THE BIOLOGY AND MOVEMENT PATTERNS OF NON-NATIVE COMMON CARP, *CYPRINUS CARPIO* (L) IN GROENVLEI, SOUTH AFRICA

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

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by

Dinah Lorraine Mukhari

G20M9832

Orchid number: http://orcid.org/0000-0001-7558-4360

Supervisor: Prof. Paul D. Cowley

Co-supervisor: Dr Josephine Pegg

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ABSTRACT

The common carp, *Cyprinus carpio* is a highly invasive fish species, first introduced into South Africa in the late nineteen century, and now widely spread throughout the country. In 1991 carp were illegally introduced to Groenvlei, within the Goukamma Nature Reserve in the Western Cape Province. Decreases in water quality and declines in biota have been attributed to the now large numbers of carp. Management measures have commenced to reduce the carp population, however these are not underpinned by science as little is known about the biology and movement patterns of resident carp.

The age, growth and maturity of carp within the lake was determined using oxytetracycline hydrochloride marked asteriscus otoliths and macroscopic gonad development staging methods. The results showed that carp in Groenvlei had similar growth characteristics to the invasive populations in North America and Australia; fast growth during the first three to five years and reproductive maturity attained between the ages of two to three years, and are long lived (maximum age of 20 years old). Their growth however differed from the only other study on a South African population.

Six acoustically tagged carp were manually tracked in order to report on their movement patterns and habitat use. Carp moved much greater distances in February compared to October and November, and occupied different areas of the lake. In November they were found to aggregate in backwaters which corresponds with their breeding activities. Literature on global carp control shows that whilst eradication of this fish can be achieved in small isolated waters using icthyocides and water drawdowns, in conservation priority areas such as Groenvlei where this is not possible, mechanical removal using multiple gears targeting vulnerable life stages can most efficient at controlling carp. This study identified where and when these methods could be focused to optimise control efforts.

DECLARATION

I, **Dinah Lorraine Mukhari**, student number: **G20M9832** hereby declare that this thesis submitted to Rhodes University, for the degree on Master of Science in Ichthyology and Fisheries Science is my original work and I have not included ideas, phrases, passages or illustrations from another person's work without acknowledging their authorship.

ETHICS CLEARANCE

Cyprinus carpio in Chapter 2 were captured using fyke and seine nets and killed as per Rhodes University Animal Research Ethics Committee (RU-AREC) Approval number: 2020-1373-4795. The additional *C. carpio* used in this chapter were donated dead from an invasive species removal project Cape Nature permit: CN-44-28-8357. *Cyprinus carpio* used in Chapter 3 were captured and tagged by qualified personnel (Prof Paul Cowley, SAIAB) as permitted by the South African Institute for Aquatic Biodiversity (SAIAB) animal ethics committee Reference number: 25/04/1/7/5.

ACKNOWLEDGEMENTS

First and foremost I would like to thank my late supervisor Prof. Olaf LF Weyl for giving me this incredible opportunity; being part of this project alongside an extraordinary team was a dream come true. I owe the biggest gratitude to my supervisors Prof. Paul D Cowley and Dr Josephine Pegg, without them this degree would not have been possible, your mentorship, support and guidance throughout this project does not go unnoticed. I would like to extend my gratitude to the following people: Prof Nick Mandrak and Dr Paul Bzonek for their expertise and collaboration on the telemetry aspect. The following people from Cape Nature are thanked for helping with this project technicalities: Natalie Baker, Thulani Ndlovu, Tobogo Botholo and Wayne Meyer. Colin Attwood and Amanda Lombard are thanked for the collaboration on the mark-recapture and validation aspect. Special thanks to Mr Johnny Snyman, Ms Nobuhle Mpanza and Mr Ferdinand Jacobs for the fieldwork, particularly late night data collection in the lake. My sincere gratitude goes to Mr Albert Libambo, Dr Chantel Elston, Dr Dumisani Khosa, Dr Josie South, Dr Lubabalo Mofu, Dr Mandla Magoro, Dr Takudzwa Madzivhandzira and Dr Taryn Murray for offering their expertise during the process of data analysis and writing. At the South African Institute for Aquatic Biodiversity; the Acoustic Tracking Array Platform (ATAP) and the Olaf Freshwater Research team are thanked for the technical support and allowing me to use their facilities throughout this project. The Department of Ichthyology and Fisheries Science and Electron Microscope Unit at Rhodes University is thanked for allowing me access to use their laboratories to process carp otoliths samples. I would also like to thank the South African Weather Service (SAWS) for providing the temperature and rainfall data from a station near Groenvlei.

On a personal note, I would like to dedicate this entire thesis to the woman who raised me to be a strong hardworking individual that I am; the late Ms Caroline Ramokone Teffu! *A moya wa gago o tšwele pele go robala ka khutšo MOTHOKWA!!! Bagologolo ba be ba opile kgomo lenaka ge ba re "kodumela moepathutse, ga go lehumo leo le tšwago kgauswi."*

Last but certainly not least, I would like to express my deepest gratitude to my family and friends for their continuous love and support throughout this journey. Thank you for everything and I am forever indebted to you.

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CHAPTER 1: General introduction

Anthropogenic activities significantly alter the earth's functioning and contribute to biodiversity declines across the world (Sala et al., 2000; Tickner et al., 2020). Globalisation has led to increased worldwide transport networks (Seebens et al., 2015) and as a result there are increased pathways for non-native species to be introduced at an unprecedented rate (Ricciardi, 2007; Hulme, 2009; Ricciardi et al., 2017; Seebens et al., 2017). Biological introductions are among the least controlled and irreversible causes of biodiversity decline (Gozlan et al., 2010; Strayer, 2010; Blackburn et al., 2019). Freshwater ecosystems are particularly vulnerable, due to the high level of endemism within these systems (Dudgeon et al., 2006; Reid et al., 2019; Tickner et al., 2020). At least 624 freshwater fish species have been intentionally introduced beyond their native range (Gozlan, 2008), for aquaculture (51%), ornamental pet trade (21%), recreational angling (12%) and food fisheries (7%) (Gozlan et al., 2010; Gozlan, 2017). In addition, accidental fish introductions are also widespread, due to aquaculture escapes, release of ballast water and the use of live bait (Weyl et al., 2020). Not all introduced fish become invasive because rates of establishment are relatively low (Gozlan, 2008), and only a small number of introduced species have measureable effects on the recipient ecosystem (Ricciardi and Kipp, 2008). However, even if as predicted only 10% of freshwater fish introductions result in adverse ecological effects (Gozlan, 2008) there remains an inherent risk that irreversible ecological consequences will result from an introduction, as evidenced by global case-studies involving invasive salmonids, tilapias, carps and catfishes (Zambrano et al., 2006; Vitule et al., 2009; De Leaniz et al., 2010).

Biological introductions occur as certain benefits arise from introductions of non-native species (Ellender et al., 2014; Gozlan, 2017; Zengeya et al., 2017). The use of non-native fish in aquaculture and fishery enhancement is driven by various factors including lack (or perceived lack) of suitable native species with fast growth rates, high fecundity and a wide environmental tolerance (Coke, 1988; McCafferty et al., 2012). For example, translocated Asian carps and African cichlids are in the top ten aquaculture produced species globally in terms of quantity and value and their production in more than 78 countries (FAO, 2020), contributes significantly to socioeconomic development through poverty alleviation and job creation (Casal, 2006; Gozlan, 2008; Weyl and Cowley, 2015). Highly successful commercial fisheries have been developed on non-native species in some African countries such as bass and carp in Lake Naivasha, Kenya (Britton et al., 2007) and Amerti reservoir in Ethiopia (Hailu, 2013). Due to water scarcity in South Africa, there is currently no commercial fisheries established inland and the present non-native species are utilised by the subsistence and recreational fishers, however the recently approved National Freshwater Wild (Inland) Capture Fisheries Policy aims to promote and formally support the establishment of small-scale fisheries (DFFE, 2021), which are likely to be based on introduced species. Other introductions of non- native fishes in Africa have been driven by the desire to develop recreational angling opportunities (Atchison et al., 2017; Weyl et al., 2020). *Micropterus*

species in southern Africa are targeted in international bass-angling tournaments and contribute to local and regional economies (Ellender et al., 2014). Some introductions continue to serve their purpose, however, a proportion of non-native fish species have concerning ecological, evolutionary and economic impacts on the recipient ecosystems (Casal, 2006; Britton et al., 2010).

Non-native fish are responsible for freshwater biodiversity loss through multiple mechanisms such as competition, predation, hybridization and introduction of diseases and parasites (Parkos et al., 2003). In the Zambezi Basin, Nile tilapia, *Oreochromis Niloticus* (Linnaeus, 1758) are relatively efficient at exploiting certain food sources and habitats compared to the native tilapia species, Kariba tilapia *O. mortimeri* (Trewavas, 1966), the three spot tilapia *O. andersonii* (Trewavas, 1966) and the greenhead tilapia *O. macrochir* (Boulenger, 1912) (Ellender et al., 2014) and this competition supresses the native fishes' growth and reproduction (Britton et al., 2007; Ellender and Weyl., 2014). Non-native fish may predate directly on native species. Pikeperch *Sander lucioperca* (Linnaeus, 1758) introduced into English waters prey on juvenile native *Rutilus rutilus* (Linnaeus, 1758) leading to changes in habitat-use as mechanism for predator avoidance (Smith et al., 1996). Extensive hybridization of non-native *O. niloticus* with the native *O. Mozambicus* (Peters, 1852), a species listed in the IUCN Red List as "vulnerable" (Bills, 2019) is reported in the Limpopo River system, South Africa and has threatened this population by genomic extinction (Moralee et al., 2000; D'Amato et al., 2007). In the United Kingdom the introduced goldfish, *Carassius auratus* (Linnaeus, 1758) hybridises with the native crucian carp *Carassius carassius* (Linnaeus, 1758) and similarly threatens its population (Hickley and Chare, 2004). Other impacts of non-native species includes introduction of diseases and parasites, for example, the Asian tapeworm *Bothriocephalus acheilognathi* (Yamaguti, 1934) that is widely distributed in six major river systems of South Africa, was introduced by non-native cyprinid vectors and it now affects other fish fauna including two native species, smallmouth yellowfish *Labeo aeneus* (Thompson, 1913) and largemouth yellowfish *Labeo kimberleyensis* (Gilchrist and Thompson, 1913) (Bertasso and Avenant-Oldewage, 2005; Stadtlander et al., 2011).

Non-native Cyprinus carpio

The common carp *Cyprinus carpio* (Linnaeus, 1758) (Skelton, 2001; Figure 1.1) is a cyprinid species native to the area of the Caspian and Aral Sea Basins (Balon, 1995; Feng et al., 2018). *Cyprinus carpio* has established in 91 of the 121 countries which it has been introduced to, and its high success rate is attributed to its life history characteristics which includes fast growth, early reproduction maturation and high fecundity, in combination with high degree of phenotypic plasticity (Balon, 1995; Matsuzaki et al., 2009; Weber and Brown, 2009). Due to successful establishment in many countries and the resulting ecological impacts, *C. carpio* is included in the "100 World's Worst invasive species" by the International Union for the Conservation of Nature (IUCN) (Lowe et al., 2001; Casal, 2006). The expanded range of *C. carpio* is the result of human mediated introductions such as stocking programmes

with secondary expansion occurring as a result of escapes into the wild and downstream larval drift facilitated by systems connectivity (Koehn, 2004; Copp et al., 2005). Early stockings of *C. carpio* across the world were facilitated by governments with the intention of contributing to social and economic developments, however, none or limited risk assessments were conducted prior (Copp et al., 2005; Vitule et al., 2009; Kara, 2012). As concerns regarding the ecological impacts of *C. carpio* in the recipient ecosystems increased (e.g., Roberts, 1995; Lougheed et al., 1998; Zambrano et al., 2001), most stocking programmes were stopped and regulations were created to limit further spread, however, presently *C. carpio* distribution continues to expand as a result of illegal introductions (Hickley and Chare, 2004; Rahel, 2004; Daniel et al., 2011). *Cyprinus carpio* are targeted and highly valued by course anglers (Vilizzi, 2012) and this group has been blamed for the introduction of *C. carpio* in previously uninvaded systems to create angling opportunities without considering their ecological impacts (Koehn et al., 2000).

Figure 1.1. Illustration of common carp *Cyprinus carpio* (Linnaeus, 1758) In: A complete guide to the freshwater fishes of southern Africa (Skelton, 2001, p. 188).

Today, *C. carpio* is a cause or contributor to environmental degradation and biodiversity loss in many regions (Parkos et al., 2003; Koehn, 2004). The impacts of *C. carpio* are more severe in some areas than others, for example in Australia and North America impacts are considered higher than in Europe (Koehn, 2004; Weber and Brown, 2009). Localised points of severe *C. carpio* impact include the Azores Archipelago (Raposeiro et al., 2017), areas in India (Singh et al., 2010) and regions of Mexico (Zambrano and Hinojosa, 1999; Tapia and Zambrano 2003). *C. carpio* are ecosystem engineers (Parkos et al., 2003; Matsuzaki et al., 2009) capable of altering the physical state of biotic and abiotic properties

within ecosystems (Koehn, 2004; Weber and Brown, 2009; Vilizzi et al., 2015). A biomass as low as 100 kg per hector of *C. carpio* can cause a dramatic decline on macrophyte abundance (Roberts et al., 1995; Zambrano et al., 2001; Kulhanek et al., 2011), vegetative cover and macroinvertebrate diversity (Bajer et al., 2009), and cause a significant increase in turbidity and phosphorus concentration (Parkos et al., 2003; Bajer and Sorenson, 2015). These impacts are associated with its benthic feeding behaviour whereby *C. carpio* uses the specialized palatal organ to sort edible items such as larvae, eggs and seeds by sucking sediments and discharging indigestible materials (Sibbing, 1988) leading to resuspension of sediments, trapped nutrients and increasing turbidity (Roberts et al., 1995; Koehn, 2004). The uprooting of submerged macrophytes in shallow lakes by *C. carpio* (Zambrano et al., 2001; Khan, 2003) can lead to transformation of macrophyte to phytoplankton dominated systems over time (Lougheed et al., 1998). In addition, *C. carpio* excretion directly increases the nutrients levels resulting in phytoplankton blooms in some aquatic systems (Koehn et al., 2000). Additional impacts of *C. carpio* includes the declines in native fish abundance over time (Zambrano et al., 2006), disease transmission, competition, egg and larval predation (Stadtlander et al., 2011). Domination of *C. carpio* in waterways has resulted in the recreational angling community losing fishing amenities in parts of Australia (Koehn et al., 2000) and South Africa (Ellender et al., 2014).

Cyprinus carpio in South Africa

In South Africa, a semi-arid country with few natural inland stillwaters, *C. carpio* was introduced into man-made reservoirs for recreational angling purposes and today occurs in all major watersheds and dominates fisheries catches (de Moor and Bruton, 1988; Weyl and Cowley, 2015). Despite being a preferred angling species by recreational anglers (bank anglers) and a table fish for subsistence in the Orange and Vaal River Basin (Ellender et al., 2014; Barkhuizen, 2015), *C. carpio* is still regarded as a highly invasive species in some parts of South Africa (Ellender and Weyl, 2014). However, there are few South African studies that formally address the local impacts of *C. carpio* (Weyl et al., 2020), the available literature reports similar impacts to elsewhere in the world, this includes reductions in water quality, high turbidity and declines in macrophytes (Dalu et al., 2020). This together with the increasing range expansion, continued illegal introductions and impacts of climate change in the South African freshwater ecosystems (Ellender and Weyl, 2014; Weyl et al., 2015), increases management concerns of this species, especially in conservation priority areas (Ellender and Weyl, 2014; Dalu et al., 2020). The present study took place in Groenvlei, located within the Goukamma Nature Reserve, in the Western Cape Province of South Africa. In this system, *C. carpio* was introduced illegally in the 1990s and currently occurs in notable abundance, exceeding 700kg per hectare (unpublished) and changes have been observed in the fish community, macrophyte abundance and water quality (Cape Nature, 2020).

Contributions of Groenvlei to the society and economy

The lake is currently used by recreational and subsistence anglers targeting mainly *M. salmoides* and *C. carpio* with rod and line. Due to the reeds on the banks around the lake, fishing from the shoreline is limited and the only public authorised access point is located from the national road (N2). Boat fishing using small row or electric motor powered boats is allowed and can be launched at this entry point (Dredge and Weyl, 2017). The lake was known for the annual bass angling tournaments, whereby approximately 1000 members of the Southern African bass angling societies participated, however these have ceased due to low catches, attributed to the increase in *C. carpio* numbers (Ellender et al., 2014). The lake is visited by tourists and used for hiking trails, canoeing and birding through the surrounding Goukamma Nature Reserve (Cape Nature, 2020). The potential of Groenvlei to contribute to inland fisheries was investigated by Dredge and Weyl (2017) who reported that the potential yield estimates ranging from 12 to 55 ton per year were too low to promote and sustain a formal commercial fishery.

Management and conservation

The National Environmental Management: Biodiversity Act (NEMBA) under the recently published Alien and Invasive Species Regulations (DEFF, 2020), *C. carpio* is listed in Category 1b; therefore in conservation priority areas such as Provincial Reserves and Mountain Catchment Areas, species within this category require compulsory control as part of non-native invasive species control programme (DEA, 2014; Wilson et al., 2018). Thereby, South African conservation management authorities, are mandated to conserve biodiversity and ensure natural ecosystem functioning (Wilson et al., 2018). The detection of *C. carpio* in Groenvlei 15 years ago has raised concerns amongst conservationists and local people (Phair et al., 2015). Phair et al. (2015) emphasized the impacts *C. carpio* might have on the populations of two native fish species *A. breviceps* and *G. aestuaria*. Cape Nature, the governmental organisation responsible for the management of Groenvlei and the surrounding Goukamma Nature Reserve have implemented gillnetting and bowfishing to reduce the *C. carpio* population biomass (Cape Nature, 2020), and from March 2020 NGO 'Gift of the Givers' established a scheme using the harvested *C. carpio* in Groenvlei to feed people impacted by the COVID-19 global pandemic (Cape Nature, 2021).

A better understanding of the biology and ecology of *C. carpio* in Groenvlei could be used to optimise the current control efforts. Therefore, this study aims to investigate the life history traits and the habitat use of non-native *C. carpio* in Groenvlei, in addition, the global literature on the control of *C. carpio* is consolidated with the purpose of guiding management interventions of this species.

The objectives of this study are:

i. Determine the age and growth characteristics including age at sexual maturity of *C. carpio* at Groenvlei to allow for growth rate comparison across other ecosystems

ii. Observe the movement patterns and spatial use of the lake by *C. carpio* during a year period and determine if any changes in movement is associated with environmental changes (i.e., temperature/rainfall) and/or the biology (i.e., life history strategy)

iii. Conduct a systematic literature review on the global control of *C. carpio* to discuss methods used and which have been successful at controlling alien *C. carpio* populations

Thesis outline

Chapter 1. General introduction

Chapter 2. The life history of non-native common carp, *Cyprinus carpio* in Groenvlei

Chapter 3. Temporal space-use and movement patterns of *Cyprinus carpio* in Groenvlei

Chapter 4. Systematic literature review on the global control of *Cyprinus carpio*

Chapter 5. General discussion and recommendations

CHAPTER 2: The life history of non-native common carp, *Cyprinus carpio in Groenvlei*

Introduction

The life history of an organism is a trade-off between growth, reproduction and survival and is constrained by individual genetic material and natural selection (Roff, 1984; Winemiller, 2005). *Cyprinus carpio* shows variable growth characteristics in its native and non-native range, with a lifespan of 15 years in the native region (Balon, 1995), it can live up to 30 years in its introduced range (Bajer and Sorensen, 2009; Bajer et al., 2015), with anecdotal evidence reporting *C. carpio* of up to 140 years in the Austrian region, although these outliers are generally considered unreliable (see Vilizzi and Copp, 2017). *Cyprinus carpio* grow fast during the first years and reach reproductive maturity as early as two to three years outside their native range (Balon, 1995; Vilizzi and Walker, 1999; Winker et al., 2011). Populations in the tropical regions tend to grow the fastest (Tempero et al., 2006; Hailu, 2013), with the shortest observed generation time of two to four years recorded in the Lake Naivasha, Kenya population, where the reproductive season extends over seven months (Britton et al., 2007; Oyugi et al., 2011). Recruitment of *C. carpio* is irregular but synchronised and it is driven by environmental factors such as changes in temperature, wind and water level fluctuations (Tampero, 2006; Weber and Brown, 2011; 2013).

The growth of *C. carpio* has been studied using calcified structures including scales (Britton et al., 2007; Oyugi et al., 2011), otoliths (Brown et al., 2004; Winker et al., 2010), vertebrae and opercles (Phelps et al., 2007; Yates et al., 2016). In *C. carpio* age and growth studies, scales are the commonly used structure due to the simplicity of the collection methods, however in areas where non-native *C. carpio* is regarded as a high "risk species" for example, Australia and South Africa, studies using scales as ageing structures only makes up 20% and 25% respectively (Vilizzi, 2018). Lack of accuracy provided by scales is of concern in its invasive range as scales are limited by seasonal reabsorption, difficulty in standardizing collection methods and inconsistent growth check formations (Britton et al., 2007; Brown et al., 2004; Oyugi et al., 2011). Asteriscii, the largest otolith in *C. carpio* has been shown to be a more reliable source of age data compared to other structures and the only validated structure using chemical mark-recapture technique (Phelps et al., 2007; Vilizzi, 2018).

Oxytetracycline hydrochloride (OTC), the most commonly used chemical marker, rapidly chelates in otoliths and produces a fluorescent mark when viewed with ultraviolet light (Campana, 1999) which creates a timestamp used in age validation studies. During this chemical validation technique, OTC marked individuals are recaptured after a known period (time at liberty) which is used to validate growth zone periodicity (Campana, 2001). Using the fluorescent marking technique, both annual and biannual growth annulus deposition have been reported on *C. carpio* populations outside its native range and the difference is attributed to climate and system productivity (Brown et al., 2004; Winker et al., 2011).

The present study will be the second to validate the growth annulus deposition on a South African population of *C. carpio* using chemical mark-recapture technique.

In addition to growth rate, age at maturity is an important metric to consider in non-native fishes (West, 1990). Age at maturity is a trade-off between reproducing at larger size (greater age) which has higher chances of success as bigger fish have the ability to produce more gametes, but also increased risk of death before reproduction (Roff 1984; West, 1990). The reproduction potential of most fish species is studied through histology and macroscopic gonad assessments (Flores et al., 2016), whereby length-class is linked to maturity stages to determine the proportion of the population that is ready to reproduce, and determines the speed at which the population density increases (Weyl and Booth, 1999). When individuals attain maturity much of the energy that was allocated to somatic growth is allocated to reproduction (Rennie et al., 2005). Global studies of *C. carpio* show that changes in gonadal development associated with spawning correlates with increases in water temperature (> 16 ºC) (Stuart and Jones, 2002; Smith and Walker, 2004), and sexual maturity is commonly reached at two and three years with some populations having extended spawning seasons while others spawn repeatedly during a single spawning season (Sivakumaran et al., 2003; Brown et al., 2005). There is variability in *C. carpio*'s reproductive behaviour across different populations, and therefore, the second objective of this chapter was to focus on the recruitment patterns of *C. carpio* in Groenvlei, South Africa.

The objectives of this chapter were to:

1. To validate *C. carpio* annulus formation on the asteriscus otolith and use these otoliths to age *C. carpio* from Groenvlei
2. To use macroscopic gonad staging method to study the reproduction biology of *C. carpio*

Materials and methods

Study site

The present study was conducted in Groenvlei (34º01'34S, 22º51'00E), a lake within the Goukamma Nature Reserve in the Western Cape Province of South Africa (Figure 2.1). It has a west-east elongated shape with a surface area of 2.34 km^2 (250 hectares), it is 3.7 km long and 0.9 km wide with a maximum depth of 5.5 m (Coetzee, 1980). The lake formed during the Late Pleistocene and Holocene through changes in sea levels and became isolated from the nearby Indian Ocean 4000 years ago (Martin, 1960; Phair et al., 2015). Groenvlei is bounded by vegetated dunes across all sides, with no influent rivers or open connections to the sea, and the water level is maintained by rainfall, aquifers and groundwater (Parson, 2009; Phair et al., 2015). Groenvlei is a near freshwater lake with a neutral to alkaline pH, the rain water makes up 71.6% while groundwater and aquifers makes up 28.4% of the lake water level (Parsons, 2014). The water levels in Groenvlei fluctuate from time to time and varies yearly, with high

water levels during the rainfall season (approximately August to January) and low water levels during the dry seasons (approximately February to July) (Figure 2.2).

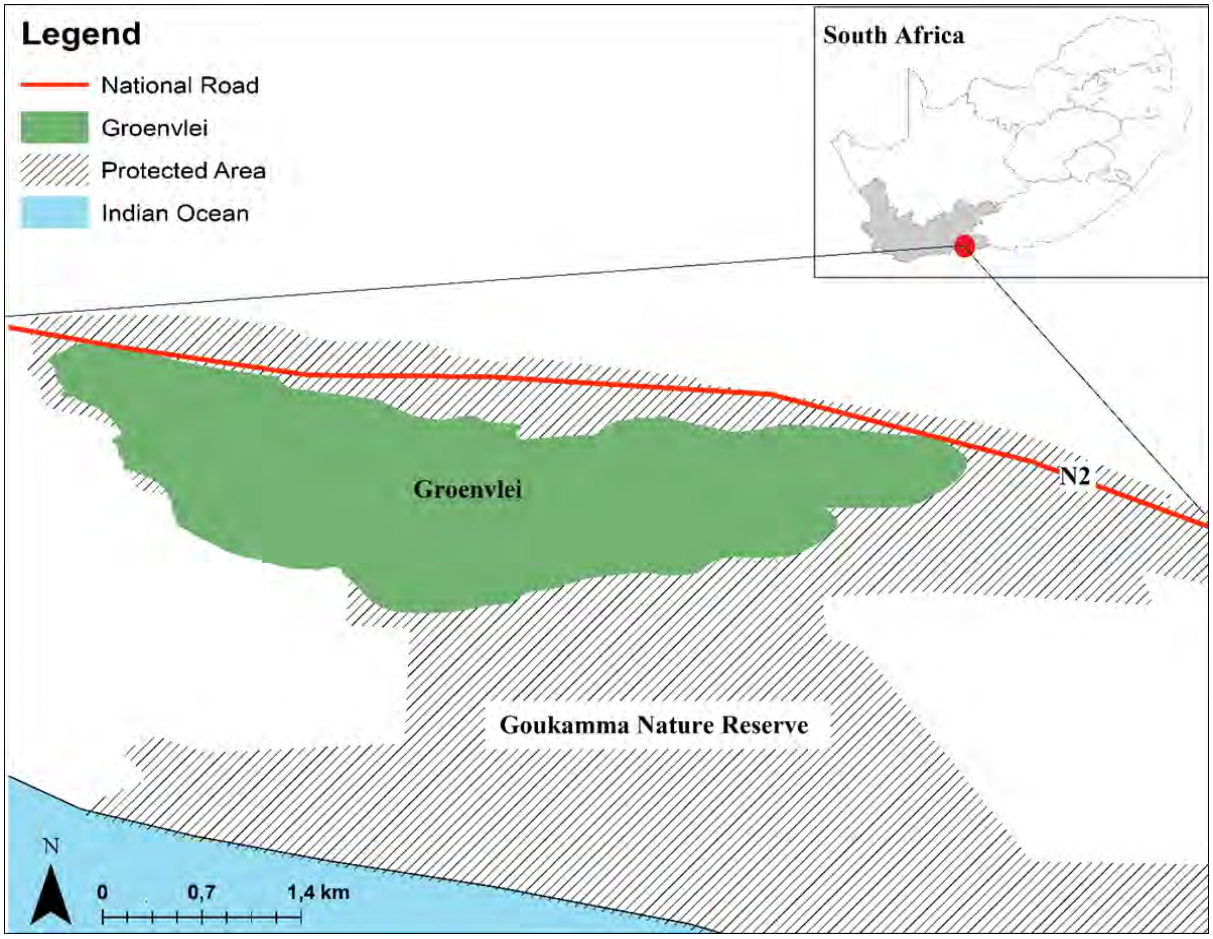

Figure 2.1. Groenvlei, located within the Goukamma Nature Reserve in the Western Cape Province, South Africa.

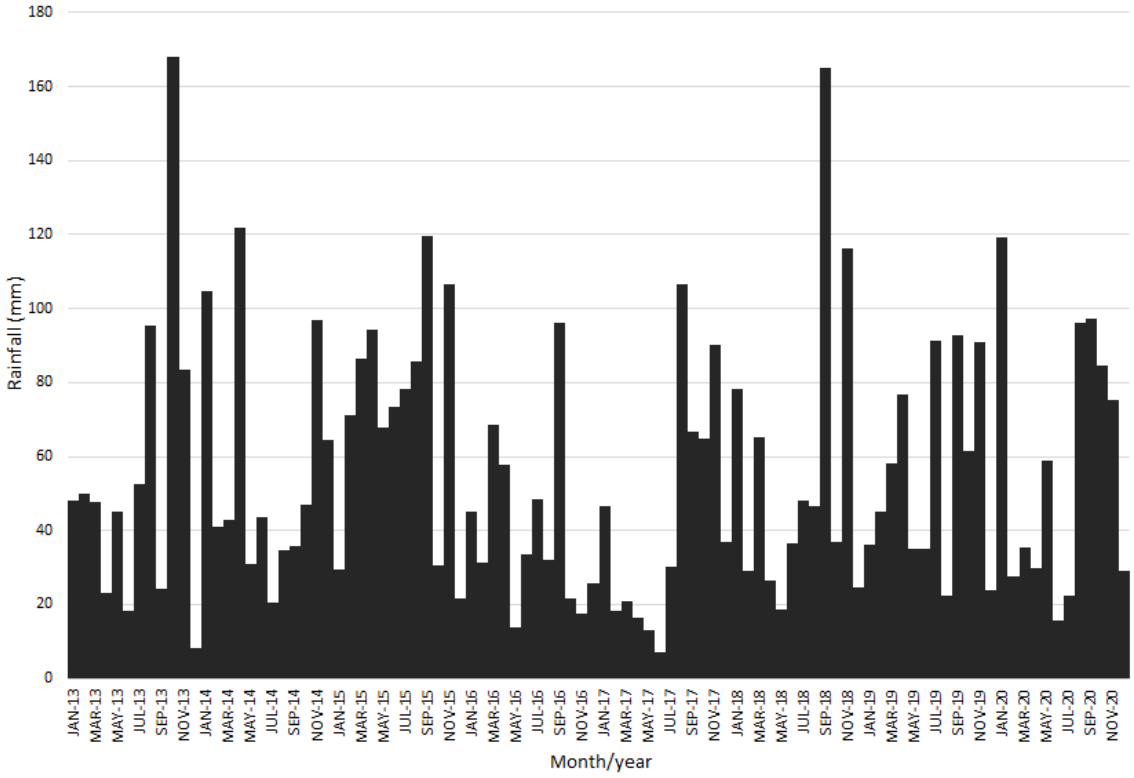

Figure 2.2. Variation in daily average rainfall from January 2013 to December 2020 measured at Knysna Station [0014123 3] (Data Source: South African Weather Services).

Environmental variables

Groenvlei experiences a mild to temperate climate and the surrounding area receives a mean annual rainfall of 780 mm (Figure 2.2) which falls predominantly during the austral winter (Parson, 2009). It is typically warm, with minimum temperatures of 15 °C in winter and 30 °C in summer (Figure 2.3).

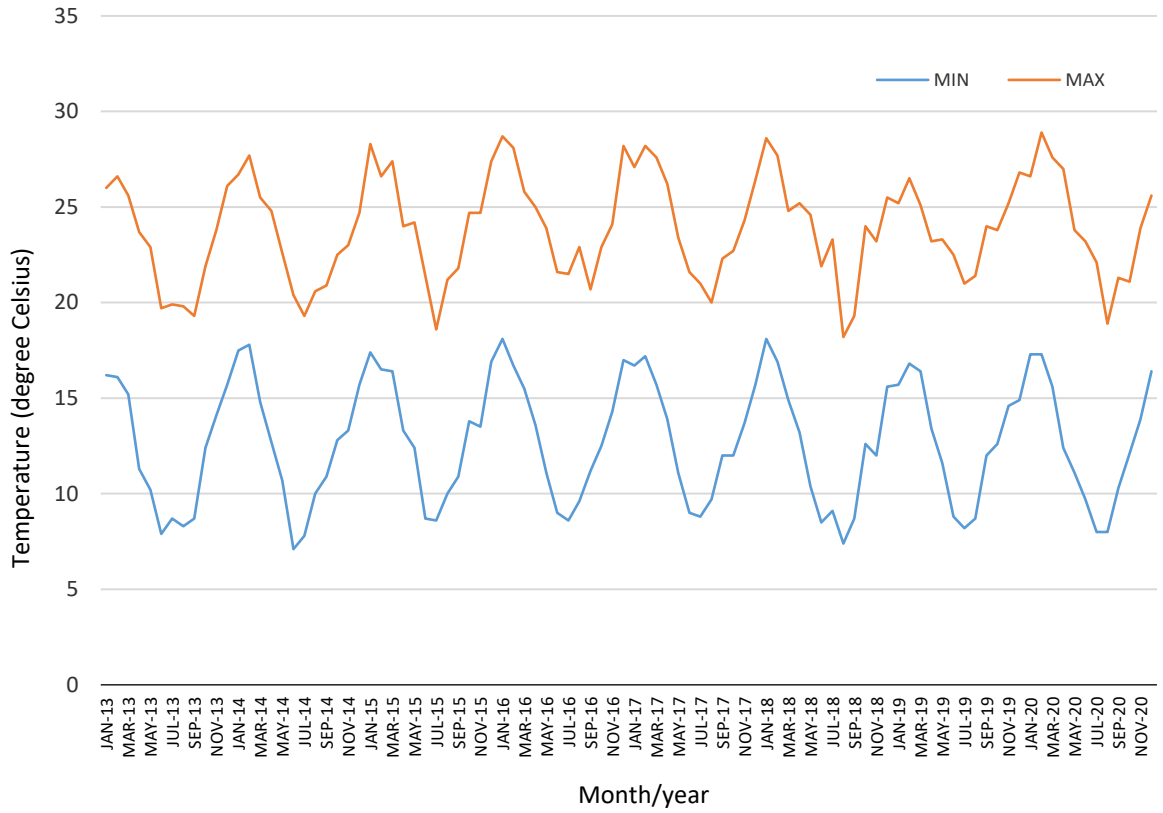

Figure 2.3. Minimum and maximum temperatures from January 2013 to December 2020 measured at Knysna Station [0014123 3] (Data Source: South African Weather Services).

Biotic characteristics

Few fish species live in Groenvlei; there are two indigenous fishes, Cape silverside *Atherina breviceps* (Valenciennes, 1835) and estuarine round herring *Gilchristella aesturia* (Gilchrist, 1913), which are of marine origin (Phair et al., 2015). Using allozymes, Ratte (1989) found that both *A. breviceps* and *G. aestuaria* populations in Groenvlei have significantly diverged from the population in Swartvlei, the nearby estuary (10.7 km away) thus these native species are of some conservation interest. There are five introduced non-native species, including common carp *Cyprinus carpio*, Mozambique tilapia *Oreochromis mossambicus*, Largemouth bass *Micropterus salmoides*, bluegill sunfish *Lepomis macrochirus* (Rafinesque, 1810) and mosquito fish *Gambusia affinis* (Baird and Girard, 1853) (Phair et al., 2015). Approximately 1.52 km^2 of the lake's surface and lake edge is covered by vegetation such as common reeds *Phragmites australis*, common bulrush *Typha capensis*, swamp sawgrass *Cladium mariscus* and bulrush *Scirpus littoralis* (all macrophytes) (Fijen, 1995). Various habitats exists within the water body and this includes (i) open water with macrophytes which makes up the majority, (ii) open water with exposed muddy bottom, (iii) reeds and (iv) open backwaters (Figure 2.4). The backwater habitats are located on the north eastern edges of the lake and are shallow (depth less than one meter) with different entry points depending on the water level of the lake.

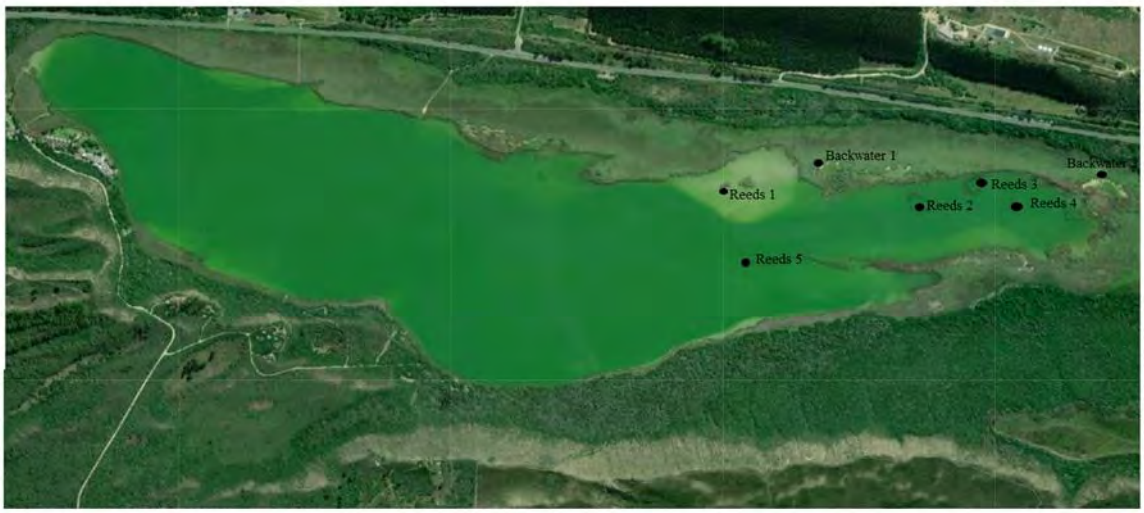

Figure 2.4. Arial map of Groenvlei showing the two main habitat types: reed habitats and backwaters. The rest of the lake consists of open water with muddy bottom and or macrophytes. (Image Source: Earth Explorer).

Fish sampling

Cyprinus carpio were caught on rod and line by volunteer anglers between 2013 and 2018. These *C. carpio* were measured, weighed and injected with oxytetracycline hydrochloride (OTC) at a dose of 0.5ml kg^{-1}. Fish were tagged with an external T-bar anchor tags before released back into the lake. A total of 18 tagged *C. carpio* were recaptured between 2019 and 2020, measured, killed and had their asteriscus otoliths removed and donated to this project; this otoliths were used for the age validation.

During this study, *C. carpio* used for age determination were captured in November 2020 using double ended fyke nets and 30 m long seine nets, with 1 cm mesh size. Any non-target species captured were released immediately into the lake. *Cyprinus carpio* were killed using percussive trauma to the skull followed by destruction of the brain, or overdose of anaesthetic (clove oil) dependent on size. Additional *C. carpio* were donated dead from the Cape Nature carp removal project which were caught using gillnets and bow and arrow (Cape Nature permit: CN-44-28-8357). Both captured and donated *C. carpio* were measured for fork lengths using a measuring board, weight was recorded from an electronic balance and the sex was macroscopically determined through direct examination of gonads following the gonadal development stage criteria (Table 2.1). The asteriscus otoliths were then extracted using a knife, pliers and forceps, dried and stored in 1.5 ml Eppendorf tubes for later age determination.

Otolith validation

One asteriscus otolith per specimen was mounted in clear polyester casting resin following Morison et al. (1998) and Anderson et al. (1992) methodologies. Once dry, a 0.4 mm transverse section through the core was removed with a Buehler Isomet low-speed diamond blade saw and mounted on a

microscope slide using DPX mounting agent. The microscope slides were viewed under the Fluorescence Microscope at the Electron Microscope Unit Laboratory at Rhodes University, and photographed under ultraviolet light and white light in the same position. Growth zones were visible as alternating translucent (light) and opaque (dark) zones under white light and the fluorescence mark was clearly visible as a yellow line under the ultraviolet light. The fluorescence mark was visible in 16 of the 18 OTC marked *C. carpio.* The number of the growth annuli post fluorescence mark were counted and this number of annuli per year validated by comparing this with known time at liberty. The readers spent time familiarizing themselves with the validated otolith morphology and annuli structure before assigning ages to specimens.

Otolith reading and age determination

Two commonly used methods of reading *C. carpio* asterescii otolith were tested, whole otoliths submerged in methyl salicylate and sectioned otoliths viewed under transmitted light. The sectioned were clearer and easier to read compared to whole otoliths and therefore this was accepted as a standard protocol for age determination for this study. Following the sectioning and mounting of otolith on the microscope slides as described above, the otoliths were read under a light microscope at varying magnifications (×10 – 40) for age determination.

Life history characteristics

In total, 140 sectioned otoliths were accepted for age determination. The otoliths were read at least twice by the first reader, then the readings were validated by a second reader who had experience in otolith reading from other fish species. The age-at-length was analysed using the three parameter deterministic von Bertalanffy Growth model (Von Bertalanffy, 1938) in the form:

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

With

$$L_\infty = \left[\frac{\exp(at_2)L_2 - \exp(at_1)L_1}{\exp(at_2) - \exp(at_1)}\right]$$

$$K = b$$

$$t_0 = t_1 + t_2 - \frac{1}{a} ln \left[\frac{\exp(at_2)L_2 - \exp(at_1)L_1}{L_2 - L_1}\right]$$

Where L_∞ is the theoretical asymptotic length of a fish, *K* is the Brody growth coefficient and t_0 is the theoretical age of a zero-length fish (Ricker, 1975). The curve fitting was performed using RStudio using the *FSA* (Ogle and Ogle, 2016), *dplyr* (Wickham and Francois, 2015) and *ggplot2* (Wickham, 2016) packages (RCore team, 2021).

Length and weight relationship

The relationships between F_L and *W* were determined by fitting the data to the equation; $W = aL^b$ (Ricker, 1975), where L is the length (mm F_L), *W* is the total weight (nearest 0.1 g), and a and b are constants. Regression analysis was employed on data for males and females separately.

Reproduction biology

Macroscopic assessment of gonadal development (Flores et al., 2015) was undertaken following a criteria summarised in Table 2.1.

Table 2.1. Macroscopic criteria used to determine gonadal developmental stage of *Cyprinus carpio* from Groenvlei, South Africa (Modified from Winker et al., 2011)

Stage	Macroscopic appearance
Juvenile	Gonads appear as very thin translucent strips. It is not possible to visibly distinguish the sex
Immature	Sex is distinguishable. Ovary are visible as translucent strips. Testes for thin but opaque white strips
Resting	Ovary translucent and increased in size. Testes are visible as white and straight strip
Developing	Ovary is orange-red and enlarged with visible oocytes. Testes increased in size and becomes lobular in shape
Ripe	Ovaries turgid with oocytes filling the entire abdominal cavity. Oocytes are olive-green in colour. Blood capillaries are abundant. Testes are enlarged, creamy white and fill more than one third of the body cavity. Sperm can be extruded from testes
Spent	Ovary and testes flaccid and reddish in appearance. Ovary occasionally with a few vitellogenic oocytes present

Length at 50% sexual maturity (Lm_{50}) was determined from 72 males and 78 females collected during October 2020, at which time spawning activities were observed. The proportion of reproductively active fish (developing, ripe or spent) was calculated by grouping specimens into 10-mm size classes (Brown et al., 2005; Winker, 2010) and fitting 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 length L and δ_L is the width of the ogive. The ogive curve fitting was performed using RStudio using the function *Ogive* (Flores et al., 2015; RCore team, 2021). Additionally, the proportion of mature males and females from each age class was calculated based on a total subsample of 42 males and 43 females with known age, following Winker (2011) actual maturity determination methods.

Results

A total of 229 *C. carpio* were measured for length and weight and 140 otoliths were sectioned and accepted for age determination. Similar to Brown et al. (2004) and Brouwer and Griffiths (2004), this study found whole otolith to be dark and challenging to read, especially on the large *C. carpio*. Apart from the opaque primordial (also known as the focus) that reduces the clarity of the first growth annulus (Brown et al., 2004), transversely sectioned *C. carpio* otoliths are clear and simple to read and therefore, accepted as standard protocol for age determination in this study.

On average the females were significantly longer (Mean ± SD; 448. 3 ± 151.7 mm F_L) compared to males (Mean ± SD; 379.9 ± 177.6 mm F_L) ($t = 1.74$; $p > 0.05$) and more were captured above 400 mm F_L (n = 68 F, n = 47 M). The smallest specimen was a 94 mm F_L weighing 14 grams. The largest specimens by weight and length were two males; 5.9 kg with 651 mm F_L length and 698 mm F_L weighing 3.5 kg, respectively. The morphometric relationships between length and weight was statistically significant and represented by the formula: Weight = $2.6\ e^{-5}$ $(\text{length})^{2.945}$ ($R^2 = 0.99$, $p < 0.05$) (Figure 2.5).

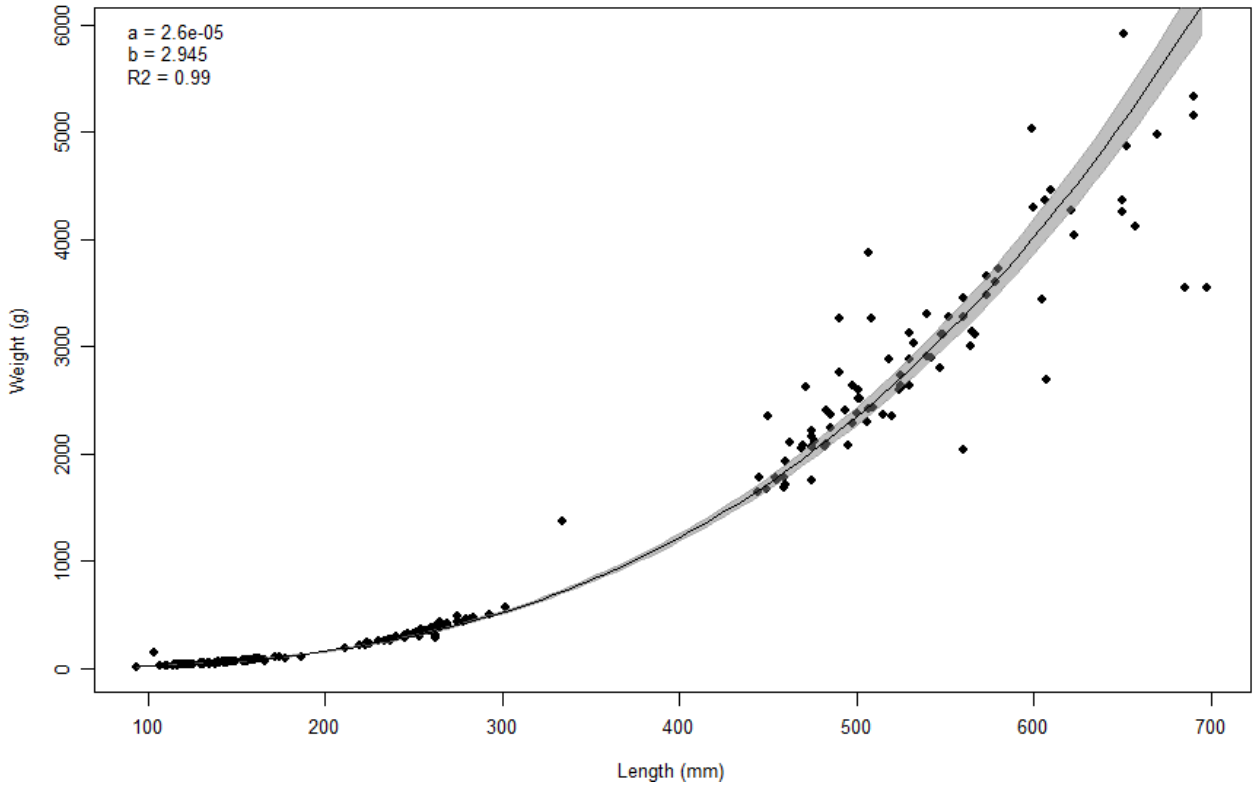

Figure 2.5. The morphometric relationship between length and weight of *C. carpio* in Groenvleiis statistically significant and represented by: Weight = 2.6 e $^{-5}$ (length) 2.945 (R2 = 0.99, $p < 0.05$).

Of all the collected specimens, 140 sectioned otolith were accepted as readable for use in this analysis. Reasons for otolith rejections included broken otoliths (during extraction and sectioning), bubbles formed during the mounting process and the occurrence of dark discontinuous bands referred to as "pseudoannulli" (Vilizzi and Walker, 1999).

Fluorescence marking

For increased accuracy and precision of otolith interpretation, only clear otoliths (thick and continuous opaque zones) with available capture information were used for growth zone counts during the validation experiment. The width of the translucent zones was initially larger but decreased with age, as the growth rate slowed down. Time at liberty of these fishes ranged from four to six years and their ages on recapture ranged from eight to 20 years. The position of the fluorescent mark was clearly visible, except on one specimen which had an opaque zone coinciding with the fluorescent mark, and the growth zone for this was counted as prior to the mark. The number of opaque zones distal to the OTC mark and the known time at liberty confirmed that one opaque and one translucent zone were deposited each year (see Supplementary table 1).

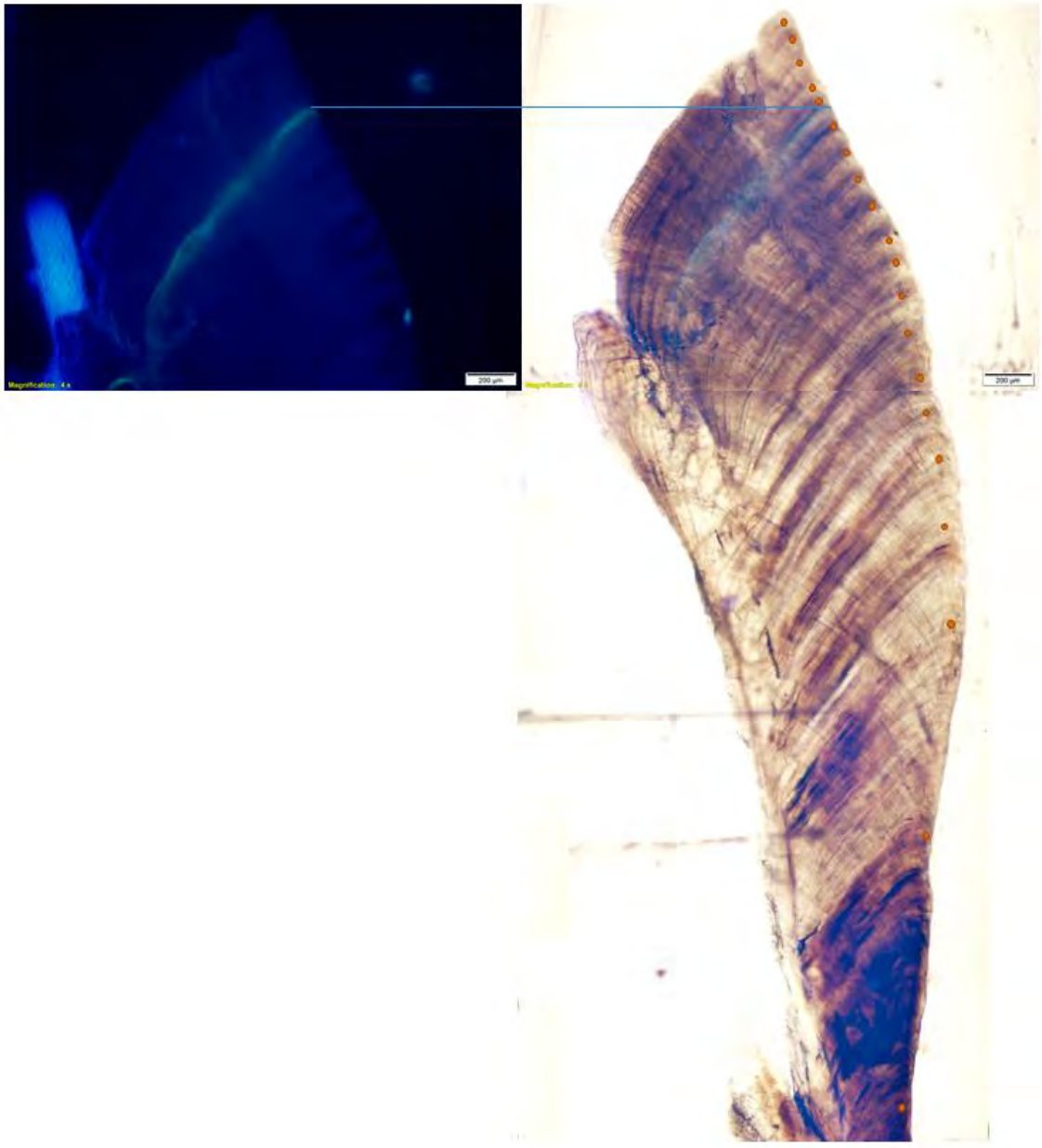

Figure 2.6. An OTC marked otolith of *Cyprinus carpio* from Groenvlei, South Africa under ultraviolet light (left) and white light (right). This specimen was 465 mm F_L, 20-years old (indicated by red circles) and had time in liberty of four years and seven months.

Length at age

The sectioned *C. carpio* asteriscus otoliths consisted of clear opaque and translucent growth zones which were counted as age and plotted against the fork length for both males and females. Based on the theoretical asymptotic length estimate (L_∞) and the distribution of residuals, the von Bertalanffy growth function adequately fitted the observed length-at-age data derived from otolith sections. The parameter values of the growth functions are shown in Table 2.2. The growth of *C. carpio* in Groenvlei differed between males and females; the biggest specimens by weight and length were males, however, females dominated the older age-classes and reached the oldest of 20 years whereas the oldest male was 18 years old (Figure 2.7; Supplementary Table 1). There was considerable variation in length-at-age especially after 500 mm F_L, consisting of individuals of ages from five to 20 years old, showing the fast growth of individuals during the first ages. The combined Von Bertalanffy growth function shows that the sample was dominated by individuals that have not reached their asymptotic length of 665 mm F_L (Figure 2.8).

Table 2.2. Von Bertalanffy parameter for males, females and the entire population of *C. carpio* in Groenvlei, South Africa.

	L_∞ (mm F_L)	K (year^{-1})	t_0 (years)
Male	642	0.23	-0.10
Female	671	0.25	0.04
Combined (M & F)	665	0.24	-0.08

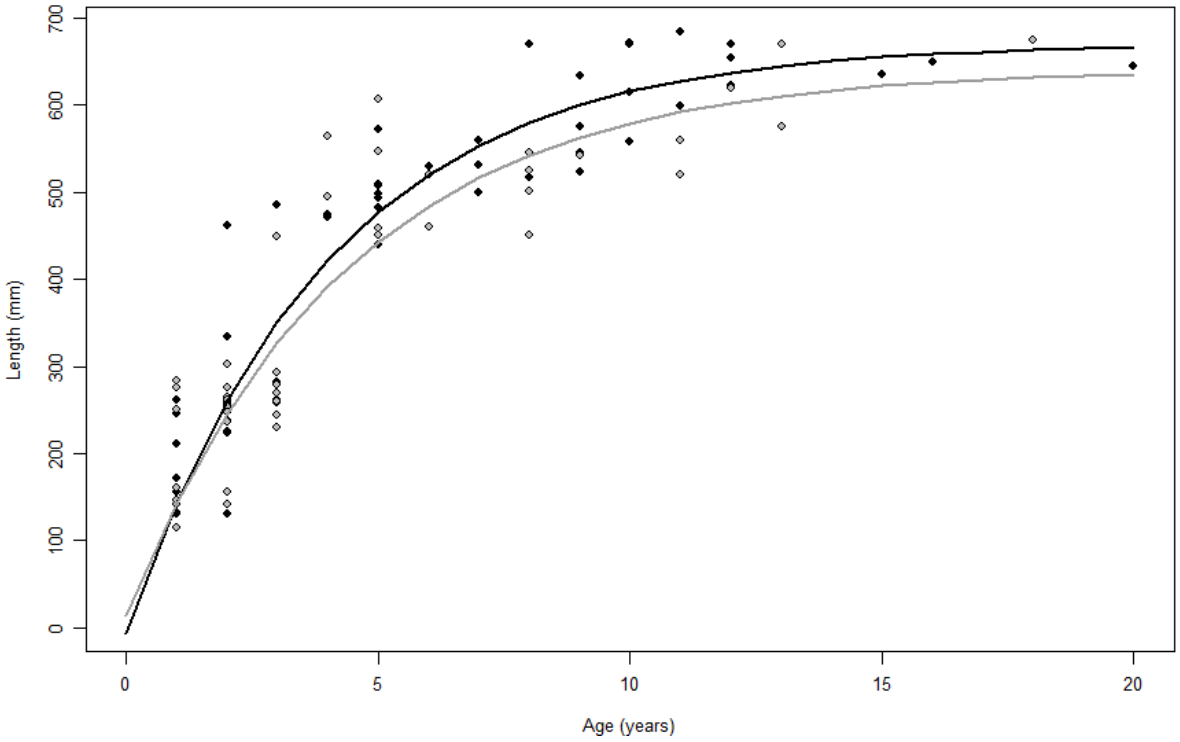

Figure 2.7. Length-at-age data for *Cyprinus carpio* using sectioned otoliths sampled in Groenvlei, South Africa. Growth was described by the Von Bertalanffy Growth Model (Von Bertalanffy, 1938). Growth curve fit for females (black) and males (grey).

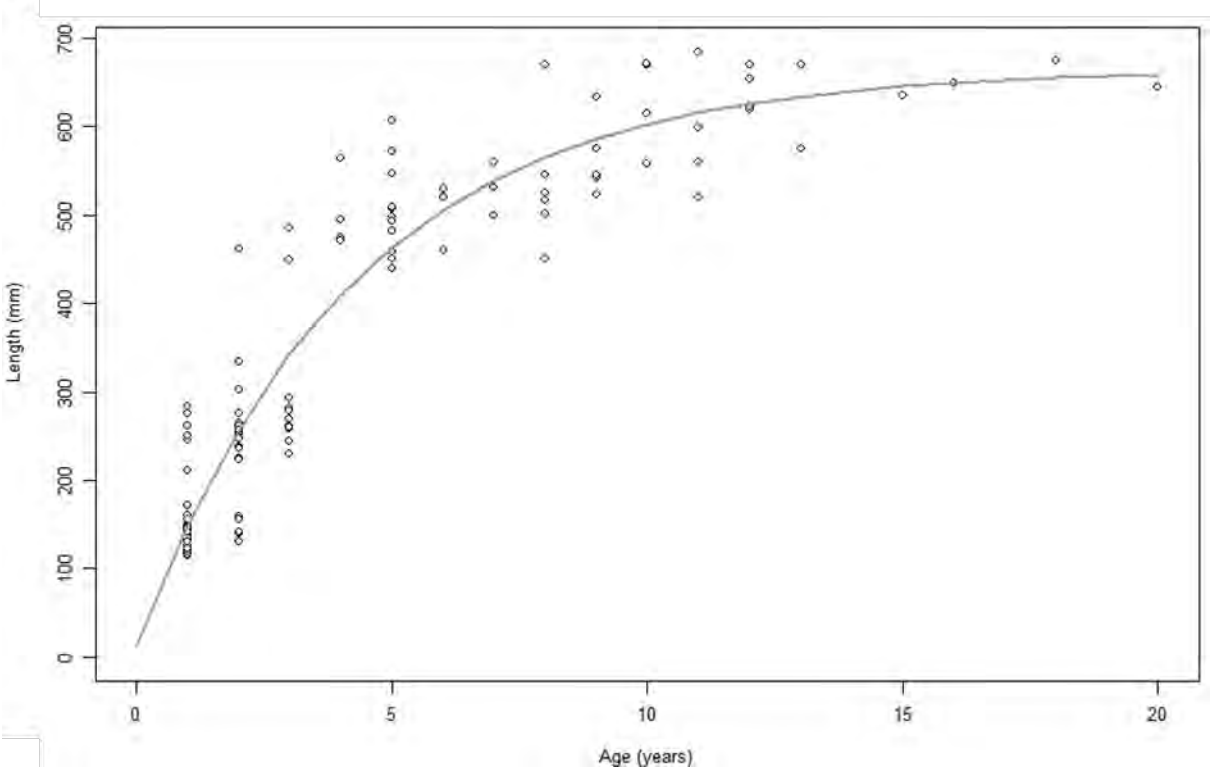

Figure 2.8. Length-at-age data for the combined (male and female) *Cyprinus carpio* in Groenvlei, South Africa. Growth was described by the Von Bertalanffy Growth Model (Von Bertalanffy, 1938).

Life history comparison

The growth performance parameter was calculated using the equation Φ' = 2log (L∞/10) + log (K) (Pauly and Munro, 1984). The comparison of *C. carpio* populations across various regions (Table 2.3) showed that introduced *C. carpio* populations at different regions have a similar growth performance, with the slowest growing population being in the Barmah Forest, Australia. Age-at 50% maturity was similar among different regions, but different across males and females, around the fork length of 200 to 300 with the exception of the Lake Naivasha population, Kenya which attained maturity at larger sizes. In general males attained sexual maturity earlier compared to females except for this study population. The lowest maximum age was from the population of Lake Naivasha, four years old whereas the oldest was from the slow-growing population of Barmah Forest. The Groenvlei population was relatively long lived (up to 20 years) compared to the only other South African population, the lake Gariep population which only lived up to seven years.

Table 2.3. Growth of *C. carpio* in other regions based on validated studies showing the *tmax*= maximum age, *Lmax*= maximum length, Lm50% = length at 50% maturity, the three parameters of VBGF model (L_∞, *K* and t_0), Φ' = 2log (L∞/10) + log (K) (Pauly and Munro, 1984).

Sex	Ageing structure	*tmax* (years)	*Lmax*	$Lm_{50\%}$ (L_F mm)	3 parameter VBG growth model			Φ	Region
					L_∞	*K*	t_0		
Female	Scales	4	694	420	755	0,75	-	3,63	Lake Naivasha Kenya[1]
Male		3	694	340	618	0,68	-	3,41	
Female	Otoliths*#	7	680	334,8	881	0,21	-0,02	3,19	Lake Gariep South Africa[2]
Male		7	661	295,9	839	0,21	-0,02	3,16	
Female	Otoliths*	28	623	328	594	0,18	-0.61	2,80	Barmah Forest Australia[3]
Male		24	570	307	489	0,25	-0.52	2,77	
Female	Otoliths*	20	698	262,2	671	0,25	0,040	3,09	Groenvlei South Africa[4]
Male		18	685	314, 2	642	0,23	-0,097	3,03	

1. Oyugi et al. (2011) 2. Winker et al. (2011) 3. Brown et al. (2005) 4. This study * sectioned otolith #whole otoliths

Reproduction

The average length at 50% maturity was estimated at 314mm F_L for males and 262 mm F_L for females (Figure 2.9). Similar to Winker et al. (2011), actual maturity was allocated to individuals in the developing, ripe and spent gonadal development stage (see Table 2.1.) and the smallest mature male and female in the sample were 230 mm F_L and 223 mm F_L respectively. From a total of 42 males and 43 females subsample, the proportion of mature males and females in various age class was calculated based on the actual age estimates derived from sectioned otoliths that were successfully read (Table 2.4). The results showed increase in maturity with age; 29% of males and 43% of females in age group 1 were reproductively mature, followed by 73% males and 90% females in age-2 group, from the age of three to the oldest specimen, all individuals had ripe gonads (Figure 2.10). In total 83.5% of all specimens were identified as reproductively active. During this study no individual had spent gonads.

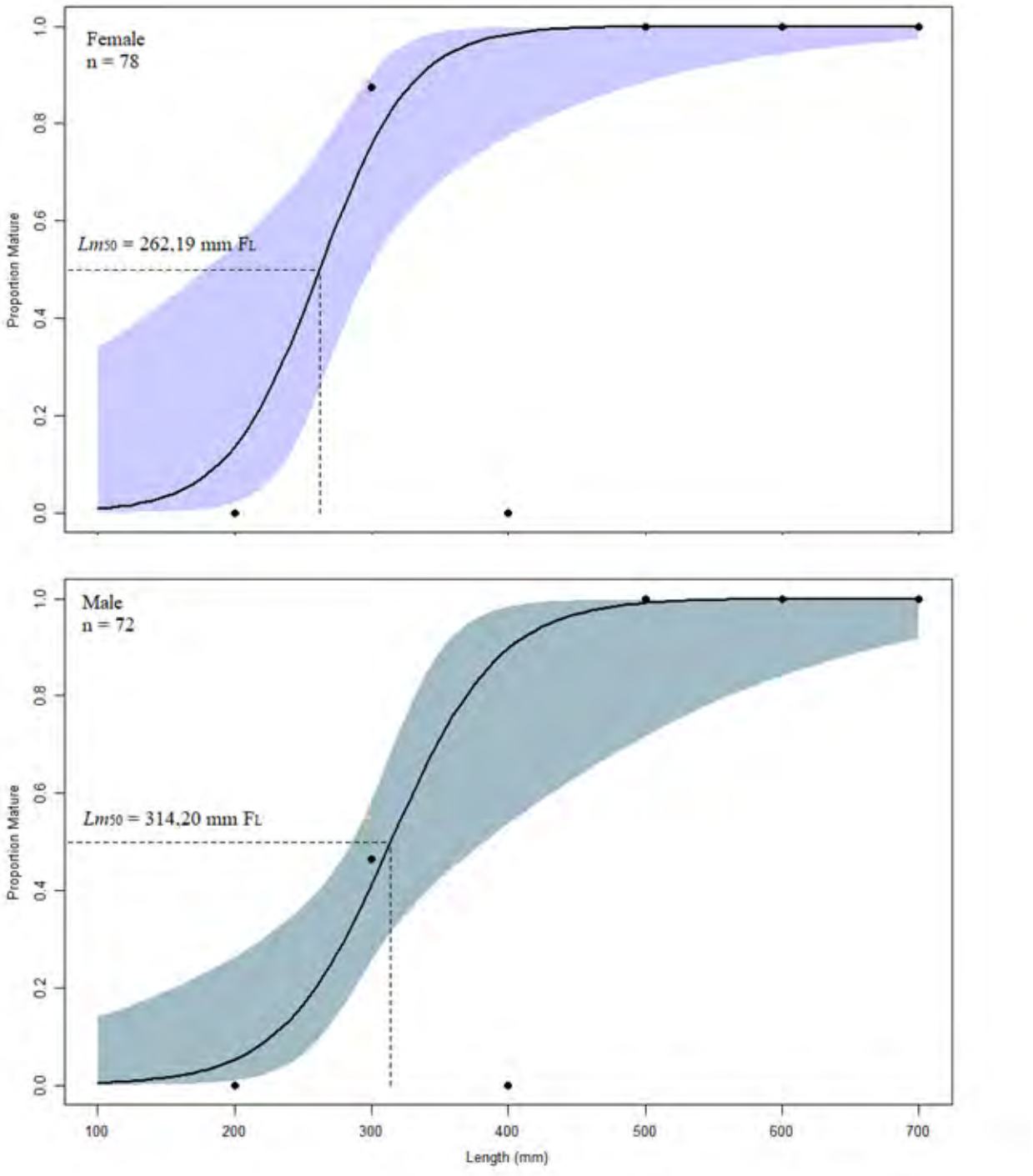

Figure 2.9. Logistic ogives fitted to the proportion of mature female and male *C. carpio* from Groenvlei, South Africa. Lm_{50} is the length-at-50% maturity.

Table 2.4. Observed proportion of mature *Cyprinus carpio* per age-class calculated from sectioned otoliths from Groenvlei collected in late October 2020 during the spawning season (peak spawning season in South Africa = November (Winker et al., 2010). The dash (–) represent lack of individuals within the age class.

Age class (years)		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Male	Fraction mature	0.29	0.73	1	1	1	1	-	1	1	-	1	-	1	-	-	-
	Sample size (n)	7	15	7	2	4	1	-	2	1	-	2	-	1	-	-	-
Female	Fraction mature	0.43	0.9	1	1	1	1	1	1	1	1	1	-	-	-	-	1
	Sample size (n)	7	10	4	2	8	2	3	2	2	1	1	-	-	-	-	1

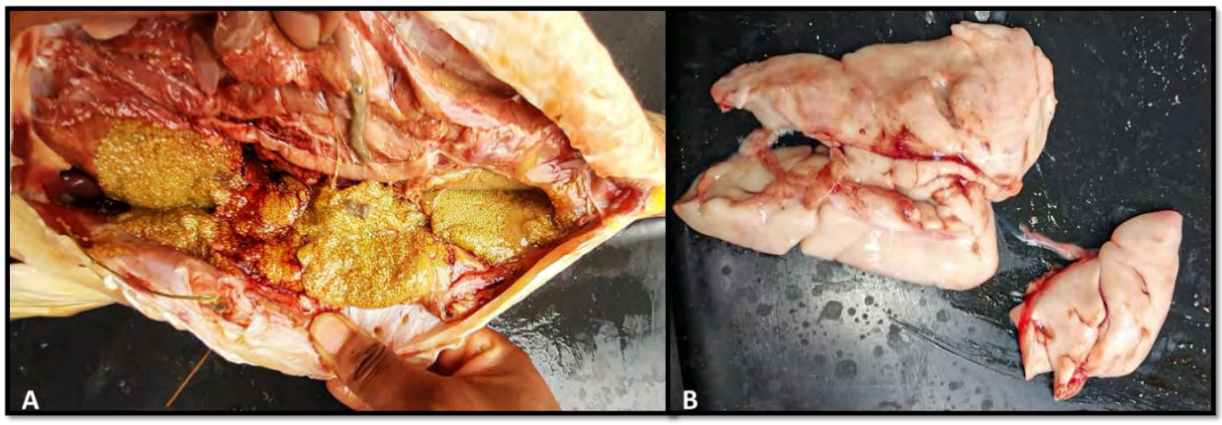

Figure 2.10. Ripe *Cyprinus carpio* gonads, (A) female ovaries turgid with oocytes filling the entire abdominal cavity and oocytes are olive-green in colour with abundant blood capillaries. (B) male testes are enlarged, creamy white and fill more than one third of the body cavity and sperm can be extruded from these testes.

Discussion

The comparison of growth performances amongst global *C. carpio* populations is often limited by lack of accurate and precise growth studies based on validated growth structures (Yates et al., 2016). Chemical marking of calcified structures and mark-recapture technique is considered the most powerful method of validation used to successfully determine the growth deposition rate on calcified structures for a wide range of fishes (Campana, 2001; Brown et al., 2004) and the present study successfully validated the growth annulus deposition rate of *C. carpio* in Groenvlei using mark-recapture of OTC marked individuals. *Cyprinus carpio* in Groenvlei were assigned age based on sectioned asteriscus otoliths, as whole otoliths submerged under methyl silicate showed poor readability and resulted in higher estimates of age. Poor readability in *C. carpio* on whole otolith is not uncommon and has been demonstrated for other populations (Yates et al., 2016; Vilizzi, 2018).

The clear florescence marking provided evidence of one growth annulus (comprised of one opaque and one translucent zone) deposited each year on the Groenvlei population of *C. carpio*, a similar growth deposition pattern was found in the Australian population using similar validation methodology (Brown et al., 2004). However, in the *C. carpio* population of Lake Gariep, South Africa, the validation technique showed strong evidence for a biannual growth zone deposition rate (Winker et al., 2010). This shows the importance of validating the annual frequency of growth zone deposition of different populations within an area prior to assigning age of fish. Although both Groenvlei and Lake Gariep are in South Africa, there is considerable variability in these two systems such as size, with Lake Gariep being larger (36400 hectors) and influenced by the harsh, unpredictable climate of the Orange River system (Winker et al., 2011), while Groenvlei is relatively smaller (2.5 hectors) and isolated with no in/out flow, thus less environmental and seasonal fluctuations (Whitfield, 2000). Additional variability in the growth of these two populations may be attributed to factors such as food availability, competition and other density-dependent processes between the two systems (Weber et al., 2010; Winker et al., 2011). The short lifespan (tmax = 7 years) of *C. carpio* at Gariep Dam may be attributed to intraspecific competition for resources with the large benthivorous cyprinid, *Labeo capensis* and the presence of *C. carpio* egg and larvae predators (*L. capensis* and *Labeobarbus aeneus*) (Burchell, 1822) (Winker et al., 2011). Furthermore, the increased longevity of *C. carpio* (tmax= 20 years) may be attributed to low to no fishing pressure at Groenvlei due to the inaccessibility of the lake (Dredge and Weyl, 2017) in comparison to Lake Gariep were *C. carpio* forms a percentage of the subsistence fisheries (Ellender et al., 2014; Winker et al., 2015; Barkhuizen, 2015).

Like other populations in its introduced range (Brown et al., 2005; Oyugi et al., 2011; Winker et al., 2011), the introduced *C. carpio* populations are fast growing compared to its native range (Balon, 1995). The large variability between the native and the introduced population is reported by the growth performance during the first five years whereby it grows faster in the introduced compared to native

regions (Vilizzi and Copp, 2017). The initial somatic growth of fishes tend to be fast because no energy needs to be allocated to reproduction (Roff, 1984; Shuter et al., 2005), and this is even faster for non-native species such as *C. carpio*, a strategy to efficiently exploit available resources (Vilizzi and Copp, 2017) referred to as the "shooting" phenomenon (Vilizzi and Walker, 1999). Introduced *C. carpio* employ the r-selected, opportunistic strategy (Vilizzi et al., 2014), with no parental care, attaining sexual maturity at an early age and with the potential to reproduce repeatedly during one spawning season, all of which maximises *C. carpio*'s colonising potential (Winker et al., 2011).

A large proportion of reproductively active *C. carpio* were recorded during this study due to data collection coinciding with the known spawning period (October/November) in South Africa (Winker et al., 2011). To obtain unbiased reproduction maturity estimates Flores et al. (2014) recommends collecting maturity data at the beginning of the spawning season to minimise the frequency of individuals with spent gonads, and during this study no *C. carpio* with spent gonads was found. The average age at 50% maturity for the entire population of *C. carpio* in Groenvlei was estimated between two to three years which was similar to other introduced populations (Vilizzi and Copp, 2017). In contrast to the findings of this study, other studies of *C. carpio* reported earlier maturity in males compared to females (Winker et al., 2011; Hailu, 2013). The reproductive characteristics of *C. carpio* often vary slightly in ecosystems, with multiple studies emphasizing the greater influence by temperature amongst other environmental variables (Smith and Walker, 2004; Tempero et al., 2006; Hailu, 2013). This observed difference in this study may be explained by the influence of low sample size within the 300 to 400 length group, skewed by the sampling methods. Furthermore due to the Covid-19 global pandemic reproductive measurements were taken from a single survey period which may also have impacted findings, and contrasts with preferred year-round methodologies commonly used in other studies. Further research would be needed to explore this anomaly.

A long-lived population of *C. carpio* of up to 30 years have been recorded in North America (Bajer et al., 2015), 28 years in Australia (Brown et al., 2005) and 20 years in the present study. In comparison to other African populations much older *C. carpio* were recorded in Groenvlei (in comparison to records of four years and seven years in Kenya and South Africa respectively). Age and growth is monitored in few exploited *C. carpio* populations, however is of importance if harvest is to form part of a management plan. The highest recorded growth rate of *C. carpio* is in Lake Naivasha, Kenya. This is attributed in part to the environmental suitability (low annual temperature range provided by the equatorial climate, and in part to established commercial exploitation. By continuously removing adults and reducing competition- no fish over the age of four years was found in this population (Oyugi et al., 2011). Studies of other fish species have shown significant changes in biology as a result of harvest (Law et al., 1989). Basic biological studies provide an opportunity to monitor changes in population dynamics facilitated by management interventions. The data in this chapter represents a baseline at the commencement of the removal interventions, and can be revisited over time.

Chapter 3: The movement patterns of *Cyprinus carpio* in Groenvlei

Introduction

Most animals live in environments where resources are patchily distributed and environmental conditions vary and therefore move in response to resource availability and changing environmental conditions (Van Moorter et al., 2016). Movement behaviour is an important aspect in species ecology as it can determine the structure of communities, the dynamics of a population and the extent of genetic mixing within and between populations (Diana, 1995). Studying animals' movement patterns in their natural environment, and understanding aspects of movement such as habitat-use, migration, productivity and survival can contribute to informed management interventions (Hockersmith and Beeman, 2012). This is particularly pertinent when it comes to invasive alien species and the development of appropriate management.

Understanding the movement of invasive species is important since dispersion of the species and is a factor in its invasiveness (Zhang et al., 2020). Historically, these data were obtained using a combination of mark-recapture studies and fisheries surveys; however, the data lacked accuracy and the resolution needed to describe fine-scale movement behaviour (Crossin et al., 2017). Acoustic telemetry, a technique developed during the mid- to late-1950s, is the most successful tool in studying the movements and ecology of animals remotely with minimal impact on their behaviour (Cooke et al., 2004; Cooke et al., 2017). It provides a means for researchers to quantify previously unobserved animal behaviours related to population dynamics and community structure at a wide range of spatial and temporal scales (Jellyman, 2009; Marsden et al., 2021). Today, telemetry is widely used in fisheries management since it allows for 'real-time' monitoring of individual fishes in relation to fluctuating environmental factors, providing fine-scale, high-resolution data. This information can be used to predict individual and population level responses to environmental changes (Bajer and Sorensen, 2009; Butler and Wahl, 2010), interactions between different species (David and Closs, 2002; Jones and Stuart, 2007), and more recently it has been applied in habitat advancement studies and management of invasive species (Jellyman et al., 2009; Daniel et al., 2011; Crossin et al., 2017). In invasive species studies, telemetry has been used to map population distribution, understand their behaviour and seasonal movements in order to establish important life history periods and areas that are vulnerable to targeted control measures (Jellyman et al., 2009; Daniel et al., 2011). Some control strategies for invasive fish populations have been based around this technology; for example, mapping maximum harvesting and barrier locations (Butler and Wahl, 2010; Crossin et al., 2017). Spawning habitats and migratory pathways tend to be the most targeted locations since these are important areas contributing to population expansion (Daniel et al., 2011).

Both radio and acoustic telemetry have been successfully used to study behaviour and seasonal movement patterns of invasive *C. carpio*, with radio telemetry often used to study the fine-scale

behaviour and habitat use, while acoustic telemetry is used in monitoring large-scale and migration behaviour (Jellyman, 2009). A large number of telemetry studies aimed at improving the control efforts of *C. carpio* have been conducted in North America (e.g., Bajer and Sorensen, 2009; Butler and Wahl, 2010; Bajer et al., 2011; Coulter et al., 2016; Coulter et al., 2017) and Australia (e.g., Jones and Stuart, 2007; Daniel et al., 2011; Taylor et al., 2012) since these are the regions that suffer from superabundance of *C. carpio* (Koehn, 2004; Bajer and Sorensen, 2009). These studies have emphasized the importance of understanding the types of habitats that are preferred by *C. carpio* and specific aspects of their life history in order to establish periods of activity that may be vulnerable to targeted control measures and therefore inform management strategies (Butler and Wahl, 2010; Bajer et al., 2011; Crossin et al., 2017; Zhang et al., 2020).

Adult *C. carpio* are reported to undertake seasonal movements, including aggregations in deeper areas of lakes and impoundments during winter, and spawning migrations during spring to summer months (Brown et al., 2004; Bajer et al., 2011; Taylor et al., 2012). Spawning migrations are generally synchronised and occur within a 2-month period in North America (Bajer and Sorensen, 2009) and Australia after which *C. carpio* return to their original place of occupation for the winter (Conallin et al., 2012). In addition to changes in seasonal habitat use, *C. carpio* shows increased mobility during summer and a few weeks prior to the spawning season, and this is shown by an increase in their home ranges and total distance moved (Conallin et al., 2012; Taylor et al., 2012). Butler and Wahl. (2010) showed that *C. carpio* movement and connectivity between different habitats in the Fox River, Illinois USA was largely influenced by the locality of spawning regions, where fish displayed less movement when spawning regions were near and vice versa. Bajer and Sorensen (2009) revealed that sexually mature *C. carpio* in the interconnected lakes of south- central Minnesota, USA migrated to shallower unstable habitats (e.g., backwater habitats with fluctuating environmental conditions) during the spawning season. These nursery habitats are often characterised as severely disturbed shallow waters with low dissolved oxygen levels, with less chances of having larval predators or native eggs thus having reduced competition (Koehn, 2004; Bajer and Sorensen, 2009).

Despite the invasion of *C. carpio* worldwide and multiple attempts in controlling this species, only a few successes are reported (Koehn, 2004; Bajer et al., 2011; Taylor et al., 2012; Dalu et al., 2020). Of the studies that used telemetry to inform targeted management efforts, most were conducted in Mid-western North America and South Central Australia where *C. carpio* is problematic (Bajer et al., 2011; Taylor et al., 2012). From this there is evidence it can be a valuable tool in tackling this species. For example deployment of barrier nets across key spawning habitats informed by telemetry, spawning of *C. carpio* was prevented at Lake Sorell and Lake Crescent, Tasmania in 2011 to 2012 and a significant biomass was harvested from these barriers (Taylor et al., 2012).

Telemetry can be divided into two basic categories based on transmission mode; the acoustic and radio transmissions which differ in energy type (mechanical or electromagnetic) and operating frequencies (Hockersmith and Beeman, 2012). Both these transmitters can be surgically installed or attached externally on the body of an animal where they transmit a signal that is detected by a receiver within the range. Radio transmitters have a relatively greater range and longer lifespan, however, the requirement of an aerial possess a disadvantage to the tagged animal as this often becomes a site for secondary infections (Jellyman, 2009; Donaldson et al., 2014). Acoustic transmitters provide better performance in high conductivity environments and are relatively affordable, their reception range is largely dependent on the background noise and physical boundaries, and this can be conducted through active or passive tracking (Jellyman, 2009). Passive telemetry involves the stationing of receivers in known locations and it can be limited by the receiver's detection range, furthermore, data from passive acoustic tracking lacks sufficient spatial and temporal resolution data needed to classify fine-scale behaviours such as daily activity patterns. In contrast, active telemetry can be used to identify fine level behaviour, and this involves the manual tracking of an animal installed with a transmitter using either a boat or a helicopter. During this study, manual acoustic tracking was used to obtain information regarding the short term fine-scale behaviour of *C. carpio*.

This study aims to investigate the seasonal area use patterns of *C. carpio* in Groenvlei which may be vulnerable to targeted control strategies to inform management of this species at this site.

The objectives of this chapter were to:

1. Determine the temporal movement patterns (monthly) and habitat-use of *C. carpio*
2. Quantify fine-scale behaviour and diel movements and space-use
3. Identify and map spawning sites in Groenvlei

Materials and methods

A detailed description of Groenvlei is provided in Chapter 2.

Tagging

The movement data of six adult *C. carpio*, ranging from 460 to 670 mm L_F (mean ± SD: 580 ± 68.1 mm) captured independently from various positions within the lake and tagged as part of an adjacent study in February 2020, were used (Cape Nature research permit number: CN-44-28-8357) (see Table 3.1 for tagging details). Acoustic transmitters (Innovasea, Halifax, Canada) were surgically implanted following the methods described by Cowley et al. (2008), whereby an incision was made on the ventral surface posterior to the pelvic girdle of an anaesthetised *C. carpio* (using 2-phenoxyethanol to the concentration of 0.5 ml^{-1}), the transmitter was then inserted into the body cavity and closed with three independent sutures. Surgery took place *in situ* on the boat and took between three to five minutes during which the gills were continuously flushed with aerated water to shorten the recovery period. External T-bar anchor tags were attached to the pelvis of *C. carpio* and released back into the lake at their respective capture locations. The transmitters (V16-4L) had a diameter of 16 mm, a length of 83 mm weighed approximately 10.3 g in water (power output = 120 dB; 50, 60, 70 kHz), and had a manufacture-estimated battery life of 390 days. To ensure that the weight of the transmitters in water did not exceed the recommended maximum of 2% of the total mass of the fish (Winter 1983), only large adult *C. carpio* were tagged. Each transmitter emitted a sonic pulse at a one second delay (1000 $m.s^{-1}$) at varying frequencies which were detected by an acoustic receiver (Innovasea, VR100) and a unidirectional hydrophone (Innovasea, VH110) was used to locate their positions in the lake manually.

Table 3.1: Tagging details of six acoustically-tagged *Cyprinus carpio* manually tracked in Groenvlei from February 2020 to February 2021. Asterisks (*) indicate the end of the study period.

Fish ID	Tagging date	Fork length (mm)	No. of days tracked	No. of positional fixes	Date of last recorded movement
1	07 Feb 2020	460	19	46	Mar 2020
2	07 Feb 2020	590	31	114	Feb 2021*
3	09 Feb 2020	570	17	37	Mar 2020
4	10 Feb 2020	600	26	86	Nov 2020
6	10 Feb 2020	590	11	22	Feb 2020
5	11 Feb 2020	670	31	111	Feb 2021*

Tracking

Manual tracking began in February 2020 and was anticipated to take place monthly for a year. However, due to the COVID-19 Global Pandemic, manual tracking was put on hold from April to September 2020 and continued from October to February 2021. As a result, the study took place in five months (February, March, October, November 2020 and February 2021) from a 4.3 m petrol-powered boat where two approaches of collecting data were used; day tracking and 24-hour tracking sessions. In February and March 2020 manual tracking was conducted for a total of 18 days with day tracking sessions conducted between 06h00 in the morning and 22h00 in the evening and position fixes of all fish recorded every four hours (Figure 3.1). From October 2020, 24-hour tracking sessions were conducted alongside day tracking sessions, largely dictated by weather conditions and during the 24-hour tracking sessions positional fixes of all fish were recorded every two hours for a period of 24 hours (started at 06h00 in the morning and finished at 04h00, the morning of the following day) (Figure 3.1). During the tracking sessions, all fish were located within the lake. The unidirectional hydrophone was held vertically into the water from a slow moving boat to scan and locate the tagged fish across all angles. Initially, the gain control function would be set to a high level (gain 48) and the hydrophone operator scans all frequency channels slowly in all directions (360 degrees) to detect a signal. Once a signal was detected, its strength was monitored to establish the direction (highest dB), and then the boat would be directed towards it whilst adjusting the gain. It was assumed that the hydrophone was directly above the fish when the transmitter signal strength was high (dB = 80–100, gain = 0) in all directions and then the GPS coordinates were recorded (Garmin 12). When a fish was encountered, water chemistry variables recorded included temperature (°C), pH and salinity using the AP800 Aquameter and the water depth (m) was recorded using the boat mounted transducer. Due to weak detection signals near reed beds, the triangulation method was used to estimate the location of *C. carpio* in these areas. Signals that were received at the same location on multiple tracking sessions were assumed as either transmitters were expelled or the fish was dead after a period of three months.

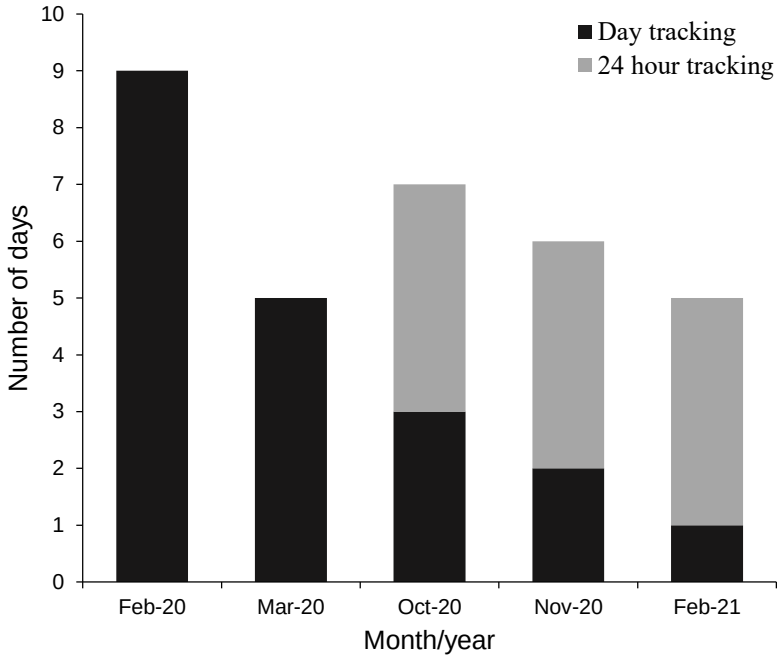

Figure 3.1. Number of days manual tracking was conducted during a five month period with each month divided by tracking method. Day tracking were conducted between 06h00 and 22h00 with at least four hour interval and 24 hour tracking sessions were conducted continuously over a period of 24 hours with two hour interval.

Public awareness

To avoid the loss of tagged fish to capture by fishers, pictures of *C. carpio* with an external tag were uploaded to the Cape Nature website (article removed) and printed in offices with a short description of the study. A reward was promised to individuals who return tagged *C. carpio* to Cape Nature once caught.

Data analysis

MS Excel was used for primary data analysis including calculating the mean and standard deviations of environmental parameters, and conducting statistical tests such as ANOVA and independent *t* test to assess the significance of the difference in environmental parameters and the diel movement patterns. For spatial movement analyses, GPS coordinates derived from active tracking were filtered to only include detections of highest positional accuracy (gain 0 dB, signal strengths 80–100 dB) and converted to a .csv file for analysis in RStudio v 4.0.3 (R Core Team, 2020). Scatterplots using location detection points throughout the lake were plotted using *ggplot2* (Wickham, 2016) on the Groenvlei Lake shape file which was loaded on RStudio using the *sf* (Pebesma, 2018), *ggmap* (Kahle and Wickham, 2013) and *mapview* (Appelhans et al., 2021) packages. All aerial photographs of Groenvlei were downloaded from Earth Explorer (Earth Explorer, 2021).

Results

Detection summary

The movement patterns of six adult *C. carpio* were monitored between February 2020 and February 2021. During which three individuals (Fish 1, 3 and 6; Table 3.1) stopped moving between 11 and 30 days post-tagging (the transmitter location was recorded at the same point for more than three months), and were therefore excluded from the analysis under the assumption that these transmitters were expelled or the fish died. A total of 472 positional fixes were recorded over a period of five months (Figure 3.2). Tagged fish showed preference for reeds habitat near the lake edge (92% positional fixes) compared to middle open waters (8% positional fixes). In February 2020, 76% of positional fixes were recorded on the eastern side while in February 2021, 97% of positional fixes were recorded on the western side of the lake.

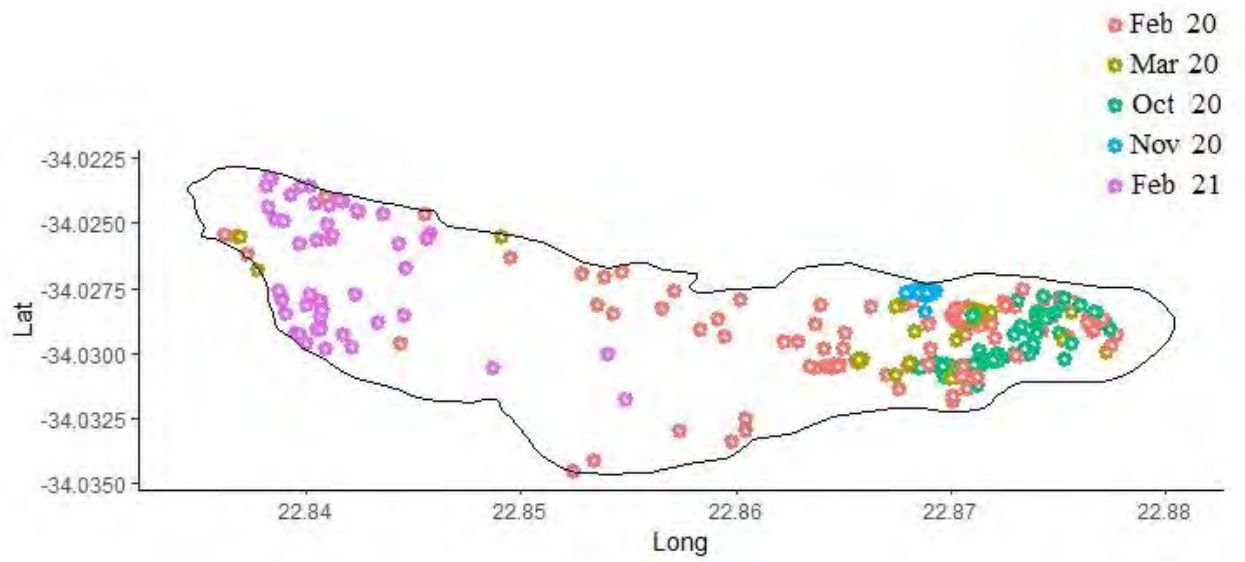

Figure 3.2. Positional fixes of *Cyprinus carpio* recorded throughout manual tracking from February 2020 to February 2021 in Groenvlei. February 2020 – Pink; March 2020 – Mustard; October 2020 – Green; November 2020 – Blue and February 2021 – Purple.

Environmental parameters

The environmental parameters where positional fixes were obtained for fish were variable between months (Table 3.2). The water depths where fish were found also fluctuated considerably, ranging from 4.2 m in February 2020 to 0.4 m in November 2020. There was a significant difference in depth used by fish across different months (ANOVA: $F = 150.50$, $df = 4$, $p < 0.001$), with water depth used by all

tagged *C. carpio* in October being significantly different to November 2020 (t-test: $t = 24.83$, $df = 28$, $p < 0.001$), and the water depth used for both months were significantly different to February, March 2020 and February 2021 (Table 3.2). Both salinity and pH of the lake remained consistant throughout the study periods, with average salinity ranging from 2.1 to 2.3 and pH ranging from 6.7 to 6.8.

Table 3.2. Environmental parameters (mean ± standard deviation) measured with positional fixes during manual tracking of *Cyprinus carpio* from February 2020 to February 2021 in Groenvlei, South Africa. Superscripts of a, b, c and d represent statistical difference.

	Water temperature (°C)	**Depth (m)**
Feb-20	26.7 ± 1.2^{a}	4.2 ± 1.5^{a}
Mar-20	24.2 ± 1.6^{a}	$3.8 \pm 0.7^{a,d}$
Oct-20	19.7 ± 0.98^{b}	1.7 ± 0.6^{b}
Nov-20	20.3 ± 0.86^{b}	0.4 ± 0.1^{c}
Feb-21	25.1 ± 0.64^{a}	3.2 ± 1.1^{d}

Spatial use

The three fish – fish 2, 4 and 5 – were successfully tracked throughout 2020, and their monthly movement patterns are shown (Figure 3.4). Individuals utilised the eastern section during the first three months (February, March and October), occupied the backwater habitat in November where their movement was limited, and then in February 2021 switched to the western section (only fish 2 and 5 were tracked) where they showed extended movements compared to other months (Figure 3.4); and the absence of transmission from fish 4 was assumed to due to capture or expired battery of the transmitter.

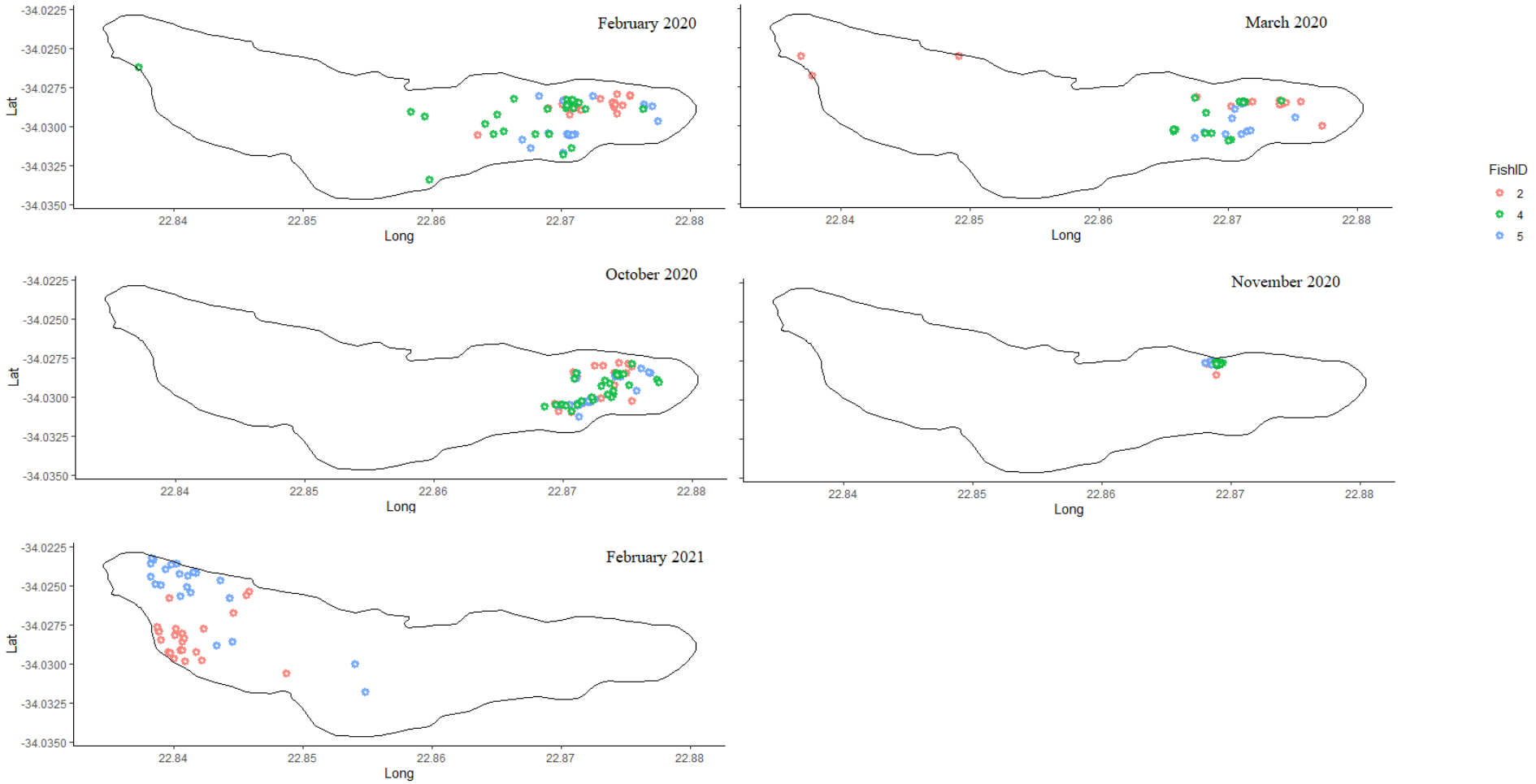

Figure 3.3. The monthly locational fixes of fish 2 (pink), 4 (green) and 5 (blue) in Groenvlei throughout the sampling period.

Twenty-four hour tracking sessions were conducted twice in October, November 2020, and February 2021 and the resultant movement patterns are shown in two figures to compare the two tracking sessions each month (Figure 3.5). Individual positional fixes of fish 2, 4 and 5 were recorded every two hours and the results show that all *C. carpio* spent at least eight hours in the same location in a period of 24-hours, the remaining time (16 hours) was spent making short strips with high chances of returning to the initial location; this trips were longer in February 2021 compared to both October and November 2020. It also noteworthy that in October and November, all individual's movements were overlapping (shared space-use), to a larger extent in November when all three fish were found within 50 m of each other for a period of 24 hours during manual tracking.

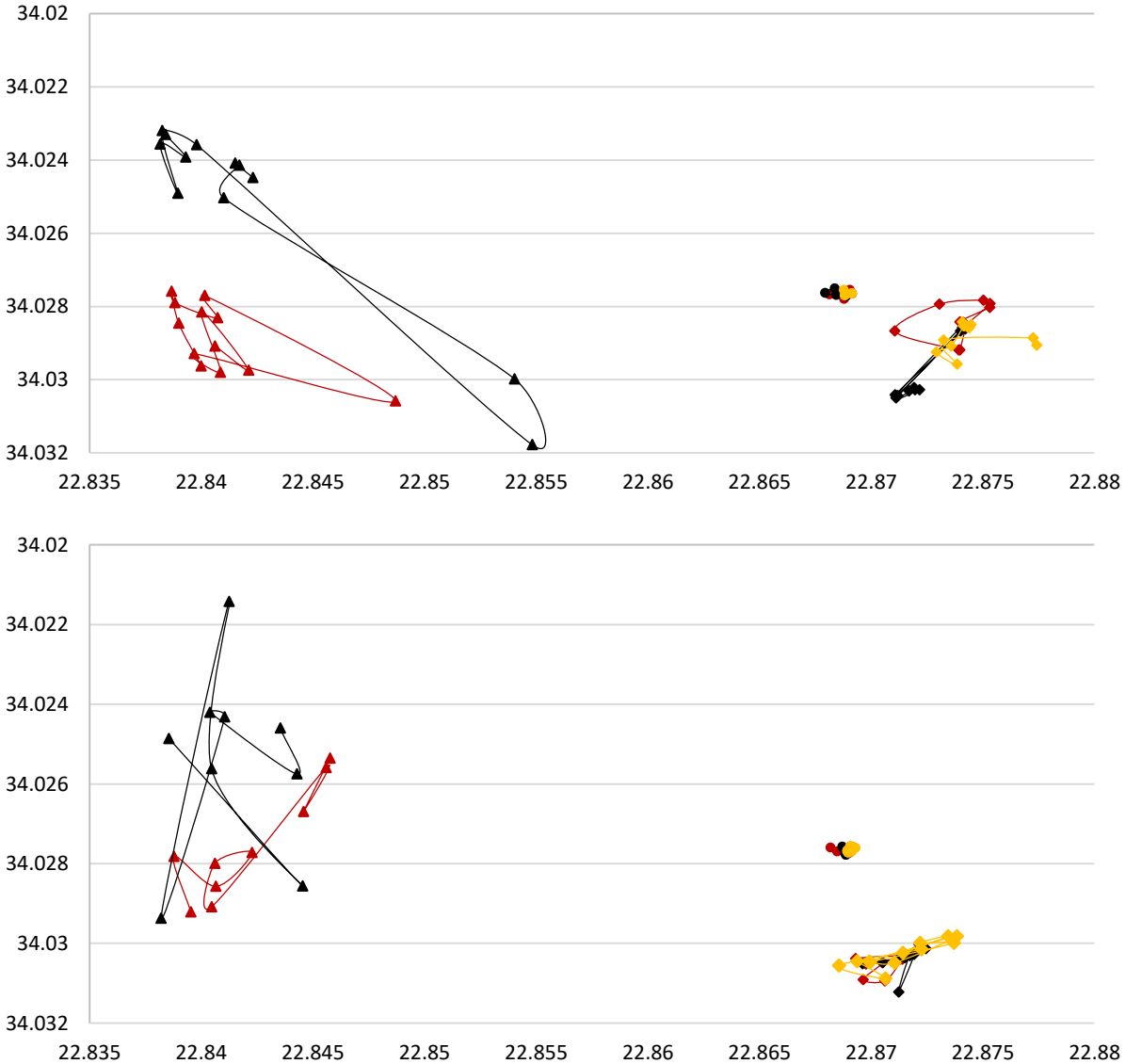

Figure 3.4. Twenty-four hour movements and space use of three *Cyprinus carpio* (fish 2–red, fish 4–yellow and fish 5–black) recorded over a period of three months during two (top and bottom) 24 hour sampling periods in Groenvlei, South Africa. October – polygon marker; November – circle marker line, February 2021 – triangle marker.

Diel movement patterns and space use

Diel movement patterns were calculated from the two 24-hour tracking sessions which were conducted in October, November 2020 and February 2021, and during all these sessions all three fish's positional fixes were logged every two hours except in February when fish 4 was not detected. The total distance moved in a single 24-hour tracking session ranged from 350 meters in November to 3740 meters in February. During the sampling period (summer-spring, day length = 12 hours), extended diel movements and long trips were undertaken in February compared to both October and November, although, there was no significant difference in the overall distance moved by all individuals during the day (6am to 6pm) and at night (6pm to 6am) (t-test: $t = 0.24$, $df = 14$, $p > 0.05$) (Figure 3.5). In most instances, high mobility by individual *C. carpio* was observed between 05h00 and 09h00 in the morning and again between 18h00 and 20h00 in the evening except in November when movement patterns were irregular. In general, fish 5, the largest fish tracked, moved greater distances compared to both fish 2 and 4 in all study months except in November 2020.

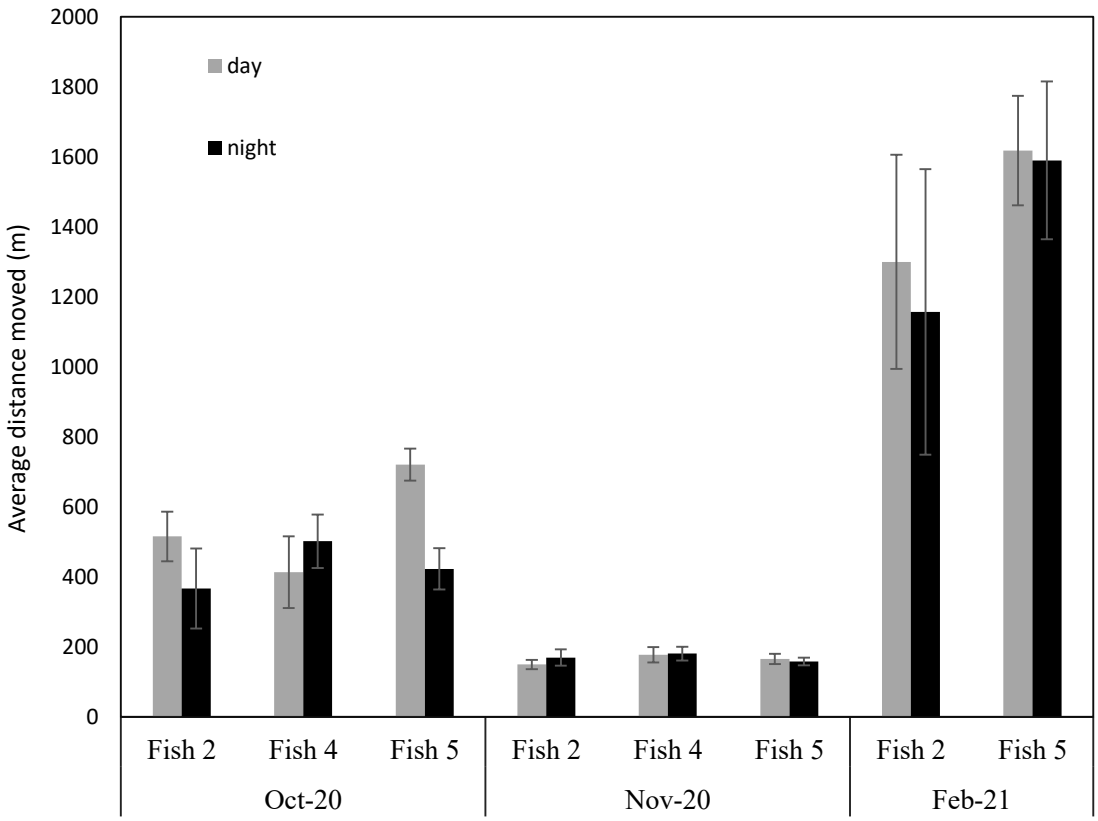

Figure 3.5. Average distance moved by each fish (day – black; night – grey) for October, November 2020 and February 2021 shown with the average water depth each fish occupied in Groenvlei. Error bars represent standard deviation.

Mapping Groenvlei habitats including spawning grounds

Throughout November 2020 manual tracking sessions (11 – 23 November 2020), all tagged individuals (n = 3) moved into the lake backwaters (B1, Figure 3.6) where their transmitter signal was undetectable from the lake until a connecting channel was found to access the backwaters. The water depth in the backwaters occupied by *C. carpio* during this period was significantly lower (t-test: t = 15.7, df = 45 p < 0.001) than the depth they occupied throughout the lake at any point (Figure 3.6). Of the two backwater habitats (B1 and B2) present in Groenvlei, only B1 had water (water depth between 0.3 and 0.6 m) in November 2020. This habitat was identified as the spawning ground of *C. carpio* in Groenvlei as aggregated individual were observed spawning during this study. The spawning period was confirmed by assessing the gonadal development stage of the captured *C. carpio* used for age determination (see Chapter 2). Although the length of the spawning period could not be determined, by February 2021, all fish had migrated out of the backwaters into the western open waters (Figure 3.3).

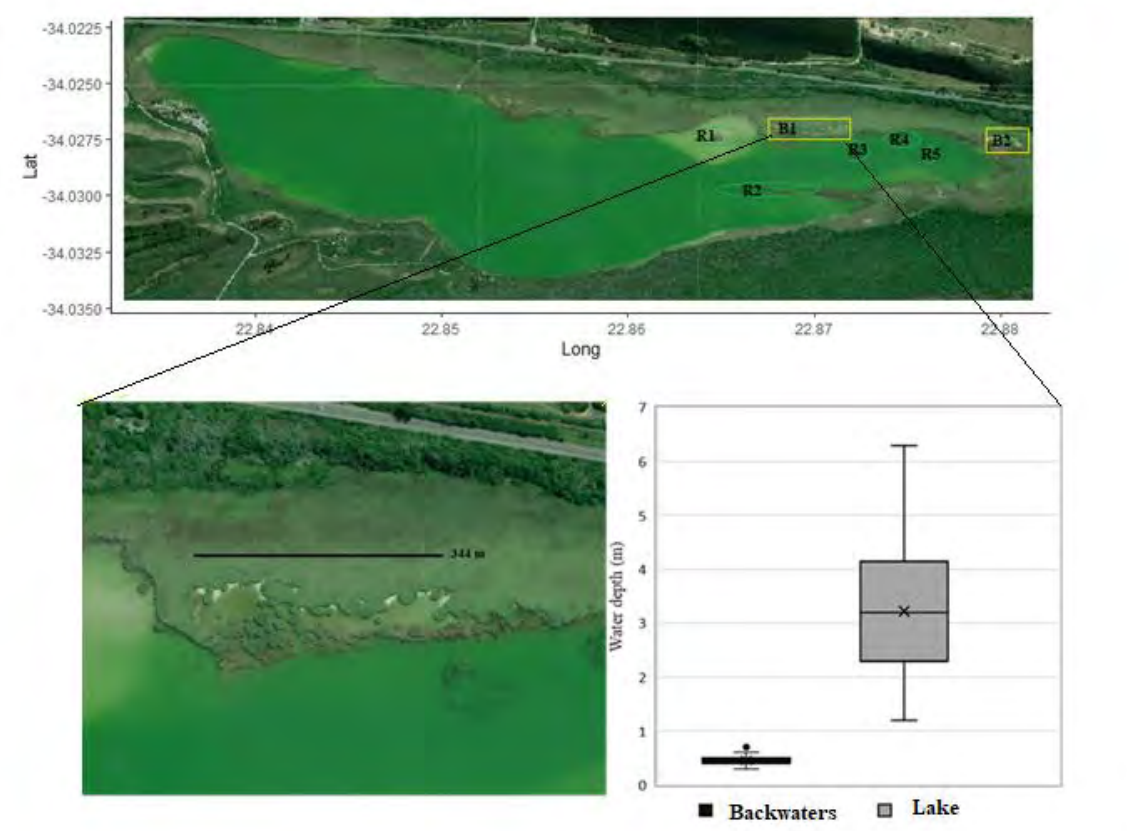

Figure 3.6. Arial map of Groenvlei showing various habitats within the water lake; R – reeds, B – backwaters and the rest of the lake consist of open water with macrophytes and muddy bottom. The insert image of backwater habitats (B1) and the water depth (blackline of backwater habitat) is where all tagged *C. carpio* were located in November 2020. (Image Source = Earth Explorer).

Discussion

Habitat and space used by *C. carpio* in Groenvlei varied across months, and this variation in movement behaviour is most likely linked to spawning behaviour. Specifically, during the spawning season (summer/spring), all tagged individuals aggregated within the shallow backwater habitats for the duration of the reproduction period, after which they dispersed and moved to deeper areas within the lake. This observed behaviour has been recorded for populations of *C. carpio* both in their native (Rodriguez-Ruiz and Granado-Lorencio, 1992) and introduced ranges (Penne and Pierce, 2008; Jones and Stuart, 2009; Bajer et al., 2011; Daniel et al., 2011) and these spawning migrations are activated by increase in temperature and the photoperiod (Conallin et al., 2012).

Cyprinus carpio are habitat generalists, and in regions where they form aggregations during winter, studies found that this was due to their shoaling behaviour rather than strong attraction to specific habitats (Bajer et al., 2009). During foraging, *C. carpio* prefers vegetated habitats such as reeds especially in slow moving impounded waters as this provides good habitat for their preferred food of macroinvertebrates (Butler and Wahl, 2010; Zhang et al., 2020); however, there is a strong variation between day and night habitat-use whereby shallow vegetated areas are commonly used at night while deep waters are preferred during the day (Benito et al., 2015; Zhang et al., 2020). During this study, there was high preference of reed habitats by tagged *C. carpio* which is likely to offer protection compared to the open water areas anytime of the day. However, this could have been influenced by the use of an engine powered boat for manual tracking. Cyprinid species show high sensitivity to sound; they have a Weberian apparatus which causes compressions in the swim bladder whenever sound waves are detected (Dennis et al., 2019), and therefore manual tracking could have influenced their movement patterns to an extent.

Cyprinus carpio movement patterns also change depending on regions and the overall environmental characteristics. In the riverine habitats they are recorded to have relatively large home ranges and long distance migratory behaviour (>100 km); however, in impounded areas or small systems, they have small home ranges and show localised movements (Stuart and Jones, 2006; Koehn and Nicole, 2016). Although the home range sizes were not measured during this study, due to the COVID19 Pandemic, variability in total distance moved was observed in the temporal movement patterns whereby there was a decrease in distanced travelled and space use towards, and during, the spawning season, and an increase afterwards. Despite a small sample size individual variability in movement was also observed whereby the largest fish (670 mm L_F) showed extended movements compared to other individuals; although, movement patterns might be related to the sex rather and the size of *C. carpio* (Stuart and Jones, 2006), further sampling would be needed to determine if sex or size-based variability is indeed present.

This study was limited by the small sample size as half of the tagged individuals were excluded from data analysis possibly due to death or transmitter expulsion. Transmitter expulsion in cyprinids is common at high water temperature areas due to tagging stress (e.g., Stuart and Jones, 2002; Økland et al., 2003; Daniel et al., 2009; Butler and Wahl, 2010), and it is possible that the three *C. carpio* could have expelled their transmitters due to the relatively high water temperature in Groenvlei. Despite the low sample size active acoustic telemetry (manual tracking) proved to be an effective tool in identifying the seasonal habitat use patterns of *C. carpio,* particularly the spawning habitats in Groenvlei, albeit from a small sample size. The spawning period (November 2020) was identified through a drastic change in movement behaviour, where fish were recorded moving to the backwater habitat, and was confirmed by the macroscopical gonad examination results in Chapter 3. The usage of the backwater habitats as the spawning sites by *C. carpio* in Groenvlei correlates with results from previous studies at other sites (e.g., Stuart and Jones, 2002; Brown et al., 2005). The management implications of this will be discussed in chapter 5.

The COVID-19 Global Pandemic halted the project's manual tracking during the winter period (April to August 2020), and as this information does not exist for *C. carpio* in Southern Africa this is an area for future exploration.

Chapter 4: Systematic literature review on the global control common carp, *Cyprinus carpio*

Introduction

Cyprinus carpio distribution

Cyprinus carpio originated in the area of the Caspian and Aral Sea Basins from where it spread into Siberia, China and far west to the Danube River during postglacial times (Balon, 1995). *Cyprinus carpio* taxonomy as described by Balon (1995) and Chistiakov and Voronova (2009) have changed over the years to three subspecies described by Zhou et al. (2004) using morphological traits; this are the *C. c. carpio* (European) which evolutionary diverged from two Asian sub-species, *C. c. haematopretus* and *C. c. rubrofuscus* about 0.9 million years ago. Nonetheless, at least two subspecies of *C. carpio* are confirmed by genetic studies; the European *C. c. carpio* and the Asian *C. c. haematopretus* (Xu et al., 2014).

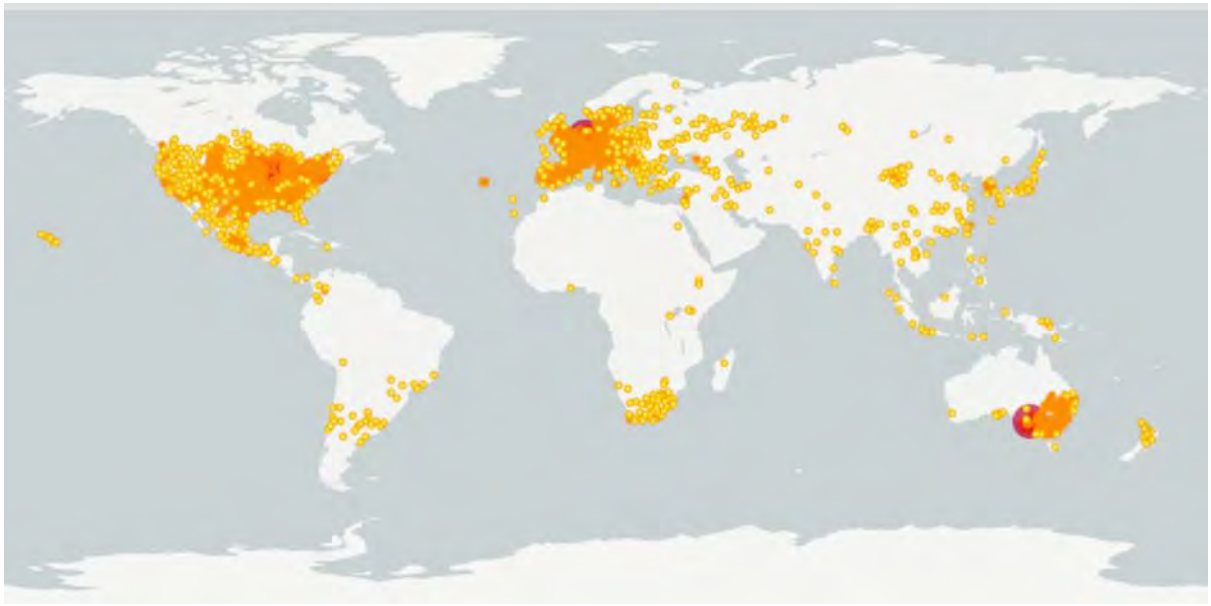

Figure 4.1. Global distribution of *Cyprinus carpio*. Native range= Eastern Europe, Russia and China (Source: Global Biodiversity Information Facility).

Cyprinus carpio have a long history of domestication, about 3000 years since their first culture (Balon, 1995), with Asia having a longer cultivation history than Europe (Chistiakov and Voronova, 2009). Since domestication, *C. carpio* distribution range has expanded through active translocation as well as downstream larval drifts, systems connectivity and escapes into the wild (Koehn, 2004; Copp et al., 2005). *Cyprinus carpio* were highly valued in Asia, Central and Eastern Europe with records of traditional culturing and harvesting techniques (Tamir, 2010), and this pattern has be seen in regions where European immigrants settled worldwide such as North and South America (Zambrano et al., 2006), Australia (Koehn, 2000) and Africa (Britton et al., 2007; Weyl et al., 2007; Ellender et al., 2010). Further *C. carpio* introductions were facilitated by humans for food and ornamental purposes, this

includes large stockings by governmental organisations especially in low-income countries for socio-economic benefits (Vitule et al., 2009). Following concerns regarding their ecological and economic impacts, *C. carpio* stocking was halted in most areas including South Africa and North America (Lougheed et al., 1998; Copp et al., 2005; Vitule et al., 2009; Kara, 2012). Over time, opinions on *C. carpio* have changed such that are now considered a species that requires management interventions (Roberts and Tilzey, 1997; Koehn, 2004; Zambrano et al., 2006). Furthermore, in regions such as Australia, both inland commercial fishers and indigenous communities support the removal of *C. carpio* due to gear-damages they caused and having little to no market value (Koehn et al., 2000).

Cyprinus carpio control efforts

Multiple control efforts are attempted to eliminate *C. carpio* with varying success, however, it is acknowledged that once established in an ecosystem, *C. carpio* are expensive and challenging to eradicate completely (Zambrano et al., 2006; Britton et al., 2010; Weber et al., 2016). Eradication of non-native species, is defined as the removal of all reproducing individuals from the population, it is therefore considered as the best option since it removes the need for further financial investment and environmental costs, however, it is likely to be successful in small enclosed systems and during the early stages of invasion (Gherardi and Angiolini, 2007). Therefore, control of the population biomass, although expensive is considered the most viable option in large-scale interconnected systems whereby the aim is to mitigate the impacts of non-native species (Gherardi and Angiolini, 2007). The costs of controlling invasive *C. carpio* was estimated from an unsuccessful Australian attempt that averaged $1 million AUD (Koehn et al., 2000), it is therefore challenging to get funding investments especially if the likelihood of success is unknown (Britton et al., 2010). This study reviews literature from regions where *C. carpio* have been introduced and is now controlled, with a focus on the past, present and future control efforts at various scales. Due to their wide global distribution, literature on the control of *C. carpio* is scattered and there is a need to consolidate and synthesise this knowledge in order to optimise available resources in a region-specific manner and motivate for future control of *C. carpio* (Casal, 2006). The aim of this systematic review is to provide a better understanding of the control methods that have been explored to date in different regions and how effective they have been at managing *C. carpio*.

The systematic review process

Peer reviewed literature was obtained and surveyed based on the guidelines of Preferred Reporting Items for systematic review and Meta-analysis (PRISMA) (Moher et al., 2009). This approach uses transparent, consistent and repeatable methods to search for and assess relevant studies for the question of interest. This includes the establishment of a search protocol, data inclusion, data extraction and analysis. The databases searched were the Institute of Scientific Information (ISI; Thomson Reuters) Web of Science online database and SCOPUS database. These databases were used to search for English literature on *C. carpio* in its non-native and invasion range. For this review, the search terms used were "common carp" OR "*Cyprinus carpio*" OR "*C. carpio*" OR "koi" AND "invasive" OR "invasion" OR "non-native" published through to the end of 2020. Koi was included because it is the coloured ornamental variant of *C. carpio* that is recognised as a pest in New Zealand (Daniel et al., 2011). The potential of each publication to contribute to this literature review was determined by reading the title, if it was not clear enough, the abstract was read and if necessary, the entire text. The initial list of potential papers was generated, this list was then refined to only include papers focusing on the control of non-native *C. carpio*. After examining all the articles selected by the inclusion criteria, the reference lists of all publications were checked for additional relevant papers and grey literature to include in the analysis (Moher et al., 2009). Additional published articles such as thesis, dissertations and reports were added. The articles obtained during both database and reference search were grouped in 5-year classes from 1975 to 2020; and the control methods are discussed.

Results and synthesis

Results presented here are based on the total number of articles found in ISI Web of Science and SCOPUS that matched the inclusion criteria, as well as the literature obtained from their reference list. The search on Web of Science yielded a total of 179 articles of which 36 matched the inclusion criteria. The same search on SCOPUS yielded 176 articles of which 29 were already obtained from the Web of Science database, however an additional nine articles were obtained. The control of non-native *C. carpio* started as early as 1973 with initial experiments such as Meadows. (1973) focusing on controlling multiple unwanted species in Europe. Even so, it was only after 2010 when the number of articles published on the control *C. carpio* increased drastically from 10 to 69 over a period of 10 years with a highest number being from the category 2016 to 2020 (Figure 4.2).

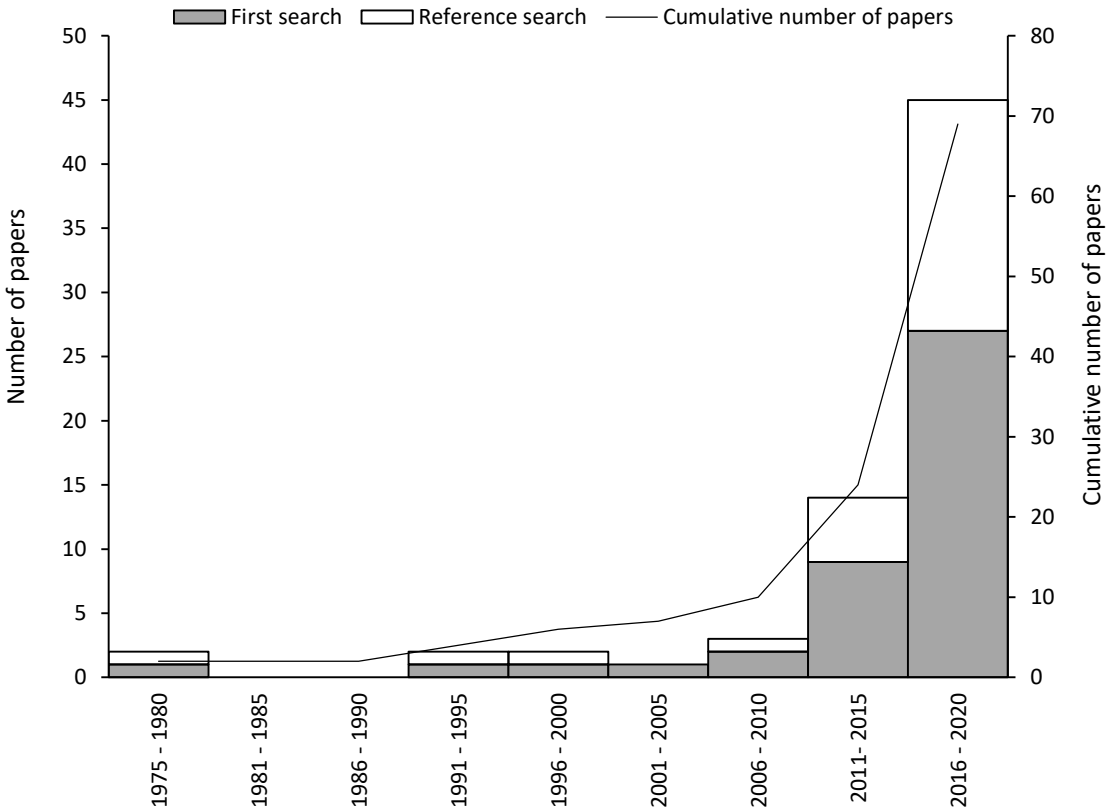

Figure 4.2. The number of papers obtained from Web of Science, SCOPUS and the reference search categorised by year published.

Eradication success of *C. carpio* is related to the size and type of the invaded systems, with complete eradication achieved only in small closed systems (e.g., Maceda-Veiga et al., 2017; Dalu et al., 2019) while no complete eradication of *C. carpio* at large scale interconnected systems (e.g., area > 50 km^2) have been reported to date, due to lack of advanced technological methods that are effective and have no impacts on non-target species (Britton et al., 2010). Management efforts are limited by economics (Weber et al., 2016; Sorenson and Bajer, 2020), In large aquatic systems they have mainly focused on reducing population biomass to non-impactful levels and minimizing their dispersal, which is achieved using long-term monitoring and integrated pest management strategies (Brown and Walker, 2004; Weber and Brown, 2009; Bajer et al., 2015). This review is divided to three parts; the control methods that have been applied to *C. carpio* since the twentieth century, recent control strategies that are specific to *C. carpio* including those still in their testing stage and finally the future of *C. carpio* control in countries that have large impactful biomass of such as North America, Australia, New Zealand, parts of Europe and South Africa.

1. *Previously used general methods*

General methods that are used to control unwanted fish populations have also been applied in the control of *C. carpio* and this includes; mechanical removal (e.g., netting and trapping), chemical toxicants, commercial exploitation, water drawdown and dam removal (Verrill and Berry, 1995; Brown and Walker, 2004; Weber and Brown, 2009; Brown and Gilligan, 2014).

a. *Mechanical removal*

Mechanical removal is the commonly used methodology to date for controlling unwanted fish species, and this is mostly done through commercial fishing using large seines, gillnets and boat electrofishing (e.g., Weber and Brown, 2009; Bajer et al., 2011; Colvin et al., 2012). Multiple gears i.e., gillnets, trawls and electrofishing at different times of the day have been tested with the aim of improving catch rates at minimum costs. For capturing adult *C. carpio*, Feeken et al. (2019) have shown high catch rates using monofilament gillnets (mean ± SD; 15.5 ± 9.8 fish/net per night) compared to multifilament gillnets (12.7 ± 7.3 fish/net per night) and high catch rates during night time electrofishing (0.3 ± 0.4 fish per min) compared to daytime electrofishing (0.1 ± 0.2 fish per min). For capturing juvenile carp, electro shocking embryos was shown to be effective in moderately conductive waters and was only effective before the embryos reach their pigmentation stage (69 hours after fertilization at 18.8 ^{o}C), during which they become resistant to electroshock (Simpson et al., 2018). Earlier application of these methods was directed by catch and release studies which lacked the accuracy in terms of locations and time of year for maximum harvest, however, recent decades have seen an increase in the use of telemetry techniques (i.e., Judas fish) to inform mechanical removal efforts and therefore optimise catch rates (Bajer et al., 2011; Taylor et al., 2012). When winter aggregations of *C. carpio* were targeted in North American mid-western lakes in 2010, up to 94% of *C. carpio* was removed using the Judas technique whereby a few individuals are equipped with transmitters that are acoustically or radio tracked to locate the group aggregation (Bajer et al., 2011).

b. *Commercial exploitation*

Overfishing can suppress *C. carpio* when a certain amount is constantly harvested, however, the exact biomass harvest that can reduce *C. carpio* biomass over the long term has not been formally identified (Weber et al., 2011; Colvin et al., 2012). In South Dakota, commercial harvest to control *C. carpio* population over a period of five years has not been effective, the removal of 230,000 *C. carpio* (up to 55 fish/ha/year) from the three interconnected lakes resulted in the population of *C. carpio* remaining stable instead of decreasing (Weber et al., 2016). Although commercial exploitation could be effective, the catch rate of less than 50% per annum is insufficient to control *C. carpio* especially in interconnected lakes (Weber et al., 2016). Mirza et al. (2012) reported that the expected yield of *C. carpio* only stopped increasing after the exploitation rates were greater than 63% in Mangla reservoir, Pakistan. When determining the effectiveness of commercial exploitation, challenges such as migration between

interconnected lakes need to be limited in order to accurately determine the density of *C. carpio* pre and post exploitation (Weber et al., 2016).

c. Chemical removal

Alternatively, though not highly favoured by the public is the chemical application of ichthyocides, such as Rotenone ($C_{23}H_{22}O_6$) (Dalu et al., 2019) and Antimycin-a ($C_{28}H_{40}N_2O_9$) (Poole et al., 2018). Rotenone, the most commonly used fish toxicant is derived from the roots of *Derris elliptica* and *Lonchacarpus*, leguminous plants native to South-east Asia. It enters the blood stream of fish directly through gills and inhibits cellular respiration in mitochondria which leads to death and have long been used in the fisheries management (Meadows, 1973; Britton et al., 2011). Rotenone is costly and not applicable in large scale due to impacts on non-targeted species, yet it remains favourable in small systems where *C. carpio* removal is a priority, usually due to the presence of endangered species (Weyl et al., 2015; Maceda-Veiga et al., 2017; Woodford et al., 2017; Dalu et al., 2019). Although often successful in small closed systems, there is evidence of *C. carpio* surviving Rotenone application in the Emiquon Preserve, located along the Illinois River, North America (Van Middlesworth et al., 2014; 2017).

d. Other previous used methods

Other previously used methods to control *C. carpio* and other non-native species includes water drawdowns and dam removal which aimed at complete eradication of unwanted aquatic organisms, however these methods are costly and affect non-targeted organisms (Britton et al., 2011). Non-target specific control methods of unwanted fish species are ecologically damaging and multiple reinvasions have occurred following their applications hence recent decades have seen an increase in development of species-specific control methods for global invasive pests such as *C. carpio* (Maceda-Veiga et al., 2017).

2. Carp-selective methods

Although still in their infancy, carp-specific control methods, both physical (structural and non-structural deterrents) and biological control show promising results during laboratory tests and field trials. These methods target life stages and behaviours of *C. carpio* that are vulnerable to exploitation, such as the spawning and winter aggregations (Stuart and Conallin, 2018). Installing structural (e.g., traps and screens) and non-structural deterrents (e.g., sound barriers and light) at specific locations informed by *C. carpio* movement studies have been the focus of *C. carpio* management efforts to limit spawning migrations in Australia and North America (Bajer et al., 2011; Taylor et al., 2012).

a. Structural deterrents

C. carpio have distinct jumping and pushing behaviour to avoid capture and structural deterrents that target this behaviour such as the William's Cage (Stuart et al., 2006; Conallin et al., 2016; Stuart and Conallin, 2018), push trap (Thwaites et al., 2010) and Clover leaf trap (Carl et al., 2016) have been built to hinder *C. carpio* spawning migration pathways while allowing a safe passage for other fish and are used as part of long-term integrated management strategy. It is noteworthy that different traps can be used to target different life stages of *C. carpio*. For capturing the juvenile *C. carpio*, Carl et al. (2016) used clover leaf traps with attractants (bloodworms and fishmeal) to lure *C. carpio* into traps and the results showed that up to 83% of age zero *C. carpio* were captured by this traps. Example of a carp-specific method applied commercially is the William's Cage (a trap that isolates *C. carpio* by their hopping behaviour), at the Lower Murray River, Australia, this was placed at known spawning locations annually for 11 years from 2009 (Stuart et al., 2006; Stuart and Conallin, 2018). The cage captured a total of 289 431 fish whereby 98% was *C. carpio*, while providing a safe passage for native species (Stuart and Conallin, 2018). Knowing the accurate spawning period and location was the key factor that contributed to the effectiveness of the trap in Australia which has proven technically, operationally and financially viable as the costs of the cage were lower ($0.18M AUD) compared to the profit ($0.90M AUD) attained from various uses for captured *C. carpio* (e.g., market for food and fertilizers) (Stuart and Conallin, 2018).

b. Non-structural deterrents

Adult *C. carpio* movements can also be blocked using non-structural deterrents such as sound, light and electricity. Acoustic and stroboscopic stimuli devices are in their research stage, with most work done in North America. Due to their sensitivity to sound, as a result of having the Weberian apparatus, the cyprinid species have compressions in the swim bladder whenever sound waves are detected (Dennis et al., 2019). Therefore, sound projected navigation locks such as pure tones (single frequency stimulus), complex sounds (multiple frequency stimulus) and air curtains (bubble systems that produce low frequency sound with a visual and a hydrodynamic stimulus), have been tested individually and in combination across cyprinids species at various life stages, in laboratory and field experiments (Dennis et al., 2019). Although, complex sound such as outboard motor sounds were found to deter *C. carpio* in lab studies, field trials on wild *C. carpio* showed that the deterring response of *C. carpio* decreased with repeated exposure to outboard motor sounds because in the wild, *C. carpio* are often exposed to various noise levels and habituate (Zielinski and Sorensen, 2017; Dennis and Sorenson, 2020). Complex sounds coupled with air curtains were effective at deterring up to 100% of *C. carpio* in a laboratory and over 95% in a hatchery raceway and a small creek (Dennis et al., 2019). Light has been tested as a deterrent in laboratory experiments with varying success; Adult *C. carpio* showed avoidance behaviour when exposed to strobe light (Kim and Mandrak, 2017) while age-zero *C. carpio* juveniles showed no change

in behaviour (Kim et al., 2019). Non-structural deterrents may be advantageous due to lower costs, as they require less installation, maintenance and do not alter the water flow compared to traps (Bzonek et al., 2020) however, they are currently not fully tested under field conditions where water depth, temperature, background noise, time of the day and biotic factors such as fish size and fish motivation which will likely affect their ultimate deterrent efficiency (Dennis et al., 2019).

c. Biological control

Biological control using organisms such as virus, pathogens and parasites have long been used in plants and animals. Disease, particularly infection by the Cyprinid Herpes Virus, CyHV-1 and CyHV-3, was a plausible hypothesis to explain the collapse of *C. carpio* in the Upper Mississipi River system, since the 1960s (Simberloff and Stiling 1996; Gibson-Reinemer et al., 2017) and the 17 mass die-offs of *C. carpio* in North America since 2004 (reviewed by Thresher et al., 2017). Cyprinid Herpes Virus is known to produce high mortality rates in *C. carpio* and its ornamental variants in the aquaculture sector (where mortality reaches up to 90%), hence its consideration as a biocontrol agent by the Australian Government (Thresher et al., 2017; Boutier et al., 2019; McColl et al., 2016; NCCP, 2017). Safety and efficacy of biocontrol agents is often the main concern especially on the non-targeted and the hybridised populations (Boutier et al., 2019; Kopf et al., 2019). Furthermore, CyHV-3 in North American river systems recently, was associated with low mortality rates compared to outbreaks in aquaculture and experimental ponds worldwide (Thresher et al., 2017) due to high genetic variability in the wild.

Biological control in the form of biomass manipulation have been used to control multiple pest fish (Colvin et al., 2012). Strategies can be top-down and or bottom-up approach, however for *C. carpio* top-down manipulation is most common and includes the introduction of piscivorous fish to predate on their eggs and fry (Bajer and Sorensen, 2010; Weber et al., 2010). Predator's preference for *C. carpio* tend to differ across species, depending on prey abundance and habitat complexity (Weber and Brown, 2011). Under controlled conditions *Lepomis macrochirus* consumed up to 95% of *C. carpio* eggs within four days, (Bajer et al., 2012; Bajer et al., 2019), however in the wild as *C. carpio* often migrate to spawn in environments where species such as *L. macrochirus* might be excluded due to narrow environmental tolerance (Lechelt et al., 2017). *Micropterus salmoids*, *Lepisosteus oculatus*, and *Amia calva* failed to predate on *C. carpio* eggs even when it was the most abundant food in the experimental set-up (VanMiddlesworth et al., 2017). To date, while no piscivorous animal has been effective at controlling *C. carpio* abundance single-handedly, *L. macrochirus* shows promising results for limiting recruitment of *C. carpio* in North America when integrated with other control techniques and restorative actions (Bajer and Sorensen, 2020).

3. *The future of C. carpio control*

Future research on the control of *C. carpio* includes the sex biasing technology, such as "daughterless" and female lethality genetic technology, with progress from laboratory testing experiments to field trials on the horizon this decade (Bajer et al., 2019). The daughter-less technologies, such as the production of super males (YY instead of the normal XY males) or YY phenotypic females can be generated through hormonal treatments which involves the blockage of aromatase, an enzyme responsible for converting male-determining androgen hormones into female-determining oestrogen hormones (Thresher et al., 2014). Once introduced into the population, this genetically modified *C. carpio* will result in high production of male offsprings. However, sample size is the biggest challenge faced by genetic technology since a large amount and multiple releases of *C. carpio* into the population which are needed are costly (Bajer et al., 2019).

In conclusion, the literature demonstrates that whilst eradication may be achieved on a small scale, in larger and connected water bodies, integrating multiple methods and preventing further spread of non-native species such as *C. carpio* can achieve some control. Whilst technological advances may improve the odds, few methods are without cost.

CHAPTER 5: General discussion

Biological invasions are a serious threat to freshwater biodiversity globally (Blackburn et al., 2019) and South Africa is no different (Ellender and Weyl, 2014), with more than 77 non-native freshwater taxa introduced to date (Weyl et al., 2020). The introduction and fast spread of *C. carpio* in South African freshwater ecosystems is a concern due to its known impacts on water quality and flora and fauna in its introduced range (Koehn, 2004; Bajer et al., 2009). In this study system, *C. carpio* was introduced illegally in the 1990s; and the present biomass currently exceeds around 700 kg per hectare (unpublished). In an attempt to rehabilitate this system, the local management authority, Cape Nature, have introduced measures to reduce *C. carpio* biomass including gill-netting and bowfishing programs (Cape Nature, 2020). However, whilst *C. carpio* is present in all major watersheds of South Africa (van Wilgen et al., 2020), information about its biology and ecology is scarce, so cannot be used to advise management.

The growth annulus deposition rate on otoliths using chemical marking (OTC) revealed that the growth zone deposition rate of *C. carpio* in Groenvlei was comparable to that recorded in other invaded locations in Australia (once a year) (Brown et al., 2005; Tampero et al., 2006), but differed from the only other study in South Africa (Lake Gariep, twice a year) (Winker et al., 2010). Furthermore growth was faster and *C. carpio* lived longer in Groenvlei than Lake Gariep (up to 20 years versus seven years). The variability in the annulus deposition rate and longevity between these two populations is attributed to factors such as environmental fluctuations, intraspecific competition, predation and fishing pressure all of which are high in the Gariep Dam compared to Groenvlei. These findings highlight the need for South African managers to consider management on a case by case basis, as despite its wide distribution the biology of *C. carpio* is likely highly variable across the country, and linked to temperature, productivity, competition and predation. The *C. carpio* in Groenvlei matured at around 262 to 314 mm fork length, between the ages of two to three years. Fisheries harvesting, regardless of purpose, can induce changes such as a decrease in body size and age at maturity (Law et al., 1989). By gathering this baseline at the early stages of management in Groenvlei it will be possible to assess if these adaptive changes occur and adjust management accordingly.

The results showed that the current removal efforts of *C. carpio* in Groenvlei could be improved through telemetry studies, and as manual acoustic tracking provides precise data on fine-scale movement patterns, it has particular value in a system like Groenvlei. *Cyprinus carpio* movement patterns were not random in space and time. We observed a synchronised migration in the lake backwater habitat during late spring (November 2020) which corresponds to the recorded reproduction period of *C. carpio* in South Africa (Winker et al., 2011) and was verified by field observations. During this period all tagged *C. carpio* were in a small area and the distance moved by individuals was much less than outside spawning season. Other case studies (Stuart and Jones, 2006; Jones and Stuart, 2009; Conallin et al.,

2011; Daniel et al., 2011) have successfully exploited the spawning season to optimise *C. carpio* capture.

Since Groenvlei is located within the Goukamma Nature Reserve, an important area for conserving biodiversity, the possibility of using chemicals such as Rotenone (as per Dalu et al., 2020) and introduction of predators as done in North America to control *C. carpio* population is impossible due to the sensitivity of the system and the effects on non-targeted species. Commercial exploitation of *C. carpio* in Groenvlei is also limited by the size and nature of the system, furthermore the potential of Groenvlei to contribute to capture fisheries reported that potential yields were too low to sustain any sort of formal fishery (Dredge and Weyl, 2017). Both structural (push and jump traps e.g., Williams Cage) and non-structural deterrents such as sound and strobe lights are costly and requires maintenance frequently. The biocontrol and other genetic control methods of *C. carpio* are still being investigated for safety and efficacy in countries such as Australia (Threasher et al., 2018) and therefore not an option in South Africa.

Of current available methods of control, only mechanical removal seems truly viable as an option, although requiring consistent effort, it is affordable at Groenvlei with less impacts on non-targeted species. Both gillnetting and bow fishing can continue to be carried out, however these methods could be optimised using the data in this study; for example specifically targeting *C. carpio* with bow and arrow in the spawning grounds during spring and summer (October to November) and placing nets to block access, or capture fish moving in and out of the backwaters spawning areas. In addition, fyke nets proved successful in capturing juvenile *C. carpio* for survey purposes, which could equally work as a control method. Ultimately this study reinforces the need and value of research informed management of non-native species in South African freshwaters.

In conclusion, this thesis answers research questions that could be used for management purposes, it will be remiss of me not to include some suggestions for future research and management interventions.

- More research on the movement patterns and habitat-use of *C. carpio* at Groenvlei to provide more data on spawning aggregations to refine the locations, as this study was largely limited by the COVID-19 Pandemic.
- A monitoring program of species changes at Groenvlei could be implemented to determine the abundance and impacts of *C. carpio* especially on the two important native species.
- Citizen science programs through NGOs such as the Gift of Givers that harvest *C. carpio* and subsistence anglers could be encouraged to target *C. carpio* with the aim of reducing its biomass.

Ultimately the decision is by local management authority to implement the suggestions or other management recommendations.

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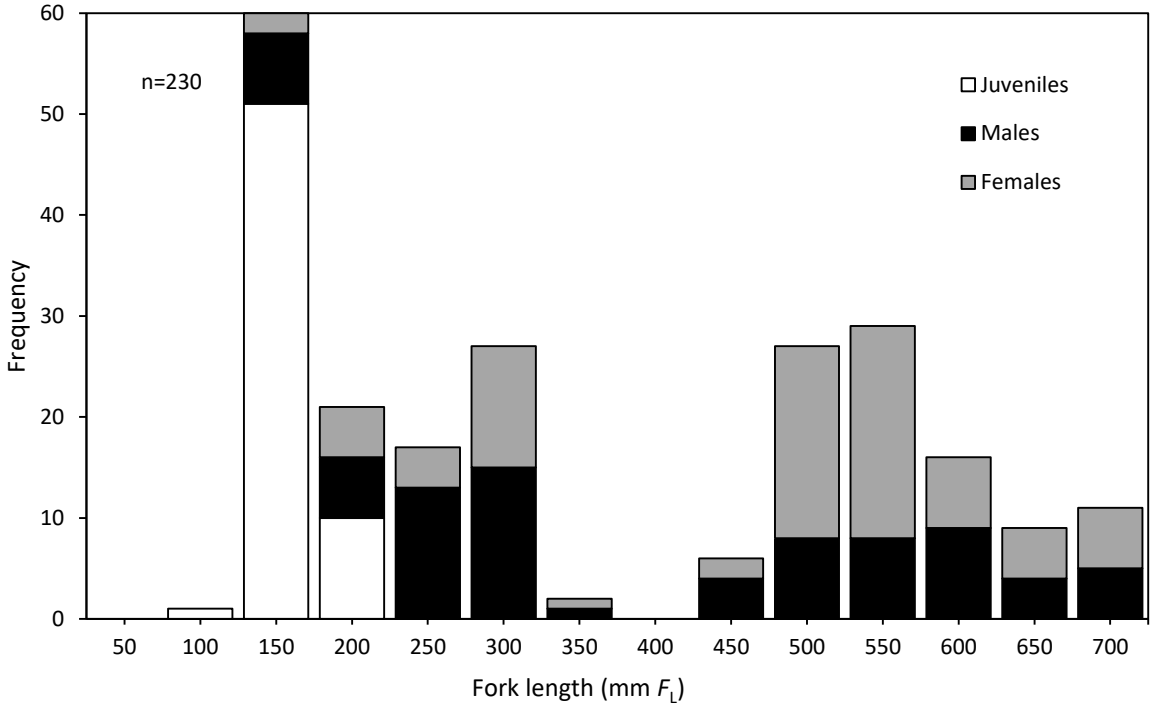
SUPPLEMENTARY DATA

Supplementary table 1. Results of the chemical marking experiment; the date of injection ($DATE_{INJ}$) and recaptured ($DATE_{RE}$), time in liberty is noted in decimal years and the number of growth increments (one opaque and one translucent zone) deposited before (Pre) and after (Post) the OTC mark. Edge appearance was categorised as translucent (T) or opaque (O).

ID	$DATE_{INJ}$	$DATE_{RE}$	Years at liberty	L_{RE} (mm F_L)	Number of growth increments			Edge
					Pre	Post	Total	
1	2013/05/26	2019/06/01	6,01	623	6	6	12	T
3	2014/02/22	2019/07/27	5,43	634	4	5	9	O
4	2015/06/14	2019/08/11	4,16	576	5	4	9	T
6	2015/03/07	2019/08/18	4,45	671	6	4	10	O
8	2015/03/08	2019/11/02	4,66	645	15	5	20	T
9	2015/06/28	2019/11/02	4,35	655	8	4	12	T
12	2015/06/13	2020/03/15	4,76	636	10	5	15	O
13	2015/01/08	2020/07/26	5,55	615	5	5	10	T
14	2015/01/08	2020/08/15	5,61	558	4	6	10	T
15	2015/06/13	2020/08/15	5,18	517	3	5	8	O
17	2014/08/18	2020/10/20	6,18	670	6	6	12	T



Supplementary figure.1. The length-frequency distribution (mm F_L) of juvenile, male and female *Cyprinus carpio* collected at Groenvlei during late October 2020 for the age determination chapter.