for a defined season of up to four months (Figure 5.1). This defined spawning season differs from the more tropical non-native populations which have extended spawning seasons of up to eight months due to sustained high temperatures throughout the year (Dadzie & Aloo, 1990; Neal, 2003). However the high bioenergetic cost associated with the extended spawning season (Neal & Noble, 2006) results in a reduction in longevity and restricts the maximum length reached by these populations (Table 5.4). This is not the case in temperate South Africa, of which Wriggleswade's *M. salmoides* population, established in 1991 when the dam filled, contains specimens up to 14 years of age (Table 5.4). Due to the relatively young nature of Mankazana's population, which were introduced into this dam by anglers in c. 2006, the longevity of this population could not yet be assessed.

The growth performance of a species encompasses its ability to meet nutritional requirements and adapt to abiotic conditions such as temperature (Jobling, 1981). Trends of *M. salmoides* growth with varying environmental variables have been assessed in both their native and introduced ranges in order to try and explain the variation in growth rates (McCauley & Kilgour, 1990; Beamesderfer & North, 1995; Helser & Lai, 2004; Rypel, 2009; Britton et al., 2010a). These studies have all documented an increase in growth or productivity with temperature (Helser & Lai, 2004; Britton et al., 2010a) or latitude as an indicator of temperature (Beamesderfer & North, 1995). Using the phi prime index which takes into consideration the interaction and dependence of the von Bertalanffy growth parameters K (rate of growth) and L_{∞} (asymptotic length) (Munro & Pauly, 1983), an increase in growth performance with an increase in mean annual air temperature was demonstrated. In addition it was illustrated that the growth of temperate South African populations was comparable to that of non-native temperate populations in Italy (Lorenzoni et al., 2002), Spain (Rodriguez-Sánchez et al., 2009) and Japan (Yodo & Kimura, 1996). Although at the lower end of the tropical and sub-tropical non-native growth scale, temperate *M. salmoides* South African populations grew at rates that were comparable to populations in temperate areas of North America (Beamesderfer & North, 1995) (Figure 5.3).

The temperate African *M. salmoides* populations therefore perform as expected, maturing at average lengths and ages, and growing at average rates to old ages. Interestingly, the subtle

changes in tactics or the observed expression of life-history traits (Frimpong & Angermeier, 2009) associated with this species across its non-native range (Table 5.4) are in accordance with the natural geographic patterns of life history strategies described by Mims et al. (2010) in association with climatic regimes. This adaptation of life history traits by *M. salmoides* populations across its non-native range demonstrates the life-history plasticity of *M. salmoides*, which are a product of phylogenetic history and current environment (Frimpong & Angermeier, 2009). To further understand the influence of environment, the diet of *M. salmoides* in the South African dams needed to be investigated.

CHAPTER 6: DIET AND CONDITION OF THE *MICROPTERUS SALMOIDES* POPULATIONS FROM WRIGGLESWADE AND MANKAZANA DAMS

6.1 Introduction

Largemouth bass *Micropterus salmoides* growth is linked to a number of interacting abiotic and biotic variables (Paukert & Willis, 2004). Influential abiotic variables include total alkalinity, chlorophyll a, conductivity, and mean depth encompassing productivity (Crawford et al., 2002; Paukert & Willis, 2004). In addition latitude, which is temperature linked (Weyl & Hecht, 1999; Neal & Noble, 2006; Britton et al., 2010a), and localized factors such as weather, water level, and aquatic macrophyte biomass (Crawford et al., 2002) are also highly influential. The biotic variables influencing growth and the production of large fish include biological factors driving population dynamics such as longevity and mortality, and the presence and abundance of prey species and habitat (Crawford et al., 2002; Paukert & Willis, 2004). The previous chapters explored the age and growth of two South African *M. salmoides* populations, and the well documented link of growth with temperature. To contribute to understanding the growth and ecology of *M. salmoides*, this chapter focuses on the differences in growth and condition of two temperate South African populations, which will be assessed with respect to the availability and abundance of prey species and the potential behavioural changes in *M. salmoides* feeding strategy.

The success of a predatory population may be driven by prey availability and size (Yako et al., 2000). Predators may consume a variety of prey items, and *M. salmoides* in particular are known for their trophic plasticity (Takamura, 2007; Britton et al., 2010b; Almeida et al., 2012). Optimal growth is determined by the ability of a species to consume key or preferred prey, that provide the highest nutritional gain (Yako et al., 2000). It is known that resource utilisation is related to body size (Werner & Gilliam, 1984) and that *M. salmoides* undergo an ontogenetic shift from zooplankton and insects to a fish dominated diet at a population dependent size resulting in increased growth and condition (Phillips et al., 1995; Olson, 1996; Garcia-Berthou, 2002). It is therefore hypothesised that *M. salmoides* that have had access to

the most appropriate prey species throughout their lives would be in better condition, and growth would be superior to that of a population in which prey availability and abundance is limiting. The situation is further complicated however by predator and prey behaviour and their interactions with structural complexity.

As *M. salmoides* are visual predators, foraging strategy and success is influenced by water clarity and structural complexity in which prey may take refuge (Howick & O'Brien, 1983; Savino & Stein, 1989; McMahon & Holanov, 1995; VanLandeghem et al., 2011; Gardiner & Motta, 2012). For example in clear water *M. salmoides* conserve energy by ambushing prey (Gardiner & Motta, 2012), while in turbid environments the energetically more costly cruising strategy may be more successful (Howick & O'Brien, 1983; McMahon & Holanov, 1995; VanLandeghem et al., 2011). Since the two dams show contrasting turbidities, it is hypothesised that the *M. salmoides* in Mankazana, a clear dam with turbidities lower than 20 NTUs, will use the ambush strategy to successfully capture prey so resulting in superior condition and growth compared to Wiggleswade's population, which may have to adopt the cruising strategy as turbidities are predominantly higher than 20 NTUs (Chapter 2). This hypothesis is however interrelated with the suitability of available prey.

In order to test these hypotheses *M. salmoides* diet was assessed using stomach content analyses seasonally in Wiggleswade and Mankazana Dams. The objectives were to determine if and when the ontogenetic shift in diet occurred in the two dams and if diet changed seasonally. In addition, the diet and condition of *M. salmoides* in the two dams was compared to determine the suitability of the prey available and the potential implications of the most likely foraging strategy used.

6.2 Methods

6.2.1 Diet with fish length and season

Fish were sampled from Wiggleswade Dam between March 2010 and March 2012, and from Mankazana Dam from February 2011 to March 2012. All *M. salmoides* were measured to the

nearest millimetre fork length (FL), weighed to the nearest gram, dissected and their stomachs examined for the presence or absence of food items. Depending on the level of digestion, fish remains were identified to species level while invertebrates were identified to family level. Prey items were then classified according to the following groups: teleosts, Potamonautid crabs *Potamonautes sidneyi*, terrestrial insects, aquatic insects and zooplankton. All organisms were counted with the exception of zooplankton, which were classified as present (1) or absent (0). The stomach contents were assessed in accordance with Hyslop (1980) as the prey abundance (%N): the number of individual prey items as a proportion of all prey items, and the frequency of occurrence (%F): the number of stomachs containing a specific prey item as a percentage of all stomachs sampled.

An ontogenetic shift in *M. salmoides* diet has been reported at both large (>200 mm) (Hickley et al., 1994; Weyl & Hecht, 1999; Weyl & Lewis, 2006) and small (<100 mm) (Phillips et al., 1995; Godinho et al., 1997; Huskey & Turingan, 2001; Garcia-Berthou, 2002; Wasserman et al., 2011) size classes depending on the biotic and abiotic environment. In order to identify any ontogenetic shifts in diet the samples from both dams were divided into length classes: <100, 100-150, 150-200, 200-250, 250-300, 300-400, >400 mm FL, compared graphically and using contingency table analysis and chi squared tests.

In order to identify seasonal trends in feeding, stomach content data from both dams were grouped into the austral four seasons: Spring (October – December), Summer (January – March), Autumn (April – June) and Winter (July – September), and the dependence of prey occurrence on season tested using contingency table analysis and chi squared tests. In addition the average number of prey per fish in the main prey categories: teleosts, *P. sidneyi* and invertebrates were plotted by season to identify any differences in prey abundance.

The average abundance (N) of the common prey items eaten by the *M. salmoides* after the ontogenetic shift (>200 mm FL) were compared between dams using *t*-tests assuming unequal variance. In order to understand the nutritional value with respect to weight of the different prey species available per dam an estimate of the average size of the teleost and *P. sidneyi* prey was needed. Of the teleost and *P. sidneyi* prey items found in stomachs, the less

digested individuals were measured to mm FL (common carp *Cyprinus carpio*, *M. salmoides*, estuarine round herring *Gilchristella aestuaria*), TL (Mozambique tilapia *Oreochromis mossambicus*) or carapace width (crab *Potamonautes sidneyi*) where possible. Averages of these lengths were then taken for each species and the associated weight estimated using length-weight relationships obtained from the literature

(*C. carpio* $w(g) = 0.000053 \times FL(mm)^{2.829}$ (Winker et al., 2011);

O. mossambicus $w(g) = 0.000021 \times TL(mm)^{2.984}$ (Weyl & Hecht, 1998);

G. aestuaria $w(g) = 0.0000061 \times SL(mm)^{3.182}$ (Harrison, 2001); *M. salmoides* see Figure 6.5). Since the same species of Potamonautid crab *P. sidneyi* was found in both dams, only average carapace widths were recorded. For both populations any conspecific prey lengths were converted to weight using the length-weight equations estimated when comparing fish condition.

6.2.2 Condition

Fish condition was quantified firstly using the length-weight relationship of the form $W = aL^b$ where W is weight in grams and L is length as mm FL. These length-weight relationships were then linearly transformed and compared using an analysis of covariance (ANCOVA) test. Secondly the relative condition factor $Kn = \frac{W}{W'}$ (Le Cren, 1951) was calculated where W is weight in grams and $W' = aL^b$, the length specific expected weight calculated from the grouped length-weight data from both populations under study. This relative condition factor displays fish condition around the value of one, whereby values greater than one indicate fish of a better than expected condition, while those with a condition factor of less than one indicate fish of a poorer condition than expected.

6.3 Results

In total 562 and 288 *M. salmoides* stomachs were examined from Wriggleswade and Mankazana Dams respectively. Of those stomachs a number of prey groups were found in both Wriggleswade and Mankazana Dams, which are summarised in Table 6.1. In addition 17

artificial lures were found in a total of 12 stomachs in Wriggleswade Dam, which were excluded from further analysis.

Table 6.1: The number (N), relative abundance (%N) and frequency of occurrence (%F) of prey items found in *Micropterus salmoides* stomachs from Wriggleswade and Mankazana Dams. Figures in bold are the totals for each prey category.

Prey	Wriggleswade			Mankazana		
	N	%N	%F	N	%N	%F
Teleostei	294	62.8	21.2	139	23.1	25.3
<i>M. salmoides</i>	17	3.6	2.7	96	15.9	15.3
<i>G. aestuaria</i>	267	57.1	17.6	-	-	-
<i>C. carpio</i>	10	2.1	1.2	-	-	-
<i>G. callidus</i>	1	0.2	0.2	3	0.5	1.0
<i>O. mossambicus</i>	-	-	-	40	6.7	9.3
Fish remains	54	11.5	9.6	11	1.8	3.8
Decapoda						
<i>P. sidneyi</i>	33	7.1	4.1	19	3.2	3.9
Other	4	0.9	0.4	-	-	-
Frog	2	0.4	0.2	-	-	-
Snail	1	0.2	0.2	-	-	-
Rodent	1	0.2	0.2	-	-	-
Insecta (terrestrial)	47	10.0	1.9	375	62.4	24.3
Formicidae (flying ants)	44	9.4	0.5	54	8.9	3.4
Anisoptera adults (dragonflies)	2	0.4	0.4	165	27.5	9.3
Zygoptera adults (damselflies)	1	0.2	0.2	109	18.1	7.9
Insecta (aquatic)	10	2.1	0.7	36	5.9	3.1
Anisoptera larvae (dragonflies)	-	-	-	15	2.5	4.9
Zygoptera larvae (damselflies)	-	-	-	32	5.3	2.1
Coleoptera (beetles)	9	1.9	0.5	-	-	-
Corixidae (river boatmen)	1	0.2	0.2	27	4.5	1.7
Gerridae (pond skaters)	-	-	-	1	0.2	0.3
Notonectidae (back swimmers)	-	-	-	8	1.3	1.4
Insect remains	15	3.2	2.7	25	4.2	8.7
Zooplankton	-	-	-	28	4.7	9.7
Artificial lures	17	3.6	2.1	-	-	-

6.3.1 Ontogenetic shift

In Wriggleswade Dam the diet of *M. salmoides* showed an increase in fish and *P. sidneyi* with increasing length, while invertebrate prey was present at low levels throughout size classes (Figure 6.1). The occurrence of prey contents in stomachs (F) was dependent on size class (contingency table 7 size classes x 4 prey categories; $\chi^2 = 46.6$, d.f. = 18, $P = 0.00$), with the first fish (*G. aestuaria*) recorded in the stomach contents of a 92 mm FL *M. salmoides*.

Alternatively in Mankazana Dam, *M. salmoides* showed a distinct shift from zooplankton and insect prey to a more fish based diet with the first fish (*O. mossambicus*) recorded in the stomach contents of a 152 mm FL fish (Figure 6.1), and the occurrence of prey contents in stomachs (F) was dependent on size class (contingency table 7 size classes x 5 prey categories; $\chi^2 = 83.7$, d.f. = 24, $P = 0.00$).

In Wriggleswade the *M. salmoides* diet was dominated by the teleost *G. aestuaria* both in frequency of occurrence (%F) and in prey abundance (%N) (Figure 6.1, Figure 6.2). In Mankazana teleost prey occurred in a large proportion of stomachs but invertebrates were the most abundant prey items utilised (Figure 6.1, Figure 6.2). The most abundant teleost prey in Mankazana were conspecifics and *O. mossambicus*. Terrestrial insects (mainly Odonates) were the most abundant prey item altogether. In addition, both populations showed an increase in the occurrence of *P. sidneyi* in the stomach contents of larger individuals (Figure 6.1, Figure 6.2).

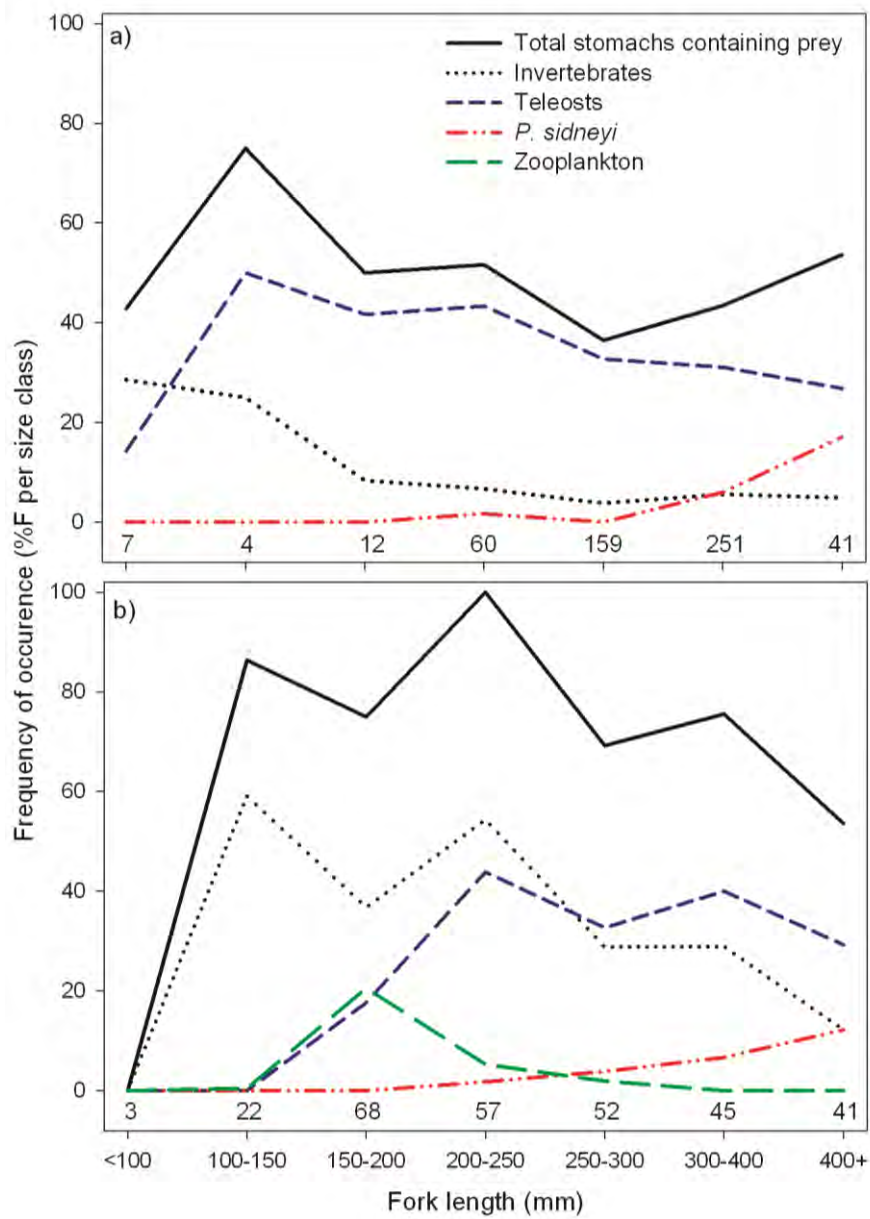


Figure 6.1: The frequency of occurrence (%F) of prey items from stomachs of *Micropterus salmoides* of different size classes sampled from (a) Wriggleswade and (b) Mankazana Dams. The number of stomachs per length class are given below the figures.

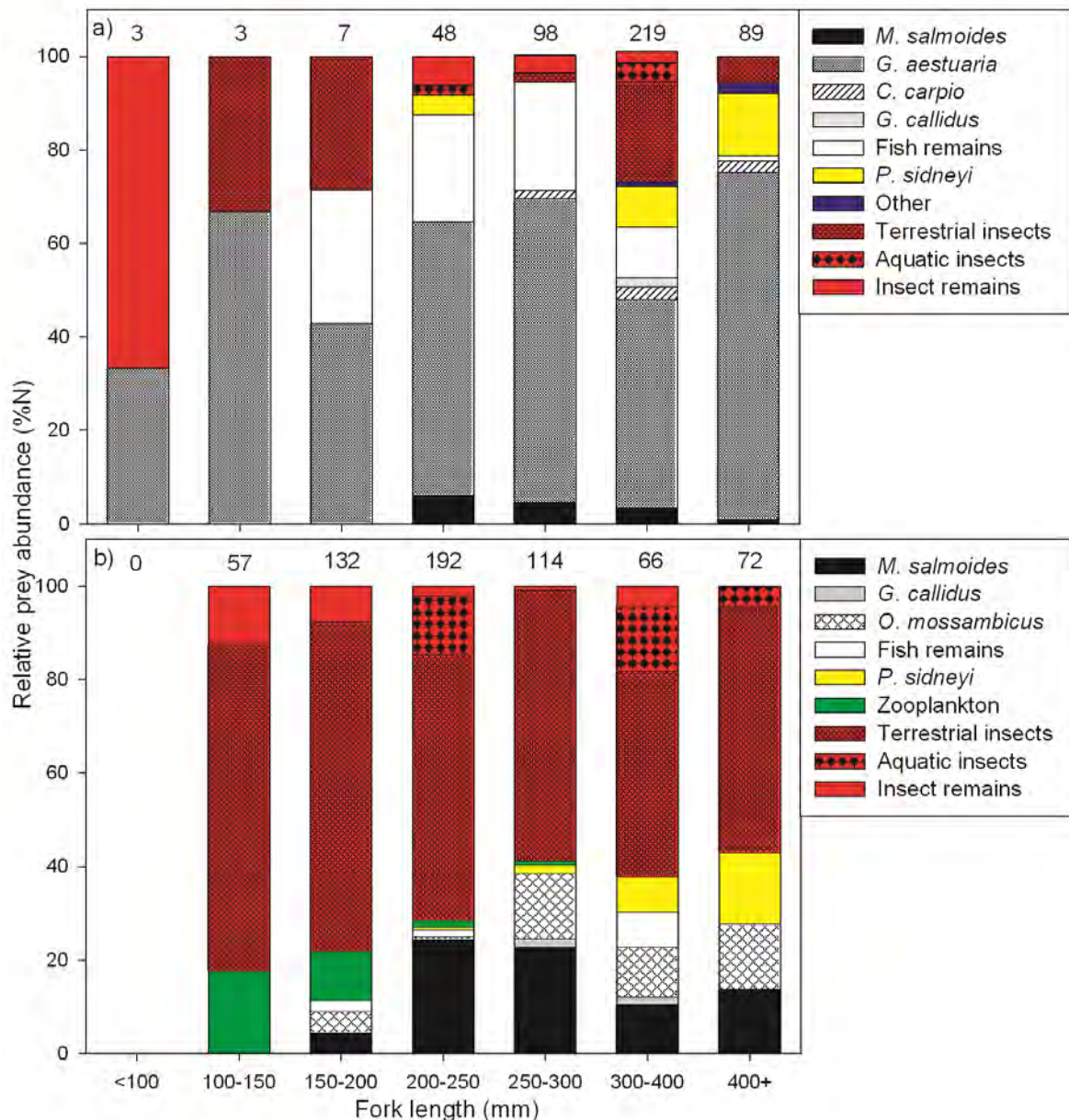


Figure 6.2: The relative abundance (%N) of prey items found in stomachs of different size classes of *Micropterus salmoides* from (a) Wriggleswade and (b) Mankazana Dams. Sample sizes of the total prey items sampled per size class are given above each bar.

6.3.2 Seasonal changes in diet

In Wriggleswade and Mankazana the presence of prey in stomachs was dependent on season (contingency table 4 seasons x 2 (empty or not empty) categories; Wriggleswade $\chi^2 = 31.6$, d.f. = 3, $P = 0.00$; Mankazana $\chi^2 = 20.3$, d.f. = 3, $P = 0.00$), with Wriggleswade's *M. salmoides* having the highest proportion of empty stomachs in spring, and Mankazana's fish having high numbers of empty stomachs in autumn and winter (Table 6.2). The average prey

abundance (N) was also dependent on season for both dams (contingency table 4 prey categories x 4 seasons; Wriggleswade $\chi^2 = 79.5$, d.f. = 9, $P = 0.00$; Mankazana $\chi^2 = 97.1$, d.f. = 9, $P = 0.00$). In Wriggleswade Dam teleost prey was important throughout the year but the highest mean number of prey per fish was recorded in winter (Figure 6.3). *Potamonautes sidneyi* abundance in the diet was highest in autumn and winter. Alternatively in Mankazana Dam invertebrates followed by teleosts were the most important prey items throughout the year, and *P. sidneyi* were only recorded in the stomach contents in spring and summer (Figure 6.3). Mean number of invertebrate and teleost prey per stomach was highest in spring and lowest in autumn and winter.

Table 6.2: The percentage of *Micropterus salmoides* with empty stomachs per season in Wriggleswade and Mankazana Dams, Eastern Cape, South Africa.

Dam	% Empty			
	Spring	Summer	Autumn	Winter
Wriggleswade	70.2	42.9	57.3	61.7
Mankazana	16.4	29.5	51.6	45.2

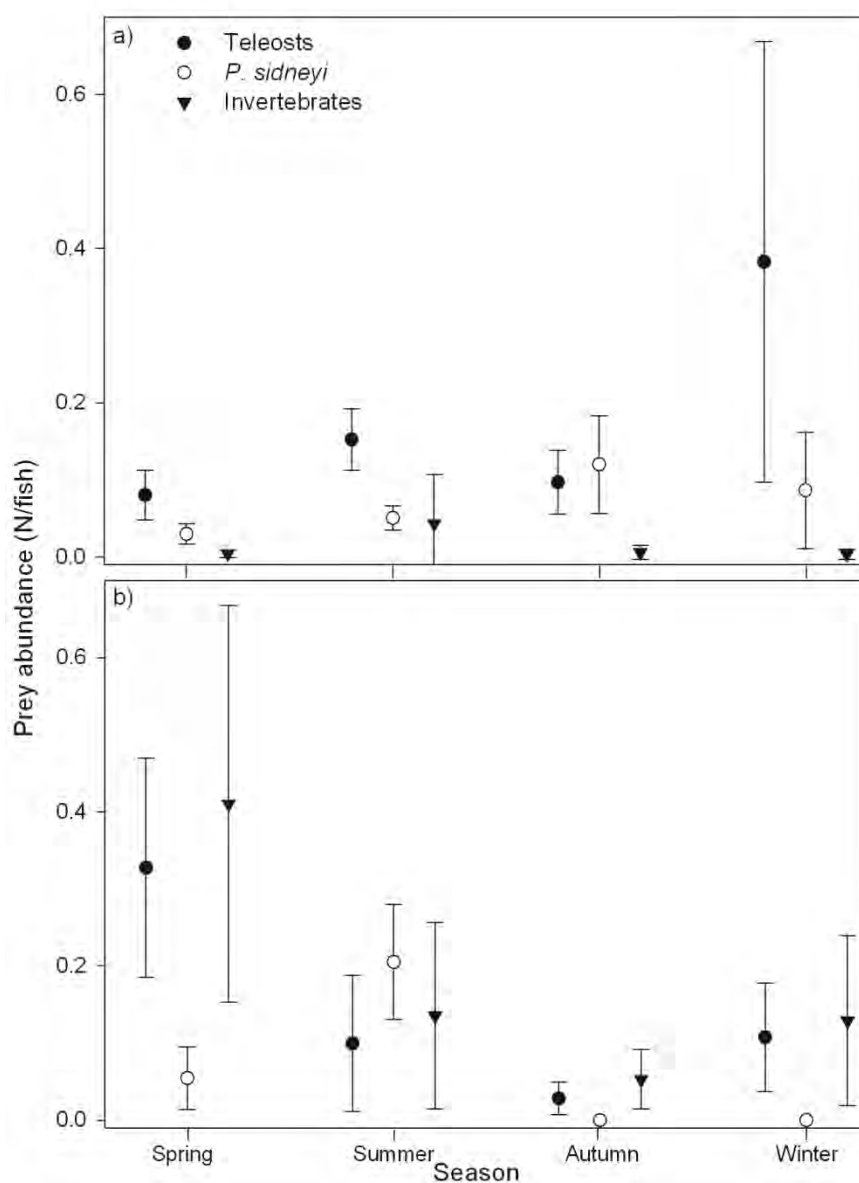


Figure 6.3: The average numbers $\pm$ SE of prey per stomach for the teleost, *Potamonautes sidneyi* and invertebrate prey per season found in *Micropterus salmoides* stomachs in (a) Wriggleswade and (b) Mankazana Dams. Wriggleswade: n = 66 in spring, 259 in summer, 41 in autumn, 137 in winter; Mankazana: n = 277 in spring, 151 in summer, 40 in autumn, and 154 prey items in winter.

6.3.3 Diet comparison between dams

For both populations of *M. salmoides* the ontogenetic shift in diet occurred at around 200 mm FL. Fish in Wriggleswade Dam fed on invertebrates and teleost prey from a small size, while the *M. salmoides* of Mankazana fed on zooplankton and invertebrates at small sizes (100-150 mm FL), and only utilised teleost prey at larger sizes (>150 mm FL) (Figure 6.1). For *M.*

salmoides larger than 200 mm FL, total numbers of prey per stomach (prey abundance N) were higher in Mankazana than in Wriggleswade for all prey categories, and in particular Mankazana's fish were significantly more cannibalistic than Wriggleswade's (one tailed t -test, $t = 4.35$, d.f. = 197, $P = 0.00$), and consumed significantly more terrestrial and aquatic insects (one tailed t -tests; terrestrial insects: $t = 4.48$, d.f. = 1290, $P = 0.00$; aquatic insects: $t = 1.85$, d.f. = 629, $P = 0.03$) (Figure 6.4). In addition a higher proportion of Wriggleswade's *M. salmoides* had empty stomachs (56%) compared to Mankazana's *M. salmoides* (37%) and the presence of prey items in stomachs was dependent on dam (contingency table 2 dams x 2 (empty or not empty) categories; $\chi^2 = 27.2$, d.f. = 1, $P = 0.00$).

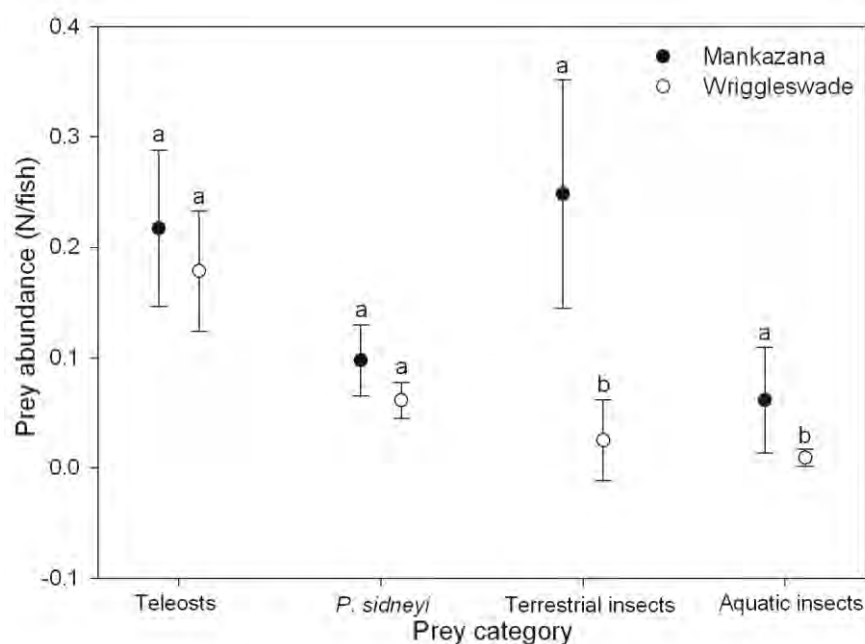


Figure 6.4: The average number of prey items $\pm$ SE for Wriggleswade and Mankazana Dams' *Micropterus salmoides* of more than 200 mm FL. The prey categories common to both dams: teleosts, *Potamonautes sidneyi*, terrestrial and aquatic insects were compared, those with significant differences between dams were labelled with different letters (a, b), those not significantly different were labelled with the same letter (a) (n = 538 stomachs in Wriggleswade Dam and 195 stomachs in Mankazana Dam).

Although the average numbers of teleost prey eaten by the *M. salmoides* in Wriggleswade and Mankazana Dams did not differ significantly (one tailed t -test, $t = 0.39$, d.f. = 1750, $P = 0.35$), the dominant teleost prey in Wriggleswade Dam *G. aestuaria* were smaller and weighed less than both common teleost prey items in Mankazana Dam (Table 6.3). In Wriggleswade the most important teleost prey (weight of prey per predator) were the *G.*

aestuaria and *C. carpio*, which were of similar importance to the *O. mossambicus* in Mankazana Dam (Table 6.3). However with respect to the average number and weight of prey items per predator stomach, conspecifics in Mankazana Dam were the most important prey compared to all other teleost prey in both dams. Although no *P. sidneyi* found in stomachs were measured in Mankazana Dam, similar proportions of *P. sidneyi* were found in both dams (one tailed *t*-test, $t = 1.00$, d.f. = 300, $P = 0.16$) (Figure 6.4).

Table 6.3: The average numbers per stomach, average lengths (mm) and their calculated weights (g), and the total weight per predator of the most common teleost prey found in stomachs of *Micropterus salmoides* from Wiggleswade and Mankazana Dams.

Dam	Prey species	Number/ stomach	Length (mm) ± SE	Weight (g)	Relative prey weight
Wiggleswade	<i>M. salmoides</i>	0.030	67.6 ± 6.57	4.18	0.13
	<i>C. carpio</i>	0.018	115 ± 55	35.81	0.64
	<i>G. aestuaria</i>	0.475	50 ± 1.44	1.55	0.74
	Total				1.51
Mankazana	<i>M. salmoides</i>	0.333	93.33 ± 33.33	11.59	3.86
	<i>O. mossambicus</i>	0.139	56.20 ± 22.24	3.49	0.48
	Total				4.34

6.3.4 Condition

Although larger specimens of *M. salmoides* were sampled from Wiggleswade Dam, the fish of Mankazana weighed more in relation to their length compared to the fish of Wiggleswade (Figure 6.5). This difference was significant with respect to the intercept (ANCOVA, $t = 10.53$, $P = 0.00$) and slope (ANCOVA, $t = 11.63$, $P = 0.00$) of the linearly transformed length-weight relationships.

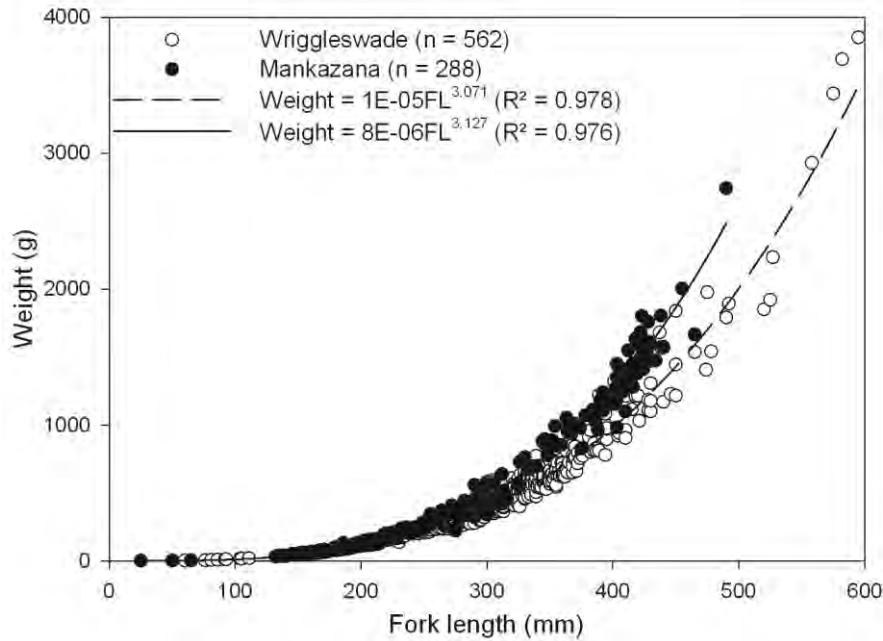


Figure 6.5: The length-weight relationships of the *Micropterus salmoides* populations of Wriggleswade and Mankazana Dams, Eastern Cape, South Africa.

In accordance with the length-weight relationships of the two populations, the relative condition (K_n) calculated using the grouped length-weight equation $W = 1E-05L^{3.049}$ shows the majority of the *M. salmoides* from Mankazana Dam had a higher relative condition than those from Wriggleswade Dam (Figure 6.6).

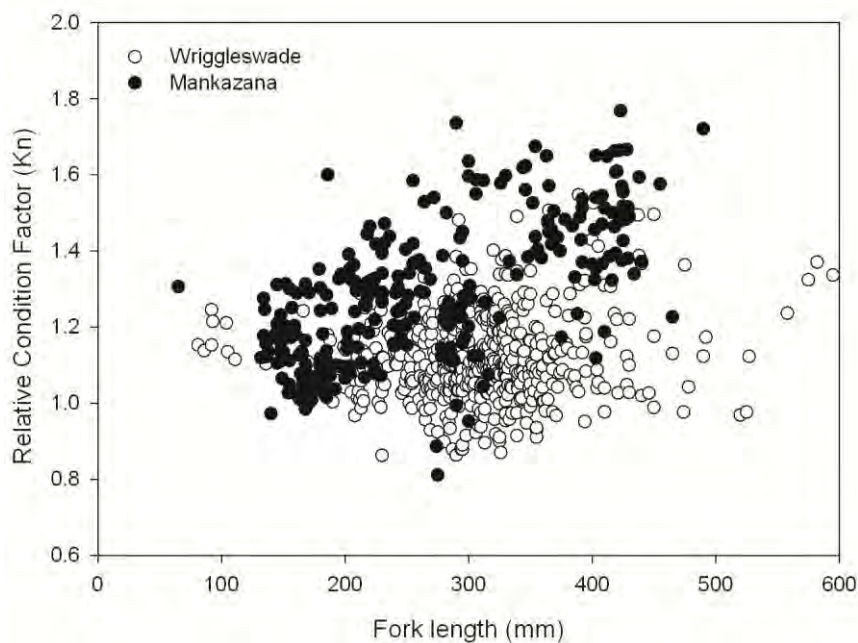


Figure 6.6: The relative condition factor for the *Micropterus salmoides* from Wriggleswade and Mankazana Dams.

6.4 Discussion

Understanding the diet and feeding behaviour of fishes is an important component of biological studies. Studies conducted elsewhere in Africa have shown that *M. salmoides* prey on all food items available in both riverine (Weyl & Lewis, 2006; Weyl et al., 2010; Wasserman et al., 2011) and lentic environments (Hickley et al., 1994; Weyl & Hecht, 1999; Britton et al., 2010a). The focus of this chapter was to assess the diet and feeding of *M. salmoides* in two temperate South African still water populations.

A shift in the diet of a species with size is a common phenomenon which reduces intraspecific competition within a population and the identification and understanding of this ontogenetic shift may be valuable when looking at nutrition and condition (Phillips et al., 1995; Olson, 1996). The *M. salmoides* of Wiggleswade and Mankazana Dams shifted from an invertebrate based diet to a more fish based diet at between 100-200 mm FL. In Mankazana Dam the ontogenetic shift was distinct and the diet dominated by insect and zooplankton prey shifted to fish and *P. sidneyi* at 150-200 mm FL, whereas the Wiggleswade population made use of the *G. aestuaria* at small sizes and the shift was a gradual decrease of invertebrates and an increase in *P. sidneyi*.

In Mankazana Dam the shift to a teleost based diet was at a similar length as that determined for the two southern African populations, Lake Chicamba and the Kowie Weir (Weyl & Hecht, 1999; Weyl & Lewis, 2006). After the ontogenetic shift, the diet of these populations however was strongly dominated by teleost prey when they were available. This differed from Mankazana's population which made use of insect prey throughout their length range. This is similar to findings by Wasserman et al. (2011) who showed that in the Kowie Weir *M. salmoides* diet was dominated by insects when fish prey were not available. The high incidence of cannibalism in Mankazana may also indicate a lack of alternative prey though the teleost prey *O. mossambicus* were available (Chapter 2).

This utilisation of large numbers of invertebrates may be as a result of the teleost prey morphology and behaviour and not a lack of this category altogether. *Oreochromis mossambicus* is a deep bodied cichlid with spiny rays on both dorsal and anal fins (Skelton, 2001) similar in body form to the sunfish family, a common prey of *M. salmoides* in their native range (Howick & O'Brien, 1983). This body form may result in an increased cost of prey capture and handling due to the possibility of injury during ingestion (Howick & O'Brien, 1983). In addition, the prey size of *M. salmoides* is gape dependent, so creating a size refuge (Savino & Stein, 1989; Garcia-Berthou, 2002; Nowlin et al., 2006) which may protect a large proportion of the rapidly growing *O. mossambicus* population that can grow to 200 mm TL within the first year of life (Weyl & Hecht, 1998; Booth & Khumalo, 2009).

Alternatively prey behaviour and the use of structural refuges may influence availability. This was illustrated in Lake Naivasha where *M. salmoides* could not access the available tilapia prey species which moved to macrophyte-covered littoral areas by day (Hickley et al., 1994). Similarly in Portugal a decrease in the abundance of submerged vegetation was reflected in an increase in fish prey in *M. salmoides* diet (Godinho et al., 1997). Mankazana is a shallow dam dominated by macrophyte-covered margins (Chapter 2) in which *O. mossambicus* may find refuge from predation (Savino & Stein, 1989).

Wriggleswade's *M. salmoides* population, on the other hand, made use of the teleost *G. aestuaria* throughout its life, with the first occurrence of this prey item in the stomach of a 92 mm FL fish. In Wriggleswade this small pelagic *G. aestuaria* is the dominant prey item making up more than 35% of the prey in all size classes of *M. salmoides* (Figure 6.2). Where present this shoaling species occurs in high abundances (Whitfield, 1998) and was sampled in all seine net pulls of Wriggleswade Dam (Chapter 2). This early ontogenetic shift to teleost prey may be attributed to a low relative invertebrate and zooplankton abundance in Wriggleswade, prey items on which juvenile *M. salmoides* would usually feed, however no data are available to support this assumption. The use of the most common prey species from a small size is not surprising as this predator has been known to adapt rapidly to prey availability (Hickley et al., 1994). Similarly an early shift to the most abundant prey available was documented in South Korea (Jang et al., 2006) where *M. salmoides* were found to prey on the most common native Cyprinidae and Gobiidae species from around 100 mm TL.

Besides the abundant *G. aestuaria*, the most common teleosts after *M. salmoides* conspecifics recorded in Wriggleswade using gill and fyke nets were *L. aeneus* and *C. carpio* (Chapter 2). *Cyprinus carpio* were found in *M. salmoides* diet in small numbers, however *L. aeneus* were never recorded in the stomach contents. As has been stated by Garcia-Berthou (2002), the prevalence of large specimens (Chapter 2) of both of these species in the population may indicate a high predation pressure on the small size classes of these cyprinids, so resulting in fast growth until the size refuge is reached. For example *C. carpio* is a fast growing species that reached 200 mm FL within the first year of growth in a South African dam (Winker et al., 2011). In addition *L. aeneus* migrates upstream to spawn in suitable gravel beds (Skelton, 2001), so potentially only recruit into the dam once they have reached the size refuge between the first and second year of life at around 200 mm FL (Weyl et al., 2009; Richardson et al., 2010; Gerber et al., 2012). These two cyprinids may therefore use the size refuge created by *M. salmoides* gape limit to avoid predation, so leaving the small *G. aestuaria* as the most common teleost food source in this dam.

Despite the differences in dominant prey between the two dams, both populations of *M. salmoides* preyed on the crab species *P. sidneyi* at larger size classes. Crabs are important prey elsewhere in Africa (Weyl & Hecht, 1999; Wasserman et al., 2011) and *M. salmoides* have been documented commonly feeding on large crustaceans such as crayfish where available (Godinho & Ferreira, 1994; Hickley et al., 1994; Huskey & Turingan, 2001; Garcia-Berthou, 2002). The occurrence of crustaceans in the diet may however have been an over representation, as one of the drawbacks of stomach content analysis is non-uniform digestion rates, and in particular hard bodied organisms such as crabs tend to be overestimated due to longer gut passage times (Hyslop, 1980).

Seasonal trends in *M. salmoides* diet have been shown to follow changes in prey abundance (Weyl & Hecht, 1999), and feeding behaviour has been related to abiotic factors such as temperature (Micucci et al., 2003). The presence of prey items in stomachs differed between dams, with Wriggleswade's population having mainly empty stomachs in spring compared to Mankazana's which had high proportions of empty stomachs in autumn and winter (Table 6.2). Since activity and metabolism are dependent on temperature (Johnston & Dunn, 1987; Rypel, 2009), it is expected that a higher proportion of stomachs would be empty in winter

than in summer (Azuma & Motomura, 1998). In addition parental care in spring may result in a decrease in feeding activity (Ridgway & Shuter, 1994; Cooke et al., 2002), so explaining the high proportion of empty stomachs seen in Wriggleswade's population at this time.

Prey ingestion rates of the three main prey categories: teleosts, *P. sidneyi* and invertebrates also differed seasonally in both dams. In Mankazana the average number of teleost prey per stomach remained relatively constant in all seasons, with a peak in spring coinciding with the influx of juvenile *M. salmoides* and *O. mossambicus* which spawn at this time (Chapter 5; Weyl & Hecht, 1998). In addition the importance of insect and crabs decreased in autumn and winter, which is in accordance with a decrease in insect activity or diapause with the onset of cool temperatures (Danks, 2002). Similar trends were observed in Lake Chicamba, Mozambique where Weyl & Hecht (1999) found reduced terrestrial insect and crab abundance in *M. salmoides* stomachs during winter.

In Wriggleswade the average number of insect prey per stomach also decreased in winter, and the numbers of teleosts and *P. sidneyi* increased in autumn and winter. This increase in average numbers of *P. sidneyi* in the diet of *M. salmoides* in Wriggleswade during autumn and winter is unusual. The increase in teleost prey in winter may be as a result of changes in prey behaviour and habitat utilisation. *Gilchristella aestuaria*, the dominant teleost prey in Wriggleswade Dam, are diverse feeders which have been shown to shift from feeding in open water on mainly zooplankton prey in summer, to a benthic insect and insect larvae based diet in the littoral areas in winter (White & Bruton, 1983; Bennett, 1989; Whitfield & Harrison, 1996). This shift inshore may increase their vulnerability to predation by *M. salmoides*, so resulting in increased numbers in the diet during winter. This focus by *M. salmoides* from more pelagic to benthic prey may also contribute to increased crab abundance. How differences in prey abundance between dams influence growth may be indicated by the relative condition.

The relationship of a fish's length to its weight may be expressed as its condition, which is a measure of its wellbeing and incorporates state of sexual maturity and degree of nourishment (Williams, 2000). Since fish from both dams were sampled over a period of a year, states of

sexual maturity were sampled equally and relative condition was taken as a degree of nourishment or long term dietary composition compared between the two populations. This may be described as being a function of prey preferences, availability and ease of capture and handling (Britton et al., 2010a). When comparing the length-weight relationship and relative condition of the *M. salmoides* between the dams it was clear that a large proportion of Mankazana's fish were in better condition than Wriggleswade's fish (Figure 6.5, Figure 6.6). This difference in relative condition may be attributed to the low relative prey weight of the teleost component of the diet in Wriggleswade, which contrasted to that of a much higher weight in Mankazana Dam (Table 6.3). This threefold weight difference in teleost prey was a result of many large conspecifics and *O. mossambicus* preyed upon in Mankazana Dam, which may have been supplemented by the abundant invertebrate prey. In contrast the *M. salmoides* from Wriggleswade Dam made use of many of the small *G. aestuaria*, however less of the larger *C. carpio* and conspecifics, and invertebrate prey were lacking. The lack of abundant suitable prey may therefore be the limiting factor in Wriggleswade Dam which has resulted in the lower relative condition of this *M. salmoides* population.

An alternative or additional explanation may be the ability of *M. salmoides* to vary feeding strategy with changes in light condition and turbidity. At low turbidities and in the presence of structural complexity, *M. salmoides* adopt the ambush strategy to effectively catch close prey without alerting other nearby prey, so allowing them to lie and wait, reducing energy expenditure and enhancing growth rates (Howick & O'Brien, 1983; Savino & Stein, 1989). Alternatively at high turbidities *M. salmoides* prefer to cruise, increasing prey encounter rates and success of capture, as at low light conditions they can detect the prey before the prey can detect them (Howick & O'Brien, 1983; McMahon & Holanov, 1995; VanLandeghem et al., 2011). Mankazana is a clear water dam with turbidities of below 16 NTUs throughout the year, differing from Wriggleswade which is considerably more turbid ranging from 20 to 60 NTUs (Chapter 2). The *M. salmoides* in Mankazana therefore had a more abundant and diverse diet, and may have conserved energy by ambushing prey, so were in better condition than the *M. salmoides* of Wriggleswade which fed predominantly on the small shoaling *G. aestuaria*, and may have had to expend energy by cruising to locate prey. This link however is still speculative and future studies could focus on the changes in feeding strategy at varying turbidities with field observations backed up by laboratory experiments.

Data therefore support both hypotheses set up in the introduction which outlined the effect of prey suitability, abundance and the choice of feeding strategy on the relative condition of the *M. salmoides* populations. Despite these differences in prey species and relative condition factors between the two dams, both populations of *M. salmoides* grew successfully to old ages, which may be attributed to the highly opportunistic nature of this predator, and in both systems it may be argued that all available prey items were being utilised.

CHAPTER 7: HUMAN IMPACTS: MORTALITY AND POST-CAPTURE DISPERSAL OF *MICROPTERUS SALMOIDES* IN WRIGGLESWADE DAM

7.1 Introduction

An overall understanding of a population in an environment requires knowledge of its biology and ecology, as well as how it is influenced by anthropogenic activity (Heino, 1998; Sloman & Wilson, 2006). In North America where largemouth bass *Micropterus salmoides* is an important sport fish, the popularity of competitive angling has increased tremendously since before the 1970s (Schramm et al., 1991a). Initially concern arose for the potential biological impacts of an increase in harvest and exploitation of the resource, which would result in reduced catch rates and depletion of species (Schramm et al., 1991a; Quinn, 1996; Cooke & Schramm, 2007). The growth of competitive angling consequently evolved to the regulated and voluntary ethic of releasing live fish from the mid-1970s (Quinn, 1996) in an attempt to raise catch rates and increase the occurrence of large fish (Clark, 1983; Schramm et al., 1991a; Quinn, 1996). The popularity of tournament angling has been reflected in a continued rise in the number of tournaments, which remain a prevalent use of inland fisheries resources in the western world today (Schramm & Hunt, 2007).

The popularity of *M. salmoides* as a freshwater angling species for competitive catch and release practices, adopted from fisheries in their native range of North America (Quinn, 1996), has been transferred to most of their introduced range (Robbins & MacCrimmon, 1974; Lever, 1996; Quinn, 1996; Quinn & Paukert, 2009; Skelton & Weyl, 2011). In South Africa an estimated 20000 anglers participated in both formal and informal bass fishing activities in 2007 (Leibold & van Zyl, 2008). Wriggleswade Dam is an important *M. salmoides* angling venue in the Eastern Cape Province, and hosts monthly tournaments for three local Bassmasters clubs, biannual provincial team trials, the annual Amatola Bass Classic, and national trials every few years (see Chapter 2). These tournaments are run according to a strict catch and release ethic in which the largest fish over a 300 mm TL

minimum size limit are targeted, weighed alive and released at a common location near the weigh-in site.

This form of competitive angling has raised a new suite of biological concerns by anglers and management agencies (Schramm et al., 1991a; Quinn, 1996). The major concerns are (i) post-release mortality associated with catch and release angling and (ii) implications of the translocation and release of large numbers of tournament caught fish at a single site (Schramm et al., 1991a; Quinn, 1996; Schramm & Hunt, 2007). More specifically, the problems of large scale translocations include alterations in the availability of fish to anglers, increased pressure on local prey resources (Schramm et al., 1991a; Driscoll et al., 2007), increased catch related mortality despite reductions in harvest, and disruption of reproductive success during the spawning season (Quinn, 1996; Cooke et al., 2000; Wilde, 2003; Wilde & Paulson, 2003). There is also concern over the long term viability of an affected fishery due to continual selection for larger fish, which may influence population dynamics and ultimately alter the genetic stock structure (Meals & Miranda, 1994; Wilde, 1998).

According to Wilde (1998) there is much variation in the rates of initial, delayed and total mortality and their consequent impacts associated with tournament angling. Initial mortality refers to those fish brought to the weigh station dead, which is usually caused by severe injury and acute stressors, while delayed mortality defines the deaths that occur due to the cumulative effects of sublethal stressors and fish usually die after being released during a tournament (Kwak & Henry, 1995; Weathers & Newman, 1997; Wilde, 1998). Both initial and delayed mortality encompass total mortality (Wilde, 1998). Tournament associated mortality has been correlated to temperature, fish size, season (i.e. if fish are spawning or not), numbers of anglers, live well holding conditions, handling methods (including time out of water), and overall tournament procedure (Meals & Miranda, 1994; Kwak & Henry, 1995; Weathers & Newman, 1997; Wilde, 1998). Wilde (1998) estimated from a collection of mortality estimates taken from the 1990s that 28.3% of tournament caught *M. salmoides* died. There is also concern that although harvest rates have declined in recent years, if the ratio of tournament caught fish to harvested fish exceeds a certain threshold, tournament mortality could decrease abundance and alter population size structure (Allen et al., 2004). Despite concerns over the causes and magnitude of the mortality associated with competitive angling,

total mortality rates have decreased substantially since 1970 in the USA where *M. salmoides* competitive angling is a mainstream activity (Allen et al., 2008). Tournament mortality is therefore unlikely to cause population declines with the low harvest rates observed in reality (Edwards et al., 2004a; Driscoll et al., 2007; Allen et al., 2008). Notwithstanding the need to mitigate potential sources of mortality during tournaments, it remains necessary to assess mortality in specific water bodies, both as a result of changes in environmental factors (natural mortality) and the utilisation of the resource (fishing mortality).

In many water bodies where competitive tournaments are a major activity, *M. salmoides* are displaced and subsequently released at a common weigh-in site, which raises the question: what are their movements from there? Movement behaviour of *M. salmoides* has received considerable research attention through the use of radio telemetry (Winter, 1977; Stang et al., 1996; Ahrenstorff et al., 2009), acoustic telemetry (Ridgeway & Shuter, 1996; Hanson et al., 2007; Hanson et al., 2008a, b), and conventional external tags (Lewis & Flickinger, 1967; Richardson-Heft et al., 2000). From these studies it is clear that most *M. salmoides* establish a home range area from which localised movements are made (Parker & Hasler, 1959; Lewis & Flickinger, 1967; Winter, 1977; Ahrenstorff et al., 2009). It would therefore be assumed that fish transported *en masse* during tournaments and released would make their way back to their home range and not concentrate around release sites. Despite this hypothesis, contrasting results from displacement studies indicate that in some water bodies the fish disperse and/or return to their capture sites (Winter, 1977; Lewis & Flickinger, 1967), while in others fish accumulate near release sites (Lantz & Carver, 1975; Stang et al., 1996; Ridgeway, 2002; Wilde & Paulson, 2003). It has also been observed that within different *M. salmoides* populations, movement behaviour is variable, with some fish moving great distances while others remain fairly sedentary (Stang et al., 1996; Richardson-Heft et al., 2000; Hanson et al., 2007).

As a result of the documented variation in mortality rates and dispersal of displaced tournament-caught fish, there is little empirical data to provide management advice to sustain the intensive catch and release tournament practices on Wiggleswade Dam. In addition, human use is a major influential factor for *M. salmoides* populations and this impact needs to be understood. Consequently, the aim of this study was to investigate these problems using

tournament catch data and a tag-recapture study on the *M. salmoides* population at this important tournament angling venue. To do this, three null hypotheses were tested: 1) the mortality rate of the *M. salmoides* population in Wriggleswade Dam is comparable to that of other populations in Africa and elsewhere, 2) tournament caught *M. salmoides* do not congregate around the release site and disperse to other areas of the dam after release, and 3) dispersal distance is not related to time at liberty or *M. salmoides* size.

7.2 Materials and methods

7.2.1 Mortality

Catch data was acquired from 2004 to 2012 from monthly club tournaments of three local clubs, and biannual South African Bass Anglers Association (SABAA) organised provincial and national tournaments. Data were also available from the annual “open” big fish classic tournaments for the years 2010, 2011 and 2012. All tournaments were two day events of 6 – 8 hours each day, except the national tournaments which were three days. At SABAA events anglers were restricted to a daily bag limit of five fish per person per day, and a size limit of over 300 mm TL. At the weigh-in the catch was awarded one point per live fish plus the weight of the fish in kilograms. For example if a fish of 2.5 kg was weighed in alive the angler was awarded $2.5 \text{ (weight)} + 1 \text{ (for the fish)} = 3.5$ points, however if this fish was dead only 2.5 points would have been awarded. As a result of such penalties all fish were kept in live wells (aerated compartments on the boat) prior to being weighed, and released after weigh-in.

Tournament data were kept by the appointed weigh master of the event, and the available data included numbers and individual or total weights of the fish caught per angler per tournament day, as well as numbers of dead fish brought in. These data provided estimates of the total number of fish caught per year, and initial immediate mortality (taken as the actual number of dead fish directly attributed to angling). During some tournaments fish were weighed individually. In these cases the individual weights of fish from the catch data could be converted to FL using the length-weight equation calculated in Chapter 6 and length frequency distributions were constructed for each year of data collection. The length frequency data were then converted to age frequency using a length–age key (Butterworth et

al., 1989) constructed from ages estimated using sectioned sagittal otoliths (see Chapter 3). This was used to calculate the instantaneous rate of total annual mortality (Z) using catch curve analysis (Ricker, 1975) and the natural logarithm of the length to age frequency distributions. In addition the annual average percentage mortality loss of the population was estimated using the equation $mortality(\%) = 100(1 - \exp[-Z])$ where Z is the instantaneous rate of total annual mortality (King, 1995).

To validate the accuracy of converting weight data to lengths before the construction of catch curves, all fish weighed in during the 2010 and 2011 Amatola Bass Classics were measured. A catch curve was then constructed from the age-length data and compared to the histograms constructed from the weight data. It must be noted however, that for the Classics the bag limit was three fish, differing from the other tournaments in which it was five fish.

In addition to show that the mortality based on tournament data does not differ from that based on standardised sampling, a catch curve was generated using the length frequency data collected from the gill and fyke nets. The Z generated from this dataset was then compared to those based on tournament data.

7.2.2 Dispersal

As part of the age validation study outlined in Chapter 4, *M. salmoides* from Wriggleswade Dam were chemically marked by injection with oxytetracycline hydrochloride and tagged externally. Data collected from the same fish were used for the dispersal experiment in this chapter.

Fish were tagged during six fishing competitions: five were monthly local club competitions involving less than 30 anglers per event, and one was a regional tournament in which 40 anglers participated. All fish were brought to the weigh station, situated at the SAC clubhouse opposite the dam wall in the main basin of the dam, and after being weighed were placed in a 100 l holding tank with aeration, prior to being tagged.

Fish to be tagged were placed in a wet measuring board with their heads covered with a wet cloth (Figure 7.1). All fish were measured to the nearest millimetre FL and TL. Tags inscribed with a unique alphanumeric code, email address and cell phone number were inserted with a stainless steel applicator (for dart tags) or pistol grip tag gun (for T-bar anchor tags) into the dorsal musculature and anchored between two inter-neural spines

(pterygiophores). Small fish of <300 mm FL were tagged with T-bar anchor (model TBA-2) tags and larger individuals of >300 mm FL were tagged with Hallprint (Victor Harbour, South Australia) plastic dart (model PDL) tags. Only fish that were swimming strongly were tagged, and all tagged fish were released by hand at the weigh station jetty. The whole tagging procedure took less than a minute per fish and mortalities were recorded around the release site after tagging.



Figure 7.1: A *Micropterus salmoides* being tagged at Wriggleswade Dam using a Hallprint plastic dart tag and stainless steel applicator.

The large competitions were monitored personally to gather information on tagged fish recaptures, and any other information on recaptures was obtained from recreational fishers or by other members of the public via e-mail or cell message. Although no reward was offered for the information, non-reporting was assumed to be low due to the lack of subsistence fishing on the dam, and the good relationship between scientists and recreational anglers. Information collected on recapture included recapture date, locality, fish length (and/or weight), whether the fish was released or not and where. A map of the dam with a 160 m grid superimposed on it was used to help identify tagged fish capture locations, and most competitive bass boats are fitted with GPS equipment and localities were often available. Recapture rates were calculated as the total number of recaptured individuals as a percentage of individuals tagged and released. Multiple recaptures of the same individual fish were treated separately and did not contribute to this value.

In order to test if dispersal distance increased with time at liberty or with fish length, the minimum distance moved was measured using the most direct path from the release site to the recapture site (Google Earth, 2012). A spearman rank correlation which measures the strength of association between two ranked variables was used to investigate the relationship between distance moved and (i) days at liberty, and (ii) fish length. In addition times at liberty were grouped and a non-parametric Kruskal-Wallis test was used to identify any differences in distance moved with time at liberty. The length at 50% maturity was 259 mm FL for the *M. salmoides* in Wiggleswade Dam (Chapter 5), and the smallest fish tagged was 213 mm FL, therefore the dispersal distance of mature and immature fish could not be compared.

Since the main aim of this aspect of the study was to assess dispersal and not to obtain a population estimate, tag retention was not quantified. However, Renfro et al.(1995) found the mortality of *M. salmoides* tagged with two different sizes of dart tags was not significantly higher than that of fish not tagged, and reported a 98% tag retention rate for large (81 mm) dart tags and 78% for smaller (69 mm) dart tags in *M. salmoides* during a 15 month study. Conversely anchor tags seem to have more variable retention rates after long time periods. Hartman & Janney (2006) indicated a 94% retention rate after 31 days, which decreased to 43% after 403 days, while Gurtin et al. (1999) reported retention rates of greater than 85% for up to 512 days after tagging *M. salmoides* with anchor tags. Gurtin et al. (1999) also found that anchor tags had no significant influence on the condition or growth of the fish. Tag retention for the time period of this study was assumed to be high for both T-bar anchor tags and plastic dart tags.

7.3 Results

7.3.1 Mortality

Available data for the total number of fish weighed during the competitions ranged from 241 in 2004 to 2159 in 2005 with an annual average of 1231 fish (Table 7.1). Initial mortality i.e. fish that were weighed in dead were very low, ranging from 21 in 2004 to two in 2010 with an average of 1.4% initial mortality per year (Table 7.1).

Table 7.1: The tournament details, total number of *Micropterus salmoides* weighed and those reported as dead to the weigh station for the period of 2004 to 2012 during competitions for which data were available, held at Wiggleswade Dam in the Eastern Cape of South Africa.

Year	Tournaments (N)	Angler days	Total fish weighed (N)	Dead fish reported (N)	Initial mortality (%)
2004	5	150	241	21	8.71
2005	18	1084	2159	9	0.42
2006	19	1086	1936	5	0.26
2007	9	736	1466	14	0.95
2008	6	368	762	5	0.66
2009	9	356	611	3	0.49
2010	5	604	693	2	0.29
2011	7	896	1436	13	0.91
2012	10	1148	1778	5	0.28

Age frequency histograms and the corresponding linearised catch curves for angling tournament data between 2004 and 2012 are illustrated in Figure 7.2. Limited data were available for individual fish weights in 2008 and this year was therefore left out of the catch curve analysis. The average Z value for all years in which data were available was 0.43 yr^{-1} , and the average mortality was estimated to result in a loss of $35.2\% \pm 0.9\%$ (SE) of the population annually.

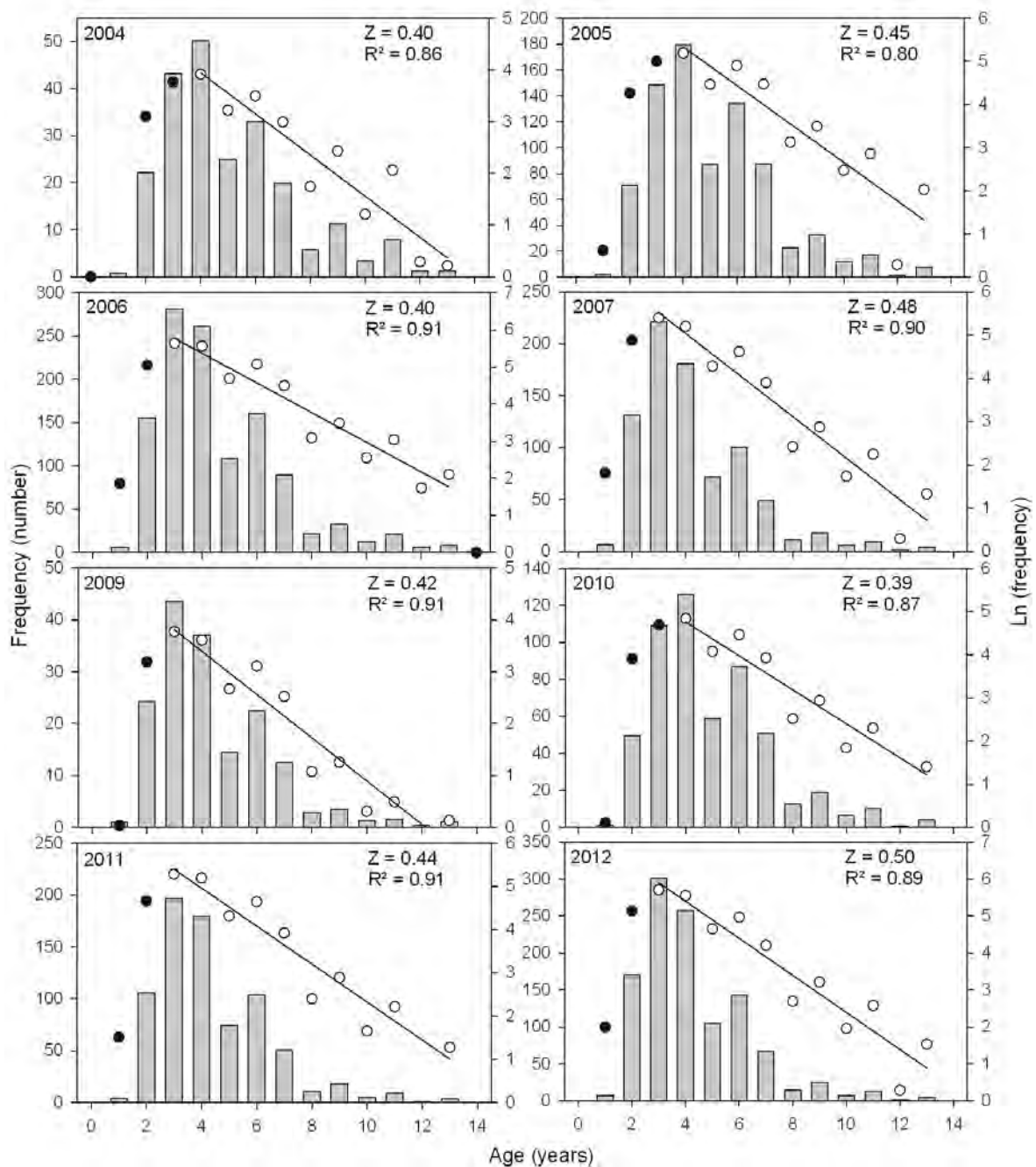


Figure 7.2: *Micropterus salmoides* age frequency histograms and the resultant catch curves generated from the accumulative weight frequency distributions obtained from angling tournaments from 2004 to 2012 in Wriggleswade Dam. The instantaneous rate of total annual mortality (Z) is the slope of the descending limb of the catch curve (open circles). The ascending limb of the catch curve (closed circles) was not used in the regression analysis.

The length frequency histogram of the *M. salmoides* measured during the 2011 and 2012 Amatola Classics illustrates the angler selection of fish larger than 300 mm TL, which

corresponds to 288 mm FL ($FL = 0.955TL + 1.526$; Chapter 5). The catch curve generated from these measured fish resulted in a Z of 0.38 yr^{-1} (Figure 7.3).

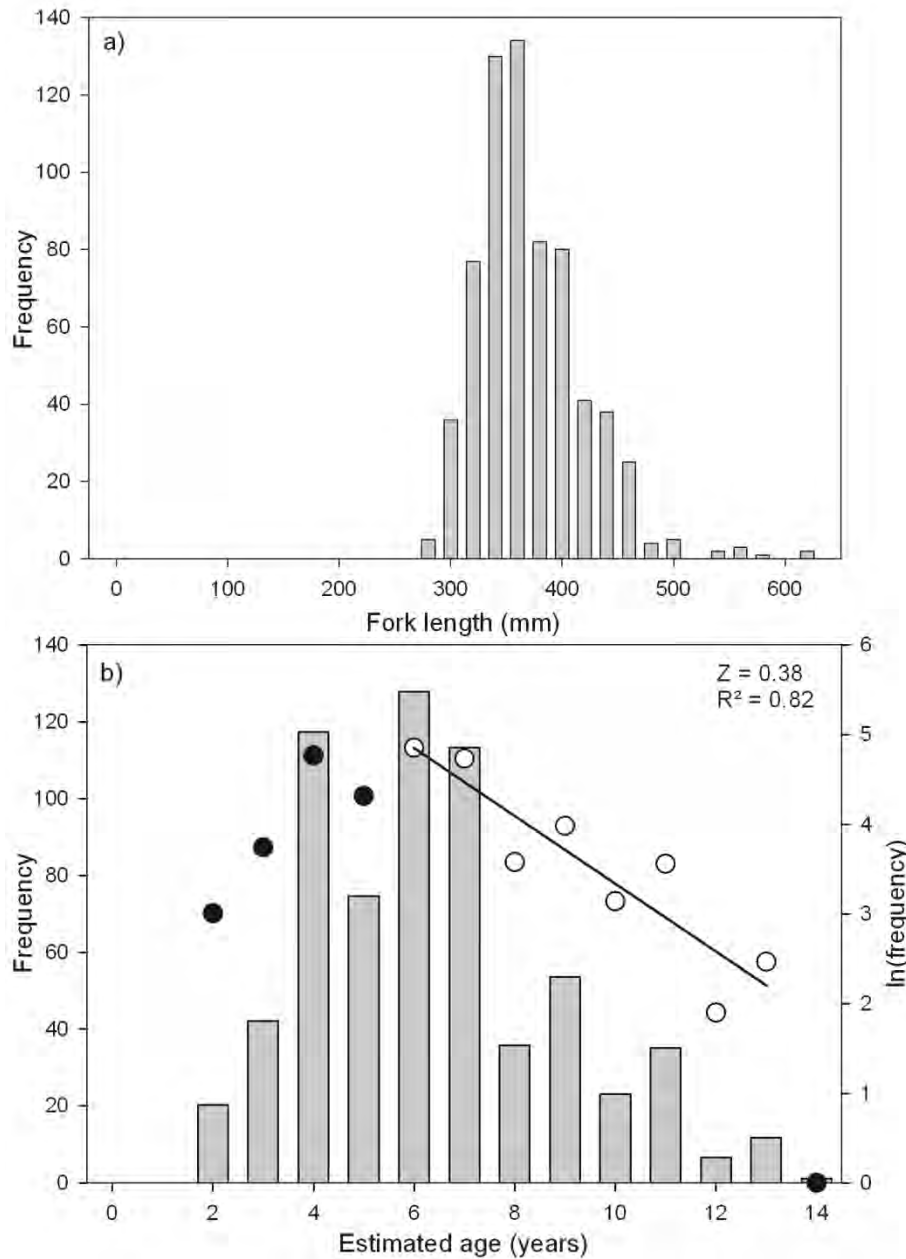


Figure 7.3: *Micropterus salmoides* (a) length and (b) age frequency histograms and the resultant catch curve generated from fish measured during the 2010 and 2011 Amatola Classics in Wiggleswade Dam. The instantaneous rate of total annual mortality (Z) is the slope of the descending limb of the catch curve (open circles). The ascending limb of the catch curve (closed circles) was not used in the regression analysis.

The catch curve created using the *M. salmoides* collected from Wiggleswade Dam using gill and fyke nets generated a Z of 0.33 yr^{-1} (Figure 7.4).

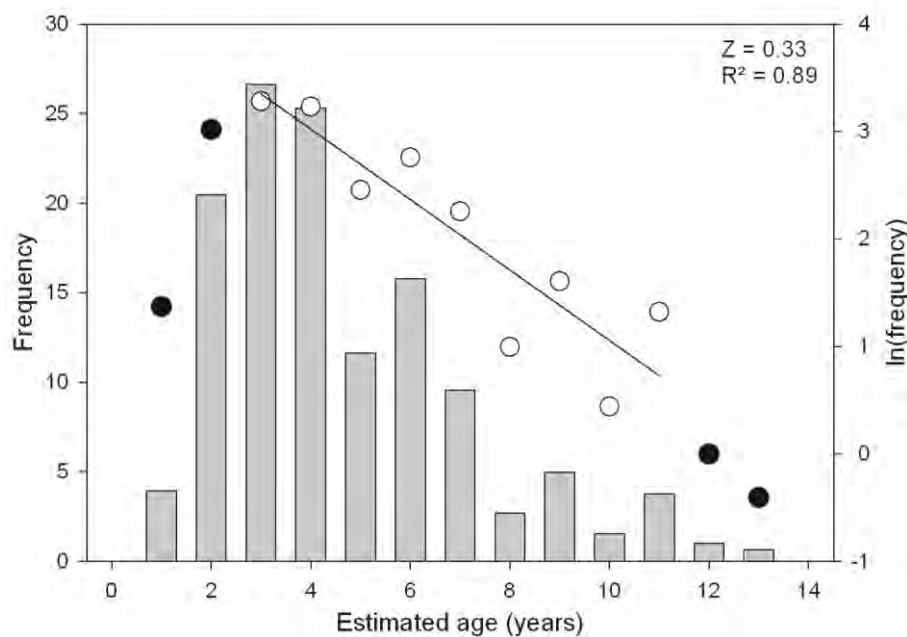


Figure 7.4: The catch curve and associated instantaneous rate of total annual mortality (Z) (slope of the descending limb = open circles) for the *Micropterus salmoides* from Wriggleswade Dam collected using standardised gill and fyke nets.

7.3.2 Dispersal

A total of 786 *M. salmoides* were tagged in Wriggleswade Dam, of which 124 were recaptured yielding an overall recapture rate of 15.6% (Table 7.2).

Table 7.2: The numbers of *Micropterus salmoides* tagged and subsequently recaptured in Wriggleswade Dam either during an identified event, or separately and reported by anglers.

Month	Event	Fish weighed	Fish tagged	Recaptured at events	Recaptured separately	Multiple recaptures
May-11	Club	No data	30			
Sep-11	Club	No data	20			
Oct-11	Club	161	154	1	2	
Nov-11	Divisionals	307	241	3	2	
Dec-11	Club	150	135	7	2	
Jan-12	Club	283	206	19	4	2
Feb-12	Club	136		6	1	1
Mar-12	Classic + Club	465 + 122		43	3	6
Apr-12	Club	98		3		1
Sep-12	Nationals	674		19		3
Oct-12	Divisionals	No data		9		3
Total			786	110	14	16

The spatial distribution of recaptured fish across Wriggleswade Dam is shown in Figure 7.5. Despite low sample sizes, fish tagged during each tournament event were subsequently recorded (recaptured) throughout the dam, at distances ranging from 0 to 10670 m from the release site. Wide dispersal was recorded from each group of fish tagged with no obvious spatial patterns (Figure 7.5). However, 18% of the fish were recaptured within 1 km of the release site (Figure 7.6).

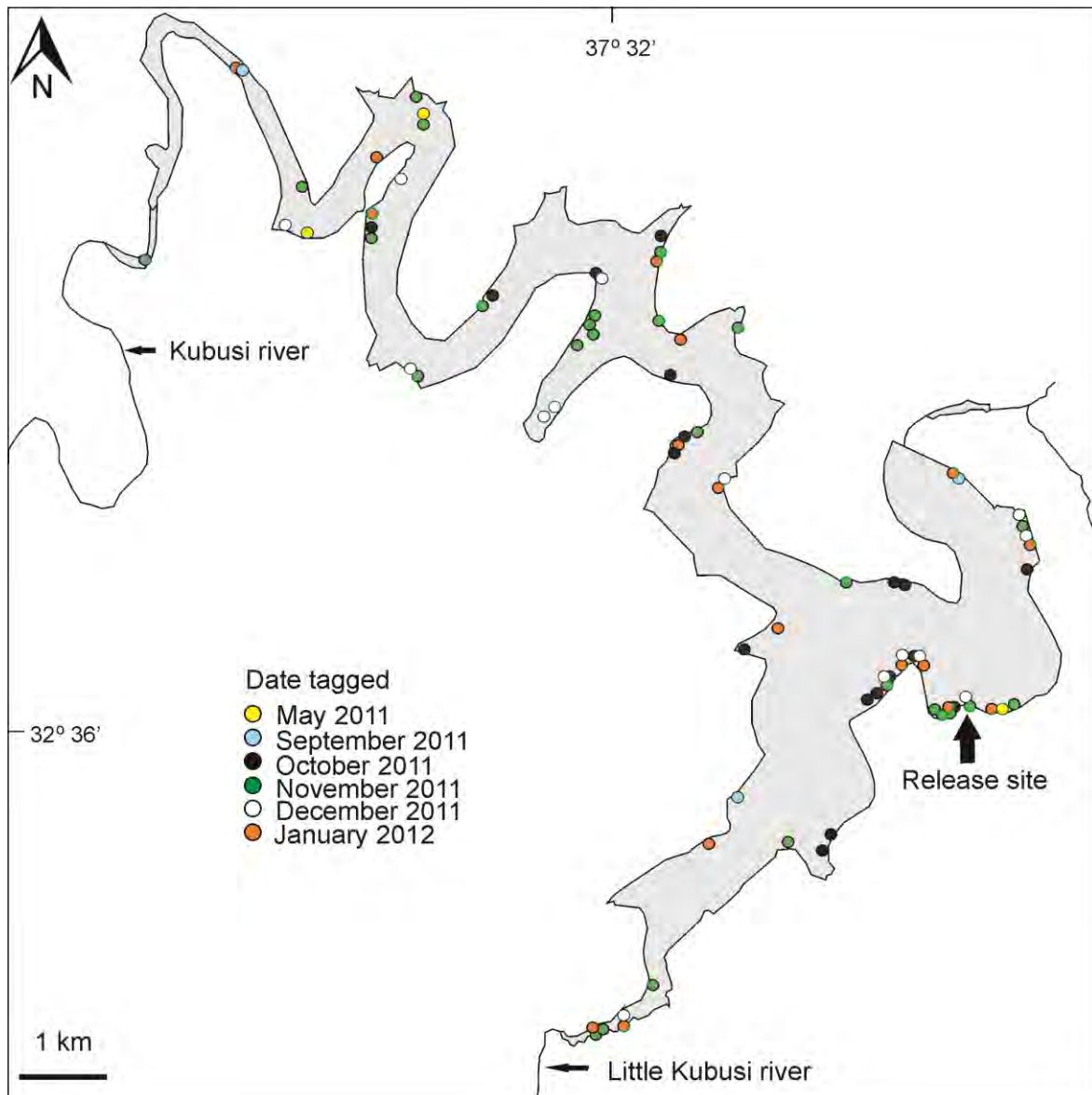


Figure 7.5: The distribution of the recaptured *Micropterus salmoides* in Wriggleswade Dam with the different colours showing the different dates of tagging.

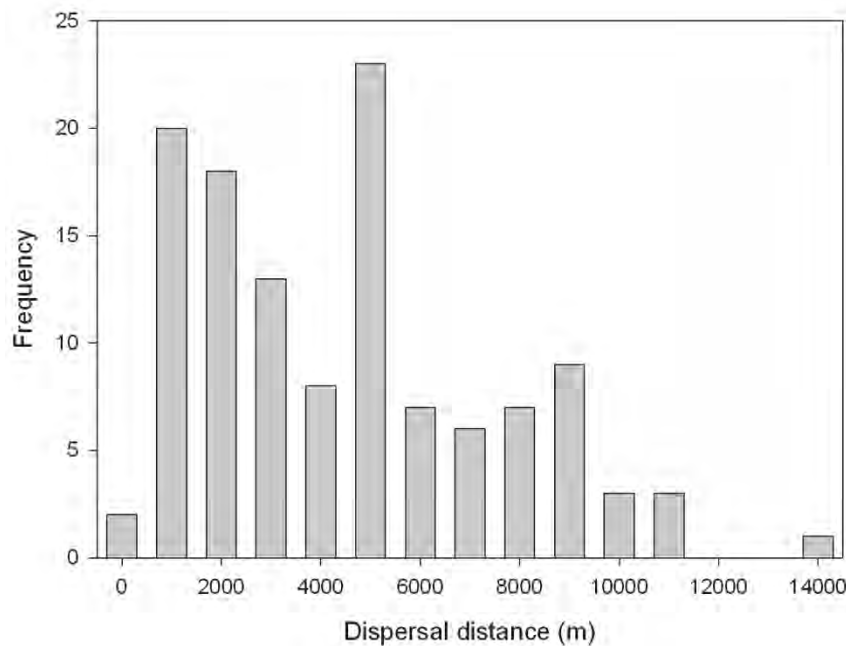


Figure 7.6: The numbers of *Micropterus salmoides* recaptured at 1000 m dispersal distance intervals in Wriggleswade Dam.

To investigate if those *M. salmoides* caught close to the release site had been at liberty for a shorter period of time than those caught further from the release site, relationships in the dispersal distance with time at liberty data were analysed using a spearman rank correlation, a Kruskal-Wallis test and *t*-tests assuming unequal variance. The average distance dispersed by the recaptured tagged *M. salmoides* in Wriggleswade Dam was 4 km, and 43% and 75% of recaptured fish had been caught within the first three and six months of tagging. Dispersal distance increased with time at liberty (Figure 7.7) and a spearman rank correlation showed a significant association between the ranks of time at liberty and distance displaced (Spearman: $r = 0.339$, $Z = 3.71$, $P = 0.00$). In addition, a non-parametric Kruskal-Wallis test showed a significant difference between the dispersal distance with time at liberty in 50 day bins (Kruskal-Wallis: $H = 24.9$, $P = 0.00$) (Figure 7.7).

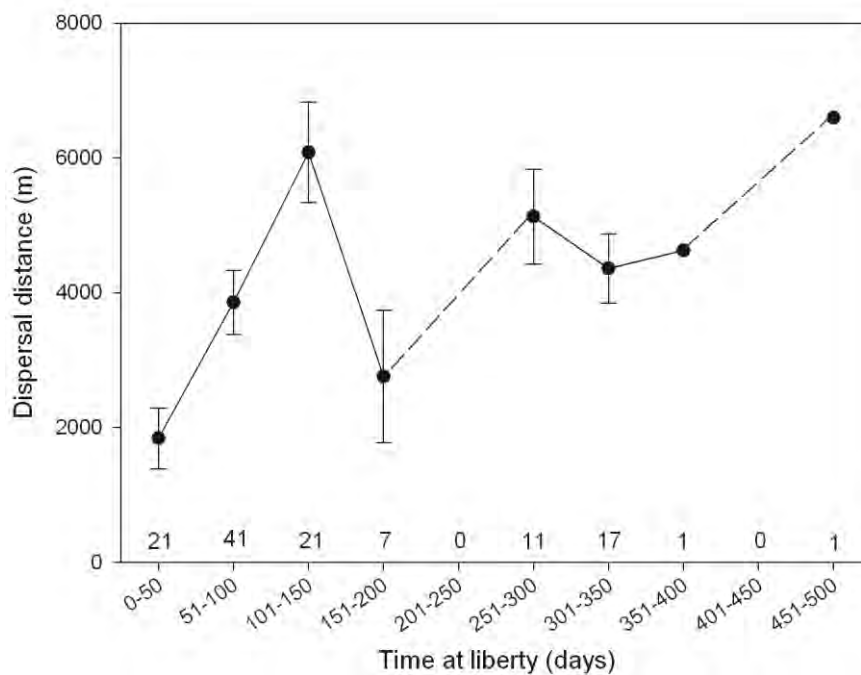


Figure 7.7: The mean dispersal distance ($\pm$ SE) with time at liberty of the *Micropterus salmoides* recaptured from Wriggleswade Dam. The dotted line illustrates the lack of data available for the time at liberty groups 201-250, and 401-450 days.

To understand where the differences in distance dispersed with time were, one tailed student's *t*-tests assuming unequal variance were carried out with times at liberty (Table 7.3). For up to 50 days at liberty the *M. salmoides* dispersal distance was significantly lower than for most of the other fish at liberty for longer periods of time (Table 7.3). Those fish recaptured after being at liberty for longer than 50 days did not show an increase in dispersal distance with time. Therefore an increase in dispersal distance with time at liberty up to 50 days was observed, after which dispersal distance seemed to not be related to time at liberty.

Table 7.3: Results from the paired *t*-tests assuming unequal variance identifying significant differences in *Micropterus salmoides* dispersal distance between time at liberty groups for the recaptured fish from Wriggleswade Dam. Significant *P* values are in bold*.

Time at liberty (days)	0-50	51-100	101-150	151-200	201-250	251-301
0-50	Dispersal distance (m)					
51-100	0.00*					
101-150	0.00*	0.01*				
151-200	0.21	0.17	0.01*			
201-250						
251-300	0.00*	0.07	0.18	0.04*		
301-350	0.00*	0.24	0.03*	0.09		0.19

Of the 124 recaptures, 16 fish were recaptured more than once, of which 14 had recorded recaptured sites, and three were recaptured three times. One of the *M. salmoides* was recaptured in its first capture site (1.5 km from the release site) only 13 days after it was released for the second time at the weigh station, three other fish were recaptured less than 1 km from their first recapture sites, and four more were recaptured between one and 4 km from their first capture sites. Therefore of the 14 *M. salmoides* recaptured more than once, eight (57%) of the second recaptures were within 4 km of their first recapture location. Of the *M. salmoides* that were recaptured three times, one was caught in the same place for recapture one and recapture three, while recapture two was made 1.8 km from the common recapture site. Two fish were recaptured for the second time only one day after the first recapture, and were less than 0.5 km from the release point (4.5 and 5 km from their first capture sites).

7.3.2.1 Size related dispersal

During angling tournaments anglers weigh in the largest five fish caught, and there is a minimum size limit of 288 mm FL (300 mm TL). The smallest *M. salmoides* tagged was 213 mm FL while the largest was a 3.6 kg fish of 582 mm FL. The smallest *M. salmoides* tagged was smaller than the minimum size limit as some “short” fish were brought to the weight station by anglers who did not have a measuring board on their boats. The sizes of the *M. salmoides* recaptured ranged from 294 to 503 mm FL with an average of 356 mm FL. Using the size range available, dispersal distance did not show a significant association with *M. salmoides* size (linear regression: $F = 2.26$, d.f. = 119, $P = 0.136$) (Figure 7.8), and a spearman rank correlation did not show a significant increase or decrease in dispersal distance with *M. salmoides* length (Spearman: $r = 0.113$, $Z = 1.2$, $P = 0.11$).

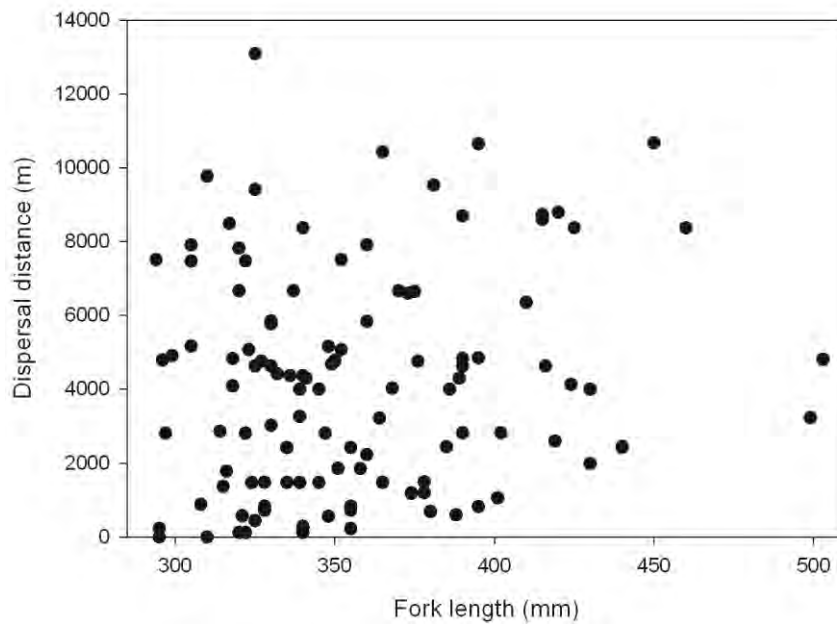


Figure 7.8: The dispersal distance with *Micropterus salmoides* length of the recaptured fish from Wriggleswade Dam.

7.4 Discussion

Allen et al. (2008) examined annual exploitation and total mortality for a number of North American *M. salmoides* competitive fisheries, and concluded that fishing mortality had halved since the 1990s, largely due to the practice of catch and release angling. In addition, they stated that the mortalities associated with this angling practice would not negate the benefits of the reduction in harvest rates unless these mortalities were extremely high. In Wriggleswade Dam the absence of harvest anglers in the form of subsistence fishers indicated that tournament associated mortality constituted a large proportion of the fishing mortality (F), which is most likely positively related to Z (Allen et al., 2008) in the form of additive mortality, or at most is only partially compensatory (Allen et al., 1998).

Instantaneous total annual mortality estimates (Z) were therefore used to assess the mortality associated with tournament utilisation in comparison with other competitive angling waters.

In Wriggleswade Dam more than 1000 *M. salmoides* were caught and displaced annually during fishing tournaments. However, this is probably an underestimate of the total number of displaced fish as smaller fish are often “culled” (released) for larger ones to increase bag

weights. The initial mortality of these fish was low (1% on average between years) compared to the average of 6.5% in the 1990s for a number of North American competitive bass angling waters estimated by Wilde (1998), and comparable to the 1.42 % estimated for two Lake Minnetonka tournaments (Kwak & Henry, 1995) and the average of 1.9% for the 1990s Bass Anglers Sportsman Society (B.A.S.S.) fishing tournaments (Wilde et al., 2002). This low initial mortality was accompanied by an average instantaneous total annual mortality rate (Z) of 0.43 yr^{-1} estimated using catch curve analysis, which is lower than the average Z of 0.73 yr^{-1} estimated for 45 Florida waters (Allen et al., 2002), the average Z of 0.99 yr^{-1} estimated for 34 competitively exploited North American populations (Allen et al., 2008), and those of 1.27 yr^{-1} and 0.89 yr^{-1} for two subtropical populations in Mozambique (Weyl & Hecht, 1999) and Puerto Rico (Waters et al., 2005) respectively. This low mortality compared to the subtropical non-native populations may be explained by the well understood relationship between mortality and temperature (Meals & Miranda, 1994; Weathers & Newman, 1997; Wilde, 1998; Neal & Lopez-Clayton, 2001; Edwards et al., 2004b). Furthermore, the low Z estimates obtained from Wriggleswade Dam, and the collection of North American waters (Allen et al., 2002; Allen et al., 2008) can be ascribed to the dominance of competitive recreational angling, whereas the Mozambique and Puerto Rico dams were subject to subsistence harvesting (Weyl & Hecht, 1999) and harvest by recreational anglers (Waters et al., 2005). Even though the fishing mortality associated with tournaments was not measured directly, it is assumed that the practice of catch and release tournament angling has minimal impact on this South African *M. salmoides* population, based on the low mortality estimates obtained from Wriggleswade Dam.

Of the 786 tagged and released tournament caught fish, 15% were recaptured at distances varying from 0 m to 13 km from the release site. This recapture rate was similar to that of the 16.7% found by (Lantz & Carver, 1975) but recovery may have been hindered during major tournaments in which anglers occasionally reported the “culling” of tagged fish from the five fish limit, from which they did not collect data for due to the lack of time or urgency to catch more fish. The dispersal of recaptured fish from which data were collected seemed randomly scattered across the dam, with an average distance of 4 km from the release site. However, there was a relationship between time at liberty and dispersal distance, with *M. salmoides* recaptures congregating within a 2 km radius from the release site until up to 50 days after release, after which dispersal distance was not related to time at liberty. A similar delay in the dispersal of acoustically tagged fish in Wriggleswade Dam was documented by

Huchzermeyer et al. (in press), who found that the majority of fish remained at the release site for two weeks, after which they dispersed various distances through an array of passive receivers. Similarly, Ridgway (2002) reported limited post-release dispersal in Rideau Lake, Ontario, as displaced fish took one week to move 200 m and Richardson-Heft et al. (2000) detected 64% of tagged fish within 0.5 km of the release site after a week. However, as was documented by Gilliland (1999) in Lake Thunderbird, Oklahoma, this high recapture rate may have been inflated by concentrated fishing effort at this stretch of shoreline (within 500 m of the release site), which was the only accessible shore angling site of the entire dam. However, if tournament released fish accumulate near the release site for up to two months, it is possible that the carrying capacity of the localised area may be exceeded resulting in reduced food availability and ultimately increasing vulnerability to angling (Lantz & Carver, 1975; Gilliland, 1999; Richardson-Heft et al., 2000).

Despite the initial delay in dispersal, 66% of the displaced *M. salmoides* in Wriggleswade Dam moved more than 3 km from the release site and there was no relationship between fish size and distance moved. The average fish dispersal distance of 4 km in the Wriggleswade Dam was similar to the 3.5 km reported by Wilde (2003), but higher than the 1.6 km reported by Gilliland (1999) and lower than the 9.6 km found by Richardson-Heft et al. (2000). *Micropterus salmoides* have been found to move directionally using landmarks or gradients (Parker & Hasler, 1959), so the high average distance moved by the *M. salmoides* in the tidewater environment documented by Richardson-Heft et al. (2000) was likely a result of orientation down a salinity gradient. In the study by Huchzermeyer et al. (in press) fish displaced more than 4 km moved back towards their original capture sites, while those displaced within 3 km of their original capture site did not show the same site fidelity. In this study it was concluded that *M. salmoides* in Wriggleswade Dam moved widely, and contrary to other literature (Winter, 1977; Gilliland, 1999) occupied home range areas of up to 3.5 km in length. A proposed 3.5 km home range size is supported by the multiple recaptures of this study, where eight out of 14 fish were recaptured less than 4 km from their first recapture sites. This finding concurs with the conclusion by Huchzermeyer et al. (in press) that displaced tournament caught *M. salmoides* in Wriggleswade Dam should return to their home ranges after release.

The main findings of this study are two-fold. Firstly, although a large number of tournament caught *M. salmoides* are displaced to a common release site in Wriggleswade Dam annually,

total mortality rates are low. This suggests that current catch and release practices (i.e. displacement) and levels of fishing mortality do not impact negatively on the population. It must be noted that the collection of more data using fisheries independent surveys would be preferable, and the limited data collected did support the fisheries estimates of Z. Secondly, although fish displaced to the common release site may take up to 50 days to disperse, there is evidence supported by the findings of the telemetry experiment by Huchzermeyer et al. (in press) to suggest that these fish exhibit homing behaviour. However, additional multiple recaptures and/or more telemetry investigations are required to strengthen this suggestion. Alternatively, an experiment where fish are tagged and released at their capture locality would provide such data.

CHAPTER 8: GENERAL DISCUSSION AND RECOMMENDATIONS FOR FUTURE RESEARCH

8.1 General discussion

Fish populations live in changing ecosystems and consequently life history parameters are adaptive (Beamish & McFarlane, 1983; Frimpong & Angermeier, 2009; Mims et al., 2010). Ecological changes also come into effect when fish are moved to new environments (Beamish & McFarlane, 1983) and understanding the concomitant changes to life history strategy improves the ability to manage invasions and fisheries. The success of largemouth bass *Micropterus salmoides* in diverse non-native environments is evidence for a life history style that is well adapted to a wide range of environmental conditions (Bruton, 1986). By comparing various biological and ecological traits of different *M. salmoides* populations in both its native and non-native range, this thesis contributes to the available knowledge base needed to manage non-native populations and control their spread.

Accurate and precise age estimates are key to defining and understanding these life history parameters in novel environments (Beamish & McFarlane, 1983; Campana, 2001). In this thesis I first identified otoliths as the most appropriate structure for ageing *M. salmoides* in the study areas (Chapter 3). Scales, although potentially useful ageing structures (Maraldo & MacCrimmon, 1979; Maceina et al., 2007), gave less precise estimates of age than otoliths. Consequently the non-lethal advantage of using scales (Carlander, 1987; Besler, 1999; Maceina et al., 2007) was outweighed by the potential bias introduced through using a less precise structure. It is also a fundamental requirement for all ageing studies to validate the periodicity of growth increment formation by proving that the technique used is accurate (Beamish & McFarlane, 1983; Beamish & McFarlane, 1987). This is because there are inconsistencies within and between species, between locations, and between age groups (Beamish & McFarlane, 1987; Heidinger & Clodfelter, 1987; Campana, 2001). Results from indirect and direct validation experiments confirmed that growth zone deposition was annual in the two study dams, as well as in two small farm dams in the Eastern Cape of South Africa

(Chapter 4). This result was consistent with that from a collection of literature (Chapter 4) and age estimates for the two populations are therefore precise and accurate. In addition, the validation study highlighted the advantages of using a direct validation method of chemical mark re-capture of fish using oxytetracycline hydrochloride, an accurate method (Campana, 2001) that has not previously been used to validate growth zone periodicity for *M. salmoides*.

With evidence of the accurate and precise estimation of age presented in Chapters 3 and 4, the growth and reproductive performance of the populations was explored in Chapter 5. Moyle (1986) listed one of the desirable characters expressed by successful invasive species as a reproductive style which possesses an unusual degree of fitness. *Micropterus salmoides* are equilibrium life history strategists (Mims et al., 2010). Males excavate a nest and guard their young after spawning (de Moor, 1996; Cooke et al., 2001). Wriggleswade and Mankazana Dam populations matured at around two years of age and at 259 and 290 mm FL respectively. Both populations tended to spawn in spring when day length increases and rising water temperatures reached approximately 18 °C (Chapter 5). Since spawning is temperature linked, an increase in latitude delays the onset of spawning season (Conover, 1992), so explaining why the spawning season of *M. salmoides* in South Africa was late (September – November) compared to that of previously assessed populations in Mozambique (August – October) (Weyl & Hecht, 1999) and in Zimbabwe (July - October) (Beamish et al., 2005). Despite these slight differences in the timing of spawning, *M. salmoides* age and length at maturity were consistent with other populations (Clugston, 1964).

The growth performance of a population reflects its ability to meet nutritional requirements and its adaptation to abiotic conditions (Jobling, 1981). Both populations performed as expected with respect to growth, which followed well known hypotheses that growth performance increases with environmental temperature (Helser & Lai, 2004; Rypel, 2009; Britton et al., 2010a). This was illustrated by the lower growth performance of Wriggleswade Dam's population which was influenced by a slightly lower mean annual air temperature of 16.4 °C, compared with Mankazana Dam's population (mean annual temperature = 18.7 °C). In addition, Wriggleswade's temperate population performed similarly to those in Italy (Lorenzoni et al., 2002) and Japan (Yodo & Kimura, 1996), which were found in similar

temperature regimes, while Mankazana Dam's warm temperate population had a comparable growth performance to that of the *M. salmoides* population from Zimbabwe (Beamish et al., 2005) (Chapter 5). Therefore growth rates were consistent with those elsewhere.

Abiotic conditions such as temperature may explain some variation in growth, however with the documented differences in relative condition factors and length-weight relationships between the two dams, diet was most likely an important contributing factor. In support of this hypothesis, (Clugston, 1964) found that *M. salmoides* with the highest condition factors for most of the year grew faster than those with lower condition factors. Frimpong & Angermeier (2009) stated that food selection is a function of availability, which is a function of time, location, and the presence of predators and competitors. All of these variables may change with location, making the diet of *M. salmoides* vary considerably between systems (Liao et al., 2002). In Wriggleswade Dam the *M. salmoides* were predominantly piscivores from a young age, feeding mainly on the small shoaling estuarine round herring *Gilchristella aestuaria* throughout the year (Chapter 6). Conversely Mankazana Dam's *M. salmoides* seemed to be more diverse feeders, predating on conspecifics and Mozambique tilapia *Oreochromis mossambicus* (Chapter 6), while supplementing their diets with large numbers of invertebrates year round. The early ontogenetic shift characterising the Wriggleswade population should have been reflected in faster growth throughout their life, however Mankazana Dam's population grew faster despite their later shift, potentially as a result of a more suitable diet before the shift to piscivory as described by Mittelbach & Persson (1998). Despite the small sample size obtained, this was supported by the lack of zooplankton prey found within the stomachs of juvenile *M. salmoides* collected from Wriggleswade Dam.

Once *M. salmoides* had shifted to a teleost based diet, the difference in nutritional value of *O. mossambicus* and conspecifics in Mankazana compared to *G. aestuaria* in Wriggleswade as discussed in Chapter 6, lead to the conclusion that the fish in Mankazana had access to more suitable prey items than those in Wriggleswade Dam. In addition, differences in relative condition were cautiously attributed to different feeding behaviours associated with the contrasting turbidities of the two dams. This speculated theory was supported by the results from the dispersal experiment conducted in Wriggleswade Dam (Chapter 7). Dispersal of translocated *M. salmoides* in this dam showed that fish moved considerably more than those

same species in similar studies (Lantz & Carver, 1975; Stang et al., 1996; Ridgway, 2002; Wilde & Paulson, 2003). This information, as has been suggested by Huchzermeyer et al. (in press), may provide evidence that *M. salmoides* moved widely in this dam to improve their likelihood of encountering their pelagic food source *G. aestuaria*. The differences in suitable prey and resulting contrasting relative conditions of the *M. salmoides* in the two dams resulted in slower growth with the population that utilised the most diverse prey items exhibiting superior growth and relative condition. Despite this, both populations were still successful. In temperate South Africa therefore *M. salmoides* reproduced successfully, had low mortality rates, utilised all available food items, and grew at rates comparable to those in their native range to old ages.

This study has therefore contributed to the literature and understanding of *M. salmoides* in Southern Africa. In addition, the study has addressed Bruton's (1986, page 207) call "although some extrapolations can be made from studies in northern temperate environments, an understanding of the ecology of invasions in southern Africa will depend on our knowledge of local interactions". Because *M. salmoides* life history is adapted to South African conditions, and because recreational fishing has little impact on populations (Chapter 6), it is likely that this species will continue to persist and establish in new impoundments.

8.2 Recommendations for future research

During this study a number of areas for future research were identified. The diet aspect of this study was constrained by the shortfalls of gut content analysis, and a lack of knowledge of the prey population dynamics. It was therefore difficult to imply the relationship between feeding and movement behaviour without more knowledge of the major source of nutrition and the movement behaviour in both dams. To improve the understanding of *M. salmoides* diet, future studies could focus on the use of stable isotope analysis to identify the assimilated diet of *M. salmoides* in both dams. In conjunction with gut content analysis, which gives a snapshot over a few hours of the material ingested, stable isotope analysis identifies the assimilated sources of nutrition over a period of a few months (Peterson & Fry, 1987; Gannes et al., 1997; Pinnegar & Polunin, 1999; Grey, 2006). This would quantify the importance of

invertebrates to the diet of *M. salmoides* in Mankazana, eliminate any bias of the significance of hard bodied prey items that have long gut passage times such as *P. sidneyi* in both dams, and give a clear picture of trends in *M. salmoides* diet which is often highly variable as a result of their opportunism (Pinnegar & Polunin, 1999; Almeida et al., 2012).

With respect to prey population dynamics, the abundance and species composition of the smaller fish species should be sampled more thoroughly. In addition, the invertebrate prey were not assessed, and an understanding of this aspect of the ecosystem would have strengthened the assumptions made in Chapter 6 about the cause of the contrasting relative condition factors of both populations through the use of selectivity indices (Pine et al., 2005).

In order to reduce the bias associated with the use of fisheries data to estimate mortality rates, unbiased data of all size classes could be collected using boat based electro fishing as is commonly used in American fisheries (Allen et al., 2002; Doe, 2002).

An extension of the movement study could focus on building the theory that *M. salmoides* in Wriggleswade Dam return to their capture sites after translocation. This could be achieved by displacing some fish from known capture locations, and releasing some after handling without displacement. In addition, a study on the movement of *M. salmoides* in Mankazana Dam could be conducted, with the aim to compare results with those from the movement of this species in Wriggleswade, which has been investigated using both acoustic transmitters (Huchzermeyer et al., in press) and conventional tags (Chapter 7). The use of a multi-state model approach (Plumb et al., 2012) would develop this tag-recapture experiment further by providing a survival estimate which could shed light on any delayed mortality from tournaments and provide another means of comparing the mortality estimates made from catch curves.

In order to broaden the knowledge base of the biology and ecology of this species in South Africa, research could be extended to a wide range of dams focussing on environmental differences as well as on genetic differences. Both the northern strain *Micropterus salmoides*

and the Florida strain *Micropterus floridanus* of largemouth bass, recently separated species that can hybridise, have been introduced into South Africa (Skelton & Weyl, 2011). It would therefore be interesting to assess the biology of the different genetic strains, and their response to different environmental conditions.

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