THE BIOLOGY OF *OREOCHROMIS MOSSAMBICUS* AND VULNERABILITY TO THE INVASION OF *OREOCHROMIS NILOTICUS*

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By

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ABSTRACT

Mozambique tilapia, *Oreochromis mossambicus,* a native southern African species now co-occurs with invasive Nile tilapia, *Oreochromis niloticus* throughout much of the distribution of the former. The spread of *O. niloticus* in South Africa has been attributed to escapees from aquaculture facilities, placing *O. mossambicus* at risk through competition for habitat and food resources, as well as through hybridisation. To better manage invasions, a comprehensive understanding of the biology, ecology and behaviour of both native and invasive species is required. The aim of this research was to comparatively assess the biology of *O. mossambicus* and *O. niloticus*, their food resource use characteristics and potential competitive interactions to infer impact risks associated with *O. niloticus* invasion dynamics.

In addition to lack of sufficient autecological knowledge on *O. niloticus* in general, the challenge in the Eastern Cape is that relatively little regional knowledge is available on the biology and ecology of the native *O. mossambicus*. To address this, a total of 101 *O. mossambicus* individuals (32 - 297 mm L_T) were sampled from the Sunday River catchment and their age and growth determined using sectioned sagittal otoliths. The largest female was 288.8 mm with a parameter estimate of L_T (mm) = 272 (1-e$^{-0.331(t=0.772)}$) and the largest male was 297 mm described as L_T (mm) = 331.9 (1-e$^{-0.167(t=1.192)}$). The growth parameter estimate age for combined sexes was best described as L_T (mm) = 322.5 (1-e$^{-0.201(t=1.027)}$). The growth rate was initially rapid for *O. mossambicus* and the asymptotic length reached after four years. The length-at-50% maturity was reached at 106.45 mm L_T ($R^2 = 0.57$) for the entire population. There was a significant difference ($\chi^2 = 8{,}047$, df = 1, p-value = 0.0045) in the sex ratio between males and females which was skewed towards males 1:1.89 (F:M). Comparisons with *O. niloticus* were based on literature and these showed that *O. niloticus* had faster growth rates than *O. mossambicus.* These results serve as a baseline study in predicting the potential impacts of *O. niloticus* if it was to be introduced in the Eastern Cape region.

Furthermore, although these two species are known to share habitat and food resources, feeding dynamics within the context of relative impact on prey resources, and competition potential between the species, are largely lacking. I used experimental functional response procedures to contrast the food consumption dynamics of each species and to assess for any multiple predator effects (MPEs) between these two closely related fishes. This was done by contrasting functional responses between individual species under single predator scenarios, predicted multiple predator functional response dynamics based on the individual species outputs, and actually observed functional responses under multiple predator conditions. Results showed that both Nile tilapia and Mozambique tilapia depicted a destabilizing Type II functional response. In both single and conspecific pairing Nile tilapia had significantly greater functional responses than Mozambique tilapia, hence greater overall predatory potential than its native congeneric Mozambique tilapia. Attack rates were also greater for Nile tilapia than Mozambique tilapia with both species showing similar handling times in single trials. However, no evidence for MPEs were detected, given lack of differences between predicted and observed functional responses under heterospecific conditions. These results suggest that Nile tilapia do not adjust their food intake in the presence of heterospecific competitors, but do consume more than Mozambique tilapia and are better at finding food when it is present at low densities.

Feeding-related morphological characteristics may influence predatory performance of a species and can further provide information on the species' capacity to locate, attack and consume different prey items. The feeding capacities between *O. mossambicus* and *O. niloticus* were compared based on morphological traits in order to determine whether differences existed, and if these differences place the invasive *O. niloticus* at an advantageous position in terms of resource acquisition and consumption over its native congener. Principal component analysis for functional morphology traits showed overlap between *O. niloticus and O. mossambicus*. *Oreochromis niloticus* had distinctively larger lower jaw closing force, gill resistance and gill raker length which facilitated greater feeding capacities for the invasive species over the native *O. mossambicus*. Trophic profiles depicted high dietary overlap between the two species. Although *O. niloticus* had a greater feeding capacity towards phytoplankton, plants, fish (ambush), fish (pursuit) and larvae, while *O. mossambicus* only showed greater feeding capacity towards zooplankton. While dietary overlap and similarities in morphological traits between native and invasive species may result in exploitative competition between the species, *O. niloticus* seems to be more versatile in its feeding and capable of consuming food web components that *O. mossambicus* may not be able to handle.

Keywords: Ecomorphology, gut content, multiple predator effects, prey consumption, sagittal otoliths, Von Bertalanffy model.

DECLARATION

I, Nobuhle Phumzile Mpanza, hereby declare that this thesis submitted for a Master of Science degree in the Department of Zoology and Entomology, Rhodes University is my own work and has not been submitted for any other degree at any other institution.

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"Ngibonga angiphezi, izandla zidlula ekhanda. Enikwenze kimi nikwenze nakwabanye"

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CHAPTER 1

GENERAL INTRODUCTION

1.1. Introduction of non-native species

Freshwater ecosystems are under pressure from a number of stressors such as pollution, habitat modifications, overexploitation as well as the introduction of invasive species (Bellard et al., 2016; Jackson et al., 2017; Venohr et al., 2018). Of the above-mentioned stressors, invasive species such as freshwater fishes have been identified as the least reversible problems currently facing freshwater ecosystems (Gozlan, 2008; Simberloff, 2003; Strayer, 2010). The introduction of these species threatens both the biodiversity and integrity of freshwater ecosystems (Jackson et al., 2017; Meyerson et al., 2019). Many of these species are moved across natural biogeographic barriers into new localities (Dudgeon et al., 2006; Meyerson et al., 2019) while others are driven by human-related activities (Dudgeon et al., 2006; Gozlan, 2008). Aquaculture, sport fishing, pet trade and fisheries are some of the main anthropogenic activities at the forefront of invasive species moving beyond their native range (Gozlan, 2008; Gozlan et al., 2010; Zengeya et al., 2015). These anthropogenic introductions have been identified as the main driving force behind an increase in invasive species establishments which are mainly caused by the expansion of transportation networks linked to global trade as well as habitat modifications (Early et al., 2016; Meyer et al., 1999) further threatening both the health and functionality of freshwater ecosystems (Ricciardi et al., 2017). Invasive species currently show no sign of increase in saturation across the globe (Seebens et al., 2017).

Non-native species potentially present adverse impacts when they invade and successfully integrate into new ecosystems and thus threatens the integrity of the novel ecosystem as well as its biodiversity (Ellender et al., 2018). Introduction of invasive species into new localities come with a number of conservation problems such as ecosystem modifications, alteration of trophic links, hybridisation with the congeneric native species, high predation pressure as well as competitive exclusion of the native species as they share habitat and food resources (Eby et al., 2006; Gozlan et al., 2005; Jackson et al., 2017).

1.2. Study species

This research project focuses on two fish species from the family Cichlidae which both fall under the genera *Oreochromis;* namely: Mozambique tilapia, *Oreochromis mossambicus* (Peters, 1852) and Nile tilapia, *Oreochromis niloticus* (Linnaeus, 1758). There are 6 indigenous and 2 non-native/introduced *Oreochromis* species in southern Africa (Skelton, 2001). *Oreochromis niloticus* in an introduced/non-native species in southern Africa while *O. mossambicus* is a native/indigenous southern African species. Both species are economically important as they are both used in support of food security through wild capture and aquaculture activities (Zengeya et al., 2017). These species are both generally tolerant to wide temperature and salinity ranges, for example *O. mossambicus* can live and breed in both freshwaters and seawaters (Skelton, 2001). Species within the *Oreochromis* genera are mouthbrooders (Skelton, 2001) meaning that females incubate the eggs in their mouth until the male finds a suitable nursery to brood the eggs and larvae (Skelton, 2001). These species show ontogenetic shifts in their diet from feeding on phytoplankton and small invertebrates as juveniles to feeding on macrophytes, diatoms, detritus, and algae as adults (Skelton, 2001; Zengeya et al., 2017).

Oreochromis niloticus is an endemic African freshwater cichlid (Zengeya et al., 2015) that is native to the Nile River basin, south-western Middle East and Senegal Rivers (Zengeya et al., 2013a; Zengeya et al., 2015; Zengeya et al., 2017). *Oreochromis niloticus* has a history as an invasive species, as it was first introduced in Lake Victoria in the early 1950s where it was found to displace native species, leading to local extinction of native congenerics (Zengeya et al., 2015). Further introductions were observed in Lake Kariba in the 1990s after *O. niloticus* escaped *in-situ* cage culture fish farms (Chifamba, 2014; Marshal, 2006; Zengeya et al., 2013a). In South African rivers *O. niloticus* was first introduced for aquaculture and has since established viable feral populations in considerable sections of the Limpopo River basin and several other river systems within the tropical and subtropical regions of the country (van der Waal & Bills, 2000; Weyl, 2008; Zengeya & Marshall, 2015; Zengeya et al., 2013a). These newly established feral populations have been implicated as having adverse impacts on the recipient river systems (van der Waal & Bills, 2000; Zengeya et al., 2015). The identified impacts include declines in endemic fish abundances and local extinction of native congenerics through competitive exclusion and hybridization (Chifamba, 1998; van der Waal & Bills, 2000; Zengeya et al., 2013a; Zengeya et al., 2015).

The success of *O. niloticus* as an invasive species has been attributed to its broad range of trophic and ecological adaptations as well as its adaptive life history traits that allows it to occupy a number of tropical and subtropical freshwaters environments. For instance, *O. niloticus* has the ability to spawn numerous broods within a single season, has high parental care, fast growth rates and rapidly attains sexual maturity (Weyl, 2008; Zengeya et al., 2013a). Furthermore, their males are more aggressive competitors which allows them to outcompete other species for spawning grounds (Zengeya et al., 2013a). *Oreochromis niloticus* further tolerates a wide range of temperatures allowing it to thrive in different environments (Zengeya et al., 2013a). The success of *O. niloticus* into new environments places native congenerics at the risk of extinction one of which is *O. mossambicus* (Zengeya et al., 2013a; Zengeya et al., 2013b).

Oreochromis mossambicus in an indigenous southern African cichlid with a native distribution range from southern Kenya into the inland and coastal regions of south-eastern Africa and southwards to the Eastern Cape region of South Africa (Bruton & Allanson, 1974*).* *Oreochromis mossambicus* is currently at the risk of extinction mainly because of its trophic and habitat overlap with *O. niloticus* that leads to both hybridization and competition among the two species (Zengeya et al., 2013a). Furthermore, these two species can interbreed with each other producing hybrids that are not sterile and are thus able to interbreed with either of the two parent species producing progenies with intermediate traits (van der Bank & Deacon, 2007). As such, the endemic gene pool of *O. mossambicus* is at the risk of extinction and thus research focusing on mitigation strategies for invasive species is needed to avoid possible loss of the native gene pool (van der Bank & Deacon, 2007).

South Africa is country with a long history of invasive species introductions. These introductions are mostly from aquaculture activities, recreation through pet trade and sport fishing while some are accidental introductions (Ellender & Weyl, 2014; Zengeya et al., 2017). The management of invasive species in South Africa is legislated by the National

Environmental Management: Biodiversity Act (NEM: BA). In terms of NEM: BA, *O. niloticus* has been listed as a prohibited species (DEA, 2014). NEM: BA legislation classifies *O. niloticus* as a category 1b species identified as being highly invasive if introduced and thus requiring compulsory control. It is important to note that *O. niloticus* has also been identified as one of the conflict species in South Africa meaning that it is considered as an economically valuable species while posing a threat to the biodiversity and integrity of freshwater ecosystems. NEM: BA further identifies *O. mossambicus as* a vulnerable species requiring urgent conservation. The economic value of *O. mossambicus* in southern Africa resides in its use as a food source for people, weed control as well as being used as prey and bait for sport fishing (van der Bank & Deacon, 2007).

1.3. Biology

1.3.1. Age and growth

Knowledge on the age and growth of fish groups is crucial for conservation and management of certain species (Bakane, 2016; Bokhutlo et al., 2015; Beamish & McFarlane, 1983). Knowing the age of a fish specimen is crucial in calculating its growth rate as well as the age at which they mature (Bokhutlo et al., 2015; Peel, 2012; Taylor et al., 2016). Age studies further forms the basis for calculating mortality rate and productivity (Campana, 2001). Fish age and growth information aids in improving our understanding of factors affecting fish recruitment processes (Bakane, 2016; Jones, 1992). In adult fish populations, age and growth studies helps in determining the impacts of exploitation on stocks, success of fisheries management strategies and life history processes (Jones, 1992).

Metabolic rates of fish are impacted by factors such as temperature, reproduction and spawning which are reflected on calcified structures such as scales, spines and otoliths which are seen as alternating opaque and hyaline growth zones (Booth & Merron, 1996; Campana, 1999; Degsera et al., 2020). Calcified structures have formation of periodic growth increments that allows the age of a fish specimen to be estimated (Campana, 2001; Peel, 2012; Peel et al., 2016). The majority of these calcified structures are vulnerable to calcium resorption which compromises the retention of growth increments (Booth & Merron, 1996; Peel, 2012). For example, sectioned spines were used in a study by Quick and Bruton (1984) where they found possible resorption of one or more rings on the majority of their sectioned spines which led to higher rejection rates. It is also important to note that the use of spines in age studies shows higher aging success in younger fish and thus spines are only reliably when working with younger fish as depicted by Van der Waal & Schoonbee (1975) in the Elands and Olifants River; while for older fish, the use of spines in aging becomes uncertain and increases the likelihood of underestimating age.

The growth zones seen on these calcified structures can be used to estimate age which is then correlated with length to determine fish growth rates (Welcomme, 2001; Weyl & Hecht, 1998). Sectioned sagittal otoliths have been used in various studies to determine age and growth of economically important cichlids (Weyl & Hecht, 1998; Peel, 2012), while other studies used scales (Dudley, 1974; van der Waal, 1985). Between these two commonly used calcified structures (otoliths and scales), sectioned sagittal otoliths are the most preferable method due to the fact that scales tend to underestimate longevity which leads to overestimated growth (Hecht, 1980; Jones, 1992). A study conducted on *O. mossambicus* by Hecht (1980) showed that the use of scales for aging hampers age and growth estimations due to false check deposition (Bruton & Allanson, 1974). This is mainly because fish scales are re-absorbed during spawning season and starvation periods (Hecht, 1980). Sagittal otoliths on the other hand are the most favourable and accurate parameter to use in age estimation studies (Weyl & Booth, 2008) as they are metabolically inert meaning that the materials that are being deposited on them are not prone to resorption (Bokhutlo et al., 2015; Carmo et al., 2018; Campana, 1999). Another advantage of using otoliths is that they grow continually throughout the entire life of the fish and thus records the entire lifespan (Bokhutlo et al., 2015; Campana, 1999). Other methods of age determination such as the use of fish scales are considered as an inferior method mainly because it underestimate the true fish age thus overestimating the growth rates (Booth & Merron, 1996; Hecht, 1980; Peel, 2012).

When assessing the age and growth of fishes, age validation is a crucial step as it allows the establishment of the relationship between growth zone/ring number and age of a fish specimen (Bokhutlo et al., 2015; Weyl & Hecht, 1998). Therefore, validation of growth zone deposition rate is considered a requirement when conducting ageing studies (Bokhutlo et al., 2015; Campana, 2001). The lack of validated age data poses a major constraint in terms of understanding the life-history of fishes and in developing management strategies because important biological information such as growth and maturity cannot be estimated (Taylor et al., 2016). Differences in growth zone deposition have been reported between populations of the same species at different localities and among species in one locality (Peel et al., 2016). For these reasons, validating the periodicity of growth zone deposition on a regional basis is considered a crucial step in age studies (Campana, 2001; Peel et al., 2016). For example, Peel et al., (2016) conducted a validation of ageing, where it was hypothesized that a single growth zone is deposited yearly. To validate this hypothesis, they used methods such as the edge analysis method which interprets otolith edges as either opaque or translucent, while plotting the relative frequency of each zone in relation to time.

Although the edge analysis method is commonly used, it is important to note that it is less reliable than other methods such as the mark-recapture method of fish that have been chemically tagged (Peel et al., 2016). Mark-recapture of fish that are chemically tagged is reliant on the incorporation of a calcium binding chemical into the calcified structures (i.e. bones, otoliths and scales), which leaves a permanent fluorescent mark in the growth increment that is formed at that specific time (Campana, 2001; Weyl & Booth, 2008). After marking, fish are released back into the wild for a year or two. Upon recapture, the number of growth zones formed distal to the mark is compared to the duration of how long the fish was tagged for (Campana, 2001; Peel et al., 2016). While the mark-recapture method is regarded as the preferred approach (Peel et al., 2016), it is often unreasonable given that the chances of recapture of an individual one to two years later are very low, even if many individuals are employed.

1.3.2. Reproductive biology

In addition to age and growth studies, reproductive biology studies are also essential for fisheries management strategies through the assessment of reproductive periodicity and estimation of size at which the fish first reaches maturity (Karna & Panda, 2011). Knowledge of the reproductive biology gives us more information on the species breeding season of which informs the implementation of closed seasons thus allowing the protection of species during their spawning time (Bokhutlo et al., 2015). This also allows the implementation of the minimum legal harvesting sizes greater than the length at which the fish reach maturity. This affords the fish the opportunity to reproduce at least once before it is harvested therefore reducing the risk of recruitment of overfishing (Kolding et al., 1992; Welcomme, 2001). Cichlids have an extended spawning season which lasts throughout the warmer summer months beginning in October and ending in April (Peel, 2012; Weyl & Hecht, 1998). During winter time, these species especially in subtropical regions are generally reproductively inert (Ellender et al., 2008).

Sexual maturity in fish marks a crucial change in its life as it presents the potential conflict between resource allocation, reproduction and growth (Wooton, 1990). Successful reproduction depends on the location and timing of reproduction (Bokhutlo et al., 2015; Wooton, 1990). The transition from allocation of resources to reproduction should only happen in environments that improves the survival rate of offspring (Lowe-McConnell, 1987). Length and age at first maturity is affected by both biotic and abiotic environmental components (Weyl & Hecht, 1998). For example, when rivers dry up, food resources become less scarcely available, hence competition for food resources arises leading to reduced fish sizes at maturity (Karna & Panda, 2011). Therefore, length at maturity is one of the important variables to look at when dealing with fish biology as it informs on closed seasons in order to allow fish to spawn. In order to make scientifically sound decisions about fish management, it is imperative to understand the biology of the species (Turan et al., 2005). Therefore, the age and growth as well as the knowledge of the reproductive biology will allow us to better understand the life history of *O. mossambicus* in relation to the invasive *O. niloticus* and thus better conserve it while managing invasions.

1.4. Functional response

Understanding and predicting the ecological impacts of invasive species is crucial in risk assessment as well as biodiversity conservation (Dick et al., 2013; Ricciardi et al., 2013). Predictive models are needed to conceptualise and understand how invasive species bring about ecological impacts and how they alter ecosystem functioning (Dick et al., 2014). These models help in the implementation of conservation strategies for native biota as well as in managing invasive species (Dick et al., 2014; Ricciardi, 2003). It is important that these models are able to explain the ecological impacts of introduced species on native species as well as how native species respond to these invasions (Dick et al., 2014). One of the models proposed for looking at invasive species impacts through food resource utilisation dynamics are functional responses (FRs) (Alexander et al., 2014; Dick et al., 2014; Dickey et al., 2020; Ricciardi, 2003). The incorporation of FRs into the field of invasion biology defines the relationship between predator and the amount of prey supplied (Dick et al., 2014; Iacarella et al., 2015). This then gives us the relationship between the amount of resources available and resource consumption rate per predator (Dick et al., 2014; Holling, 1959; South et al., 2018). Based on Holling (1959; 1965), this relationship can be displayed in three general categories of functional responses namely, Types I, Type II and Type III (Figure 1.1). Type I occurs when the capture rate increases in direct proportion to prey density until it reaches a state of stativity. There is a constant proportion of available prey eaten regardless of how much prey is available thus a linear increase in feeding rates is depicted. Type I FR is evident in filter feeding organisms where the resource utilisation is not limited by handling time (Khosa et al., 2020; South & Dick, 2017). Type II depicts a decrease in predation rate as the amount of prey available increases. This inversely density-dependent FR type suggests that there is high food resource consumption at low food resource densities and is thus associated with the risk of food resources becoming depleted due to the fact that food available in low densities are used at high rates (Khosa et al., 2020; Alexander et al., 2014; South et al., 2017).

Lastly, Type III occurs when declines in predation rate occurs at both the low and high prey densities thus depicting a positively density-dependent relationship (Holling, 1959). The FR types displayed by different consumers are crucial in understanding consumer impacts and the community dynamics because the functional response type can contribute to the stability and persistence of the resource (Dick et al., 2014). Within the invasion context, FRs are useful for assessing how novel consumers in receiving environments may interact with native food resources. Invasive species are able to utilise resources more rapidly and efficiently in comparison to native species (Chapple et al., 2012; Johnson et al., 2008; Weis, 2010). Indeed, invasive species have been shown to have higher per capita effects on food resources when compared to native species (Dick et al., 2013; Alexander et al., 2014). As such, FRs have been identified as a largely reliable and affordable tool for predicting ecological impacts of non-native species on native species (Alexander et al., 2014; Dick et al., 2014; Mofu et al., 2019a). For instance, comparative FRs allows us to understand and assess the dynamics that exists between native and invasive species which is very useful in assessing and predicting potential competition that might exist among consumers (Mofu et al., 2019b).

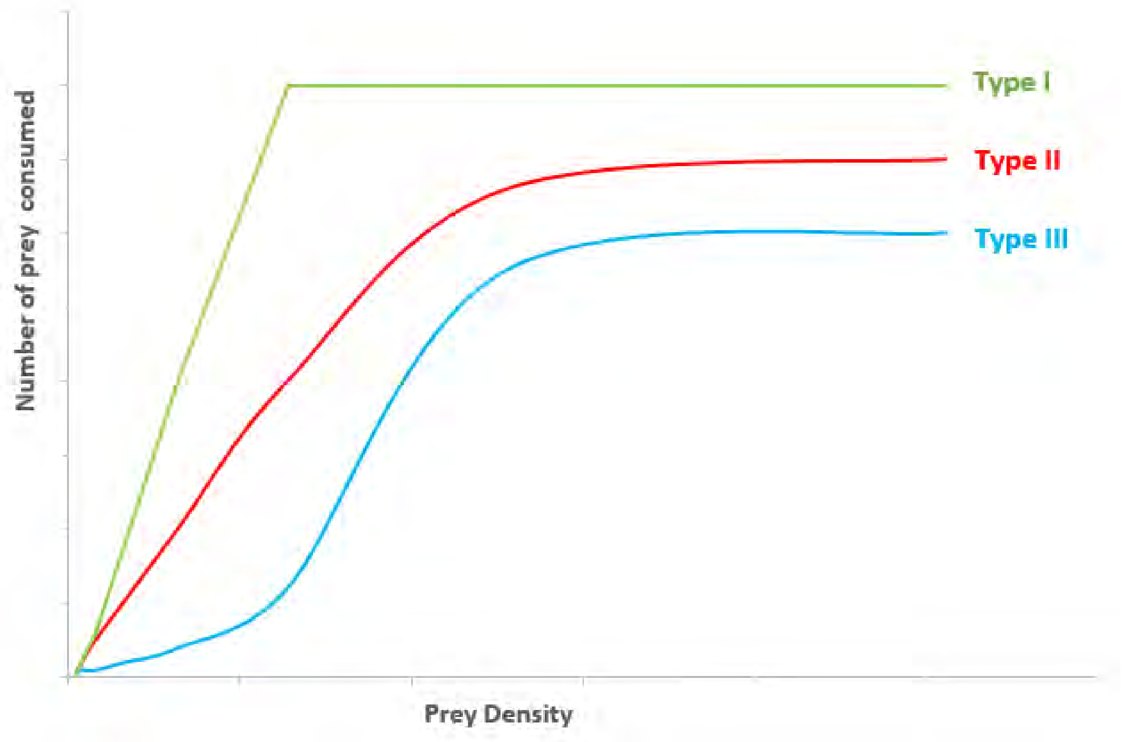

Figure 1.1: The different types of functional responses based on the relationship between prey density and rate of prey capture (Redrawn from Pritchard et al., 2017).

Upon entry into new ecosystems introduced species will interact with resident species, resulting in heterospecific interactions (Jackson et al., 2017). There is thus a need to better understand the effects of multiple species interactions in invasion and biotic-resistance contexts (Wasserman et al., 2016). These interactions between multiple species are fundamental to the structure and functioning of ecological communities and are important regulators of predator-prey dynamics (Barrios-O'Neill et al., 2014). Interactions between predators can lead to multiple predator effects (MPEs) with regard to prey consumption dynamics. Predator-predator interactions can result in additive prey consumption, synergistic food resource consumption (e.g. increased prey risk MPE) or reduced food resource consumption (e.g. decreased prey risk MPE). Multiple predator effects allows us to compare predicted and observed functional responses based on individual predator and multiple predator combinations as well as their consumption rates (Barrio-O'Neil et al., 2014; Wasserman et al., 2016). Given the variable impacts combinations of predator species may have on food resources, quantifying MPEs are vital for understanding how predator-prey interactions may be altered under multiple predator scenarios, (Sokol-Hessner & Schmitz, 2002; Wasserman et al., 2016) with implications for invasive-native consumer interactions. Functional responses are also regarded as being useful for the assessment of MPEs, given that they cater for prey depletion effects associated with multiple predator lab-based studies (Sentis & Boukal, 2018; McCoy et al., 2012; Wasserman et al., 2016; Mofu et al., 2019b).

Studying the interactions between invasive and native species will allow us to provide evidence to conservation managers which will aid in management and mitigation strategies of invasive species. Experimental approaches further provide an important complement to field observations to predict and disentangle complex predator-prey interactions and resource density in order to inform management and mitigation strategies. Since invasive species are characterised by high FR, comparing resource utilisation (e.g., prey consumption) between native species and the invaders might help predict the invaders impact and allow for better legislation regarding limiting the spread of *Oreochromis niloticus*. For example, *O. niloticus and O. mossambicus* are morphologically similar but the latter grows larger. If this invasive species also has higher FRs (attack and consumption) rates or reduces with *O. mossambicus* feeding efficiency, then greater care needs to be taken to limit their spread.

1.5. Functional morphology

Morphological traits are biological physical attributes that can be measured on an individual and can influence the performance of a species and thus its fitness (Violle et al., 2007). These traits can then be used to quantify the functional diversity of communities and help assess how environmental and anthropogenic constraints affects community structure (Mason et al., 2008). Incorporating the morphological traits of a species into diversity analysis has been used as a way to construct a more generalised understanding of patterns and processes in community ecology (Pease et al., 2015). Based on Pease et al., (2015) examining the functional structure of a species may reveal numerous factors linked to mechanisms by which ecological communities function as a response to environmental changes. Therefore, traits-based approaches have the potential of improving conservation applications, such as bio-assessment metrics utilised in evaluating ecological integrity (Pease et al., 2015). Morphological traits aid in determining the capacity of a species to find, attack and eat different prey items. The similarity in morphological traits allows us to see if there are any dietary overlaps and similarity in trophic profiles between invasive and native species (Luger et al., 2020; Nagelkerke et al., 2018).

The type of prey item a fish consumes as well as the effort involved in acquiring that particular food source is determined by the morphological traits of the species (Sibbing & Nagelkerke, 2000). The Food-Fish Model (FFM) is used to predict differences in trophic morphology between species and further depicts implications inferred by these predicted differences on the capacity to utilise certain food resources (Nagelkerke et al., 2018). Based on Sibbing & Nagelkerke (2000), the FFM model further gives information on which food properties are crucial in feeding and how fish can better cope with them. Furthermore, this allows one to analyse the trophic interactions in fish communities as well as the cascade effects of changes within that particular environment. This approach is an important tool when it comes to developing fishery management plans and biodiversity conservation as it allows conservation managers to understand and compare feeding capacities of native and invasive species based on their morphological differences (Sibbing & Nagelkerke, 2000).

Parameters such as food properties where the size, shape, escape speed and mechanical properties are evaluated when working with feeding in fish (Nagelkerke et al., 2018). The FFM model will then show the food properties that are most crucial in resource consumption and how different fish species are morphologically built to cope with these food items. Highly demanding food types can be either large in size, fast mobility, suspensions of plankton, and benthic prey imposes incompatible morphological requirements on fish (Sibbing & Nagelkerke, 2000) and its ability to outcompete its competitors for food resources (Nagelkerke et al., 2018). Fish species prey on a variety of items including phytoplankton, seeds, detritus, zooplankton, benthic insects and fish (Sibbing & Nagelkerke, 2000; Taylor, 2016). Two activities are involved in feeding, that is foraging, and food processing and fish have various morphological, physiological and behavioural specializations that gives them an advantage in utilizing different food sources. Some food types are highly demanding when foraging (fast prey) while others are highly demanding when processing such as macrophytes (Nagelkerke et al., 2018).

Comparative functional morphology between native and invasive species allows comparison in feeding capacities between native and invasive species based on morphological differences and similarities (Sibbing & Nagelkerke, 2000). Functional morphological will help us to better understand whether there are any similarities in feeding-related morphological traits between *O. mossambicus* and *O. niloticus* and if these differences places the invasive *O. niloticus* at an advantageous position in terms of resource acquisition and consumption and hence aid in better management of invasions.

1.6. Research approach and thesis outline

This research project aims to assess the comparative biology of *Oreochromis mossambicus* and *Oreochromis niloticus* as well as their food resource use characteristics and competitive interactions in order to infer potential invasion risk of *O. niloticus* so as to better manage future invasions.

The objectives for this research are as follows:

(i) Assess the biology of *Oreochromis* using sectioned otoliths to determine the growth rates and determine the sex structure as well as the age at maturity using gonadal development stages of *O. mossambicus* in the Sundays River catchment.

(ii) Contrast the consumer-resource dynamics and competitive interactions through resource utilisation between *Oreochromis mossambicus* and *Oreochromis niloticus* using functional response experiments.

(iii) Make morphological trait comparisons between *O. mossambicus* and *O. niloticus* in order to determine whether there are differences in feeding-related morphological traits between these two species, and if these differences place the invasive *O. niloticus* at an advantageous position in terms of resource acquisition and consumption.

To achieve the above objectives, this research thesis was organised into five chapters. Chapter one was a general introduction. Chapter two assessed the biology of *O. mossambicus* by determining the age and growth as well as the reproductive of *O. mossambicus* in Sundays River, Eastern Cape and made comparisons with *O. niloticus* based on published literature. Resource utilisation was investigated in Chapter three. Here I evaluated and compared prey consumption between *O. mossambicus* and *O. niloticus* using both single and mixed functional response experiments. In this chapter I tried to identify whether the invasive species has a greater overall predatory potential, and if the invasive species potentially reduces consumption by the native fish species when they co-occur, through interference competition. Chapter four compared the functional morphology of both *O. mossambicus* and *O. niloticus* in order to detect morphological similarities between these two species and if these differences favour the invasive species. Lastly, Chapter five synthesized and discussed the data chapters while providing recommendations for the future.

1.7. Ethical clearance and permits

The collection of animals for this research was carried out in compliance with the Department of Environmental Affairs (DEA permit no. 50738210617105722 & 50738210617114244); the Eastern Cape Department of Economic Development and Environmental Affairs (DEDEA permit no. HO/RSH/20/2021) and ethical clearance was approved by the Rhodes University Animal Research Ethics Committee (RU-AREC reference no. 2021-2695-5969).

CHAPTER 2

AGE, GROWTH AND REPRODUCTIVE BIOLOGY OF *OREOCHROMIS MOSSAMBICUS* IN THE SUNDAYS RIVER CATCHMENT, EASTERN CAPE

Introduction

Knowledge of the age of fish is crucial in estimations of its growth, maturity and mortality rates (Campana, 2001; Campana & Thorrold, 2001; Peel et al., 2016; Taylor et al., 2016). Age and growth studies assists in determining exploitation impacts on fish stocks, efficacy of fisheries management as well as improving our understanding of factors that might affect recruitment processes (Booth & Merron, 1996; Jones, 1992). Thus accurate age estimations are fundamental in calculating population age structure and growth rates for fish species (Booth & Merron, 1996; Weyl & Hecht, 1998). Calcified structures such as scales and otoliths are useful when estimating fish age (Campana, 2001; Carmo et al., 2018; Peel et al., 2016; Taylor et al., 2016), which when correlated with fish length can be used to determine growth rates (Carmo et al., 2018; Jenkins, 1952; Sneed, 1951; Welcomme, 2001; Weyl & Hecht, 1998).

Of the above-mentioned calcified structures, sectioned sagittal otoliths have been used in various studies to determine age and growth of cichlids (Booth & Merron, 1996; Degsera et al., 2020; Peel, 2012; Weyl & Hecht, 1998), while other studies used scales (Dudley, 1974; van der Waal, 1985). The use of scales has been found to be less accurate and unreliable as they tend to under-estimate longevity thus over-estimating fish growth and mortality rates (Booth & Merron, 1996; Campana & Thorrold, 2001; Booth & Merron, 1996; Weyl & Booth, 2008). For example, a study conducted by Hecht (1980) on Mozambique tilapia, *Oreochromis mossambicus* (Peters, 1852) showed that the use of scales hampers age and growth estimation due to deposition of pseudo checks and also because fish scales are easily re-absorbed during spawning periods or starvation. Sectioned sagittal otoliths are the most accurate and suitable method used in age estimation studies (Peel et al., 2016; Weyl & Hecht, 1998; Weyl & Booth, 2008). This is mainly because sagittal otoliths are metabolically inert meaning that the materials deposited on them are not prone to resorption (Campana, 1999; Weyl & Booth, 2008). The present study utilizes the sagittal otoliths method because of its advantageous attributes mentioned above.

Besides the knowledge of the growth rate of fish species, it is also imperative to study their reproductive cycles so as to better understand and manage freshwater ecosystems. For instance, proper and accurate estimation of size at first maturity is very useful for fish stock management (Karna & Panda, 2011). An individual needs to be identified based on whether they are sexually mature or immature. This is done by categorising the ovaries and testes into different gonadal stages macroscopically (Karna et al., 2012; Weyl & Hecht, 1998). Sexual maturity marks a crucial change in the life cycle of a species as it presents potential competition between resources allocation, survival and growth (Weyl & Hecht, 1998; Wootton, 2012). The reproductive success of a species is determined by the place and timing of reproduction (Wootton, 1990). A change in resource allocation from reproductive to competitive activities should only happen in habitats where they will improve survival rates of future offspring (Lowe-McConnell, 1987). Therefore, reproductive studies enable the implementation of minimum legal harvesting sizes that are greater than the length at maturity, which affords fish the opportunity to reproduce at least once in its lifetime before being harvested (Welcomme, 2001). Furthermore, knowing when species are in their breeding season is important as it gives information on the design of closed seasons allowing species protection during their spawning season (Welcomme, 2001).

Nile tilapia*, Oreochromis niloticus (*Linnaeus, 1758) has a history as an invasive species ranging from as early as the 1950s where it first was introduced in Lake Victoria leading to the local extinction of native congeneric (Zengeya et al., 2013a). The success of *O. niloticus* as an invasive species is attributed to number of variables, such as its ability to spawn multiple broods within one season, high parental care, fast growth rates, rapidly attains sexual maturity (Weyl, 2008; Zengeya et al., 2013b) and having aggressive male competitors that allows them to outcompete other species for spawning grounds (Bwanika et al., 2007; Zengeya et al., 2013a). Within South Africa, *O. niloticus* was first introduced for aquaculture activities, where it escaped establishing viable feral populations in the Limpopo River and other freshwater ecosystems within the tropical and subtropical regions of the country (Weyl, 2008; Zengeya & Marshall, 2015; Zengeya et al., 2013a). These newly established populations of *O. niloticus* have been implicated as having adverse impacts on recipient ecosystems (van der Waal & Bills, 2000), such as the local extinction of native congenerics through competitive exclusion and gene pollution due to hybridization (Chifamba, 1998; van der Waal & Bills, 2000; Zengeya et al., 2013a). One of the native congenerics identified as being at risk of extinction is *O. mossambicus*, a native southern African cichlid (Bruton & Allanson, 1974; Zengeya et al., 2013a).

Proper assessment and management of fisheries requires an understanding of the growth and reproductive life history events of species. With the knowledge of the age and growth as well as the reproductive biology of the native *O. mossambicus* in relation to the invasive *O. niloticus,* we will be able to develop sustainable management strategies for the Sundays River catchment and possible management across the whole of the Eastern Cape Province. Basic knowledge of biology of these species will allow us to make scientifically sound decisions in terms of management strategies. Our hope with this study is to contribute to a better understanding of factors driving invasion establishment of the globally invasive *O. niloticus*, within the context of its impacts on the native and closely related *O. mossambicus*. There is a lack of published data in the Eastern Cape on the age and growth of *O. mossambicus* thus our work aims to bridge that data gap while providing information of the potential impacts of the invasive *O. niloticus* on native species. Furthermore, there are no records of *O. niloticus* as an invasive species in the Eastern Cape thus this work is a baseline study in predicting its potential impacts if introduced.

The aim of this study was to assess the biology of *Oreochromis mossambicus* using sectioned otoliths in order to determine growth rates and determine the sex structure as well as the age at maturity using gonadal development stages of *O. mossambicus* in the Sundays River catchment. This will then be used to make comparisons with an invasive *Oreochromis niloticus* based on literature. The objectives for this chapter were as follows: (i) determine the age and growth of *O. mossambicus* using sectioned sagittal otoliths in order to provide growth rate estimates and (ii) determine sex structure and age at maturity of *O. mossambicus* using reproductive gonadal staging.

Materials and Methods

Ethical clearance and permits

The collection of *O. mossambicus* was carried out in compliance with the Eastern Cape Department of Economic Development and Environmental Affairs (DEDEA permit no. HO/RSH/20/2021) and ethical clearance was approved by the Rhodes University Animal Research Ethics Committee (RU-AREC reference no. 2021-2695-5969).

Study site

Fish for this study were sourced from the ML Swart (-33.4094329; 25.4843039) irrigation pond which forms part of the Sundays River irrigation pond system. The Sundays River has a catchment area of approximately 20 792 km^2 and is about 310 km long. The Sundays River irrigation ponds are located within a semi-arid region in Eastern Cape, South Africa (Kadye & Booth, 2013). The ML Swart pond is 86 m long and 57 m wide covering an area of 4 902 m^2. During the sampling period, the temperature in the pond was 21.5°C and the pH was 8.3.

Biological data collection

A total of 101 *O. mossambicus* specimens were collected using a 30 x 2 m seine net with 12 mm mesh wings and a 8 mm mesh cod-end during the month of April 2021. Upon capture, *O. mossambicus* were euthanized with an overdose (40 mg/L) of clove oil. Non-target/bycatch species were immediately released back into the system from which they were sampled. All fish were measured for total length (to the nearest 1.0 mm), weighed (to the nearest 0.1 g), dissected and sexed. Sagittal otoliths were extracted, dried to remove any membranous tissue and blood and stored in labelled 1.5 ml Eppendorf tubes for later processing. Otoliths were prepared and read following recommendation by Weyl & Hecht (1998). The otolith processing procedure took place in the general laboratory of the Department of Ichthyology and Fisheries Science, Rhodes University.

Otolith processing

Otoliths were set in clear polyester casting resin, sectioned transversely through the nucleus using a double-bladed diamond edge saw at a thickness of 0.4 mm. Sections were labelled and mounted onto microscope slides using DPX microscopy mountant (Merck PTY LTD). Sections were then examined under a binocular microscope using transmitted light at various magnification (10–45 X) to count pairs of opaque and hyaline growth zones and to assess the appearance of the otolith margin. The number of opaque rings were counted to determine the age estimates of the fish. Each opaque ring was approximated to be equal to one year (Figure 2.1), as has been verified in other studies (Beamish & McFarlane, 1983; Peel et al., 2016). Growth zones were identified as alternating translucent and opaque rings and counted as the number of opaque rings from the nucleus to the marginal edge of the otolith. This was used to validate growth zone formation. Each otolith was read twice, and an estimate of age was recorded if the two readings yielded the same result (Peel, 2012). Should the two age estimate readings differ, a third reading was taken and thereafter an average of the three readings recorded. If an otolith could not be assigned an age it was discarded as unreadable.

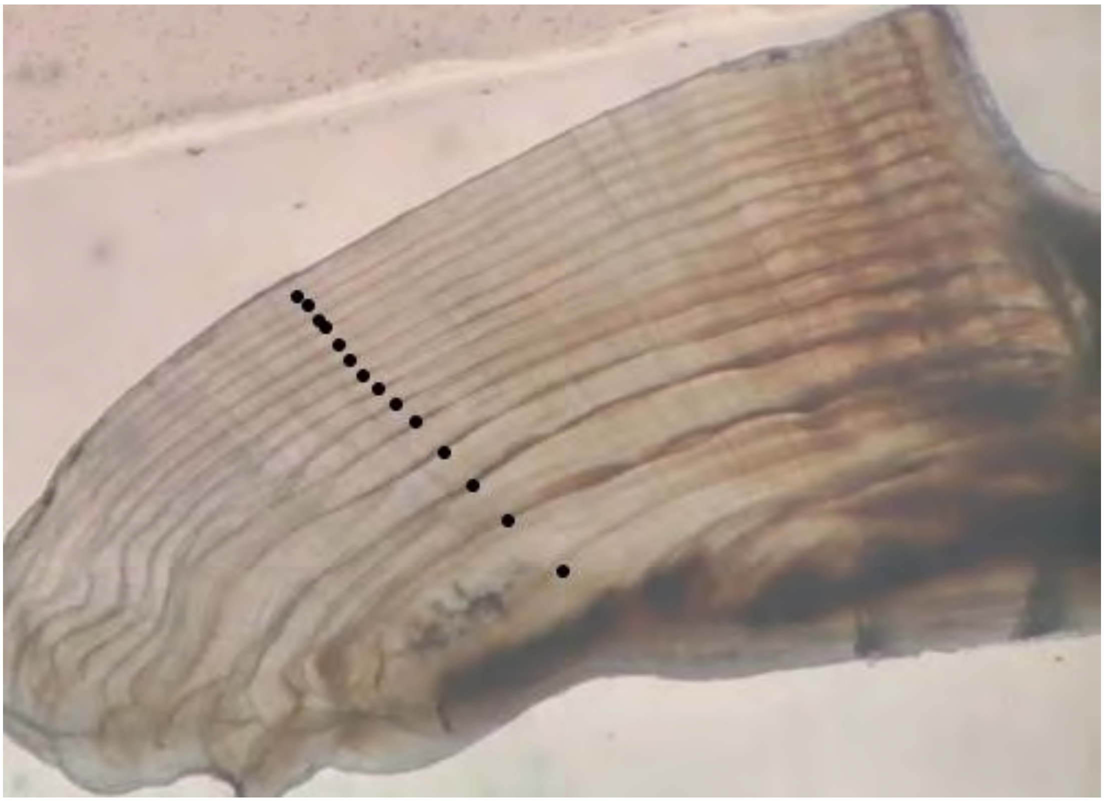

Figure 2.1: A sectioned sagittal otolith showing the translucent and opaque growth zones on a 297 mm L_T 14 year old (denoted by the black dots) *O. mossambicus* specimen sampled from ML Swart pond in the Sundays River catchment.

Gonadal development staging

Fish were sexed and their reproductive stages were determined macroscopically using the visual staging described by Weyl & Hecht (1998) (Table 2.1). Fish were considered mature if they were assigned a gonadal development stage from 3–5 (developing, ripe or spent). Stages of maturity from 1–2 were considered juveniles or immature. The length at first maturity was determined as the smallest fish sampled that contains developing or ripe gonads.

Table 2.1: Macroscopic criterion used to determine the reproductive stages of maturity of males and females of *Oreochromis mossambicus* (reproduced from Weyl & Hecht, 1998).

Stage	Gonad Development	Gonadal appearance
1	Juvenile	Gonads appear as thin translucent strips. Sex indistinguishable macroscopically.
2	Resting	Sex distinguishable. Ovaries appear white/yellowish. Oocytes macroscopically distinguishable. Testes appear as thin white bands.
3	Developing	Ovaries enlarged in size, oocytes readily visible and yellow. Testes appear as broadened, distended and cream in colour.
4	Ripe	Oocytes of maximum size, dull yellow in colour. Testes appear white and swollen to maximum size.
5	Spent	Ovaries flaccid with irregular oocytes sizes. Testes reduced in size with a grey colour.

Statistical analysis

All data analysis were performed using R programming (version 4.0.3) and Microsoft Office (Excel). R was used to fit the Von Bertalanffy model for growth as well as determining the length at which 50% of the population has matured. Microsoft Excel was used to determine the length-weight relationship, condition factors and the male to female sex ratio.

Length-Weight relationship

The Length–Weight relationship was estimated using the formula

$$W = aL^{b}$$

(1)

In the above formula, W is the measured weight (g), L is the measured total length (mm), while a' and b' are model parameters (Booth & Khumalo, 2010).

Growth modelling

The length and age data were correlated and plotted to form growth curves which were fitted to a Von Bertalanffy growth model of the form

$$L_t = L_\infty(1 - \mathrm{e}^{-k[t-t0]})$$

(2)

Where L_t is the total length in mm at age t (years), L_∞ is a predicted asymptotic length, K is the Brody co-efficient (year^{-1}) and t_0 is the theoretical age (years) at zero length as per Ricker (1975).

Condition factor

The condition factor (K_n) is a measure of the condition of a fish. Bagenal & Tesch (1978) hypothesised that heavier fish of a particular length are in a better condition physiologically. Therefore, condition factor is useful in monitoring feeding intensity, reproduction season, growth rate, age, physiological state, relative robustness and the general well-being of intra and inter-populations (Dan-Kishiya, 2013). To make comparisons between mean condition factors between the species, the relative condition factor (K_n) was calculated for the combined sexes, whereby,

$$\boldsymbol{K_n} = \frac{\boldsymbol{W}}{\mathrm{a}L^{b}}$$

(3)

Where K_n is the condition factor, W is the weight of fish in grams, T_L is the Total length of fish in mm, a and b are the exponential form of the intercept and slope from the logarithmic length-weight equation (Le Cren, 1951).

Sex ratio

A *Chi-square* test was used to test for unity between the females and the male population of *O. mossambicus* from the ML Swart, Sundays River system, whereby

$$\boldsymbol{X_c^2} = \sum \frac{(\boldsymbol{O_i} - \boldsymbol{E_i})^2}{\boldsymbol{E_i}} \tag{4}$$

In the above formula, c' is the degrees of freedom, O' is observed value and E' is expected value.

Length at 50% maturity (L_{50})

Sample size was too small to calculate sex-specific length at maturity. As a result, males and females were grouped for analysis. To estimate length at maturity, the proportion of mature fish in each 10 mm L_T size class was first calculated. Length at 50% maturity (Lm_{50}) was estimated by fitting these data into a two-parameter logistic model form

$$\boldsymbol{\Psi_L} = \frac{\mathbf{1}}{\mathbf{1} + \boldsymbol{exp}^{-(L - Lm50)}/\boldsymbol{\delta}} \tag{5}$$

In the above formula, Ψ_L is the predicted proportion of mature fish at length L and & δ is the width of the logistic ogive (King, 2013).

Results

A total of 101 fishes ranging from 32 mm to 297 mm L_T were examined. The oldest female was 6 years old with a total length of 288.8 mm and the oldest male was 15 years old with a total length of 297 mm. The juvenile's total length ranged between 32 mm and 83 mm and their age was either zero or one year old. The age for most of the analysed fishes varied from 0 years to 6 years old, with only two exceptions from males which were above this range (Figure 2.2).

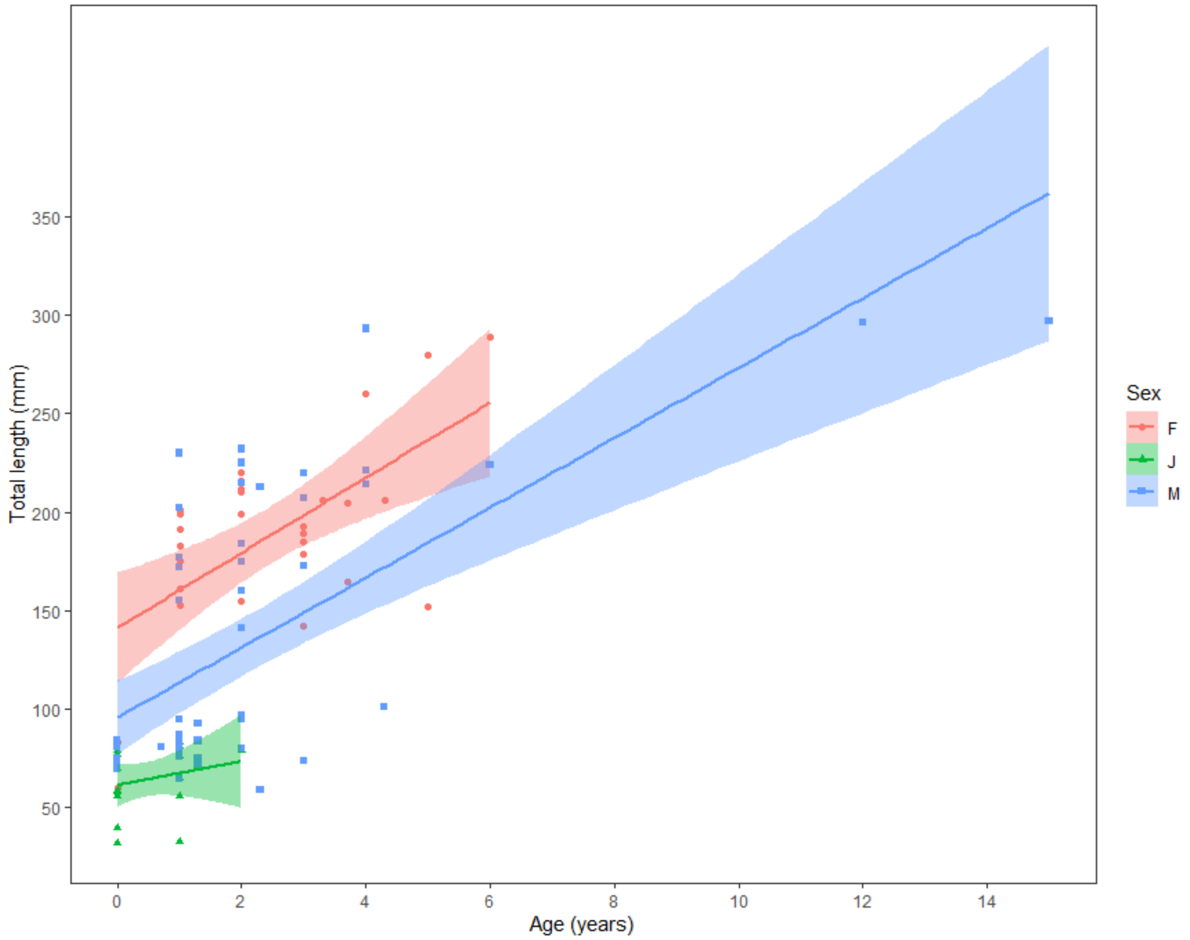

Figure 2.2: Age-length variation of males, females and juveniles for *O. mossambicus* sampled in ML Swart, Sundays River catchment in the Eastern Cape, South Africa.

Length- weight relationship

The relationship for total length and weight for combined sexes was best described by W (g) = 8E-05$L_T^{2.6885}$ on the original scale (Figure 2.3). The model exhibits a good fit to the transformed data with the goodness of fit indicated by R^2 = 0.944. The equation of the best-fit line is *(W)* = 0.0165 $L_T^{2.688}$ on the transformed scale. There was a linear increase in weight (g) with an increase in total fish length (mm) (Figure 2.4). The growth exponent for *O. mossambicus* was b = 2.688 and showed an allometric growth with a *b*-value ranging between 2.557 and 2.819 (95% CI). There was a significance difference in length-weight between males and females (*t*-value = 40.865, df = 99, *p*-value < 0.05) (Table 2.2).

Table 2.2: Estimates of a and b from the linear regression model for relationship between log transformed total length (mm) and log-transformed weight for *Oreochromis mossambicus* from Sundays River catchment.

	Coefficients	*St. Error*	*t-value*	*p-value*	*Lower 95%*	*Upper 95%*
Intercept	-4,106	0,316	-29,891	2.34e-51	-4,378	-3,833
X Variable	2,688	0,066	40,865	8.64e-64	2,557	2,819

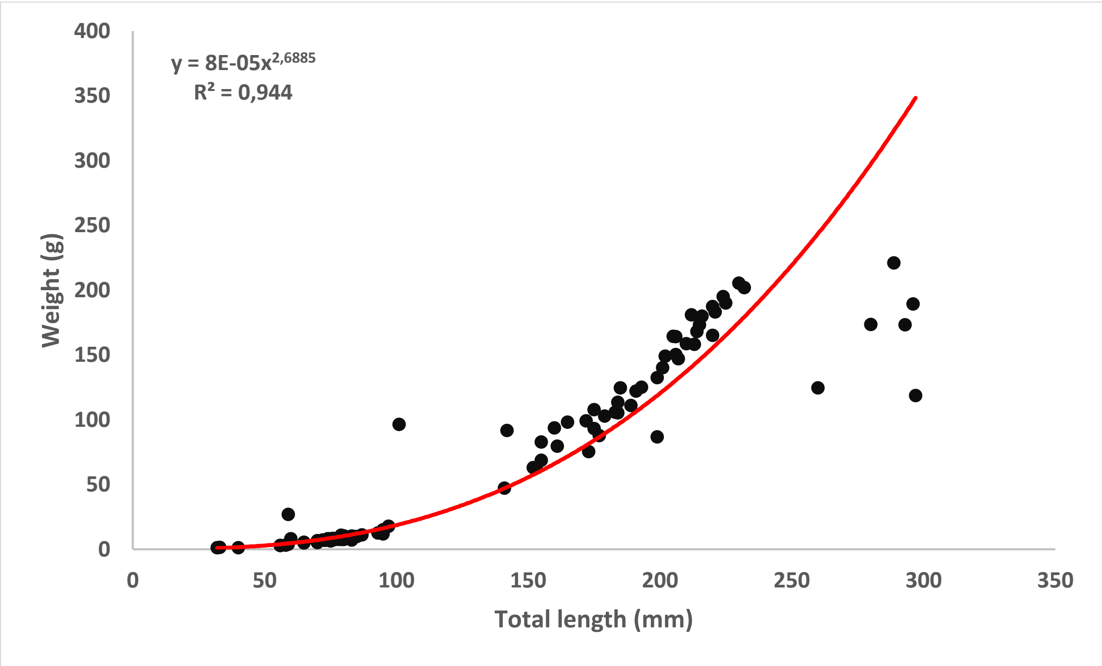

Figure 2.3: The total length (mm) and weight (g) relationship for combined sexes *O. mossambicus* (n = 101), sampled from the ML Swart pond in Sundays River catchment, Eastern Cape, South Africa. (Observed = dots, predicted = line).

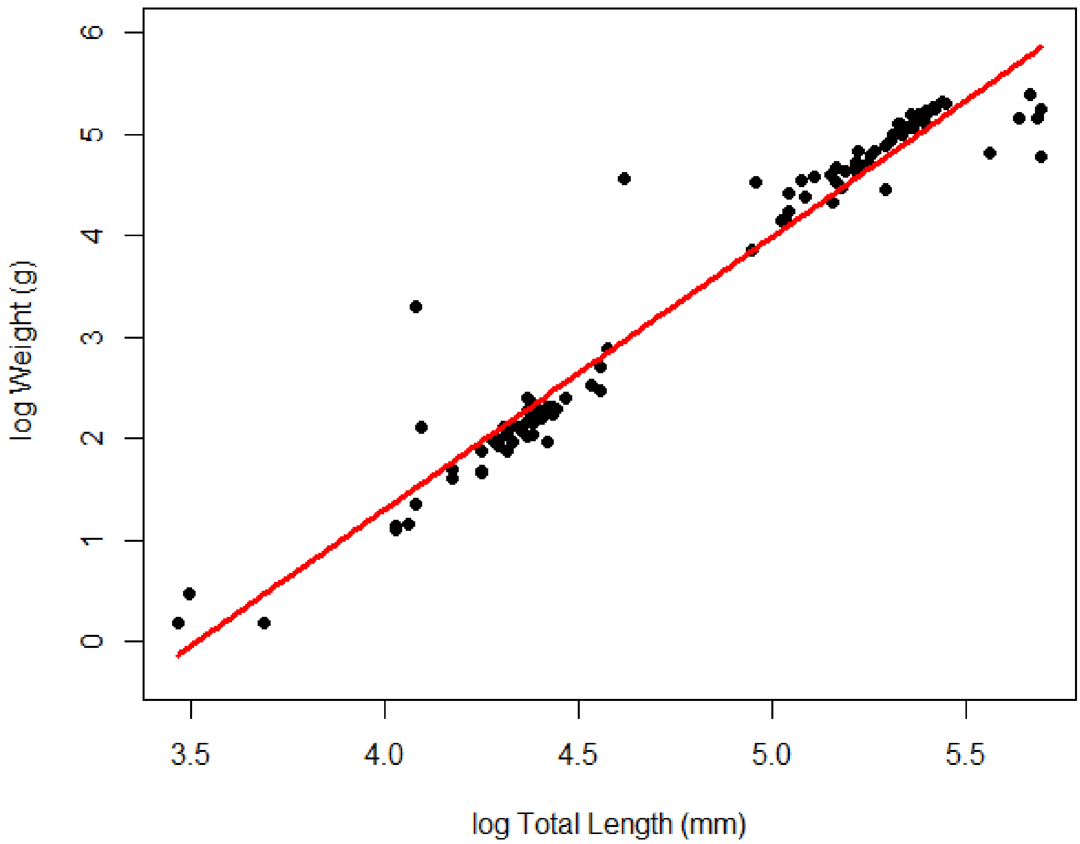

Figure 2.4: Log transformed total length (mm) and weight (g) of *O. mossambicus* for combined sexes sampled from the ML Swart pond, Sundays River catchment, with best-fit line superimposed.

Growth

Parameter estimates for *O. mossambicus* are summarised in Table 2.3, along with those of and *O. niloticus* for comparison. The parameter estimates from the von Bertalanffy model for *O. mossambicus* from the current study were comparable to parameter estimates for *O. niloticus* based on published data. The parameter estimates for *O. mossambicus* males was best described as L_T (mm) = 331.9 (1-$e^{-0.167(t=1.192)}$) and for females it was best described as L_T (mm) = 272 (1-$e^{-0.331(t=0.772)}$). The theoretical age of fish at zero (t_0) for males, females and combined sexes were all positive (1.192, 0.772 and 1.027 respectively) and their growth coefficients (K) were -0.167 yr^{-1}, -0.331 yr^{-1} and -0.201 yr^{-1} respectively. (Table 2.3). The L_T age for *O. mossambicus* (combined sexes) was best described as L_T (mm) = 322.5 (1-$e^{-0.201(t=1.027)}$). The growth rate for *O. mossambicus* was initially rapid and the asymptotic length reached after 4 years (Figure 2.5). The growth of *O. mossambicus* was comparable to that of *O. niloticus* and the greatest attainable length (L_∞) was found in *O. niloticus*. Furthermore, *O. niloticus* had a higher growth coefficient (K) *than O. mossambicus* (Table 2.3).

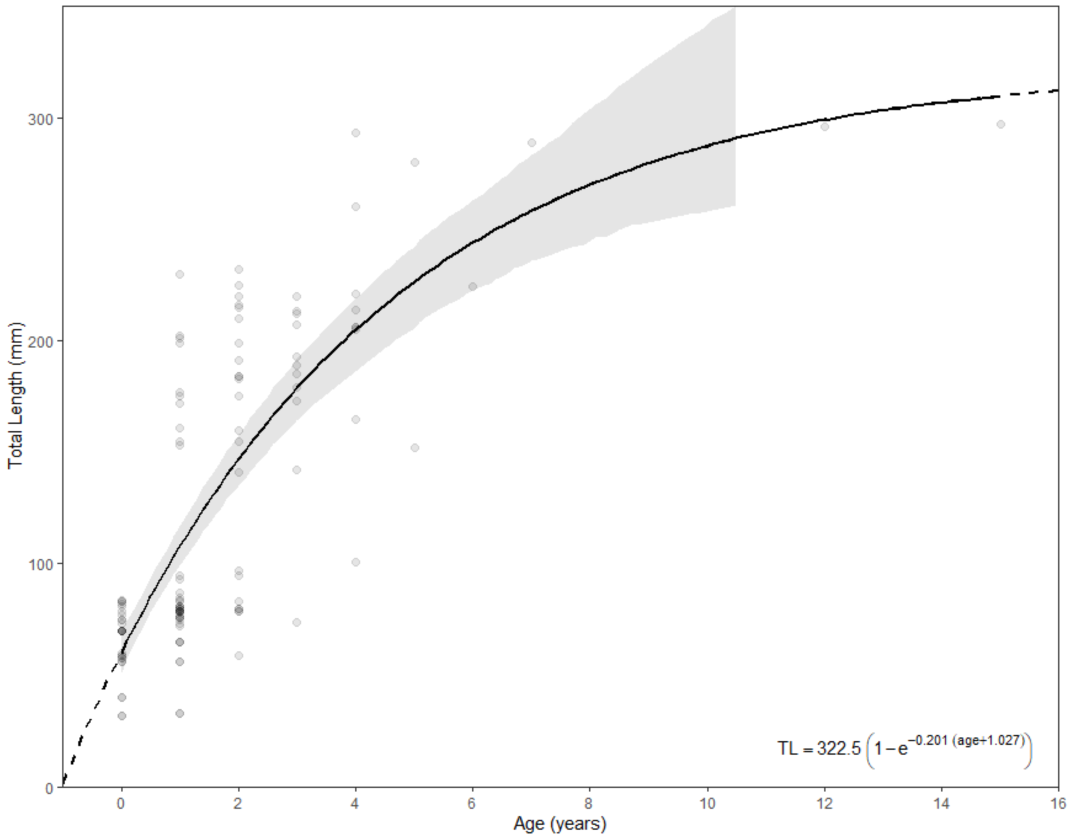

Figure 2.5: Von Bertalanffy growth curve for *O. mossambicus* from ML Swart pond, Sundays River catchment in the Eastern Cape Province, South Africa. The L_T at age was described by the Von Bertalanffy growth equation as L_T (mm) = 322.5 (1-e)$^{-0.201(t=1.027)}$). (Observed = dots; predicted = line).

Table 2.3: Growth parameter estimates for *O. mossambicus* (current study) and *O. niloticus* from other studies using the Von Bertalanffy growth model.

Parameter	L_∞	K	t_0	Reference
O. mossambicus				
Males	331.9	-0.167	1.192	Current study
Females	272.0	-0.331	0.772	
Both sexes	322.5	-0.201	1.027	
O. niloticus				
Males	501.2	-0.45	-0.115	Bwanika et al. (2007)
Females	411.2	-0.53	0.099	
Both sexes	463.5	-0.41	0.050	
Both sexes	458.0	0.180	-3.002	Nyirenda (2017)
Both sexes	451.0	0.210	0.560	Degsera et al. (2020)
Both sexes	646.0	0.250	0.560	Getabu (1992)

Note: K = Brody growth coefficient; L_∞ = asymptotic length in mm; t_0 = theoretical age of fish at zero length.

Sex ratio and L_{m50} maturity

A preliminary assessment of reproductive gonadal stages showed that juvenile, resting, developing, and ripe were present in the *O. mossambicus* population during the sampling period (April 2021). Sixty percent of the females were ripe and 84% of males were ripe. Only 17% were in their juvenile stages (Figure 2.6). The weight of the juveniles ranged between 0 and 78 g and their total length ranged between 0 and 100 mm. The adults (males and females) ranged between 50 and 250 g in weight with a total length of above 100 to 300 mm (Figure 2.7). The relative condition factor was found to be equal to 1.09 for *O. mossambicus* in the ML Swart, Sundays River catchment. The overall sex ratio of females to males was 1:1.89. Chi-square test showed a significant difference (goodness of fit test x^2 = 8,047, df = 1, *p*-value = 0.0045) in the sex ratio between males and females. The Length-at-50% maturity (L_{m50}) for *O. mossambicus* was calculated at 106.5 mm L_T (R^2 = 0.57) (Figure 2.8) and best-fit logistic model was best described as Y = $\frac{1}{1+exp^{-(-3.424+0.032})}$

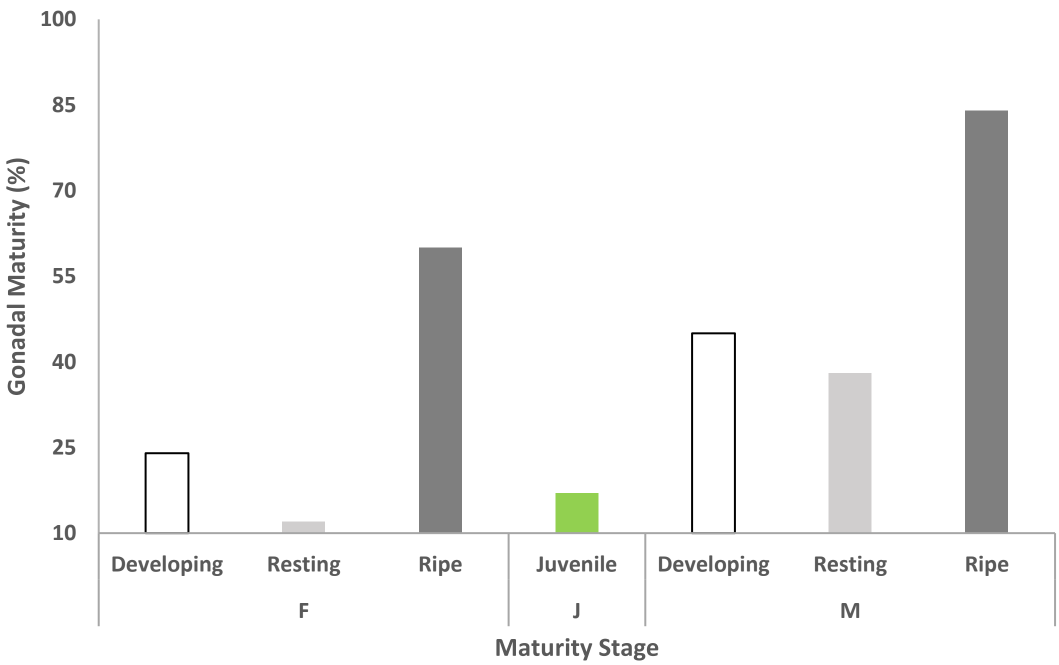

Figure 2.6: Reproductive gonadal stages for females (F), juveniles (J) and males (M) sampled in the ML Swart, Sundays River catchment for *O. mossambicus*.

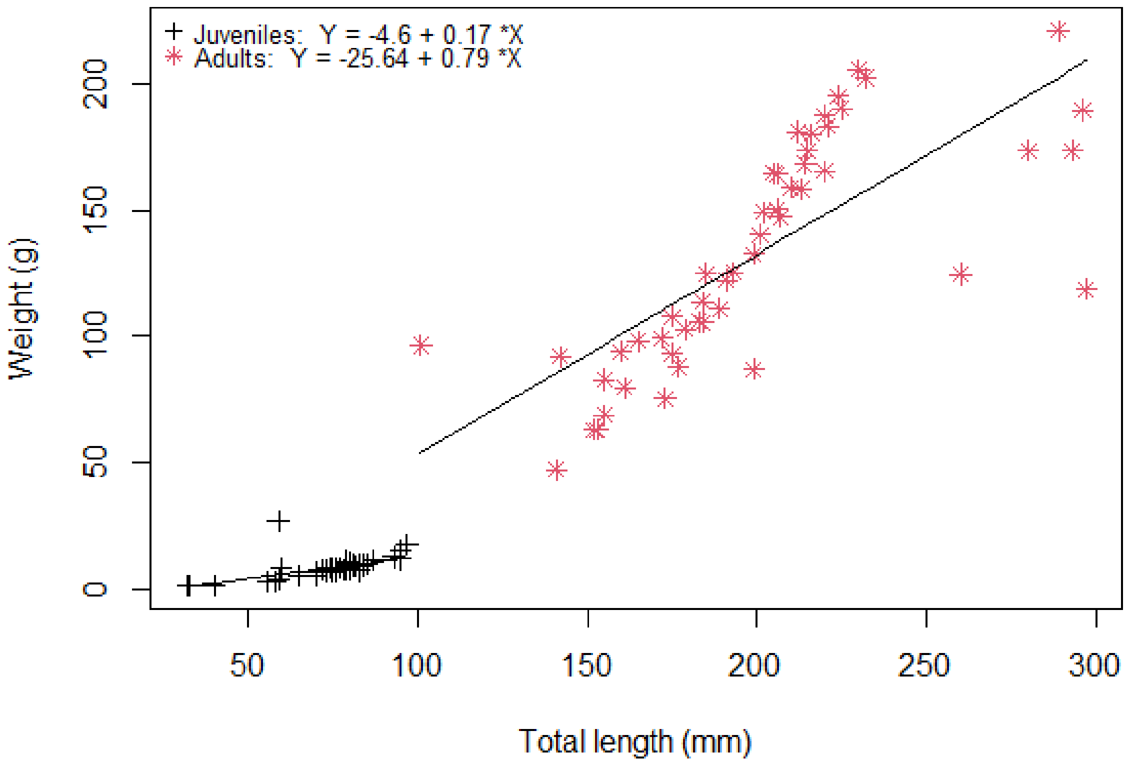

Figure 2.7: Length-weight relationship of adults (males and females) as well as juveniles of *O. mossambicus* from the Sundays River catchment.

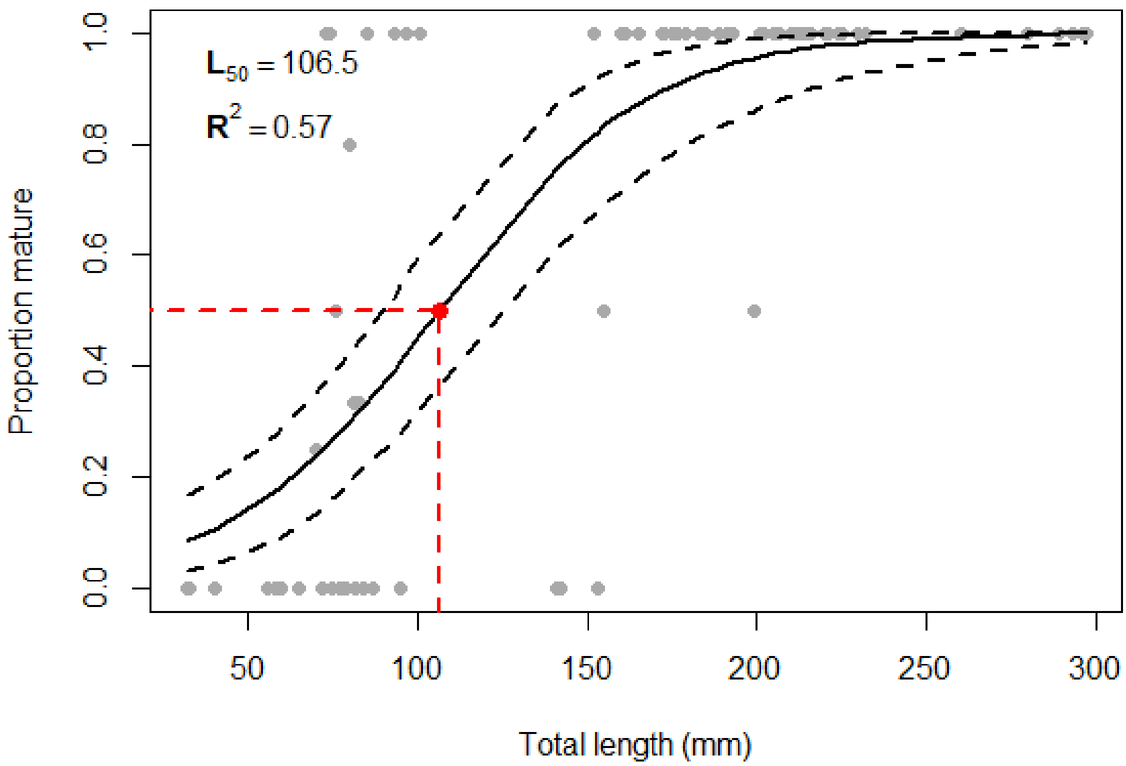

Figure 2.8: Logistic ogive fitted for the proportion of reproductively mature male and female *O. mossambicus* from ML Swart, Sundays River catchment. L_{50} = length-at-50% maturity.

Discussion

The present study showed that for the age and growth of *O. mossambicus*, it is possible that growth zones on sectioned sagittal otoliths can be assessed without needing to burn the otolith as they were visible and easily readable without the need for enhancing visibility through burning them as outlined in various studies (Booth et al., 199; Peel, 2012). This study further showed that cichlids can easily be aged using sectioned sagittal otoliths which allowed the comparison of growth rates between *O. mossambicus* and *O. niloticus*. The age and growth as well as the reproductive maturity of *O. mossambicus* was compared to that of *O. niloticus* based on literature in other regions. Life history characteristics are crucial in depicting the success of introduced species into new environments, as they determine the ability of a species to withstand and overcome environmental pressure imposed on them (Taylor & Weyl, 2017).

Growth

The Von Bertalanffy provided a good fit to length-at-age data for *O. mossambicus*. The estimated length-at-age relationship for *O. mossambicus* was comparable to that of *O. niloticus* based on literature from other studies in other localities. Growth was almost linear up to 4 years, followed by a reduced growth that coincided with the species approaching first maturity. Growth patterns for cichlids in tropical and sub-tropical regions are consistent with a decrease in the rate of somatic growth as fish start allocating more energy to gonadal growth when they approach sexual maturity (Bruton & Allanson, 1974; Bwanika et al., 2007; Weyl & Hecht, 1998). The sex-specific differences in the asymptotic lengths in the present study may be attributed to sexual selection for larger, faster-growing males linked to their breeding behavior which suggests size advantage for the territory defending males in tilapia species (Bwanika et al., 2007; Lowe-McConnell, 1987; Oliveira et al., 2005).

The estimated asymptotic length of *O. mossambicus* found in the present study was 322.5 mm L_T which was much higher when compared to other L_∞ estimated for *O. mossambicus* in other environments. This means that the *O. mossambicus* population from the Sundays River catchment attained greater lengths than other *O. mossambicus* populations from other localities. For instance, a study by Weyl & Hecht (1998) found an estimated L_∞ of 266.06 mm in Lake Chicamba. In the Luphephe impoundment, Hecht (1980) found an estimated L_∞ of 273 mm which was also much lower than that found in the present study. When the *O. mossambicus* population from the Sundays River catchment was compared to *O. niloticus* populations from other localities based on literature, *O. mossambicus* was found to have slower growth than *O. niloticus* (Bwanika et al., 2007; Nyirenda, 2017). Bwanika et al., (2007) found a very high asymptotic length (L_∞) of 463.5 mm for *O. niloticus* in Lake Nabugabo and Lake Wamala. Another study by Nyirenda (2017) found a similar pattern in Lake Kariba where *O. niloticus* had a very high asymptotic length (L_∞) of 458 mm with a growth coefficient of 0.180. Theresa et al., (2011) found similar results at Kafue River where they showed that the highest attainable size by *O. niloticus* was 477 mm. Degsera et al., (2020) also found similar results for *O. niloticus* in Lake Tana Basin where the L_∞ was 451 mm with a growth coefficient of 0.208. Both Nyirenda (2017) and Degsera et al., (2020) found very high growth coefficients as compared to that of *O. mossambicus* found in the present study. An important factor to consider in fish growth is temperature as growth rates tend to increase until an optimum threshold is reached and the growth slows than and eventually stops (Elliot, 1975; Lappalainen et al., 2008). Furthermore, some studies have found that cooler temperatures tend to slow down fish growth (Handeland et al., 2008; Tadesse et al., 2003). Hence the slower growth rates seen in *O. mossambicus* in this region may be attributed to the cooler climates experienced in this region, which might have slowed down their growth. These results serve as evidence that the invasive *O. niloticus* has faster growth and attains greater sizes than its native congeneric *O. mossambicus*.

A number of factors may be attributed to the variations observed in the growth of different species. These factors include food availability as well as the size of the system and its catchment area (Degsera et al., 2020). For instance, rivers are more productive than lakes and other standing water bodies (Bwanika et al., 2007; Junk et al., 1989). The attributes depicted by *O. niloticus* as an invasive species further places it at an advantageous level when compared to native species. These attributes include *O. niloticus* having a broader diet and hence being able to utilise a wide range of food resources which may be a factor contributing to their fast growth rates (Bwanika et al., 2007; Zengeya et al., 2013a). *O. niloticus* and *O. mossambicus* have high diet overlap and this could result direct competition for food resources when these species co-occur (Zengeya et al., 2015). This could ultimately result in the displacement of *O. mossambicus* from the Eastern Cape region if *O. niloticus* was to be introduced in this region, as *O. niloticus* has been identified as a highly aggressive competitor (Theresa et al., 2011;

Zengeya et al., 2013a). Furthermore, *O. niloticus* have higher performance growth and better reproduction strategies such as bigger egg sizes, thereby increasing its abundance and giving it higher survival chances compared to the indigenous *O. mossambicus* (Theresa et al., 2011).

Sex ratio and Lm_{50} maturity

Gonad preliminary assessments showed a high percentage of mature gonads in the *O. mossambicus* population for both males (80%) and females (60%) and this was during the month of April. These results were consistent with findings from other studies that found cichlids to extend their spawning season throughout the warmer summer months from October to April (Chimatiro, 2004; Merron, 1991; van der Waal, 1985). Weyl & Hecht (1998) also found that reproductive activity of cichlids were confined to summer months (September to May) at Lake Chicamba. Therefore, we can conclude that the *O. mossambicus* population from the Sundays River catchment was sampled at its spawning peak as a high percentage of the population was found to be reproductively mature during April.

The mean relative condition factor for *O. mossambicus* was 1.09 which depicted a good condition/physiology (Le Cren, 1951) for the population at the ML Swart, Sundays River catchment. There are a number of factors that affect the physiological condition of fishes in tropical and subtropical river systems and these can either be biotic or abiotic entities (Le Cren, 1951). For instance, food availability, feeding regimes, environmental factors and the state of gonadal development are some factors that affect fish physiology (Le Cren, 1951; Ogidiaka & Esenowo, 2015). Furthermore, the sex ratios for the *O. mossambicus* in the Eastern Cape region was found to be skewed towards males. This may be attributed to the fact that the males tend to show territorial aggressive behavior, where they establish and defend breeding territories as well actively courting their mating partners (Gomez-Marque, 2008; Lowe-McConnell, 1987; Oliveira et al., 2005; Zengeya et al., 2013a).

The length-at-50% maturity for *O. mossambicus* was found at 106.45 mm L_T. The variation in size at sexual maturity in cichlids is attributed to environmental conditions experienced by fish populations (James & Bruton, 1992; Merron, 1991). For example a study by Chimatiro (2004) found that *O. mossambicus* matured at smaller size due to fishing pressure and hydrologically unstable environments. Furthermore, a study by James and Bruton (1992) found that the length of *O. mossambicus* ranged between 110 to 265 mm in small reservoirs in the Eastern Cape region. Other research on tilapia species that were consistent with the results from the present research were from van der Waal, (1985) who found that *Coptodon rendalli* reached 50% maturity at 109 mm in Lake Liambezi.

Oreochromis niloticus introductions into new ecosystems is a cause for concern for native species such as *O. mossambicus* which is at the risk of extinction due to genetic pollution caused by hybridization between these two species (Zengeya et al., 2013a; Zengeya et al., 2015). Furthermore, there is habitat and trophic overlap between *O. niloticus and O. mossambicus* which further poses a threat to the native *O. mossambicus* (Chifamba, 1998; Zengeya et al., 2013b; Zengeya & Marshall, 2015). The success of *O. niloticus* as an invasive species has been attributed to its wide range of trophic and ecological adaptations as well as its adaptive life history traits that allows it to occupy a number of tropical and subtropical freshwaters environments. For instance, *O. niloticus* has the ability to spawn multiple broods within a single season, exhibits high parental care, has fast growth rates and rapidly attains sexual maturity (Weyl, 2008; Zengeya et al., 2013a).

Conclusions

This chapter provided information on the age and growth as well as the length-at-50% maturity for *O. mossambicus* in the Eastern Cape region. The key observation from this study and the comparison with *O. niloticus* based on literature was that *O. niloticus* is superior in its biology (age, growth and L_{m50}) when compared to the native *O. mossambicus*. Such information is important in stock assessment and in the implementation of sustainable management strategies (Karna & Panda, 2011). Currently there is very little published literature on the growth of *O. mossambicus* in the Eastern Cape region hence this research fills that data gap on *O. mossambicus*.

Furthermore, it is important to note that there are a lot of restrictions on the invasive *O. niloticus* in South Africa that are regulated by the National Environmental Management: Biodiversity Act (NEM:BA) legislation (DEA, 2014), yet there is still very little research published literature on the impacts it has on receiving environments (Zengeya et al., 2013a). Currently the distribution of *O. niloticus* as an invasive species in South Africa does not include the Eastern Cape region although it has been found in some parts of South Africa including KwaZulu-Natal, Limpopo and the Western Cape regions (van der Waal & Bills, 2000; Weyl, 2008; Zengeya et al., 2013a). Therefore, this research is a baseline study in predicting potential impacts of *O. niloticus* on its closely related congenerics such as *O. mossambicus* in the Eastern Cape region. *Oreochromis niloticus* is currently being farmed in the Eastern Cape (per obs.), hence the threat of introduction is high in parts of the region due to possible farm escapees as has been the case in other parts of South Africa (Zengeya et al., 2013b). Furthermore, the Orange-Fish Sundays inter basin water transfer scheme further serves as a possible pathways for invasive species, leading to increased number of invasive species entering the Sundays River catchment through the irrigation canals transferring water to small irrigation farm ponds in this area (Kadye & Booth, 2013; Woodford et al., 2013). Such systems provide an opportunity for possible introductions of *O. niloticus* in the Eastern Cape, hence clear understanding of their life history parameters are needed in order to implement management strategies and conservation of native species.

CHAPTER 3

RESOURCE UTILISATION COMPARISONS BETWEEN *OREOCHROMIS MOSSAMBICUS* AND *OREOCHROMIS NILOTICUS* USING FUNCTIONAL RESPONSE EXPERIMENTS

Introduction

Biological invasions threatens both the biodiversity and integrity of freshwater ecosystems (Jackson et al., 2016; Meyerson et al., 2019). These invasions come with a number of conservation problems such as genetic pollution of native species through hybridization as well as competition exclusion as they compete for habitats and food resources (Eby et al., 2006; Gozlan et al., 2005; Jackson et al., 2017). Although the introduction pathways of invasive species are well understood (Copp et al., 2005), their establishment success seems to be controlled by a number of factors such as predation and competitive interactions (Latombe et al., 2017). Thus, understanding factors influencing establishment success or failure of invasive species is of great importance in invasion biology (Sato et al., 2010). Particularly important in this regard are biotic interactions between native and non-native species, which can have strong implications for community dynamics (Britton et al., 2010). With regards to resource utilisation, invasive species have the ability to utilise resources more rapidly and efficiently in comparison to native species (Dick et al., 2013; Ricciardi et al., 2013). This may cause declines and possible depletion of resources such as native prey species (Dick et al., 2014). When non-native species enter new communities, they interact with native species and this results in heterospecific interactions (Jackson et al., 2017).

Communities have multiple predators that share resources, thus bringing about competition (Barrios-O'Neill et al., 2014; Sih et al., 1998; Wasserman et al., 2016). These predators not only interact with their prey but they also interact with each other in their pursuit for mutual resources (Johnson et al., 2009; Polis et al., 1989; Wasserman et al., 2016). For example, one predatory species can hinder the feeding of another through interference competition (Mofu et al., 2019b). Similarly, certain heterospecific or conspecific predator combinations can result in disproportionately increased prey consumption through facilitation, such as is observed of predators attacking shoals of fish (Hebshi et al., 2008). These multiple predator effects (MPEs) can be significant, with implications for community structure. It is, therefore, important to conduct research that aims at better understanding the effects of multiple species interactions (Wasserman et al., 2016), as these interactions are crucial in the structure and functioning of ecological communities and are well-known controllers of predator-prey dynamics (Barrios-O'Neill et al., 2014). However, within the invasion context we have little knowledge on how invasive species will impact certain native species, through such MPEs. This chapter focuses on the potential impact of the invasive Nile tilapia, *Oreochromis niloticus* (Linnaeus, 1758) on the native Mozambique tilapia, *Oreochromis mossambicus (*Peters, 1852). Nile tilapia was first introduced in southern African rivers for aquaculture and has since established viable feral populations in considerable sections of the Limpopo River basin (van der Waal & Bills, 2000; Zengeya et al., 2013a; Zengeya et al., 2015) and numerous river systems within the tropical and subtropical regions (Skelton, 2001; Weyl, 2008; Zengeya et al., 2012). Nile tilapia poses a threat to the native Mozambique tilapia given, amongst other issues, their shared habitat and food (Zengeya et al., 2015).

Experimental approaches such as functional responses are a useful, dependable and affordable tool used when predicting ecological impacts of invasive species on native species (Alexander et al., 2014; Dick et al., 2014; Mofu et al., 2019b). Functional response (FR) experiments have been used as a method of measuring and quantifying impacts of invasive species across a range of species (Alexander et al., 2014; South et al., 2019). These FRs depicts the relationship between the amounts of resources available and how much of those available resources are being consumed (Denny, 2014; Dick et al., 2014; Iacarella et al., 2015; Holling, 1959; Holling, 1965). Furthermore, we explore multiple predator effects (MPEs) which are useful in comparing the predicted FRs to the observed FRs for both single and multiple predator experiments (Mofu et al., 2019a; Wasserman et al., 2016). The MPEs integrate gut content analysis which is a method used to complement direct functional response approaches when assessing multiple species interactions. Gut content integration approach minimizes biasness in functional responses as it uses direct enumeration of prey items present in the predator's gut (Mofu et al., 2019b). MPE approach allows us to quantify single prey consumption from gut content in order to assess the predator prey functional responses of species under multiple predator scenarios.

Understanding and predicting the ecological impacts of invasive species is important for risk assessment as well as for biodiversity management (Dick et al., 2013; Mofu et al., 2019a, Ricciardi et al., 2013). For instance, it is important to understand how predator-prey interactions are altered by the addition of another predator and how one predator may affect the predatory success of another. Functional response experiments further provide an important complement to field observations in predicting and disentangling complex predator-prey interactions and the amount of prey available (South et al., 2019). Invasive species have been shown to consume higher rates of available prey when compared to native species (Dick et al., 2013; Alexander et al., 2014).

Based on Holling (1959), functional responses can be described in three general categories namely, Types I, Type II and Type III. Type I occurs when the prey capture rate increases with an increase in prey density until a state of equilibrium is achieved (Holling, 1959; Holling, 1965). There is a constant proportion of available prey consumed regardless of how much prey is available thus a linear increase in feeding rate is depicted (Holling, 1959). Type II depicts a decrease in prey capture rate as the number of prey available increases (Holling, 1959). Furthermore, Type II shows high rates of resource consumption when the resources available are at low densities. The Type II FR is thus known as destabilizing because it is associated with the risk of resource depletion as resources are being used at high rates when they are available in low densities (Alexander et al., 2014). Lastly, Type III shows a positively density-dependent relationship because resource consumption rates decreases at both the low and high resource/prey densities (Holling, 1959; Holling, 1965). The type of functional response depicted by a certain species changes with the influence of a number of environmental factors such as temperature, the amount of light available as well as habitat type (Dick et al., 2013). Therefore, the FR types depicted by different predators are crucial in understanding predator impacts and community dynamics because the FR type can contribute to the stability and persistence of particular resources (Ward et al., 2008; Dick et al., 2017).

The aim of this study was to contrast resource utilisation of *Oreochromis mossambicus* and *Oreochromis niloticus* through functional response experiments in order to infer the potential or increased resource utilisation by *O. niloticus* and competitive exclusion of *O. mossambicus*.

The objectives for this are as follows: Identify (i) if the invasive species has a greater overall predatory potential, (ii) if competition within each species facilitates disproportionate prey consumption through facilitation, and (iii) if the invasive species potentially reduces consumption by the native fish species when they co-occur, through interference competition. To achieve this, a multiple predator effect (MPE) comparative FR design was employed, whereby a) single predators, b) conspecific pairs of predators, and c) heterospecific pairs of predators were exposed to the full FR design.

Single predator models (a) were used to determine if i) the invasive species has a greater overall predatory potential. These models (a) were then used to calculate theoretical multiple predator models (through additive single predator data use). These predicted multiple predator models (based on single predator performance) were then compared with observed (actual) multiple predator scenario data (b & c). Deviations from predicted multiple predator scenarios (e.g., reduced or increased FRs) by observed multiple predator scenarios (conspecific or heterospecific) are referred to as MPEs and will inform on ii) if conspecific pairs increase consumption through facilitation, and iii) if the native species reduces consumption in the presence of the invasive fish species, through interference competition.

Materials and Methods

Ethical clearance and permits

The sourcing and keeping of animals was carried out in compliance with the Department of Environmental Affairs (DEA permit no.50738210617105722 & 50738210617114244) and ethical clearance was approved by the Rhodes University Animal Research Ethics Committee (RU-AREC reference no. 2021-2695-5969).

Animal collection and maintenance

The fish for this study were purchased from Rivendell fish farm, Eastern Cape. All fish purchased for the functional response experiments were in their juvenile stages. These FR experiments were conducted within the South African Institute for Aquatic Biodiversity (SAIAB) facilities in Makhanda, Eastern Cape. While in transit from the Rivendell fish farm to SAIAB (12 kms), fish were transported in 10 L plastics bags filled with 5 L of water to ensure aeration during transportation. There was 100% survival rate for *O. niloticus* and 2 *O. mossambicus* lost while in transit.

Experimental setup

Upon arrival at SAIAB, animals were housed separately in four glass holding tanks of dimensions (length × height × width): 1190 mm × 410 mm × 440 mm; 900 mm × 380 mm × 320 mm; 900 mm × 370 mm × 320 mm and 870 mm × 380 mm × 310 mm containing 216 L; 180 L; 180 L and 180 L of water, respectively. Each holding tank contained conspecific specimens and was fitted with a continuous air supply and filtration system. Aerated water was replaced twice a week to maintain good water quality. All specimens were maintained on a standardized chironomids diet to control for prior experience to prey in a temperature-controlled laboratory (25 °C) and under 12 hr dark and 12 hr light regimes. All fishes were size-matched with respect to total length to reduce the influence of size-related differences on their feeding. Prey used for this study were chironomid larvae which were obtained from commercial suppliers (Ocean Nutrition™). Chironomid larvae were selected as prey to avoid using live prey for ethical reasons. Furthermore, chironomid heads are not easily digested in the gut which makes it easy to quantify and verify prey consumption by counting the heads present in the fish gut (Mofu et al., 2019b).

Multiple predator effect (MPE) comparative FR design was employed, whereby a) single predators, b) conspecific pairs of predators, and c) heterospecific pairs of predators were exposed to the full FR experimental design. The experiments were carried out in 20 L buckets filled with 9 L aerated water. The number of specimens were selected as follows: Single fish component (a), 56 per species were required (1 fish x 6 prey densities × 6 replicates × 2 species). For the conspecific multiple predator component (b), 48 per species were required (2 fish x 6 prey densities × 6 replicates × 2 species). For the heterospecific component (c), 36 of each species were required (2 fish × 6 prey densities × 6 replicates).

Twenty-four hrs prior to experiments, an individual specimen, or multiple (2 specimens- either a conspecific pair or a heterospecific pair) were selected randomly from the holding tanks and each placed in a 20 L bucket according to their allocated experimental group (i.e. single, conspecific pair, heterospecific pair), where they were held without food to allow for standardization for hunger levels. Thawed chironomids prey were then supplied at six densities (2, 4, 8, 16, 32 and 64), with six replicates per density to the two different *Oreochromis* species or multiple predator combinations in the experimental 20 L bucket and allowed to feed for two hours. Prey consumption was examined after two hours of feeding by counting the number of remaining prey (verified later through gut content analysis; see below). Fish were not re-used as this is a potential confounding factor given predator learning dynamics.

Once the experiments were complete, the fish were removed from the buckets and euthanized using clove oil (400 mg/L) dissolved in ethanol, by submerging the specimen in water containing the clove oil for 10 minutes. Fishes were then dissected to assess their gut content by counting the number of chironomids heads present in the gut in order to verify the number of prey items consumed (this is particularly relevant for the multiple predator scenarios).

Statistics analysis

All statistical analyses were conducted using R version 4.1.2 (R Core Team, 2021).

Single predators

Binomial generalised linear modelling was used to categorise functional response types for the single predator experiments (Juliano, 2001; Pritchard et al., 2017). The same approach was used for categorising functional responses as depicted by gut content of *O. niloticus* and *O. mossambicus* in the heterospecific pair experiments. Type II functional response is shown by a significantly negative linear coefficient as a response to increasing prey density, whereas Type III functional responses are shown by a significantly positive first order term and significantly negative second order term. In the case of prey not being replaced after consumption during the course of the experiment, Rogers' random predator equation was used to model functional responses (Rogers, 1972):

$$N_e = N_0(1 - \exp(a(N_e h - T))) \tag{1}$$

Where N_e is the number of prey items eaten, N_0 is the initial prey density supplied, a is the attack constant, h is the handling time and T is the total experimental period. The Lambert W function was used to fit the model to the data (Bolker, 2008; Pritchard et al., 2017). Roger's random predator equation is robust to prey depletion in parameter estimation (Cuthbert et al., 2019b).

In the instance that there was no significant evidence for Type II or Type III functional response, a flexible version of the FR model was fitted on the data which included the scaling exponent q (Real, 1977; Pritchard et al., 2017):

$$N_e = N_0 (1 - \exp(bN_0^q(hN_e - T))) \tag{2}$$

where N_e is the number of prey eaten, N_0 is the initial prey density supplied, b is the search coefficient (analogous to attack rate a), q is the scaling coefficient, h is the handing time and T is duration of the experiment. Whereas a Type II functional response is analogous to q being fixed at 0, functional responses are increasingly sigmoidal (i.e. approaching Type III) where $q > 0$. Using Akaike's information criterion (AIC; where lower values depict a better fit), fits from Rogers' random predator equation (1) were compared to flexible functional response models with q free vary (0–1) and with q fixed at 1 (analogous to a Type III functional response), to select the best model which minimised information loss. The final functional response models were bootstrapped 2000 times to generate unbiased 95 % confidence intervals (Pritchard et al., 2017).

Multiple predators

In order to predict the multiple predator feeding rates, the attack rate (a) and handling time (h) estimates from single predator (i.e. in the absence of conspecifics or heterospecifics) functional responses (equation 1) were used. These were then compared to the observed multiple predator feeding rates. This was done separately for multiple predator groups (i.e. Nile tilapia + Nile tilapia; Mozambique tilapia + Mozambique tilapia and Nile tilapia + Mozambique tilapia) using the corresponding single predator functional response parameters. Predictions of functional responses were calculated following McCoy et al., (2012) and Sentis & Boukal (2018):

$$\frac{dN}{dt} = -\sum_{i=1}^{n} f_i(N)P_i \tag{3}$$

where N is the prey population density, P is the predator population density, a is the attack rate and h is the handling time obtained from the single predator functional response estimates. This model assumes no emergent multiple predator effects and its predictions can be compared to actual (observed) multiple predator feeding trials in order to determine the sign and strength of mutiple predator effects. To generate predictions of expected prey survival from the multiple predator combinations, initial values of N and P are set at the experimental initial prey and predator densities corresponding to the experimental treatment. For each predator treatment and prey density, equation 3 was integrated over the full experimental time to get the expected number of surviving prey.

In order to estimate variances around predictions, a global sensitivity analysis that uses the 95 % confidence intervals of each functional response parameter estimate and their variance-covariance matrix (covariance is assumed to be zero when unknown) to generate 100 random parameter sets using a Latin hypercube sampling algorithm (Soetaert & Petzoldt, 2010). For each parameter set (n = 100), equation 3 was then integrated over time and expected prey survival calculated using the 'sensRange' function in the R package 'FME' (Soetaert & Petzoldt, 2010). Confidence intervals between predicted and observed functional responses were compared to dictate differences (i.e. multiple predator effects) across prey densities.

Results

Single predators (individuals, observed)

Nile tilapia exhibited significant evidence for a Type II functional response, owing to a significant negative first order term (GLM: estimate = -0.007, z = -2.796, p = 0.005). Mozambique tilapia did not show any statistically clear evidence for a particularly functional response, although feeding rates tended to decrease with increasing prey density (GLM:

estimate = -0.003, z = -1.050, p = 0.294). The Type II functional response minimised information loss compared to the flexible functional response model irrespective of the scaling exponent *q* for Mozambique tilapia (i.e. lower AIC).

Significant functional response parameters were returned for Nile tilapia attack rates and handling times (*a*: estimate = 0.660, z = 10.999, p < 0.001; *h*: estimate = 0.012, z = 2.912, p = 0.004) and attack rates but not handling times for Mozambique tilapia (*a*: estimate = 0.290, z = 8.053, p < 0.001; *h*: estimate = 0.012, z = 1.091, p = 0.275). Attack rates were therefore substantially greater in Nile tilapia compared to Mozambique tilapia, whereas handling times were more similar between species (notwithstanding a lack of functional response asymptote at high prey densities). Across all available prey densities, functional responses of Nile tilapia were significantly greater in magnitude than that of Mozambique tilapia, as evidenced by a lack of overlap between 95 % confidence intervals (Figure 3.1; Table 3.1).

Table 3.1: Parameter estimates and significance levels from the generalised linear model (GLM) of the proportion of prey consumed against the initial prey density supplied, with significance levels of functional response (FR) parameters (*a*, *h*) as depicted by the Roger's random predator equation.

Treatment	Species	GLM			FR Parameters					
		estimate	***z***	***p***	***a***	***z***	***p***	***h***	***z***	***p***
Single	Nile tilapia	-0.007	-2.796	0.005	0.660	10.999	<0.001	0.012	2.912	0.004
Single	Mozambique tilapia	-0.003	-1.050	0.294	0.290	8.053	<0.001	0.012	1.091	0.275
Heterospecific, gut content	Nile tilapia	-0.006	-1.823	0.068	0.599	7.408	<0.001	0.013	1.972	0.049
Heterospecific, gut content	Mozambique tilapia	-0.002	-0.552	0.581	0.312	6.410	<0.001	0.007	0.547	0.585

a = attack rate; h = handling time

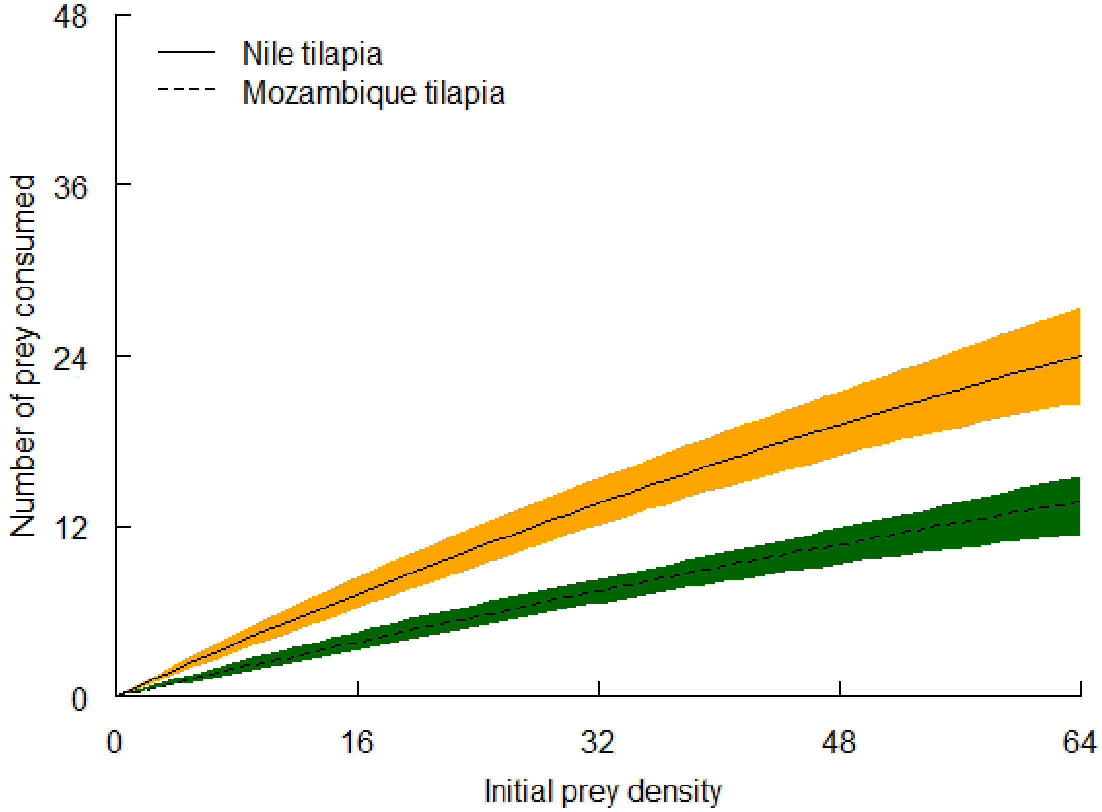

Figure 3.1: Type II functional responses of Nile tilapia and Mozambique tilapia individually. Lines represent fits from the random predator equation, whereas shaded areas are 95 % confidence intervals from non-parametric bootstrapping.

Single predators (heterospecific, gut contents)

Neither Nile tilapia (GLM: estimate = -0.006, z = -1.823, p = 0.068) nor Mozambique tilapia (GLM: estimate = -0.002, z = -0.552, p = 0.581) exhibited significant evidence for a Type II functional response based on gut contents in heterospecific pairs. For both predators, however, the Type II functional response fit had the lowest AIC compared to the flexible form of functional response considering scaling exponent q.

Significant functional response parameters were returned for Nile tilapia (a: estimate = 0.599, z = 7.408, p < 0.001; h: estimate = 0.013, z = 1.972, p = 0.049), but only for the attack rate and not handling time considering Mozambique tilapia (a: estimate = 0.312, z = 6.410, p < 0.001; h: estimate = 0.007, z = 0.547, p = 0.585). Attack rates were accordingly greater in Nile tilapia, whereas handling times were shorter (albeit non-significant) for Mozambique tilapia. Nevertheless, across all prey densities, functional responses of Nile tilapia were again significantly higher than Mozambique tilapia (Figure 3.2; Table 3.1), with some evidence for convergence at the highest density.

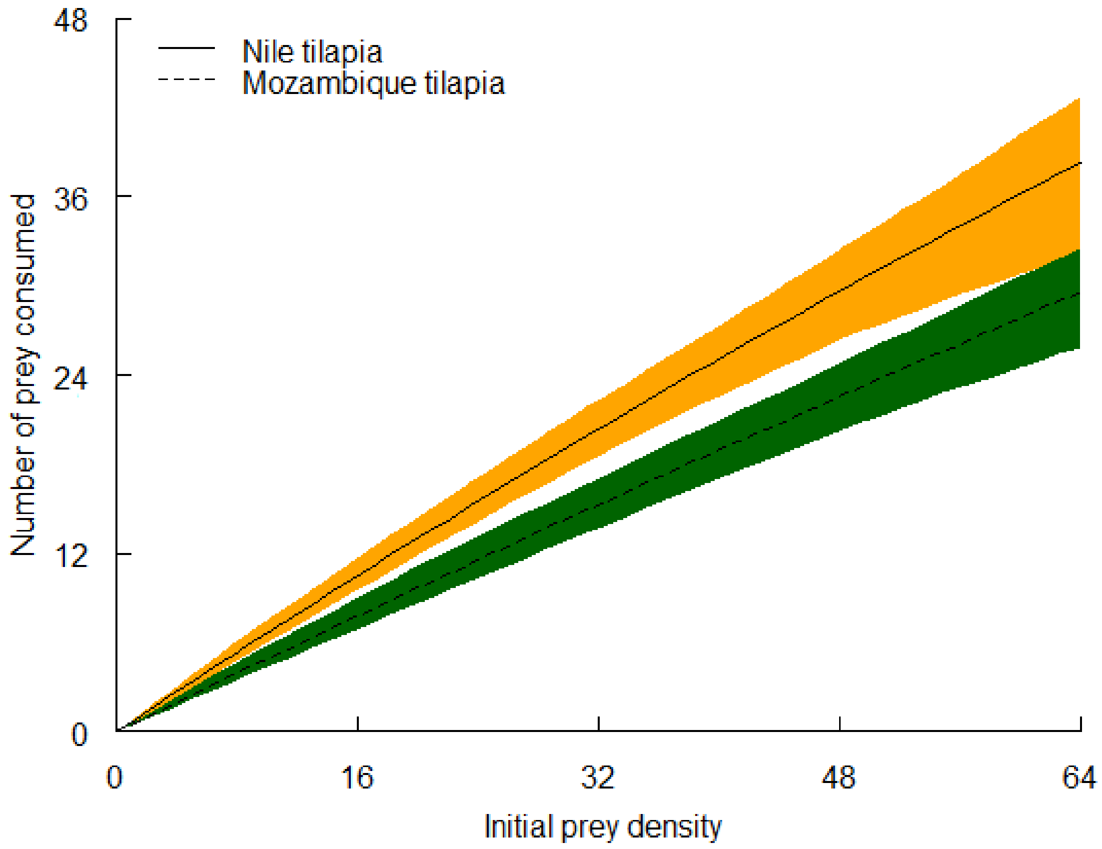

Figure 3.2: Type II functional responses of Nile tilapia and Mozambique tilapia in heterospecific pairs based on gut contents. Lines represent fits from the random predator equation, whereas shaded areas are 95 % confidence intervals from non-parametric bootstrapping.

Multiple predators (conspecific, heterospecific)

Both conspecific pairs of Nile tilapia and Mozambique tilapia, observed (i.e. actual models from conspecifics) and predicted (i.e. expected models of conspecifics, simulated from individuals) functional responses were statistically similar, owing to overlapping 95 % confidence intervals (Figure 3.3a, b). Conspecific Nile tilapia consumed more prey than Mozambique tilapia based on either observations or predictions (Figure 3.3a, b). For heterospecific pairs of Nile tilapia and Mozambique tilapia, observed functional responses again were again similar to predicted functional responses, given the overlapping of 95 %

confidence intervals (Figure 3.3c). Accordingly, multiple predator effects (MPE) were not significantly evidenced in any intraspecific or heterospecific fish pairing.

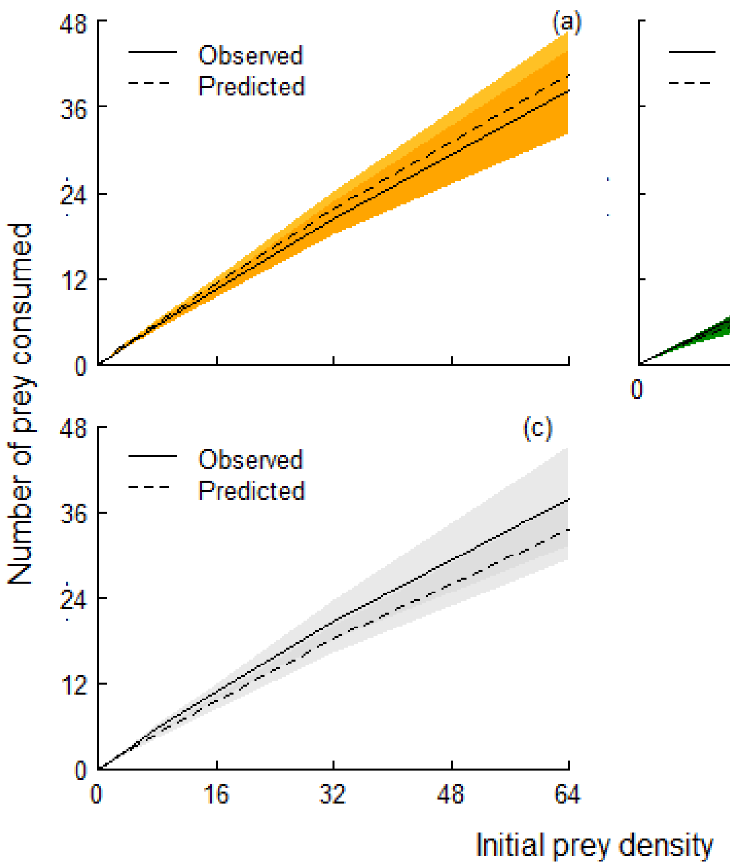

Figure 3.3: Experimentally-observed and simulated Type II functional responses of (a) conspecific Nile tilapia, (b) conspecific Mozambique tilapia and (c) heterospecific Nile tilapia and Mozambique tilapia. Lines indicate functional response fits and shaded areas are 95 % confidence intervals. Observed functional responses were empirically recorded, whereas predicted functional responses were simulated from single predator attack rate and handling time parameters.

Discussion

Results from this chapter depicted a destabilising Type II functional response (Alexander et al., 2012; Taylor & Collie, 2003) for both the native Mozambique tilapia and the invasive Nile tilapia in the single predator experiments. A Type II functional response depicts how predators tend to consume prey at low densities, with theoretical implications for localised prey extinction effects (Alexander et al., 2014; Barrios-O'Neill et al., 2016; Murray et al., 2013). Within the key questions, our results showed that 1) the invasive Nile tilapia had higher functional responses towards chironomids at single predator level than the native Mozambique tilapia, as evidenced by the lack of overlap between the 95% confidence interval. The outcomes from the conspecific multiple predator experiments showed that 2) neither Nile tilapia or Mozambique tilapia exhibited synergistic feeding. Similarly, under heterospecific conditions 3) the observed functional responses were similar to predicted functional responses suggesting a lack of interference competition.

Differences in attack rates and handling times highlight how predator-predator interactions are dependent on the amount of prey available (Sun et al., 2018). When contrasting attack rates between the two species, the invasive Nile tilapia showed significantly greater attack rates than the native Mozambique tilapia. Based on Holling (1959), the attack rate parameter estimate is an indication of the success of a species in finding and consuming food at low prey densities. Our results showed that the invasive Nile tilapia based on attack rates was more successful in searching and acquiring prey than native Mozambique tilapia. The handling time parameter estimate is an indication of the time it takes the species to eat and digest its prey (Jeschke et al., 2004; South & Dick, 2017). Here, it was shown that the handling times were similar for both *O. mossambicus* and *O. niloticus*. Overall, these results showed that the invasive species has a greater overall predatory potential than the native species. Furthermore, our results showed that prey consumption by native species is reduced when it co-occurs with the invasive species. It is evident that higher prey consumption in invasive Nile tilapia may alter food intake of the native Mozambique tilapia, which in turn may bring about changes in native population dynamics hence threatening native biota (Palacios et al., 2018).

According to Barrios-O'Neil et al., (2016), predator-prey interactions and the type of functional response affects population stability of species. For instance, the present study showed potential for the invasive Nile tilapia to outcompete the native Mozambique tilapia given that Nile tilapia consume more prey than native congener. Furthermore, the higher FRs depicted by Nile tilapia in conspecific specific pairing experiments further suggest that the invasive species does not reduce its food intake in the presence of conspecifics and that the single predator scenarios can be extrapolated to multiple conspecific scenarios. In heterospecific combinations, however, the presence of Nile tilapia did not seem to have a negative impacts on the native Mozambique tilapia. While this suggests that the presence of Nile tilapia does not hinder the feeding of Mozambique tilapia through some form of interference competition, it also highlights that no negative MPE towards Nile tilapia was evident. This suggests that Mozambique tilapia offer little biotic resistance with regards to interference competition when it comes to Nile tilapia presence in a receiving environment.

Results from this study strongly suggest that the invasive Nile tilapia may have adverse impacts on native prey items when compared to the effects of Mozambique tilapia. It is therefore crucial to understand the factors driving invasions and their impacts on native species and functional response experiments are an important method of measuring and quantifying impacts of invasive species across a range of species (Alexander et al., 2014; South et al., 2019). Nile tilapia has been shown to have a broader diet and hence able to utilize a wide range of food resources (Zengeya et al., 2013b). This further places invasive Nile tilapia at an advantageous position over native species that utilized the same resources. Based on Zengeya et al., (2013a) there is a trophic overlap between Nile tilapia and Mozambique tilapia where they co-occur, and this overlap has placed the native Mozambique tilapia at the risk of extinction (Zengeya et al., 2013a; Zengeya et al., 2013b). While field surveys on diet and distribution of species are useful, they offer limited insight into mechanisms through which invasive species may threaten native fauna. In this regard, comparative functional responses are increasingly prevalent in invasion ecology investigations, given that they can provide better understanding of biotic resistance as well as predicting the success of an invasive species (Cuthbert et al., 2018; Dick et al., 2017). Invasive species continue to have adverse impacts on native species and thus methodologies such as functional responses are needed in order to understand their establishment success and spread (Cuthbert el al., 2018). The structure and functionality of communities is driven by interspecific interactions between species hence understanding and assessing these interactions such as competition for resources and predator-prey dynamics is important (Mofu et al., 2019b).

This chapter further integrated gut content analysis which is an underutilised approach used to complement direct functional response approaches assessing multiple species interactions. Gut content integration approach minimizes bias in functional responses as it uses direct enumeration of prey items present in the predator's gut (Mofu et al., 2019b). This allowed us to determine the single level functional responses for both Nile tilapia and Mozambique tilapia using chironomids prey under multiple predator scenarios following the multiple predator effect approach (Wasserman et al., 2016). This approach allowed us to quantify single prey consumption from gut content in order to assess the predator prey functional responses of both the invasive Nile tilapia and native Mozambique tilapia under multiple predator scenarios, hence masking the presence of multiple predator effects if respective predatory facilitation and disruption occur simultaneously between two predator species, with no observed non-additive effects on prey (Mofu et al., 2019b).

Conclusions

Results from this chapter provided more information on the functional responses of the native Mozambique tilapia and invasive Nile tilapia based on feeding experimental approaches using chironomids. The study showed that the invasive Nile tilapia had greater predatory potential than the native Mozambique tilapia, even under conspecific scenarios. However, there was no evidence of synergistic feeding in conspecific multi-predator scenarios for either species. Similarly, it was also found that there was limited interference interactions between the invasive Nile tilapia and native Mozambique tilapia. While this lack of MPEs at the heterospecific level indicates that the invasive species does not hinder prey resource acquisition by the native Mozambique tilapia when available, it also suggests that the latter offers little in the form of biotic resistance to invasions by Nile tilapia. It is also important to note that the fish used in this study were sourced from the same fish farm which is beneficial in knowing they had similar backgrounds prior to our experiments, however as strains from fish farms are bred to grow quickly this may have enhanced their feeding rates above what might be expected from wild fish. In conclusion, differences in feeding dynamics between the invasive Nile tilapia and native Mozambique tilapia may aid in successful invasion of Nile tilapia at the expense of the native Mozambique tilapia, should prey resource limitations occur. The lack of interactions between the two species investigated also indicate that the Nile tilapia does not adjust its feeding in the presence of a closely related comparative species.

CHAPTER 4

FUNCTIONAL MORPHOLOGICAL TRAIT DIFFERENCES BETWEEN *OREOCHROMIS MOSSAMBICUS* AND *OREOCHROMIS NILOTICUS*

Introduction

The introduction of invasive species globally is one of the main causative factors driving biodiversity loss through displacement of native biota (Meyerson et al., 2019). Therefore, to better conserve native species and manage invasions, a thorough understanding of the factors facilitating invasive species success is needed (Siddik et al., 2016). One such factor deals with food resource use and acquisition, as invasive species can outcompete native species for food. Given their important role in exploitative competition dynamics, feeding-related morphological features are an important element to consider in invasion biology (Luger et al., 2020; Nagelkerke et al., 2018).

The assessment of feeding-related morphological features can aid in the detection of factors driving resource consumption and possible competitive exclusion of native species by the non-native species (Luger et al., 2020). Feeding-related morphological characteristics are integral to the predatory performance of species (Van Deurs et al., 2017; Luger et al., 2020) and can further provide information on the species capacity to search, attack and consume different prey items (Sibbing & Nagelkerke, 2000). Any constraints in these morphological traits can have an influence on the feeding performance of a species and thus affect resource utilisation patterns of individual species (Mihalitsis & Bellwood, 2017). Therefore, understanding the way in which an invasive species is specialised morphologically in comparison to its native analogues can help in informing assessment and management strategies used in determining mechanisms that facilitate invasive species impact (Luger et al., 2020; Nagelkerke et al., 2018; Siddik et al., 2016).

Morphological features such as the mouth shape and body length of the fish are crucial in determining the type of prey items a species will eat (Paul et al., 2017). For instance, the opening of the mouth depicts how successful a species will be in acquiring food resources

(Magnahagen & Heibo, 2001; Paul et al., 2017) as well as in controlling the size of prey captured by the species (Cunha & Planas, 1999; Paul et al., 2017). Bardash (1972) further showed that features such as the spacing, thickness and length of gill rakers are able to show us the feeding habits used by different tilapia species. For instance, large gill rakers indicate that a species feeds on larger prey items while numerous, narrow gill rakers are characteristics depicted by planktivorous species. Diet predictions from morphological features are important in fish ecology as they depict the extent to which unknown diets of some fishes can be predicted based on the known diets of species that have similar functionality (Albouy et al., 2011; Bardash, 1972). Furthermore, dietary overlap and similarities in trophic profiles are imbued from these morphological trait similarities between native and non-native species and these may result in exploitative competition leading exclusion of native species (Luger et al., 2020; Nagelkerke et al., 2018).

Feeding-related morphological traits have been identified as one of the causal factors driving invasive species establishment success (Azzurro et al., 2014; Blanchet et al., 2010). For instance, a number of studies have reported that introduced species that successfully established into new localities differed both morphologically and functionally from the native biota present in recipient ecosystems (Blanchet et al., 2010; Marchetti et al., 2004; Olden et al., 2006; Toussaint et al., 2018). These species introduced into new localities were found to be larger in size and displayed more diversity in the type of diet they consumed (Toussaint et al., 2018). Hence, it is important to incorporate an assessment of feeding-related morphological trait differences between native and non-native species as these can give us a clear indication of factors responsible for high resource consumption in non-native species leading to possible exclusion of native species (Luger et al., 2020).

Mozambique tilapia, *Oreochromis mossambicus* (Peters, 1852), a native southern African cichlid is currently at risk of extinction through habitat and trophic overlap with Nile tilapia *Oreochromis niloticus* (Linnaeus, 1758) and has been identified as a vulnerable species under the IUCN red list of threatened species (IUCN, 2021; Zengeya et al., 2013b). Furthermore, the hybridization between these two species could lead to genetic loss for *O. mossambicus* as their broods are able to reproduce with either one of the parent species as well as with each other (Cambray & Swartz, 2007; Van der Bank & Deacon, 2007; Zengeya et al., 2013b). Hence, the introduction of *O. niloticus* into new localities is a cause for concern (Luger et al., 2020; Meyerson et al., 2019).

The functional morphology of these two species have yet to be contrasted, limiting our understanding on how morphological features may facilitate a competitive advantage of *O. niloticus* over *O. mossambicus.* As such, this chapter explores the feeding capacities of both *O. mossambicus* and *O. niloticus* using a functional morphology approach, as outlined by Sibbing & Nagelkerke, (2000). The aim of this chapter was to make morphological trait comparisons between *O. mossambicus* and *O. niloticus* in order to determine whether (i) there are differences in feeding-related morphological traits between these two species, and (ii) if these differences place the invasive *O. niloticus* at an advantageous position in terms of resource acquisition and consumption.

Materials and Methods

Ethical clearance and permits

The collection of species was carried out in compliance with the Department of Environmental Affairs (DEA permit no(s). 50738210728112716 and 50738210728122315) and ethical clearance was approved by the Rhodes University Animal Research Ethics Committee (RU-AREC reference no. 2021-2695-5969).

Specimen collection

The fish used for this chapter were sourced from Chapter 3 in order reduce the number of animals killed (see Chapter 3 for sourcing details). A total of 62 fishes (31 *O. mossambicus* and 31 *O. niloticus*) were euthanized with an overdose of clove oil (400 mg/L) and frozen before measuring feeding related morphological traits. Size matched specimens of *O. mossambicus* (60–110 mm) and *O. niloticus* (60–115 mm) were used for this chapter.

Morphological traits measurements

A total of twenty-three feeding-related morphological traits were measured to compare the trophic capacities of *O. mossambicus* and *O. niloticus* following criterion by Nagelkerke et al., (2018) and Sibbing & Nagelkerke (2000) (outlined in Table 4.1 & Figure 4.2). These morphological traits were then used to characterise the ability of each species to utilise a particular food type as depicted by Sibbing & Nagelkerke (2000). Measurements of body dimensions of fish were recorded (to the nearest 0.1 mm) using electrical callipers (e.g. Figure 4.1). The length and distance of gill rakers were measured (to the nearest 0.1 mm) under a dissecting microscope using an eyepiece graticule. All morphological measurements were done at the Department of Zoology and Entomology, Rhodes University. Morphological measurements used for further analyses are outlined in the supplementary material (Table S1).

Figure 4.1: Total length (TL) of fish measured using electrical callipers.

Statistical Analysis

R programming (version 4.0.3) was used for all data analysis. PCA was conducted on both the morphological traits to compare the overall trophic morphology of the two species as well as on the trophic profiles for an overall interpretation of trophic capacities.

All morphological trait values were calculated as ratios following a criterion by Sibbing & Nagelkerke (2000) to reduce the influence of body size. The coefficient of variation per species and variable were assessed. Then the correlation of variables was assessed using Kendall's tau correlation. After correlation was done, the trait ratios were standardised. A multivariate principal component analysis (PCA) was used to assess the significant variation among the morphological traits measured for both *O. mossambicus* and *O. niloticus*. Lastly, food specialist profiles (Table S2) were loaded and correlated based on selected morphological trait variables. This was done using a food fish model (FFM) to relate the measured morphological traits to its capacity to consume certain prey types following a criterion by Sibbing and Nagelkerke (2000).

Table 4.1: Morphological traits associated with feeding measured for both *Oreochromis mossambicus* and *Oreochromis niloticus* (adapted from Sibbing & Nagelkerke, 2000; Nagelkerke et al., 2018).

Morphological trait	Abbreviation
Anal fin base	AFiB
Anal fin length	AFiL
Body depth	BD
Body width	BW
Caudal peduncle depth	CPD
Eye diameter	ED
Total length	TL
Gill inter-raker distance	GiRD
Gill raker length	GiRL
Gill raker profile	GiRP
Gut length	GuL
Head length	HL
Hyoid length	HyL
Lower jaw in-lever for closing	LJin
Lower jaw out-lever	LJout
Lower jaw length	LJL
Operculum depth	OpD
Oral gape height	OGH
Oral gape width	OGW
Oral gape area	OGA
Postlingual organ width	PLOW
Postorbital length	POrL
Protrusion length	ProtL

This model was used as follows: Firstly, the effects of the measured feeding-related morphological traits on the capacity to eat a suite of aquatic food resources were established and expressed as positive, negative, or zero values (ranging between -2 and +2, with zero values indicating no evidence for any effect). The combined values of all effects for an aquatic resource formed a hypothetical food specialist profile (FSP), expressing the ideal relative sizes of morphological traits to exploit that resource. Secondly, the hypothetical profile values for each food resource were correlated with the measured morphological trait of each species using Kendall's tau correlation which resulted in the correlation coefficient considered as a measure of the predicted capacity of the fish to feed on the different food resources.

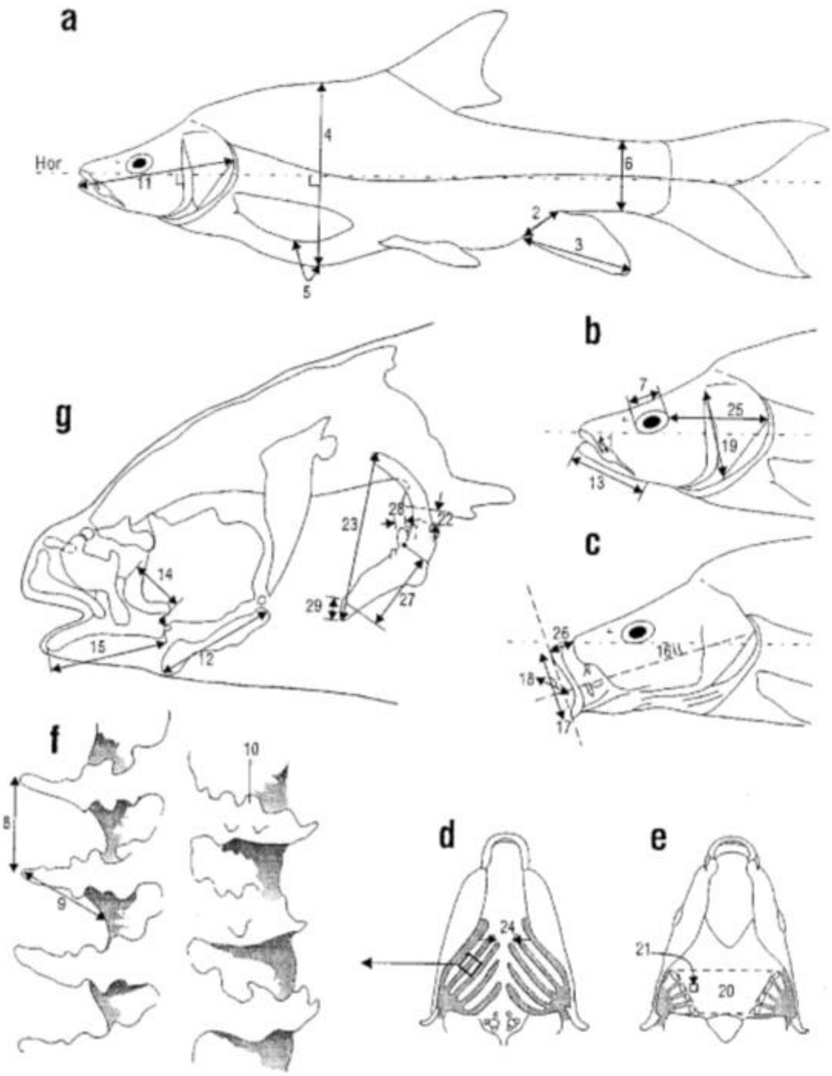

Figure 4.2: Image extracted directly from Sibbing & Nagelkerke (2000) outlining trait measurement used. Trait measurements were made as follows: (a) external fish characteristics, (b) head with closed mouth, (c) head with open mouth, (d) oro-pharyngeal floor, (e) oro-pharyngeal roof; (f) Gill arch showing the raker profile and (g) Skeletal part of the head.

Results

The PCA of the morphological trait variables explained only 44.5% of variance of the total variation along the axis of the first two dimensions of the PCA (Figure 4.3a). The PCA did, however, show overlap between *O. niloticus* and *O. mossambicus* in the morphological trait, with *O. niloticus* more on the right half of the ordination and *O. mossambicus* more on the left half of the ordination. Lower jaw closing force, gill raker length, gill resistance, body depth and operculum area were clearly larger for *O. niloticus*. Lower jaw closing force, gill resistance and gill raker length are crucial variables in feeding capacities of hence allowing *O. niloticus* to feed on various food items than native *O. mossambicus* (Figure 4.3a, b).

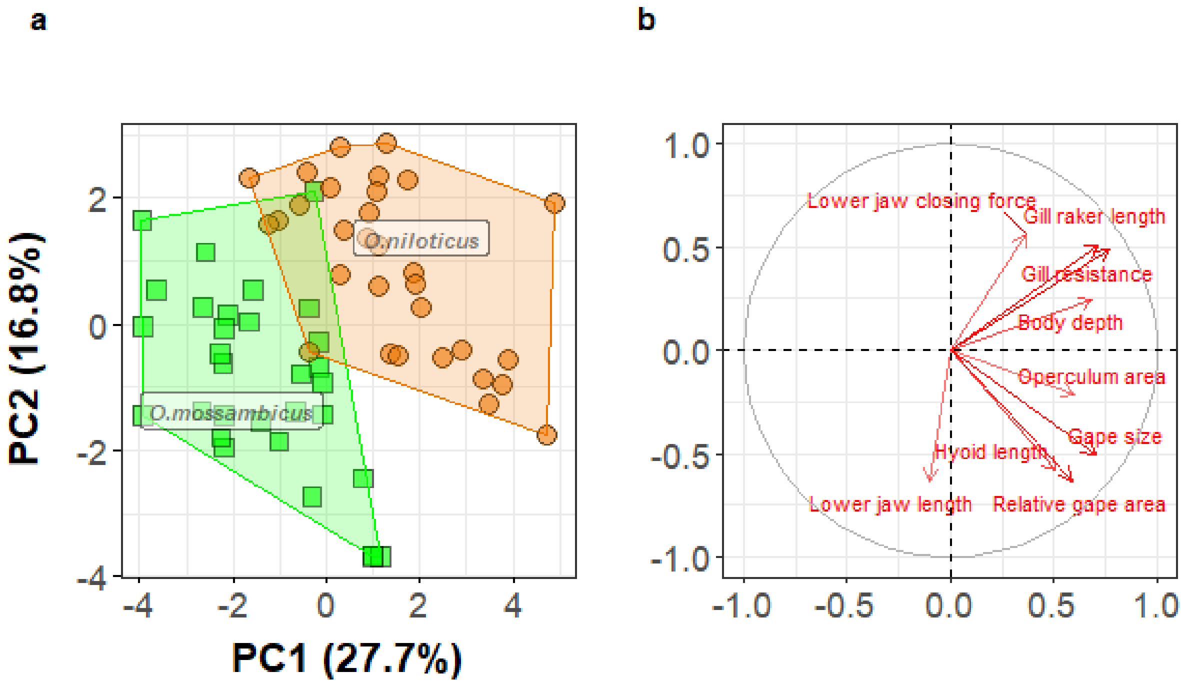

Figure 4.3: Principal component analysis (PCA) ordination of invasive *Oreochromis niloticus* and native *Oreochromis mossambicus* based on feeding-related morphological features. Markers on a) depict *Oreochromis niloticus* (orange circles) and *Oreochromis mossambicus* (green squares) and the arrows on b) depict the loadings of the most influential variables on the PC-axes.

The PCA of trophic profiles for the two species explained 69.7% of the total variance along the first two axes (Figure 4.4a). The dietary overlap between *O. niloticus* and *O. mossambicus* was relatively high. The invasive *O. niloticus* showed greater feeding capacity towards phytoplankton, plants, fish (ambush), fish (pursuit) and larvae, which was evident of the species being omnivorous. Both species had similar feeding capacities towards sessile algae, molluscs and insects, with *O. mossambicus* only having greater feeding capacity towards zooplankton (Figure 4.4a, b).

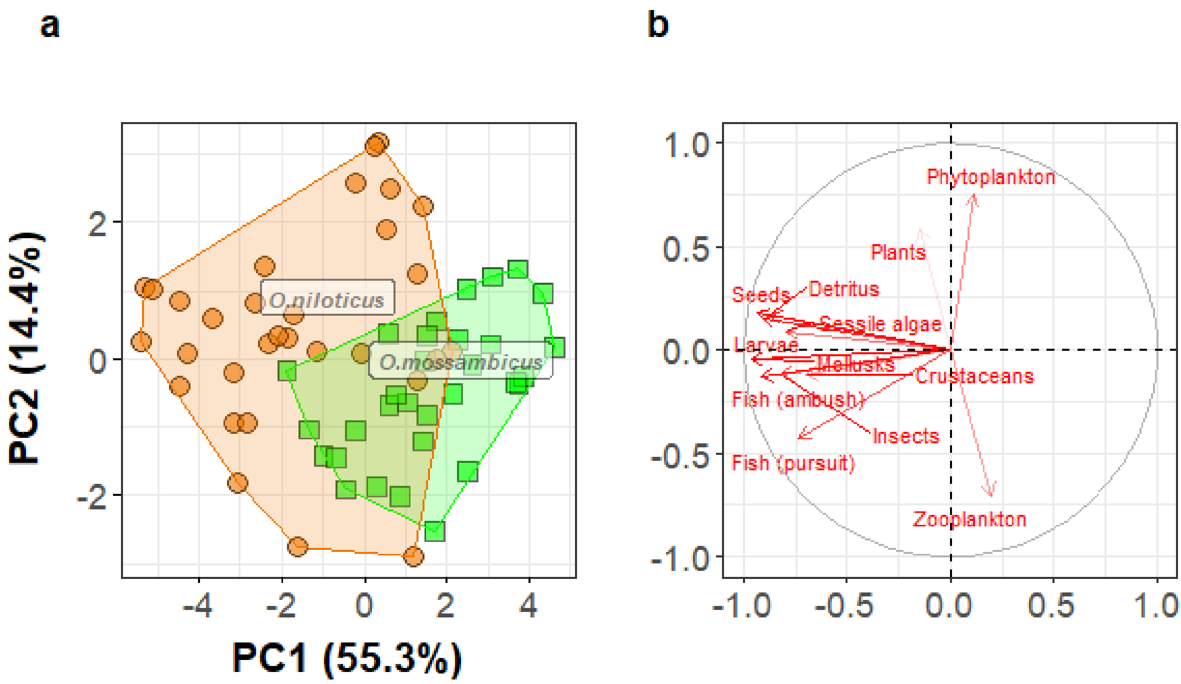

Figure 4.4: Principal component analysis (PCA) ordination of invasive *Oreochromis niloticus* and native *Oreochromis mossambicus* based on trophic profiles. Markers on a) depict *Oreochromis niloticus* (orange circles) and *Oreochromis mossambicus* (green squares) and the arrows on b) depict the loadings of the most influential food items on the PC-axes.

Discussion

Results showed that when comparing the functional morphology of the invasive *O. niloticus* and native *O. mossambicus* the two species had high morphological overlap (Figure 4.3a, b). With *O. niloticus* having larger lower jaw closing force, gill raker length, gill resistance, body depth and operculum area than *O. mossambicus*. Greater lower jaw force in *O. niloticus* suggests that the invasive can handle hardier invertebrate prey with increased lower jaw strength than its native analogue. Greater lower jaw force further allows the species to acquire larger prey and causes increased speed when biting thus promoting greater jaw protrusion (Cooper et al., 2010). Furthermore, the gill raker length and gill resistance are crucial for facilitating feeding in fishes and hence places the invasive species at an advantageous state over the native when it comes to acquiring and consumption of food items (Pease et al., 2015).

Differences in morphological traits suggest that there might be differences in feeding capacities for these two species providing opportunity for resource partitioning and opportunity for the invasive species to becoming successfully integrated into the receiving ecosystem (Jere, 2021; Nagelkerke et al., 2018).

When looking at the species capacity to feed on different aquatic food items, the PCA of trophic profiles explained 69.7% of the total with relatively high dietary overlap between *O. niloticus* and *O. mossambicus* (Figure 4.4a, b). This dietary overlap suggests that these two species have similar feeding capacities, meaning there is a potential for competitive interactions (Eloranta et al., 2015; Pilger et al., 2010) between the species, should food resource limitation be an issue. While both species are known omnivores, *O. niloticus* showed evidence of being a more diverse feeder, with high feeding capacities towards phytoplankton, plants, fish (ambush), fish (pursuit) and larvae. The ability to eat different food items indicates the high feeding plasticity for *O. niloticus*, with implications for its success across different aquatic habitats. Both species, however, had similar feeding capacities towards sessile algae, molluscs and insects, with *O. mossambicus* having greater feeding capacity towards zooplankton.

A recent study by Jere (2021) on dietary overlap between *O. niloticus* and native species conducted in the upper Kabompo River in Zambia found that the invasive *O. niloticus* has high dietary overlap with native species such as *O. macrochir* and *T. sparrmanii* and this indicates high interspecific competition potential between these species. Such competition may have implications for food web dynamics and eventually lead to decline in native biota and hence loss of biodiversity (Eloranta et al., 2015; Jere, 2021), should the invasive species outcompete native analogues. *Oreochromis niloticus* has been identified as being an opportunistic feeder allowing it to withstand and overcome competition for food resources as it is able to use a wide range of available resources (Jere, 2021; Winemiller & Kelso-Winemiller, 2003). More research on the diet of *O. niloticus* and native species has found similar results where *O. niloticus* was found to share food resources with native species and consuming more than their native counterparts (Jere, 2021; Marshall, 2011; Zengeya et al., 2015). Dietary overlap and similarities in trophic profiles are imbued from morphological trait similarities between native and non-native species and these similarities may result in exploitative competition leading possible extinction of native species (Luger et al., 2020; Nagelkerke et al., 2018).

Conclusions

Prior to this investigation, the functional morphology of *O. niloticus* and *O. mossambicus* had yet to be contrasted, limiting our understanding on how their feeding-related morphological traits may facilitate a competitive advantage of *O. niloticus* over *O. mossambicus.* Incorporating an assessment of feeding-related morphological trait differences between native and invasive species can give a clear indication of factors responsible invasive species generally having high feeding capacities than their native analogues which might lead to possible extinction of native species (Luger et al., 2020).

This chapter showed that there is high overlap in the functional morphology and trophic profiles between the invasive *O. niloticus* and native *O. mossambicus*. The trophic overlap between these two species is evident of potential competition existing between these two species. However, subtle differences between the species were evident, particularly for morphological traits. Feeding-related morphological traits are one of the main driving factors in invasive species establishment success (Blanchet et al., 2010). Previous research has reported that introduced species that successfully established into new localities were morphologically different from the native species found in recipient ecosystems (Blanchet et al., 2010; Marchetti et al., 2004; Toussaint et al., 2018). These newly introduced species displayed more diversity in the type of diet they consumed as detected by their morphological features (Toussaint et al., 2018). The results in this chapter are reflective of this, with the invasive species highlighted as being the more diverse feeder.

CHAPTER 5

GENERAL DISCUSSION

An overview of the three data chapters provides insights into similarities and differences between two congeneric species, within the context of biological invasions. Specifically, aspects of the biology of the native Mozambique tilapia, *Oreochromis mossambicus* (Peters, 1852) in relation to the invasive Nile tilapia, *Oreochromis niloticus* (Linnaeus, 1758) was assessed. The thesis further offers information on feeding dynamics within the context of competition potential and how the incorporation of feeding-related morphological traits elucidate how feeding capacities differ between these two species, with implications for invasion success dynamics.

In order to be able to predict integration success or failure of invasive species one needs to have a clear understanding of their life history parameters (Mooney & Hobbs, 2000). For instance, factors such as rapid growth and early maturity are important variables in the success of invasive species (Beamish & McFarlane, 1983, Jones, 1992). Currently there is lack of published data on the biology of Mozambique tilapia in the Eastern Cape region. Therefore, in an attempt to fill this data gap I assessed the biology of Mozambique tilapia in this region and made comparisons with that of an invasive Nile tilapia (Chapter 2). This study showed that age of Mozambique tilapia can be easily assessed using sagittal otoliths (unburnt). Key findings showed sex-specific differences in growth where males grew faster and larger than females. This is linked to their breeding behavior as males are needed to be larger for defense of breeding grounds (Bwanika et al., 2007; Lowe-McConnell, 1987). A high percentage of the sampled Mozambique tilapia population was found to be reproductively mature, highlighting that this species spawns during the summer season as sampling was conducted in April. When comparing the age and growth of Mozambique tilapia to that of Nile tilapia based on published data, the invasive Nile tilapia had faster growth rates than its native congeneric Mozambique tilapia (Chapter 2). The faster growth of the invasive congeneric will presumably enable earlier prey size refuge dynamics, placing the Nile tilapia at an advantage over the Mozambique tilapia in the wild as fast growth has been previously linked to reducing susceptibility of juveniles to predation (Kadye, 1986). Such fundamental results are an important step in predicting mechanisms that would facilitate the potential impacts of invasive Nile tilapia in the case of it being introduced in the Eastern Cape region. However, basic biological information alone is not sufficient to suitably inform on invasion dynamics, and as such the study of biological interaction dynamics are also regarded as key in this regard (Latombe et al., 2017).

Chapter 3 dealt with predator-prey dynamics, an important aspect of invasion biology (Dick et al., 2017). Nile tilapia pose threats to food webs in receiving environments in that their prey consumption dynamics may be dissimilar to that of native congeners such as the native Mozambique tilapia. In addition, because of the potential shared habitat and food resources, direct and interference competition dynamics may ensue between the two species. Feeding dynamics within the context of competition potential are, however, largely lacking for Nile tilapia and Mozambique tilapia. Therefore, I used experimental functional response procedures to contrast the food consumption dynamics of both Nile tilapia and Mozambique tilapia and assess for any multiple predator effects (MPEs) within and between these two closely related species. Major findings showed that at the single and conspecific predator level, invasive Nile tilapia consumed more prey than its native congeneric. Although both species had similar prey handling times, Nile tilapia had greater attack rates than the native species. Furthermore, Nile tilapia were better at finding food when it is present at low densities (Chapter 3). At the heterospecific predator level, Nile tilapia did not adjust their food intake or interfere with feeding of the native but still consumed more than Mozambique tilapia. While Nile tilapia was found to impose no interference competition on Mozambique tilapia, the native species similarly offers limited biotic resistance potential, with Nile tilapia. This experimental chapter offers important insight into how Nile tilapia may shape food webs when compared to native Mozambique tilapia. When these results are considered within the context of the differences in growth rates (Chapter 1), the potential of Nile tilapia to be more detrimental to food resources shared with Mozambique tilapia is further highlighted. It is acknowledged that the experimental settings for this chapter, although widely used, are highly constrained given the artificial nature of the feeding arenas used. As such, care needs to be taken when extrapolating these results to field scenarios. To fully understand trophic dynamics in this regard, integration of these findings with additional information such as levels of dietary overlap, prey handling and consumption ability are required.

The final data chapter (Chapter 4) assessed morphological traits between Mozambique tilapia and Nile tilapia in an attempt to provide additional information on competition potential dynamics between the two species. This chapter showed that there is overlap in feeding related morphological traits between the two species, facilitating dietary overlap, which has also been observed in other field studies (Zengeya et al., 2015). However, Nile tilapia were shown to have the ability to consume a greater diversity of food web components, many of which Mozambique tilapia may not be able to handle. This was attributed to Nile tilapia having a distinctively greater lower jaw closing force, gill resistance and gill raker length. These key features have all been shown to be advantageous when it comes to feeding, through facilitating greater levels of predatory potential and omnivory (Cooper et al., 2010; Pease et al., 2015). The versatility in feeding displayed by the invasive species may play an important role in its establishment success if it was to be introduced in the Eastern Cape region as it would afford Nile tilapia the opportunity to exploit a broader range of food resources than Mozambique tilapia. Furthermore, differences in feeding-related morphological traits depict some differences in feeding capacities of species, providing opportunity for resource partitioning and opportunity for successful integration of invasive species into new ecosystem, under certain circumstances (Jere, 2021; Nagelkerke et al., 2018). Yet despite these important differences between the species, there was still a considerable amount the high dietary overlap between the congeners. This implies that exploitative competition for food resources may still play a role in structuring community dynamics when food resource become scarce. These findings suggest that direct competition between Nile tilapia and Mozambique tilapia are inevitable should food resources be limiting or under certain food web scenarios. This highlights how direct comparisons such as those conducted in Chapter 3 are ecologically relevant for these congeners, and that the results of the functional response study, despite being highly artificial may still offer insight into food web dynamics in systems invaded by Nile tilapia.

Conclusion and recommendations

In combination, the three data chapters in the thesis present a cohesive overview of how biological and ecological features of the Nile tilapia and Mozambique tilapia may facilitate invasion success of the former in receiving environments in southern Africa. Currently there is very little data available on the biology of Mozambique tilapia in the Eastern Cape region. Therefore, this research forms a baseline study in age and growth of Mozambique tilapia in this region and in predicting potential impacts the invasive Nile tilapia might pose upon invasion. Prior to this investigation, the functional morphology of invasive Nile tilapia and native Mozambique tilapia had also yet to be contrasted, limiting our understanding on how their feeding-related morphological traits may facilitate a competitive advantage of the invasive species over Mozambique tilapia. Hence incorporating an assessment of feeding-related morphological trait differences between native and non-native species in Chapter 4 gave a clear indication of morphological traits that are responsible for invasive Nile tilapia having high predatory potential/feeding capacities than Mozambique tilapia. Chapters 3 and 4 thus provided crucial information on feeding dynamics of Nile tilapia and Mozambique tilapia, with complementary feeding related morphology traits analysis highlighting major differences between these species which allowed the invasive Nile tilapia to consume a more diverse suit of food resources and able to exploit resources that the native might not be able to handle. Such information clearly shows that possible competition might arise between the species at the expense of the native species. This information therefore calls for the implementation of management strategies for invasions to avoid possible loss of the native species. As such, our findings could be useful in identifying problematic invasive species such as Nile tilapia and potentially quantifying their impacts. Furthermore, similar studies can be implemented in the future in order to identify priority species that require conservation.

Future work should consider assessing the biology of Mozambique tilapia in other Eastern Cape catchments in order to make comparisons of the life history of Mozambique tilapia across the entire region. Furthermore, sampling should be done seasonally to better understand the spawning season of these species which could be useful in stock assessment and management strategies. It is also important to increase sample size for all age classes in order to assess a full range of size classes. A comprehensive study of the reproductive biology of Mozambique tilapia including the length and age at maturity for each sex is needed, this further feeds into stock assessment and implementation of conservation. Other autecological information would also be useful, such as physiological characteristics of both species, and how this is likely to facilitate or hinder population successes under shifting climate and pollution level dynamics. Additional studies looking at how growth rates may facilitate prey refuge effects would also be useful, as would additional studies on direct competition dynamics between Nile tilapia and Mozambique tilapia. There are, however, other very important considerations that require mention as they relate to impacts on Mozambique tilapia by Nile tilapia and these need to be considered for future work. Arguably the greatest impact that Nile tilapia will have on Mozambique tilapia is through genetic pollution. Both species belong to the *Oreochromis* genus, and members of this genus are well-known for their ability to interbreed (Skelton, 2001; van der Bank & Deacon, 2007; Zengeya et al., 2015). Mozambique tilapia is currently under threat through much of its native range given extensive invasions by Nile tilapia, primarily through hybridization of the two species (Zengeya et al., 2013a). The hybrids produced are viable and can interbreed with each other or either one of the parent species producing progenies with intermediate traits (van der Bank & Deacon, 2007, Zengeya et al., 2015). As such, the endemic gene pool of Mozambique tilapia is at risk of becoming extinct. Thus, further research focusing on mitigation strategies for invasive species is needed to avoid possible loss of native gene pools. The Eastern Cape populations of Mozambique tilapia are also thought to be among the last with no genetic pollution from Nile tilapia, highlighting the importance of native stocks in the region.

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SUPPLEMENTARY MATERIALS

Table S1: Raw data for measurements used in principal component analysis for Nile tilapia, *Oreochromis niloticus* and Mozambique tilapia, *Oreochromis mossambicus* in Chapter 4. All measurement units are in millimetres.

Spec.	AFiB	AFiL	BD	BW	CPD	ED	TL	GiRD	GiRL	GiRP	GuL	HL	HyL	LJL	Ljin	Ljout	OGAx	OGH	OGW	OpD	PLOW	POrL	ProtL
Nile	14	19,84	30,42	10,46	12,1	8,83	99	4,3	3,2	1	294,2	27,55	8,03	5,39	4,67	7,61	26,45	10,94	4,4	13,43	5,92	11,93	3,69
Nile	10,4	16,22	24,74	7,97	9,29	6,52	76,77	3,9	3,4	1	251,73	22,13	4,89	3,03	5,03	5,03	20,54	9,05	3,6	10,91	3,23	9,43	1,53
Nile	11,75	18,43	26,95	8,08	9,84	7,14	89,47	4,5	3,6	1	452,08	23,54	7,58	4,5	4,54	7,21	22,14	9,69	4,01	11,75	3,81	11,27	2,5
Nile	12,53	17,64	25,45	6,92	9,66	6,78	81,61	4,3	3,1	1	377,62	23,66	6,55	4,85	4,77	7,38	21,41	9,2	4,07	11,52	3,76	10,04	3,22
Nile	11,8	18,75	25,74	6,64	10,47	6,99	85,15	4,5	3,4	1	274,45	24,07	6,92	4,44	4,8	7,5	23,3	8,81	3,89	11,48	3,84	10,51	2,54
Nile	11,39	18,33	25,48	6,59	9,79	6,34	81,32	4,1	3,2	1	247,09	22,44	7,02	5,88	4,79	7,58	2,01	8,8	3,01	10,85	3,91	10,48	3,27
Nile	12,07	18,24	26,45	7,95	10,82	6,26	88,6	4,8	3,8	1	352,28	24,39	6,48	5,49	4,52	7,48	24,19	9,22	3,08	11,5	3,81	10,6	2,67
Nile	11,01	17,25	24,33	6,2	9,96	6,8	82,04	4,4	3,6	1	216,25	22,9	5,82	3,8	3,86	5,01	21,64	6,99	2,41	9,8	3,25	9,88	2,43
Nile	11,98	18,34	25,08	6,9	9,91	6,37	83,84	4,7	3,2	1	188,66	23,11	6,24	2,93	3,88	5	22,41	6,97	2,07	9,15	3,07	9,94	2,98
Nile	13,92	23,5	31,95	8,9	12,25	7,66	103,28	5,1	4,2	1	312,97	27,33	8,01	6,28	4,66	7,42	27,86	9,82	3,66	12,85	4,3	12,63	3,63
Nile	12,42	18,27	25,6	7,46	9,83	6,1	85,78	4,6	4,2	1	345,23	23,95	6,25	4,38	3,02	5,17	23,37	6,89	2,77	11,08	3,27	10,08	2,47
Nile	9,26	15,72	24,44	6,07	9,18	6,03	78,46	4,6	3,5	1	302,21	22,52	6,28	4,49	3,05	5,29	21,62	5,53	2,42	10,74	3,08	9,21	2,6
Nile	10,17	16,52	24,52	7,14	9,73	6,04	78,1	4,6	3,2	1	198,1	21,28	5,94	4,29	3,01	5,5	21	5,76	2,49	11,02	3,09	9,1	2,36
Nile	12,37	18,71	26,51	7,47	10,03	6,95	86,71	4,4	3,4	1	444,84	23,24	7,56	5,4	3,78	6,48	22,52	6,66	2,29	11,63	3,9	10,39	2,52
Nile	14,52	25,51	32,5	9,57	12,65	8,26	107,54	6,4	4	1	467,45	28,64	8,23	6,38	4,8	7,79	28,63	10,34	3,81	15,56	4,64	13,03	2,4
Nile	12,41	19,79	28,22	8,35	11,01	7,61	88,72	4,4	2,5	1	298,95	24,77	8,29	5,29	4,16	7,53	23,43	7,59	3,49	11,16	3,39	10,4	2,97
Nile	10,58	16,57	25,65	7,38	10	7,33	84,54	5,4	3,7	1	247,97	23,5	6,03	4,83	3,74	6,55	22,95	6,62	2,15	10,67	3,31	10,27	2,53
Nile	12,18	18,3	27,58	7,41	10,77	7,45	89	4,6	3,4	1	460,69	25,33	9,02	5,12	4,08	7,25	24,13	7,84	3,69	11,7	3,65	11,27	2,67

Nile	10,19	15,84	23,96	6,59	9,73	6,25	80,47	4,6	2,7	1	259,59	2,28	4,7	3,54	2,79	5,71	21,68	5,86	1,98	9,59	3,26	10,16	2,02
Nile	11,32	17,39	25,97	7,66	9,38	6,82	84,76	4,1	3,5	1	396,58	23,87	5,6	3,8	3,4	6,09	22,84	6,44	2,79	10,23	3,73	11,14	2,67
Nile	11,94	19,38	26,73	7,84	9,89	6,76	88,31	4	4,2	1	318,07	24,7	5,16	4,54	3,92	6,83	23,78	7,76	2,78	11,38	3,01	10,68	2,44
Nile	13,97	21,42	30,85	9,98	12,28	8,13	99,5	4,5	2,7	1	554	26,97	6,2	5,3	4,39	7,57	25,87	8,51	3,48	12,42	4,52	12,23	2,23
Nile	13,69	20,09	27,58	8,64	10,75	6,7	89,45	4,6	1,6	1	371,38	24,88	5,94	5,28	4,15	7,51	24,07	7,8	2,57	12,11	3,03	10,29	2,76
Nile	12,14	18,5	27,35	7,95	9,21	6,39	84,47	4,7	2,9	1	435,26	24,36	5,53	4,74	3,76	6,36	24,06	7,23	2	11,68	3,16	10,15	2,31
Nile	11,29	17,58	24,55	6,9	9,05	6,45	82,62	4,4	3,1	1	518,23	23,66	4,96	3,88	2,96	5,82	22,48	6,43	1,98	10,41	3,5	10,27	2,25
Nile	11,92	17,6	24,65	7,26	9,27	6,34	82,06	4,5	2,5	1	460,78	22,64	5,02	4,22	3,67	5,72	21,86	7,72	2,02	9,5	2,71	9,72	2,08
Nile	12,65	19,35	27,26	7,9	10,01	7,15	88,41	4,6	3	1	387,88	24,6	5,17	4,48	4,09	6,59	23,6	7,32	2,05	10,8	3,72	10,83	2,22
Nile	11,63	16,61	24,73	7,85	10,4	7,08	84,08	4,6	3,3	1	286,13	23,78	5,1	4,67	4,28	6,14	21,99	6,88	2,03	10,16	2,98	9,98	2,24
Nile	12,94	19,52	27,26	7,75	10,02	6,71	85,75	4,9	3	1	301,03	23,9	4,45	3,54	3,85	6,6	22,98	7,59	2,1	9,98	3,81	10,79	2,78
Nile	8,88	15,54	23,66	6,91	9,08	6,46	76,25	4,6	3,1	1	442,88	21,66	4,2	4,36	3,26	6,16	20,23	7,95	1,88	9,78	3,76	9,17	2,51
Nile	8,76	16,07	24,18	6,78	9,55	5,84	80,03	4,2	2,5	1	303,73	22,16	4,16	4,76	4,22	6,63	21,48	7,23	1,75	9,16	3,33	9,82	2,33
OMO	13,35	21,58	29,78	9,15	11,71	6,79	97,86	4,9	1,9	1	287,25	26,6	8,41	6,17	4,09	14,12	24,48	11,68	3,74	13,85	3,21	11,54	2,91
OMO	12,38	18,77	26,11	7,61	10,72	6,27	88,9	5,4	2,1	1	348,16	25,26	8,17	4,7	5,76	13,29	22,94	10,1	2,99	11,41	3,19	10,19	2,63
OMO	12,38	18,94	25,4	6,98	10,3	6,31	84,85	4,9	1,7	1	385,04	22,87	8,21	5,71	5,03	13,32	21,08	9,21	3,11	11,59	3,23	10,18	2,74
OMO	12,03	17,8	27,18	8,11	11,11	6,33	90,39	4,4	1,3	1	326,52	25,37	8,91	5,63	5,3	13,31	24,02	9,97	2,67	11,03	4,2	11,12	2,24
OMO	14,01	22,62	30,5	8,26	11,79	6,98	100	4,7	1,6	1	272,81	27,4	8,19	6,41	5,32	14,02	25,18	10,78	2,53	11,72	3,39	12,59	2,29
OMO	12,67	22,43	27,63	7,51	11,53	6,92	99	4,4	1,2	1	259,01	25,48	8,19	5,7	5,22	13,62	25,1	9,25	2,7	11,58	3,4	11,21	2,83
OMO	12,77	18,73	26,61	7,25	10,42	6,04	90,36	5,1	1,1	1	318,58	24,13	8,14	4,33	5,18	13,48	24,75	10,07	2,33	10,81	3,95	11,37	2,47
OMO	12,22	18,25	26,39	6,6	10,41	6,12	86,32	4,8	1,3	1	370,72	23,38	8,59	5,33	5,12	13,36	22,33	9,41	2,82	12,64	3,38	10,6	2,2
OMO	12	17,6	26,61	7,37	10,67	6,3	89,99	4,7	1,6	1	389,83	24,11	7,17	5,6	5,76	7,22	24,04	9,31	3,31	10,97	3,28	10,57	2,36

OMO	10,53	15,4	22,28	6,11	8,88	5,79	77,85	4,6	1,3	1	308,66	21,25	7,54	5,32	3,8	7,36	19,95	7,02	2,68	6,85	2,18	9,14	1,54
OMO	11,41	16,73	27,2	7,68	10,44	5,99	88,9	5,4	2,2	1	354,69	22,13	5,97	5,08	3,37	6,1	21,93	7,94	3,02	9,43	3,04	10,42	2,04
OMO	11,86	18,45	27,81	7,94	11,4	5,68	90,1	5,9	3,8	1	216,74	24,38	5,78	6,31	3,5	7,04	23,88	7,52	3,3	11,09	2,92	10,76	2,02
OMO	10,25	16,19	23,83	7,04	9,44	5,45	81,59	5,3	1,7	1	453,46	20,98	5,84	5,24	3,1	6,49	20,08	6,5	2,84	9,92	2,5	9,55	1,86
OMO	10,18	17,57	23,57	6,31	9,95	6,21	82,02	5,6	3	1	212,84	21,3	5,59	5,27	3,05	6,02	21,09	6,77	2,66	11,97	2,15	9,63	1,78
OMO	11,54	19,28	28,96	7,37	11,26	6,66	95,21	6,1	3,3	1	365,69	26,05	7,9	6,45	4,41	6,99	24,12	7,73	2,56	12,13	3,22	11,55	2,32
OMO	11,84	17,18	27,03	7,29	11,2	5,91	92,03	5,2	1,7	1	554,95	22,94	6,22	5,33	3,58	6,02	22,73	7,2	2,38	11,37	2,77	10,49	2,23
OMO	10,1	14,27	24,3	7,2	9,99	5,9	80,33	4,9	1,9	1	274,59	22,07	4,67	4,3	3,49	5,7	20,68	7,16	2,03	11,15	2,53	9,68	2,16
OMO	13,19	20,08	29,45	8,44	11,39	6,58	98,24	5	1,8	1	391,83	27,1	7,21	6,08	4,63	7,68	24,02	8,7	3,71	12,33	3,14	12,12	2,7
OMO	10,67	15,8	26,01	6,88	10,11	5,85	85,44	4,8	1,7	1	369,3	23,48	4,4	4,6	3,91	6,58	21,48	7,98	3,14	11,83	3,49	10	2,12
OMO	10,98	17,56	25,8	6,66	10,38	5,47	88,62	5,3	2,1	1	379,32	22,62	4,26	4,15	4,25	5,64	21,74	7,6	2,66	11,59	2,9	10,42	2,27
OMO	10,98	17,38	27,06	8,7	10,5	7,7	86,98	4,9	2,3	1	39,36	24,66	4,95	5,37	4,39	5,8	22,3	7,84	2,38	10,36	3,63	11,11	1,77
OMO	1,25	17,81	24,11	7,59	9,35	6,71	83,41	5	1,1	1	326,65	22,09	4,11	4	2,66	5,24	19,62	7,36	1,56	9,05	2,82	9,48	1,65
OMO	9,29	13,1	22,83	6,69	9,01	6,12	76,11	4,8	1,3	1	39,45	21,1	4,23	4,31	2,4	5,02	20,54	5,88	1,49	9,02	2,86	9,19	1,62
OMO	11,5	18,01	25,85	8,02	10,07	6,01	87,99	5,6	1,4	1	288,67	23,71	5,02	4,4	3,57	6,33	22,08	6,85	2,91	10,1	3,33	10,19	2,09
OMO	10,21	14,48	22,58	6,5	8,85	5,59	77,23	5,1	1,1	1	347,78	20,54	4,3	4,31	3,69	5,9	19,79	6,03	2,01	9,91	2,58	9,64	2,33
OMO	12,45	17,5	26,02	7,95	10,4	7,02	93,59	5,8	1	1	435,15	25,12	5,92	5,69	4,17	7,4	24,41	7,37	2,2	10,35	3,22	11,12	2,28
OMO	12,92	19,88	28,6	8,9	11,77	7,03	98,45	6,2	1,4	1	409,67	25,99	6,23	5,58	4,11	7,46	25,04	8,22	2,5	12,38	3,81	11,11	2,66
OMO	15,64	24,65	32,42	9,05	12,91	7,36	112,8	6,8	1,7	1	611,37	31,43	5,43	7,17	4,87	10,38	28,75	9,26	3,93	15,69	4,32	14,07	3,12
OMO	16,74	22,86	30,69	8,98	12,2	6,68	110,08	6,7	1,4	1	504,85	29,09	5,24	7,14	4,25	9,55	27,41	8,48	2,95	14,61	3,68	12,35	3,33
OMO	12,71	20,46	28,87	7,99	12	6,49	99,62	6,4	2,7	1	446	26,32	5,03	6,13	4,6	8,03	25,49	8,42	2,12	13,52	3,08	10,91	2,68
OMO	12	18,22	26,77	7,44	10,16	6,12	90,79	5,5	1,1	1	277,92	23,43	3,82	4,7	3,71	7,8	21,97	7,28	1,81	11,72	3	10,49	2,35

Table S2: Raw data for food specialist profiles (FSP) used to relate the measured morphological traits to the species capacity to consume certain prey types following a criterion by Sibbing and Nagelkerke (2000).

Food Specialist	**Body depth**	**Caudal peduncle depth**	**Head length**	**Eye diameter**	**Protrusion length**	**Gut length**	**Lower jaw length**	**Gill raker length**	**Gill raker distance**	**Postlingual organ width**	**Lower jaw closing force efficiency**	**Volume capacity operculum**	**Operculum area**	**Gill arch resistance**	**Relative gape area**	**Velocity suction**	**Hyoid length**	**Gape size**	**Oral gape axis**	**Barbels**	**Oral teeth presence**	**Pharyngeal papilliform teeth**	**Pharyngeal molariform teeth**
Phy_t	-1	-1	1	0	0	1	0	2	-2	0	0	0	0	2	1	0	0	2	-1	0	0	1	1
Phy_p	0	0	1	0	0	1	0	2	-2	0	0	1	1	2	0	0	0	1	-1	0	0	1	1
Algae	0	0	-1	0	0	1	-1	1	-1	0	1	0	0	0	0	0	0	0	0	0	0	1	1
Plants	0	0	-1	0	-2	0,5	-2	0	0	1	2	0	0	0	0	0	0	0	0	0	1	1	1
Seeds	1	0	0	0	1	0	0	0	0	0,5	0	0	0	0	0	0	0	0	0	0	1	1	1
Detr	1	0	0	0	2	2	0	1	-1	0	0	0	0	0	0	0	0	-1	1	2	1	0	0
Micr_t	-1	-1	1	0	0	0	0	2	0	0	0	0	0	2	1	0	0	2	-1	0	0	1	1
Micr_p	0	0	1	1	0	0	0	2	-2	0	0	1	1	2	0	0	0	1	-1	0	0	1	1
Crust	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	1	1
Larvae	1	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	-1	1	2	1	0	0
Insect	0	1	1	0	1	0	1	-1	0,5	1	-1	1	1	-0,5	0	0	0	0,5	0	0	1	0	0
molluscs	1	0	0	0	1	0	0	0	0	0,5	0,5	0	0	0	0	0	0	0	0	0	1	1	1
Fish_p	-2	-2	1	0	0	0	2	-2	1	2	-2	1	0	-2	1	0	0	2	-1	0	1	0	0
Fish_a	0	2	2	0	2	0	2	-2	1	2	-2	2	2	-1	0	-1	1	1	0	0	1	0	0