Assessing the extent, effects, and management strategies for aquatic invasive alien species in protected areas in Mpumalanga, South Africa

By

Fannie Mfaniseni Masina

201705117

orcid.org/ 0000–0003–1727–2830

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Supervisor: Prof Tatenda Dalu (SUN), Dr Farai Dondofema (UNIVEN),
Dr Pule Mpopetsi

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ABSTRACT

Aquatic invasive species pose a significant threat to biodiversity and ecosystem functioning, including in protected areas meant to preserve native and often endemic species. However, despite growing awareness of their ecological and economic impacts, the management of aquatic invasive species is still not fully integrated or consistently prioritised within broader conservation strategies. The study aimed to assess the presence of aquatic invasive species, their occurrence, and their effects on non–native species, as well as evaluate the effectiveness of current management strategies for aquatic invasive species within the protected areas of the Mpumalanga Province, South Africa. This body of work represents fieldwork, laboratory experiments, and social components undertaken from May 2023 to June 2025. Only one invasive species, *Xiphophorus helleri* (Swordtail), was recorded, and it occurred exclusively at the SANBI–Lowveld National Botanical Garden. In that protected area, *X. helleri* was also the most abundant species, while it was absent from the other five protected areas. The study further revealed that *X. helleri* exhibited rapid growth and competitive superiority, which contributed to its ability to outcompete native species, including *Micralestes acutidens* (sharptooth tetra), *Pseudocrenilabrus philander* (mouthbrooder), *Oreochromis mossambicus* (mozambique tilapia), and *Enteromius eutaenia* (orangefin barb). Mortality rates were found to be low, suggesting that there were few negative factors affecting the *X. helleri* population in the SANBI Lowveld National Botanical Garden. Moreover, the study examined the feeding interactions between the native mouthbrooder (*P. philander*) and the non–native swordtail (*X. helleri*) when offered a readily consumed prey item (*Chironomidae*). The results revealed that predator–predator interactions were primarily additive, with minimal non–trophic effects observed, suggesting that swordtail invasion could increase pressure on prey communities if total predator abundances concomitantly increased. Furthermore, the results revealed significant gaps in aquatic invasive species management, including the absence of species checklists, inconsistent monitoring, limited formal training, and inadequate funding. While some participants drawn from semi–structured interviews with workers responsible for invasive species management in protected areas reported collaborative efforts and the use of adaptive strategies, many reserves lacked baseline data and clear decision–making frameworks. The findings suggest that although awareness of aquatic invasive species threats exists, practical implementation of management strategies remains limited and fragmented. Constraints such as inadequate funding and insufficient targeted training impede the effective implementation of aquatic invasive species management strategies. Strengthening aquatic invasive species management in Mpumalanga’s protected areas requires long–term funding, targeted training, improved documentation of invasive species data and management strategies, and inter–agency collaboration.

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PREFACE

This thesis is organised into seven chapters. Chapter 1 provides a general introduction outlining the background, justification, and objectives of the study. Chapter 2 presents a literature review, while chapters 3 to 6 comprise a series of data chapters, each presented in the format of a scientific paper, focusing on different aspects of aquatic invasive species in protected areas. Chapter 7 presents a general synthesis and conclusion. A combined reference list is provided at the end of the thesis to minimise repetition across chapters and ensure consistency in citation formatting.

Additional outputs completed during this thesis:

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1. Masina, F.M., Munyai, L.F., Mpopetsi, P., Dondofema, F., Cuthbert, R. and Dalu, T., **2025**. Demographics, status, and dietary habits of swordtail fish *Xiphophorus helleri* Heckel, 1848 in a protected botanical garden and surrounding areas. *BioInvasions Records*, *14*.
2. Masina, F.M., Cuthbert, R.N., Munyai, L.F., Mpopetsi, P.P., Nkosi, M.S., Dondofema, F. and Dalu, T. **2026**. No evidence for multiple predator effects between a non–native and native wetland fish. *Biological Invasions*, *28*(2), p.47.
3. Masina, F.M., Cuthbert, R.N., Munyai, L.F., Mpopetsi, P.P., Dalu, M.T.B., Dondofema, F. and Dalu, T. Evaluating the effectiveness of current management strategies for aquatic invasive species in protected areas. **(Under review)**
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Conference presentations

1. Masina, F.M., Munyai, L.F., Mpopetsi, P., Dondofema, F., Cuthbert, R.N. and Dalu, T., 2024. Demographics, status, and dietary habits of swordtail fish *Xiphophorus helleri Heckel*, 1848 in a protected botanical garden and surrounding areas. ***NRF SAIAB Student Symposium 2024. Safeguarding Africa's Aquatic Future. 29***

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DECLARATION

I, Fannie Mfaniseni Masina, student number 201705117, hereby declare that I am fully aware of the University of Mpumalanga's policy on plagiarism, and I have taken every precaution to comply with the regulations. This document has been submitted through a similarity detection software, and the report was reviewed by my supervisor(s). I declare there is no plagiarism in this dissertation.

Signature: Masina Date: December 2025

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CHAPTER 1: INTRODUCTION

1.1 Background

Protected areas are legally designated geographical spaces established to conserve biodiversity, protect threatened species and fragile ecosystems, and maintain natural processes (Olmos–Martínez et al., 2022; de Hemptinne, 2023). They are widely recognised as effective environmental policy tools, preserving largely intact ecosystems and providing a range of valuable ecosystem services (Olmos–Martínez et al., 2022). In particular, protected areas play a vital role in biodiversity conservation through affording enhanced protection to fragile ecosystems, endemic species, and vulnerable vegetation types that are most vulnerable to extinction (Velazco et al., 2022; Omar et al., 2025; Gatti, 2025). The highest level of protection is typically available within legislatively designated areas (Margules and Pressey, 2000; Breen et al., 2021). However, protected areas face various ongoing threats, including habitat degradation resulting from land–use changes, illegal hunting and poaching of wildlife, pollution from surrounding human activities, and the proliferation of invasive alien species that can outcompete native flora and fauna (Foxcroft et al., 2019). Invasive alien species are defined as non–native animal or plant species whose introduction and spread cause, or have the potential to cause, harm to native biodiversity, ecosystems, human livelihoods, or the economy, often as a result of human activities (Russell and Blackburn, 2017; Sá, 2025). Invasive alien species in ecosystems can be introduced accidentally, such as when boats travel between different bodies of water and carry hitchhikers, such as *Dreissena polymorpha* (zebra mussel) (Russell and Blackburn, 2017; Marbuah et al., 2014; Hendrickson et al., 2025). Some invasive alien species, however, are introduced intentionally; for instance, *Rhinella marina* (cane toad) was introduced to Australia in the early 20th century as a means of pest control (Mulig et al., 2024). Unfortunately, these poisonous amphibians have proliferated in number, leading to a decline in native predators on the island (Russell and Blackburn, 2017).

While numerous studies (e.g., Bănăduc et al., 2022; Paganelli et al., 2024; López–Cañizares et al., 2025) have addressed the prevention, management, and control associated with terrestrial invasive alien species, there is a limited number of studies focused on aquatic invasive alien species in protected areas in particular, studies that provide practical management actions, policies, or plans to effectively control these species (Hulme, 2014). Aquatic invasive alien species refer to aquatic organisms, such as fish, invertebrates, or plant species, that are non–

native species introduced into a new aquatic environment beyond their natural range (Rahel et al., 2008; Jones et al., 2021; Bir et al., 2022). Once established, these species can rapidly proliferate through several pathways, including natural dispersal via water currents, human–mediated transport such as boats and fishing equipment, as well as accidental releases from aquaculture and the aquarium trade (Daly et al., 2023). The absence of natural predators in their new environment often enhances their proliferation (Rahel et al., 2008; Daly et al., 2023).

Consequently, they pose a significant threat to native species by outcompeting them for resources and causing harm (Rahel et al., 2008; Shaheryar et al., 2025). Some aquatic invasive alien species can alter the physical and chemical characteristics of aquatic habitats, such as altering water quality or disrupting the structure of underwater vegetation, which negatively affects native species that rely on these habitats (Shiferaw et al., 2018; Bir et al., 2022). Hence, they disrupt the functioning of entire ecosystems, causing species loss and extinctions in sensitive ecosystems (Daly et al., 2023). Therefore, the invasion of ecosystems by aquatic invasive alien species must be managed to prevent further loss of biodiversity in protected areas (Guimarães et al., 2024; Hulme et al., 2025).

In South Africa, several government policies address biological invasions (Lukey and Hall, 2020). However, specific legislation and management instruments focused on aquatic invasive alien species remain limited. The National Environmental Management: Biodiversity Act 10 of 2004 (NEM:BA) and its Alien and Invasive Species Regulations (2014) place broad obligations on organs of state to monitor, control, and eradicate invasive species, including in aquatic systems, yet comprehensive regulatory mechanisms tailored exclusively to aquatic invasive alien species are still lacking. It is therefore necessary to have a full list of aquatic invasive alien species in protected areas in order to monitor the precise scale of their invasion and conduct further research (Adam et al., 2017; Carneiro et al., 2024). These will allow for a better understanding of how to manage the threats they pose.

Plants and animal species from other countries have been introduced to South Africa as early as 200 AD (van Wilgen et al., 2020). Since the 19th century, this trend has continued to rise exponentially, and the invasion of invasive alien species has begun disrupting ecosystem services (van Wilgen et al., 2020). In a globalised world, increasingly sophisticated transport networks that supply the demand for international commodities are the pathways for the spread of invasive alien species (Hulme et al., 2025). Although protected by law, protected areas are not immune to the introduction of new invasive alien species. An understanding of invasion pathways and their risk assessment is an important tool for preventing infestation (Hulme, 2014). Despite strategic plans, such as global endeavours to manage invasive alien species in protected areas, a study by Shackleton et al. (2019) revealed that most invasive alien species continue to proliferate in these areas, with the number of invasive alien species increasing in 31% of the world's protected areas. In South Africa, approximately 55% of protected areas are proactively managed for invasive alien species control, and 45% have implemented additional management approaches (Shackleton et al., 2019). However, considering the presence of 1 422 documented naturalised invasive plant and animal species in South Africa (Richardson et al., 2020), it is crucial to conduct further research on management plans to prevent their occurrence in protected areas and effectively manage their spread if already present (van Wilgen et al., 2020). Invasive alien species presence lists are important, but because species numbers and names are subject to fluctuation, these lists must be dynamic and regularly updated, necessitating constant monitoring (van Wilgen et al., 2020).

1.2 Justification

The absence of a comprehensive list of aquatic invasive species within South Africa's protected areas poses a significant challenge for biodiversity conservation and management (van Wilgen et al., 2025). This gap hampers the understanding of how aquatic invasive species affect native species and ecosystems, and it limits the effectiveness of control and monitoring programs (Woodford et al., 2017; van Wilgen et al., 2025). For example, without knowing which aquatic invasive species are present in a protected area, managers cannot detect early invasions, prioritise high–risk species, or evaluate whether current interventions are reducing their spread. While numerous studies on invasive alien species within protected areas have primarily focused on terrestrial environments, relatively few studies have examined aquatic invasive alien species occurring within protected freshwater ecosystems (Moorhouse and Macdonald, 2015; Reid et al., 2019). Without a clear understanding of which aquatic invasive species occur in these areas, their dispersal pathways, reproductive strategies, and potential ecological impacts remain uncertain. This lack of knowledge hampers the ability of conservation managers to implement timely and effective control measures. As a result, many aquatic ecosystems face increasing risks of water–quality degradation, habitat modification, and loss of indigenous species posed by the introduction and spread of aquatic invasive alien species (Hermoso et al., 2011; Chamier et al., 2012; Rendón–Hernández et al., 2025).

Gaining a thorough understanding of the distribution, abundance, and ecological impacts of aquatic invasive species in these protected areas will provide insights into their extent and potential threat. Such knowledge will inform the development of a dedicated national inventory of aquatic invasive alien species, guide the design of management strategies, and enhance the long–term protection of freshwater biodiversity and ecosystem services within South Africa's protected areas.

1.3 Aims

The study aimed to assess the presence of aquatic invasive alien species, their occurrence, population structures, and effects on biodiversity within the protected nature reserves of the Mpumalanga province, South Africa. One of the primary objectives of this project was to develop an effective provincial aquatic invasive species control strategy for the management authority.

1.4 Objectives

1. To identify and document aquatic invasive alien species presence in the protected areas, including mapping the distribution and abundance of invasive alien species within the areas.
2. To assess the distribution of non–native fish *Xiphophorus helleri* in the Lowveld National Botanical Garden and the nearby Crocodile River, by investigating its growth, mortality rate, population structure, and diet composition.
3. To examine the feeding interactions of the two co–occurring freshwater fish species, the native mouthbrooder (*Pseudocrenilabrus philander*) and the non–native swordtail (*Xiphophorus helleri*), towards a readily consumed prey (Chironomidae), under multi–predator scenarios using a comparative functional response (FR) approach, in a pond situated within a protected area.
4. To assess the effectiveness of existing management strategies for controlling aquatic invasive species in protected areas, with a focus on identifying the most successful approaches and potential areas for improvement.

1.5 Hypothesis

1. The occurrence of aquatic invasive species would differ among protected areas, since variation in human activity, connectivity, and habitat conditions makes some sites more vulnerable to invasions than others.
2. *Xiphophorus helleri* will be established in the Lowveld National Botanical Garden and the nearby Crocodile River, with its population structure, growth, and diet expected to indicate successful colonization and potential impacts on native fish species.
3. The mouthbrooder, although potentially a generalist, would exhibit higher attack rates and efficiency at low prey densities, as native species are typically well adapted to local prey types and foraging conditions, giving them a competitive advantage over non–native species at lower resource levels.
4. Limited budgets will hinder the effectiveness of aquatic invasive species management strategies in protected areas.

1.6 Thesis outline

This thesis, as outlined in the preface, comprises seven chapters. Chapter 1 provides a general introduction that presents the background, justification, and objectives of the study. Chapter 2 offers a comprehensive literature review, synthesising existing research on aquatic invasive species, their ecological impacts, and management. Chapter 3 investigates the distribution of an invasive fish species within fish communities across protected areas in the Mpumalanga Province of South Africa. Building on this, Chapter 4 focuses on one of these invasive species, the swordtail fish (*Xiphophorus helleri* Heckel, 1848), assessing its demographics, status, and dietary habits within a protected botanical garden and its surrounding aquatic systems. To further understand the ecological role of this species, Chapter 5 evaluates predator–prey interactions by assessing the presence or absence of multiple predator effects between a non–native *X. helleri* and a native *P. philander* wetland fish species. Finally, Chapter 6 synthesises these findings to evaluate the effectiveness of current management strategies for controlling aquatic invasive species in protected areas.

A general synthesis and conclusion are presented at the end of the thesis (Chapter 7), integrating the key findings from all chapters and discussing their implications for the conservation of aquatic biodiversity and the management of aquatic invasive species in South Africa's protected freshwater systems. A consolidated reference list is included to maintain consistency and minimise repetition across chapters.

CHAPTER 2: LITERATURE REVIEW

2.1 Aquatic invasive species in South Africa

Aquatic invasive species pose a significant threat to freshwater biodiversity and ecosystem integrity in South Africa (Weyl et al., 2020; Whitfield et al., 2021; van Wilgen et al., 2022a). Defined as non–native organisms introduced into aquatic ecosystems that establish, spread, and cause ecological or socio–economic harm (Hill et al., 2020; Ndou, 2024), these species alternative community structures, displace indigenous taxa, and compromise ecological functioning (Ellender and Weyl, 2014; Bernery et al., 2022; Feio et al., 2023; Seebens et al., 2025**.** South Africa's extensive freshwater network, comprising rivers, lakes, wetlands, and impoundments, offers a range of niches susceptible to invasion (Weyl et al., 2020; Van Niekerk et al., 2022; van Wilgen et al., 2022a; Adam, 2024). The vulnerability of these systems is exacerbated by anthropogenic pressures, including dam construction, eutrophication, and habitat modification (van Wilgen et al., 2020).

South Africa harbours numerous aquatic invasive plants, fish, and invertebrates that have become well established across both protected and urban landscapes (Otero et al., 2013; Francis et al., 2019; Blanckenberg et al., 2020). According to Hill et al. (2020) and Borbhuyan and Das (2025), the most prevalent aquatic invasive plants include *Pontederia crassipes* (water hyacinth), *Salvinia molesta* (salvinia), *Azolla filiculoides* (red water fern), *Myriophyllum aquaticum* (parrot's feather), and *Alternanthera philoxeroides* (alligator weed). These species have proliferated in nutrient–rich and slow–flowing waters, particularly in regions affected by agricultural runoff and effluent discharge (Dalu et al., 2025; Khotsa et al., 2025). The invasive macrophytes form dense surface mats that impede light penetration, reduce dissolved oxygen, and hinder the growth and reproduction of submerged native flora (Hill and Coetzee, 2017). Such effects cascade through the ecosystem, reducing habitat availability for aquatic macroinvertebrates and fish, which rely on native vegetation for refuge and for feeding grounds (Hill et al., 2020; Mangi, 2024; Ojha et al., 2025).

Equally concerning are invasive fish species such as *Micropterus salmoides* (Florida bass), *Oncorhynchus mykiss* (rainbow trout), and *Cyprinus carpio* (common carp), which were introduced primarily for recreational and aquaculture purposes (Ellender et al., 2014; Long and Seguy, 2024; Khotsa et al., 2025; Phonmat et al., 2025). These species prey on and outcompete native fishes, contributing to the decline of endemic taxa such as *Pseudobarbus* spp. (redfins) and *Sandelia capensis* (Cape kurper) (Whitfield et al., 2021; Cerrilla et al., 2022). Weyl et al. (2020) emphasise that non–native fish introductions have had profound ecological consequences, including altered trophic structures, homogenisation of fish communities, and loss of evolutionary distinctiveness. The introduction of alien invertebrates such as the freshwater snail *Tarebia granifera* (quilted Melania) has similarly transformed benthic communities by displacing indigenous molluscs and modifying detrital processing rates (van Wilgen et al., 2020; Pearson et al., 2024). The drivers facilitating aquatic invasions in South Africa are multifaceted. Historical introductions often stemmed from colonial–era acclimatisation programs that sought to improve fisheries and ornamental trade (Ahmed et al., 2025). Contemporary pathways include the aquarium and horticultural trades, ballast water discharge, and intentional releases for biological control or aquaculture (Hill et al., 2020; O'Shaughnessy et al., 2025). Additionally, climate change has expanded the potential distribution range of many aquatic invaders, particularly tropical and subtropical taxa, which are now capable of surviving in temperate regions (Weyl et al., 2020; Osland et al., 2023).

Although protected by law, protected areas are not exempt from these pressures. Despite strategic plans such as global endeavours to manage invasive alien species in nature reserves, a study by Shackleton et al. (2019) revealed that most invasive alien species continue to proliferate in these protected areas, with invasive species increasing in 31% of the world's protected areas. In South Africa, approximately 55% of protected areas are proactively managed for invasive alien species control, and 45% have implemented additional management approaches (Shackleton et al., 2019). Foxcroft et al. (2017) document the presence of aquatic invasive plants and fishes within several South African National Parks (SANParks) units, including Kruger and Addo Elephant National Parks. Many protected waterbodies receive inflows from catchments outside their boundaries, allowing propagules of invasive species to enter and establish, despite internal management controls (Saunders et al., 2002; Pittock et al., 2015). Furthermore, limited surveillance and enforcement of national regulations such as the National Environmental Management: Biodiversity Act (NEM:BA, 2004) exacerbate the problem, as invasive species often spread before detection or eradication is feasible (Green and Grosholz et al., 2021; Ndou, 2024; Roy et al., 2024).

The cumulative impacts of aquatic invasions have made them one of the leading causes of biodiversity loss in the country's freshwater ecosystems. The National Biodiversity

Assessment (Sebola and Willis, 2025) recognises invasive alien species as a major driver of ecosystem degradation, second only to water abstraction and pollution. While significant efforts have been made to control these invaders through mechanical, chemical, and biological means (Hill and Coetzee, 2017; Djihouessi et al., 2023), many remain widespread and resilient. Thus, aquatic invasive species in South Africa represent a complex ecological and policy challenge. Their persistence in both natural and protected systems highlights the need for integrated catchment–level management and strengthened monitoring frameworks. As subsequent sections will show, understanding the mechanisms of biological invasion, assessing their ecological consequences, and developing effective control strategies are central to mitigating their impacts on biodiversity within South Africa's protected areas.

2.2 Invasion of aquatic invasive alien species

Biological invasion is a multistage process encompassing introduction, establishment, and spread (Richardson and Pyšek, 2012; Ellender and Weyl, 2014; van Wilgen et al., 2022b). Introduction refers to the arrival of a species outside its native range, often through human–mediated pathways (Ellender and Weyl, 2014; Sinclair et al., 2020; Ahmed et al., 2025). Establishment occurs when the introduced species survives, reproduces, and forms a self–sustaining population (Cordeschi et al., 2022). Spread is the stage where established species expand their range into new areas, often altering native communities and ecosystem functions (Bradley et al., 2024). In the South African context, aquatic invasive species follow these stages through diverse pathways driven by human activity. Early introductions were motivated by colonial acclimatisation schemes that sought to "improve" inland fisheries and enhance recreational angling (Hill and Coetzee, 2017; Cooke et al., 2023). Subsequent decades saw deliberate and accidental introductions via the aquarium and ornamental plant trade, aquaculture, and water–transfer schemes (Hill et al., 2020; Ndou, 2024). According to the propagule pressure hypothesis, invasion success increases with the number and frequency of introductions (Woodford et al., 2017). Repeated releases of invasive fish have led to the establishment of self–sustaining populations across multiple catchments (Healy et al., 2022). Floating aquatic plants, by contrast, spread rapidly downstream through vegetative fragments (Thomaz et al., 2025). The absence of natural enemies in recipient systems enhances the establishment success of introduced species (Hill et al., 2020).

Hill et al. (2020) indicated that aquarium trades and horticulture are the principal sources of macrophytes, notably *P. crassipes* and *Myriophyllum aquaticum* (parrot's feather). Fragments of these plants are easily transported between catchments through boating, fishing gear, or floods. Similarly, *Cyprinus carpio* (common carp) and *M. salmoides* have been widely distributed through intentional stocking and translocation for recreational purposes (Hill and Coetzee, 2017; Long and Seguy, 2024). Once established, these species can display traits such as rapid reproduction, broad environmental tolerance, and high dispersal ability, enabling colonisation of new habitats (Daly et al., 2023; Cooke et al., 2023).

Anthropogenic alterations to aquatic habitats have accelerated the invasions of non–native species (González–Ortegón and Moreno–Andrés, 2021; Haubrock et al., 2025). Dam construction and flow regulation have created lentic conditions ideal for floating macrophytes (Hill and Coetzee, 2017). Nutrient enrichment from agricultural runoff stimulates dense growth of invasive plants, while climate warming extends the suitable range of tropical invaders (Weyl et al., 2020). Invasive fishes exploit disturbed habitats where native predators or competitors are absent (Mar–Silva et al., 2021). Ndou (2024) notes that poor enforcement of regulatory frameworks under NEM: BA (2004) enables the continuous introduction and secondary spread of listed species.

Although protected areas are designed to conserve biodiversity, they are often permeable to invasive species (Le Saout et al., 2023). Rivers and dams within national parks often receive inflows from invaded catchments, importing propagules despite local control (Foxcroft et al., 2017). For example, the Sabie and Crocodile Rivers entering Kruger National Park carry upstream infestations of *P. crassipes* and *Salvinia molesta* (giant salvinia) (Macdonald et al., 1988; Coetzee et al., 2011). The Addo Elephant National Park's aquatic systems have been invaded by alien fish dispersed from surrounding farms (Cole et al., 2024). Therefore, aquatic invasions in South Africa are driven by a combination of anthropogenic vectors, ecological opportunity, and policy shortcomings. Understanding these invasion pathways is crucial for designing effective preventative measures and reducing the flow of propagules into protected ecosystems.

2.3 Impact of aquatic invasive species on biodiversity

Aquatic invasive species influence biodiversity through direct and indirect mechanisms (Peller and Altermatt, 2024). Their effects manifest at genetic, species, and ecosystem levels (Weyl et al., 2020; Saidova et al., 2024). Invasive macrophytes such as *P. crassipes* and *S. molesta* form dense mats that block sunlight, reduce dissolved oxygen, and alter nutrient cycling (Hill et al., 2020; Madzivanzira et al., 2023). These conditions suffocate benthic fauna, reduce phytoplankton diversity, and ultimately simplify food–web structures (Madzivanzira et al., 2023; Dalu et al., 2025). Similarly, invasive fish exert intense predatory and competitive pressures on native species (Sanches et al., 2012; Dominguez et al., 2021). *Micropterus salmoides* (Florida bass) preys on small indigenous cyprinids and cichlids, while *O. mykiss* competes with native salmonids for habitat and prey (Ellender et al., 2014; Costantini et al., 2023). The outcome is often the extirpation of endemic taxa and the homogenisation of fish communities (Scott and Helfman, 2001; Pool and Olden, 2012).

According to Goto et al. (2020), invasive species modify trophic dynamics and ecosystem processes. *Cyprinus carpio* disturbs sediments during feeding, increasing turbidity and releasing nutrients that promote algal blooms (Huser et al., 2022). Dense plant mats impede gas exchange, causing diel oxygen fluctuations detrimental to fish and macroinvertebrates (Hill and Coetzee, 2017). The National Biodiversity Assessment (2019) identified invasive alien species as a principal driver of freshwater ecosystem degradation in South Africa, contributing to the poor ecological condition of over 60% of assessed river systems.

In addition to these ecological disruptions, aquatic invasive species exert extensive environmental impacts across South Africa's freshwater and riparian ecosystems (Dallas and Rivers–Moore, 2014; Le Maitre et al., 2016; Millicent, 2024). Their influence extends beyond biotic interactions to large–scale alterations in ecosystem processes and hydrological balance (Bănăduc et al., 2024; Peller and Altermatt, 2024). Invasive plants are known to reduce both surface–water runoff and groundwater recharge while intensifying habitat degradation and wildfire frequency through changes in vegetation structure and litter accumulation (Gorgens and van Wilgen, 2004). The World Wide Fund for Nature (WWF) estimates that invasive vegetation accounts for an annual loss of approximately 3.3 billion m^3 of water in South Africa (Rebelo et al., 2025). For example, *Acacia mearnsii* (black wattle) is one of the most widespread invaders, occupying nearly 2.5 million hectares nationally. Its high transpiration rate depletes streamflow and groundwater reserves, severely affecting water availability, biodiversity, and the stability of riparian ecosystems (Le Maitre et al., 2023).

Beyond hydrological changes, aquatic invasive species can drive the local extinction of native species by outcompeting them for essential resources, modifying habitats, and altering environmental conditions (Peller and Altermatt, 2024; Khan et al., 2025). These cumulative effects can lead to profound biodiversity loss and the destabilisation of aquatic and coastal ecosystems (Khan et al., 2025). Cross–border trade and human–mediated dispersal continues to facilitate the introduction of invasive species valued for their medicinal, ornamental, or nutritional uses (Kopecký et al., 2013; van Wilgen et al., 2012; Hulme, 2021).

The ecological success of many invasive species in South Africa can also be interpreted through the enemy release hypothesis (ERH). This theory posits that species introduced into new environments often escape their natural predators, pathogens, or competitors, enabling them to reproduce and spread rapidly (van Wilgen et al., 2004). The ERH has been widely validated across taxa and regions. The invasion success of *Chromolaena odorata* (Siam weed) in South Africa has also been linked to the ERH. In its native range in Central and South America, the species is heavily regulated by specialist herbivores and pathogens; however, in South Africa, these natural enemies are largely absent. This reduction in biotic resistance has enabled *C. odorata* to form dense, monospecific stands and spread rapidly across savannas and coastal forest ecosystems (Zachariades et al., 2021). In South Africa, the absence of effective natural enemies for species such as *P. crassipes* and *S. molesta* similarly contributes to their rapid expansion and persistence in aquatic habitats (Coetzee et al., 2011).

2.4 Economic impacts of invasive species

Invasive alien species contribute significantly to economic losses through their detrimental impacts on agriculture, biodiversity, and water resources (Moodley et al., 2022; Di Lernia et al., 2025). Globally, invasive alien species continue to spread across both undisturbed and human–modified ecosystems, causing ecological and socio–economic disruptions (Pyšek et al., 2020). The financial burden associated with invasions primarily stems from the costs of control, eradication, and management efforts (Pimentel et al., 2005; Cuthbert et al., 2022). Pimentel (2011) estimated that invasive alien species inflict an annual global economic loss of approximately US$345 billion (equivalent to about 5.15 trillion ZAR).

In South Africa, the management of invasive species represents a substantial and recurring expense (van Wilgen et al., 2025). The Department of Environmental Affairs (DEA) reported that approximately R600 million is required annually to clear over 10 million hectares of land invaded by alien plant species. The management of aquatic macrophyte invasions, particularly those caused by *P. crassipes*, is especially costly. Between 2010 and 2018, the Department of Forestry, Fisheries, and the Environment (DFFE) spent approximately R42 million on herbicide–based control of water hyacinth, averaging around R1,800 per hectare (Millicent, 2024). However, the total cost of control varies by location, invasion extent, and management approach (Hill et al., 2020).

Van Wyk and van Wilgen (2002) compared three main strategies for managing water hyacinth, chemical, biological, and integrated control, and found significant cost differences among them. Herbicide application was the most expensive at R3,663 per hectare, while biological control cost substantially less at R664 per hectare. The most cost–effective approach, however, was integrated management, which combined mechanical, biological, cultural, and chemical techniques, providing the highest return on investment at roughly R571 per hectare.

2.5 Case studies of affected protected areas in South Africa

In the Addo Elephant National Park, Woodford et al. (2024) documented the presence of non–native fish species, including bass and tilapia, in the park's aquatic systems. Their study showed that river hydrology strongly mediates invasion dynamics: intermittent flows limit dispersal, whereas perennial connectivity facilitates colonisation. These invasions have reduced native fish abundance and altered invertebrate assemblages (Kim et al., 2021). Additionally, the Kruger National Park, as identified by Foxcroft et al. (2017), recorded over 870 alien species among the aquatic invasives. Water hyacinth and salvinia infestations along the Sabie River impede flow, reduce water quality, and increase mosquito breeding. Control is complicated by transboundary river systems and continual reinvasion from outside park boundaries. Lastly, the Cape Floristic Region, although renowned for terrestrial biodiversity, has also been invaded by aquatic aliens in its wetlands and rivers. van Wilgen et al. (2025) reported ongoing infestations of *M. aquaticum* and *P. crassipes* despite sustained management. Their assessment revealed that persistent reinvasion, funding limitations, and lack of cross–agency coordination hamper long–term success. Across South Africa's protected–area network, aquatic invasions follow similar trends: high connectivity with surrounding landscapes, limited staff capacity for monitoring, and slow response times (Kajee et al., 2023). Even remote high–altitude wetlands in uKhahlamba–Drakensberg Park now host alien trout populations introduced decades ago (Weyl et al., 2020).

2.6 Management and control efforts of invasive species in South Africa

The management of aquatic invasive species in South Africa employs a combination of mechanical, chemical, biological, and regulatory approaches (Hill and Coetzee, 2017; Ndou, 2024). The National Environmental Management: Biodiversity Act (NEM:BA, 2004) and its Alien and Invasive Species Regulations provide the legal basis for controlling species introductions. Ndou (2024) found, however, that implementation is inconsistent due to limited institutional capacity, poor interdepartmental coordination, and inadequate monitoring.

South Africa is globally recognised for pioneering biological control programmes against aquatic weeds (Hill and Coetzee, 2017). Host–specific agents such as *Neochetina eichhorniae* weevils for water hyacinth and *Cyrtobagous salviniae* for salvinia have achieved notable reductions in plant biomass. Nevertheless, effectiveness varies with climatic conditions and nutrient levels. Physical removal and herbicide applications remain common where infestations threaten water supplies or recreational areas. However, these methods are costly and can damage non–target species (Hill et al., 2020). South African National Parks implements monitoring and rapid–response programs, yet coverage is uneven. Foxcroft et al. (2017) emphasise the importance of early detection, stakeholder engagement, and community participation. Public–awareness campaigns and citizen–science initiatives have improved reporting but require sustained support (Lamerira et al., 2025). Recent trends favour adaptive, integrated management that combines control methods with restoration of native vegetation and hydrological regimes (van Wilgen et al., 2025). Such holistic strategies address underlying drivers rather than symptoms of invasion.

In addition to the management of invasive aquatic plants, control efforts in South Africa also extend to non–native fish and other aquatic fauna. However, these are often more complex and less straightforward (Ellender and Weyl, 2014; Jones et al., 2021; Whitfield et al., 2021). For instance, Woodford et al. (2017) detail how conservation agencies face significant challenges in managing alien freshwater fishes under national legislation (NEM: BA), leading to the development of a prioritisation tool for deciding whether to eradicate, manage, or monitor specific invasive fish populations. Moreover, Weyl et al. (2015) highlight that allowing recreational use of alien fishes in protected areas (e.g., angling) can hinder long–term eradication efforts, as dependencies on these populations develop and complicate control strategies. According to the 2022 national status report, the removal of invasive fish, such as *Micropterus dolomieu* (smallmouth bass), in some rivers has led to a partial recovery of native fish communities, demonstrating both the potential and challenges of faunal control in freshwater systems.

2.7 Challenges in managing aquatic invasive species

Despite progress, invasive species management remains hindered by overlapping mandates between national departments, fragmented funding, and insufficient enforcement of NEM: BA regulations (Ndou, 2024). Many protected areas lack trained personnel and the relevant resources necessary to sustain effective control programs (Foxcroft et al., 2017). Data on species distributions, invasion rates, and ecological impacts remain incomplete (Foxcroft et al., 2017). The absence of long–term monitoring prevents the evaluation of management outcomes. Some invasive fish support recreational angling, creating resistance to eradication (Ellender et al., 2014). Control within parks is undermined by reinfestation from external catchments (van Wilgen and Richardson, 2014). Addressing these obstacles requires sustained funding, coordinated governance, capacity building, and public involvement.

2.8 Conclusion

Aquatic invasive species constitute a pervasive and escalating threat to biodiversity in South Africa's protected areas. They compromise ecological integrity, reduce native species richness, and disrupt ecosystem processes. The literature demonstrates that both biological and socio–economic drivers underlie their spread. Although South Africa has made significant advances in biological control and legislative frameworks, persistent challenges, particularly inadequate enforcement and cross–boundary reinvasion, limit effectiveness.

CHAPTER 3: DISTRIBUTION OF AN INVASIVE FISH SPECIES IN FISH COMMUNITIES OF PROTECTED AREAS IN MPUMALANGA PROVINCE OF SOUTH AFRICA

Abstract

Aquatic invasive species threaten global biodiversity, disrupt ecosystem services, and impose severe economic and social costs. Their impacts on native communities include competition for resources, alteration of food webs, and degradation of ecological processes. In protected freshwater ecosystems, such invasions undermine conservation goals and ecosystem resilience, particularly when they combine with other stressors, such as habitat modification and climate change. Despite their significance, data on the occurrence and distribution of aquatic invasive species in protected areas in South Africa remain limited. This knowledge gap hinders managers' ability to implement proactive conservation measures and assess the vulnerability of protected areas to biological invasions. This study aimed to assess the occurrence and distribution of aquatic fish species across six protected areas in Mpumalanga. Field surveys were conducted between October 2023 and March 2025 using multiple fish sampling methods, covering spring, autumn, and winter seasons. A total of 3 420 individual fish representing 29 species from 12 families were recorded, with only one invasive species, *Xiphophorus helleri* (swordtail), at the SANBI–Lowveld National Botanical Garden. The species' presence, likely linked to the garden's location at the river confluence and high visitor activity, highlights that even protected areas can be vulnerable to human–mediated introductions. These findings underscore the role of geographic isolation, habitat integrity, and regulated access in preventing invasions. The results can guide targeted monitoring in high–risk areas, inform early detection systems, and support policy frameworks to safeguard freshwater biodiversity in protected landscapes.

Keywords: Invasive fish species; Freshwater ecosystems; Fish communities; Protected areas.

3.1 Introduction

Invasive alien species pose a significant risk to global biodiversity, disrupt ecosystem services, and have a negative impact on economies and public health (Blackburn et al., 2019; Gentili et al., 2021; IPBES, 2023). The ecological consequences of invasive alien species include competition for resources and habitat, disruption of food webs, alterations in nutrient cycling, and changes in physical attributes, resulting in cascading effects on biodiversity across all trophic levels, from individual extinctions to entire ecosystems (Gallardo et al., 2016; Peller and Altermatt, 2024). The economic impacts of invasive alien species stem from various sources, including damage to productive sectors, infrastructure, and public health, as well as the costs associated with prevention, control, and eradication measures. (Epanchin–Niell, 2017; Cuthbert et al., 2021; Rico–Sánchez et al., 2021; Warziniack et al., 2021). The Intergovernmental Science–Policy Platform on Biodiversity and Ecosystem Services reported that the yearly worldwide economic cost of invasive alien species surpassed US$423 billion in 2019, with expenses at least tripling every decade since 1970 (IPBES, 2023).

Invasive alien species often interact with other environmental pressures, such as habitat alteration and climate change, amplifying their overall impact (Pyšek et al., 2020; Finch et al., 2021; IPBES, 2023). Climate change has further accelerated species redistribution in recent years, increasing the likelihood that invasive species will continue to establish and spread (Gallardo et al., 2016; Finch et al., 2021). As a result, they are projected to remain a major driver of global biodiversity loss (Perrin et al., 2024). Estimates suggest that invasive alien species could increase by 36% over the next 30 years, posing significant challenges and requiring substantial resources for effective management (Seebens et al., 2021; Roy et al., 2024).

Aquatic invasive alien species threaten ecosystem health by disrupting native community structure and altering essential ecological processes (Francis and Chadwick, 2012; Emery-Butcher et al., 2020; Cuthbert et al., 2021). These species can lead to shifts in species composition, reduce biodiversity, and weaken the natural resilience of ecosystems to further invasions (Havel et al., 2015; Emery-Butcher et al., 2020). Introducing non–native fish can disrupt resource distribution and have cascading effects across linked ecosystems (Mollot et al., 2017). In freshwater habitats, invasive species have been linked to the collapse of food webs, the decline of native species, and the degradation of water quality (Britton, 2023). They may also negatively affect economic activities dependent on freshwater resources, including fisheries, aquaculture, and freshwater infrastructure (Dimitriadis et al., 2021; Carneiro et al., 2024). These ecological and economic disruptions can lead to broader social consequences, such as job losses and declining local well–being (IPBES, 2023).

Biological invasions are among the most significant threats to protected areas, undermining the very ecological functions they are meant to safeguard (Foxcroft et al., 2013; Braun et al., 2016; Carneiro et al., 2024). Human–induced changes to these landscapes, such as development, tourism, and infrastructure, create opportunities for invasive species to enter and establish (Saunders et al., 2002; Foxcroft et al., 2013; Aththanayaka et al., 2023). One of the major obstacles to effective management is that, by the time invasive species are visibly detected, they are often already well established across the ecosystem (Pyšek et al., 2020; Stefani et al., 2024). This issue is particularly acute in freshwater systems of the Global South, where data on the presence, spread, and impact of aquatic invasive species remain sparse or absent (Acreman et al., 2020; Rico–Sánchez et al., 2020). Early detection and rapid response systems are widely recognized as the most cost–effective tools for managing invasions, yet they rely heavily on timely and accurate information (Martinez et al., 2020). This study aimed to address these information gaps by identifying invasive fish species in selected protected areas of Mpumalanga Province. Through systematic field surveys and species–level identification, the research aimed to generate actionable evidence to strengthen conservation and management interventions.

3.2 Methods

3.2.1 Ethics and permissions

The study was ethically approved by the University of Mpumalanga Animal Sciences Research Ethics Committee, number: AS/TDalu 01–150322. The Mpumalanga Tourism and Parks Agency: MPB5936 granted permission to carry out the study.

3.2.2 Study area

The study was conducted in protected areas within Mpumalanga Province, South Africa (Figure 3.1). This province shares borders with Limpopo, Eswatini (formerly Swaziland), Mozambique, and the Kruger National Park. Spanning approximately 76 495 km², Mpumalanga is predominantly rural, with agriculture as a primary livelihood source for many local communities. The region's natural vegetation is primarily composed of grasslands, which cover around 65% of the province, along with savannah, warm–temperate, and subtropical forests. Management of the protected areas is divided among three central conservation authorities: the Mpumalanga Tourism and Parks Agency (MTPA), South African National Parks (SANParks), and the South African National Biodiversity Institute (SANBI). The MTPA is a provincial body responsible for managing several nature reserves and promoting tourism in the province. The SANParks is a national authority that oversees the country's national parks, including sections of the Kruger National Park located within Mpumalanga. SANBI, established under the National Environmental Management: Biodiversity Act, is a national institution dedicated to biodiversity research and the management of national botanical gardens. Collectively, these organizations manage ecologically rich landscapes, including rivers, wetlands, grasslands, and forests, some of which are home to numerous endemics and threatened species such as the *Enteromius treurensis* (Treur River barb), endangered *Chiloglanis bifurcus* (suckermouth catfish), and locally restricted plants such as *Protea curvata* (Ladysmith sugarbush) and *Eucomis vandermerwei* (Vandermerwe's pineapple lily). For this study, six protected areas were selected to capture variation in management authorities and aquatic habitat types, ensuring accessibility for field surveys. Four of these are managed by the MTPA (Barberton Nature Reserve, Songimvelo Nature Reserve, Ohrigstad Dam Nature Reserve, and Skertspruit Nature Reserve), one by SANBI (Lowveld National Botanical Garden), and another by SANParks. The surveys were conducted in October 2023, April 2024, July 2024, and March 2025.

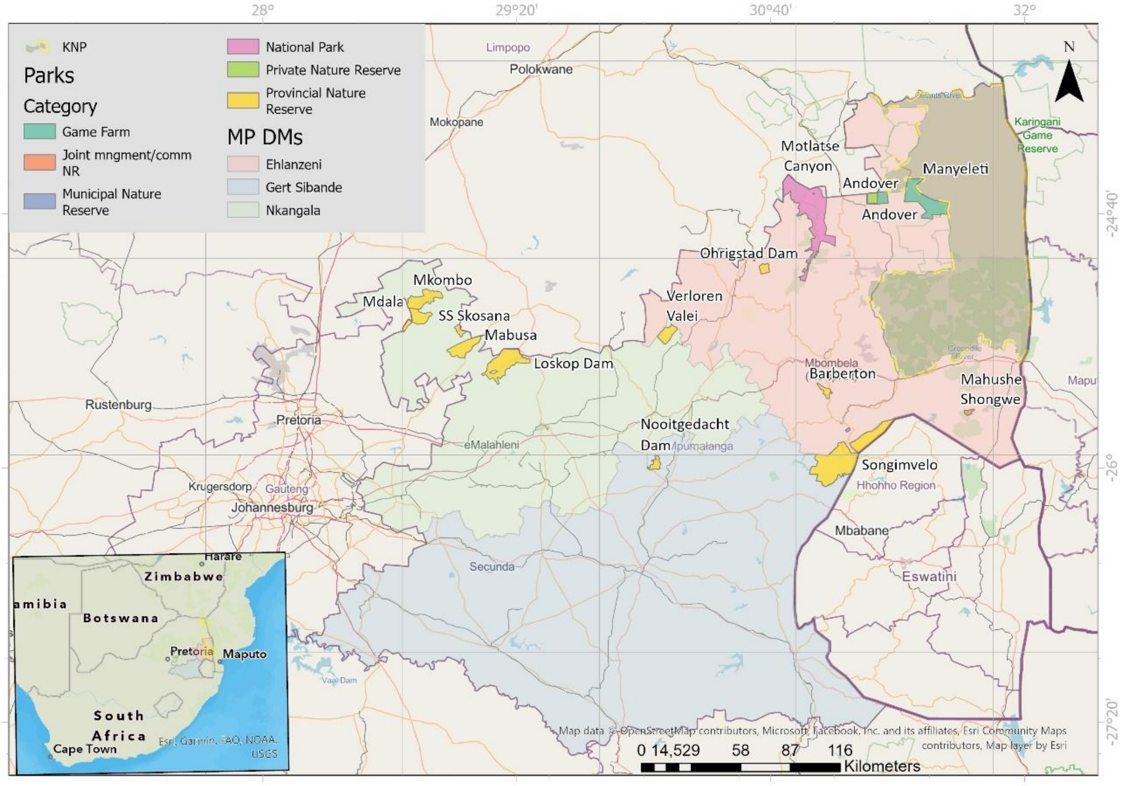

Figure 3.1. A map showing the location of protected areas in Mpumalanga Province, South Africa.

3.2.3 Environmental variables

Environmental variables, including electrical conductivity (µS cm^{-1}), salinity (ppt), pH, water temperature (°C), dissolved oxygen (mg L^{-1}), and total dissolved solids (mg L^{-1}), were measured *in situ* at each site using a portable handheld multiparameter Cyberscan Series meter (Eutech Instruments, Singapore) from two different points across the site and these were taken prior to fish collection.

3.2.4 Sampling of fish

Fish were sampled using a variety of sampling methods, including cast netting, electrofishing, fyke netting, and seine netting. Electroshocked fish were collected with a hand–held net (mesh size 500 µm). Five seine hauls with a mesh size of 18 mm were performed for the seine netting. Moreover, two single–ended fyke nets with a net mesh of 24 mm, connected by a 12.5 m long net, were deployed overnight (i.e., from 16:00 to 08:00), with an average soak time of 14 hours. Using multiple techniques ensured a more representative sample of the fish community across different habitats. Captured fish were placed in 25–L aerated buckets containing source water, and the recorded data included species identity, GPS coordinates, number of individuals, and standard length. All captured fish were released back to their respective habitats, and for those that could not be identified in the field, a photo was taken using a digital camera for further identification at the University of Mpumalanga laboratory.

3.2.5 Data analysis

Species richness, evenness, and the Shannon–Wiener diversity index was calculated for each protected area using SPSS statistical software (version 25) to assess within–site diversity. Thereafter, beta diversity was compared among the protected areas to evaluate differences in community composition. In addition to diversity analysis, the occurrence and relative abundance of fish species were examined for each site. To assess the influence of environmental variables on fish community structure, a canonical correspondence analysis (CCA) was conducted using PAST 4.03. This ordination technique was applied to examine the relationships between fish species and environmental variables across sites and protected areas. Cluster analysis using the Bray–Curtis similarity index was performed in PAST 4.03 software to group sites based on fish assemblage composition. Finally, indicator species analysis (IndVal) was employed to identify species that are significantly associated with protected areas.

3.3 Results

3.3.1 Environment variables

Water pH varied across the protected areas, with acidic conditions observed at Skertspruit (pH 6.68), Ohrigstad (pH 6.77), and SANBI (pH 6.90). In contrast, the other sites had neutral to alkaline pH, ranging from 7.72 at SANParks and 7.75 at Songimvelo to 7.99 at Barberton. Mean water temperature ranged from 18.13°C at Skertspruit and 19.8 °C at Ohrigstad to 22.3°C at both SANBI and Barberton, with the highest value recorded at Songimvelo (27.7°C). Electrical conductivity was lowest at Skertspruit (24.16 µS cm^{-1}) and Ohrigstad (66.3 µS cm^{-1}), intermediate at Barberton (206.6 µS cm^{-1}), SANParks (213.1 µS cm^{-1}), and Songimvelo (250.9 µS cm^{-1}), and highest at SANBI (403.9 µS cm^{-1}). Total dissolved solids (TDS) followed a similar pattern, ranging from 12 mg L^{-1} at Skertspruit and 32.9 mg L^{-1} at Ohrigstad to 91.9 mg L^{-1} at Barberton, 104.3 mg L^{-1} at SANParks, 125 mg L^{-1} at Songimvelo, and peaking at 175.5 mg L^{-1} at SANBI. Salinity values were lowest at SANBI (19.5 ppt), followed by Ohrigstad (29.2 ppt) and Skertspruit (32.9 ppt), while higher values were recorded at Barberton (154.0 ppt), SANParks (194.7 ppt), and Songimvelo (208.5 ppt). Dissolved oxygen (DO) concentrations were relatively high across all protected areas, ranging from 6.09 mg L^{-1} at Skertspruit and 7.48 mg L^{-1} at Barberton to 7.55 mg L^{-1} at Songimvelo, 8.57 mg L^{-1} at SANBI, 9.79 mg L^{-1} at SANParks, and 10.07 mg L^{-1} at Ohrigstad. The two–way ANOVA revealed that both site and seasonal variations significantly influenced most water quality variables. Temperature, pH, conductivity, TDS, and salinity all showed significant differences among sites and across seasons ($p < 0.05$), with significant site–season interactions indicating that seasonal patterns varied across locations. In contrast, dissolved oxygen (DO) showed no significant differences among sites ($p = 0.985$), although it varied significantly across seasons ($p < 0.001$), and no interaction between the two factors was detected (Table 3.1).

Table 3.1. Two–way analyses of variance (ANOVA) based on water variables for sites and seasons.

Variables	**Sites**			**Seasons**			**Sites x Seasons**		
	df	**F**	***P***	**Df**	**F**	***P***	**df**	**F**	***P***
Temperature °C	3	42.416	<0.001	2	39.797	<0.001	2	20.656	<0.001
pH	3	12.885	<0.001	2	4.180	0.023	2	6.735	0.003
Conductivity µS cm^{-1}	3	14.874	<0.001	2	39.964	<0.001	2	11.260	<0.001
Total Dissolved Solids mg L^{-1}	3	13.877	<0.001	2	26.102	<0.001	2	11.575	<0.001
Dissolved Oxygen mg L^{-1}	3	0.049	0.985	2	38.745	<0.001	2	0.102	0.904
Salinity ppt	3	7.641	<0.001	2	24.853	<0.001	2	3.345	<0.001

3.3.2 Fish species

A total of 3 420 individual fish representing 29 species from 12 families were caught across the six protected areas (i.e., Songimvelo, Ohrigstad, Skertspruit, Barberton, SANBI, and SANParks). The most abundant species by far was the non–native *Xiphophorus helleri* (*n* = 1 963), followed by *Pseudocrenilabrus philander* (*n* = 224), *Oreochromis mossambicus* (*n* = 102), *Labeobarbus marequensis* (*n* = 88), *Micralestes acutidens* (*n* = 45), and *Tilapia sparrmanii* (*n* = 34) (Table 3.2).

The Cyprinidae was the most species–rich family, represented by seven *Enteromius* species and larger–bodied taxa such as *L. marequensis* and *Labeo molybdinus*. Other families included Mochokidae (five *Chiloglanis* species), Amphiliidae, Clariidae, Anguillidae, and Mormyridae. Cichlids were also diverse, represented by *O. mossambicus*, *P. philander*, *Tilapia sparrmanii*, and *Coptodon rendalli*. The non–native *X. helleri* was by far the most abundant species, dominating the community (see Table 3.2).

Table 3.2. Fish species and their distributional status across the protected areas in Mpumalanga, South Africa. Abbreviations: SON– Songimvelo; OHR– Ohrigstad; SKE– Skertspruit; BAR– Barberton; SANBI– South African National Biodiversity Institute; SNK– South African National Parks; LC– Least Concern; NT–Near Threatened; CR–Critically Endangered; VU–Vulnerable

Species	**SON**	**OHR**	**SKE**	**BAR**	**SANBI**	**SNK**	**Mean SL (± SD)**	**N**	**Native/ Invasive**	**IUCN Status**
Amphilius uranoscopus				✓			6.06 ± 4.02	3	Native	LC
Anguilla mossambica				✓			35 ± 49.49	2	Native	NT
Chiloglanis anoterus						✓	2.1 ± 2.96	2	Native	LC
Chiloglanis paratus				✓		✓	4.93 ± 0.96	4	Native	LC
Chiloglanis pretoriae				✓		✓	4.07 ± 0.91	9	Native	LC
Chiloglanis bifurcus				✓			5.72 ± 1.58	9	Native	CR
Chiloglanis swierstrai						✓	3.71 ± 0.51	14	Native	LC
Clarias gariepinus				✓		✓	12.45 ± 0.77	2	Native	LC
Coptodon rendalli						✓	4.88 ± 1.98	9	Native	LC
Enteromius annectens						✓	3.55 ± 0.49	2	Native	LC
Enteromius anoplus	✓	✓	✓	✓			6.35 ± 0.37	14	Native	LC
Enteromius eutaenia				✓	✓		6.52 ± 1.57	13	Native	LC
Enteromius radiatus						✓	3.9 ± 1.27	1	Native	LC
Enteromius trimaculatus	✓			✓		✓	7.05 ± 1.84	29	Native	LC
Enteromius unitaeniatus				✓		✓	6.24 ± .1.03	20	Native	LC
Enteromius viviparus	✓			✓		✓	3.55 ± 0.48	36	Native	LC
Glossogobius giuris						✓	7.05 ± 0.07	2	Native	LC
Labeobarbus marequensis	✓			✓		✓	10.77 ± 4.11	88	Native	LC
Labeo cylindricus						✓	10.75 ± 6.71	2	Native	LC
Labeo molybdinus			✓	✓		✓	18.7 ± 5.65	18	Native	LC
Marcusenius macrolepidotus						✓	11.7 ± 1.82	2	Native	LC
Marcusenius pongolensis				✓			12.45 ± 11.38	2	Native	LC
Mesobola brevianalis						✓	3.75 ± 0.58	10	Native	LC
Micralestes acutidens				✓	✓	✓	6.62 ± 1.17	45	Native	LC
Oreochromis mossambicus	✓			✓	✓	✓	9.14 ± 7.31	102	Native	VU
Opsaridium peringueyi						✓	4.78 ± 1.13	2	Native	LC
Pseudocrenilabrus philander	✓	✓		✓	✓	✓	6.67 ± 1.45	224	Native	LC
Tilapia sparrmanii	✓			✓		✓	10.05 ± 1.82	34	Native	LC
Xiphophorus helleri					✓		6.26 ± 1.62	2719	Invasive	LC

Historical records indicate the presence of alien fish in protected area water bodies, including *X. helleri* at SANBI (2025), *Cherax quadricarinatus* (redclaw crayfish) and *Hypophthalmichthys molitrix* (silver carp) at SANParks (2017–2021), and mirror/common carp in Ohrigstad, based on citizen reports. In contrast, no historical records of alien fish were found for Skertspruit, Barberton, and Songimvelo (Table 3.3).

Table 3.3. Historical records of invasive fish species in protected–area water bodies of Mpumalanga, South Africa, including first–record year, site, and source.

Protected area	Alien taxon (historical)	Approx. year/note	Source
SANBI	*Xiphophorus helleri* (swordtail)	2025—reported invasion in a pond and the Crocodile River	Masina et al., 2025
SANParks	*Cherax quadricarinatus* (redclaw crayfish)	2017 (first records reported in Crocodile River / Kruger).	SANParks news / Koedoe paper summary by Khosa et al., 2022
	Hypophthalmichthys molitrix (silver carp)	2019–2021 onward—range expansion into large river systems feeding into Kruger has been documented.	Crookes et al., 2020
Ohrigstad	Mirror/common carp	Citizen records (no formal published paper found).	FishBrain/ local angling reports.
Skertspruit	No historical alien–fish records found		
Barberton	No historical alien–fish records found		
Songimvelo	No historical alien–fish records found		

In terms of species richness, the SANParks and Barberton sites had the highest diversity, each recording 22 and 18 species, respectively. This was followed by Songimvelo and SANBI, which recorded 7 and 5 species, respectively. The lowest species richness was observed at Ohrigstad and Skertspruit, with only 2 species each (Table 3.4). The Shannon–Wiener diversity index ranged from 0.33 at SANBI to 2.68 at Barberton. Evenness (E) ranged from 0.21 at SANBI, indicating strong dominance by a few species, to 0.96 at Skertspruit, where species were more evenly distributed. Barberton and SANParks exhibited both high diversity and high evenness, while SANBI showed low richness and low evenness, suggesting dominance by a small number of taxa (Table 3.4). Notably, only one invasive fish species was identified across all sites: *X. helleri,* recorded at the SANBI (Table 3.2). Results from the non–parametric Kruskal–Wallis test showed no significant variation (*p* > 0.05) in Shannon–Wiener diversity, species richness, or evenness across the protected areas.

Table 3.4. Diversity indices (Shannon–Wiener, taxa richness, and evenness) of fish communities across the six protected areas.

Protected area	**Taxa richness**	**Shannon –Wiener**	**Evenness**
Barberton	18	2.68	0.93
Songimvelo	7	1.52	0.78
Ohrigstad	2	0.48	0.69
Skertspruit	2	0.67	0.96
SANBI	5	0.33	0.21
SANParks	22	2.63	0.85

3.3.3 Relationship between fish communities and protected areas

The Indicator Species Analysis (IndVal) identified several species that were significantly associated with specific protected areas (Figure 3.2). For example, *Anguilla mossambica* (African longfin eel) and *Amphilius uranoscopus* (slender mountain catfish) exhibited strong indicator values for Barberton, suggesting that these species are characteristic of this system. Similarly, *Chiloglanis anoterus* (upside–down catfish), *Chiloglanis swierstrai* (swierstra's suckermouth catfish), *Coptodon rendalli* (redbreast tilapia), *Enteromius annectens* (largescale barb), *Enteromius radiatus* (striped barb), *Glossogobius giuris* (tank goby), *Labeo cylindricus* (slender labeo), *Marcusenius macrolepidotus* (elephantfish), *Mesobola brevianalis* (lake sardine), and *Opsaridium peringueyi* (southern chub) were strongly associated with SANParks, indicating their restricted distribution and potential sensitivity to the environmental conditions in this area. In contrast, *X. helleri* was strongly associated with SANBI and some protected areas, such as Ohrigstad and Songimvelo, had few or no significant indicator species, reflecting a more generalist fish assemblage.

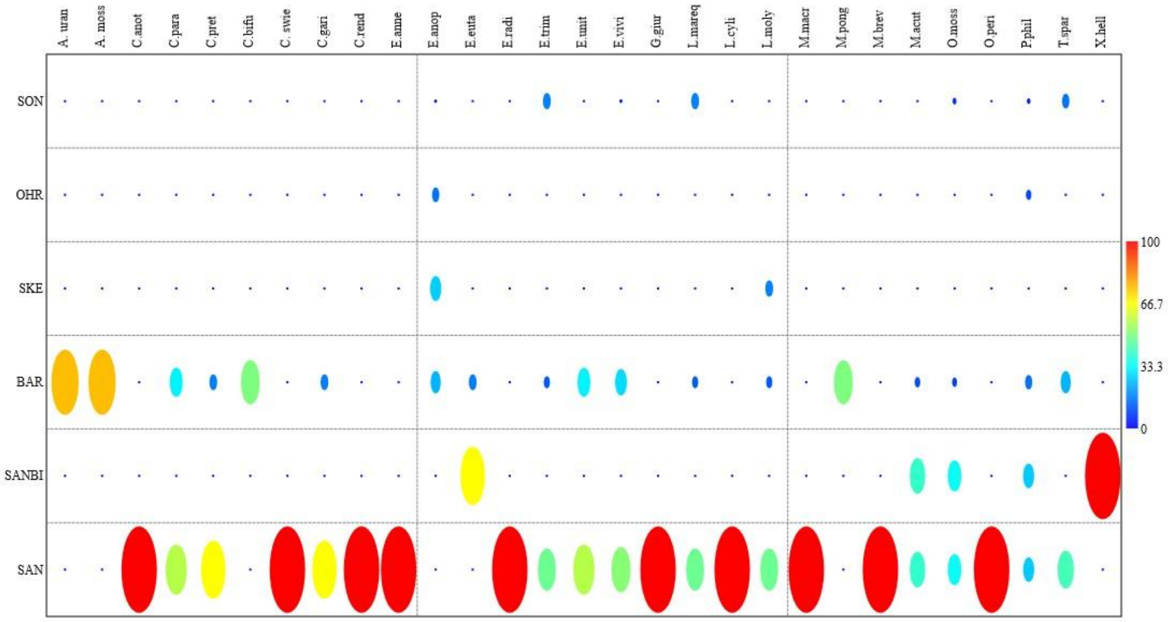

Figure 3.2. Indicator Species Analysis (IndVal) of fish communities showing species significantly associated with each protected area. Abbreviations: SON– Songimvelo; OHR– Ohrigstad; SKE– Skertspruit; BAR– Barberton; SANBI– South African National Biodiversity Institute; SNK– South African National Parks; A.uran–*Amphilius uranoscopus*; A. moss–*Anguilla mossambica*; C.anot–*Chiloglanis anoterus*; C.para–*Chiloglanis paratus*; C.pret–*Chiloglanis pretoriae*; C.bifu–*Chiloglanis bifurcus*; C. swie–*Chiloglanis swierstrai*; C.gari–*Clarias gariepinus*; C.rend–*Coptodon rendalli*; E.anne–*Enteromius annectens*; E.anop–*Enteromius anoplus*; E.euta–*Enteromius eutaenia*; E.radi–*Enteromius radiatus*; E.trim–*Enteromius trimaculatus*; E.unit–*Enteromius unitaeniatus*; E.vivi–*Enteromius viviparus*; G.giur–*Glossogobius giuris*; L.mareq–*Labeobarbus marequensis*; L.cyli–*Labeo cylindricus*; L.moly–*Labeo molybdinus*; M.macr–*Marcusenius macrolepidotus*; M.pong–*Marcusenius pongolensis*; M.brev–*Mesobola brevianalis*; M.acut–*Micralestes acutidens*; O.moss–*Oreochromis mossambicus*; O.peri–*Opsaridium peringueyi*; P.phil–*Pseudocrenilabrus philander*; T.spar–*Tilapia sparrmanii*; X.hell–*Xiphophorus helleri.*

Based on cluster analysis, the first group consisted of Barberton and SANParks, which showed the highest similarity (~0.6), with Songimvelo joining this subgroup at a similarity of approximately 0.45 (Figure 3.3). The South African National Biodiversity Institute was loosely associated with this cluster, merging at a lower similarity (~0.3). The second group comprised Ohrigstad and Skertspruit, which were relatively similar to each other (~0.5) but clearly distinct from the first group. The two major clusters were separated at a similarity of ~0.2, indicating substantial variation in fish assemblages across the surveyed protected areas.

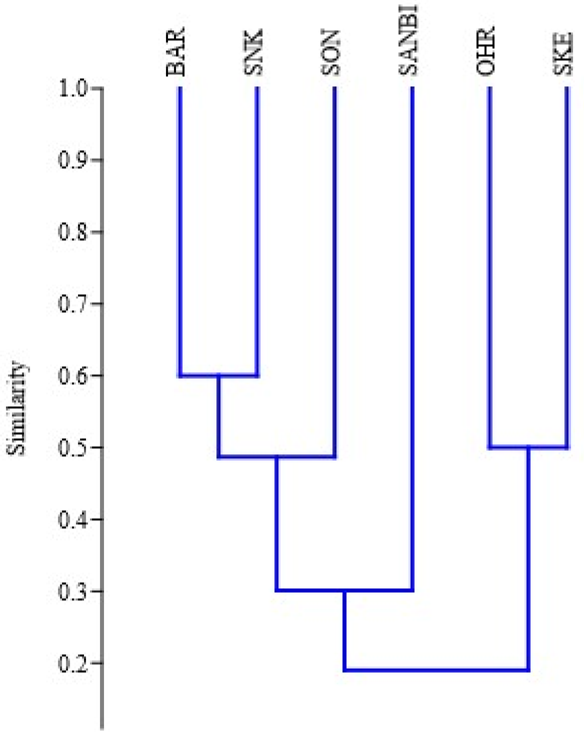

Figure 3.3. Cluster dendrogram showing fish assemblages across protected areas in Mpumalanga based on Bray–Curtis similarity. Abbreviations: Abbreviations: SON – Songimvelo; OHR – Ohrigstad; SKE – Skertspruit; BAR – Barberton; SANBI – South African National Biodiversity Institute; SNK – South African National Parks.

3.3.4 Relationship between fish community composition and environmental variables

The Canonical Correspondence Analysis (CCA) revealed clear associations between fish communities, environmental variables, and protected areas (Figure 3.4). Three main site groupings were identified: (i) Barberton and SANParks, which clustered together and were characterized by native species such as *M. acutidens* and *O. mossambicus*; (ii) SANBI, Ohrigstad, and Skertspruit, which grouped closely, with SANBI being notable for the occurrence of the invasive *X. helleri*; and (iii) Songimvelo, which separated from all other sites and was linked to higher salinity, temperature, and pH, supporting species such as *T. sparrmanii* and *E. viviparus*. Environmental variables played a significant role in structuring communities: dissolved oxygen was positively associated with *P. philander* and *O.*

mossambicus, while conductivity and total dissolved solids explained the distribution of several other species.

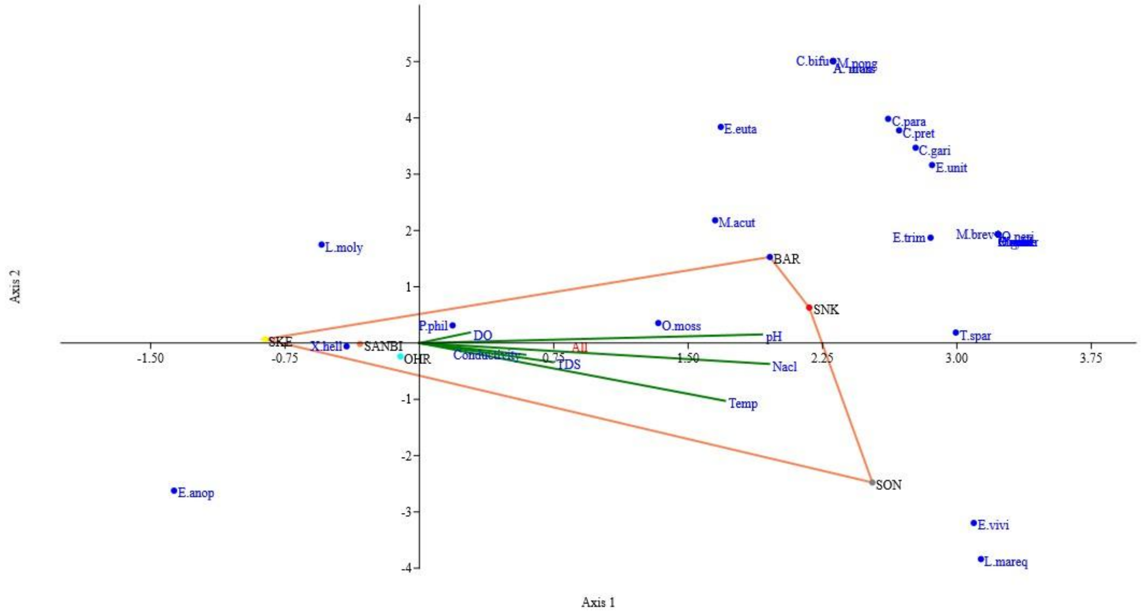

Figure 3.4. Canonical correspondence analysis ordination triplot diagram showing the relationship between measured significant environmental variables with fish species across the protected areas. Abbreviations: Abbreviations: SON– Songimvelo; OHR– Ohrigstad; BAR– Barberton; SANBI– South African National Biodiversity Institute; SNK– South African National Parks; A.uran–*Amphilius uranoscopus*; A. moss–*Anguilla mossambica*; C.anot–*Chiloglanis anoterus*; C.para–*Chiloglanis paratus*; C.pret–*Chiloglanis pretoriae*; C.bifu–*Chiloglanis bifurcus*; C. swie–*Chiloglanis swierstrai*; C.gari–*Clarias gariepinus*; C.rend–*Coptodon rendalli*; E.anne–*Enteromius annectens*; E.anop–*Enteromius anoplus*; E.euta–*Enteromius eutaenia*; E.radi–*Enteromius radiatus*; E.trim–*Enteromius trimaculatus*; E.unit–*Enteromius unitaeniatus*; E.vivi–*Enteromius viviparus*; G.giur–*Glossogobius giuris*; L.mareq–*Labeobarbus marequensis*; L.cyli–*Labeo cylindricus*; L.moly–*Labeo molybdinus*; M.macr–*Marcusenius macrolepidotus*; M.pong–*Marcusenius pongolensis*; M.brev–*Mesobola brevianalis*; M.acut–*Micralestes acutidens*; O.moss–*Oreochromis mossambicus*; O.peri–*Opsaridium peringueyi*; P.phil–*Pseudocrenilabrus philander*; T.spar–*Tilapia sparrmanii*; X.hell–*Xiphophorus helleri.*

3.4 Discussion

In this study, we provide an updated assessment of the occurrence and distribution of fish species within protected areas in Mpumalanga Province, South Africa. Generating accurate and current species occurrence data in these protected areas is essential for guiding effective, long–term management strategies (Foxcroft et al., 2013). Information on invasive species within protected areas should receive the same level of priority as data collected for threatened or endemic species, as both are critical for informing ecosystem restoration, biodiversity conservation, and measures to prevent the spread of invasive species (Forner et al., 2022).

The observed clustering patterns suggest that environmental filtering plays an important role in structuring fish assemblages across the protected areas. The similarity between Barberton, Songimvelo, and SANParks likely reflects comparable environmental conditions that favour species with similar ecological tolerances. In contrast, the distinctiveness of Ohrigstad and Skertspruit may indicate localized habitat characteristics or subtle environmental variables influencing species composition. The separation of SANBI appears to be strongly influenced by the dominance of the invasive *X. helleri*, highlighting how biological invasions can modify community structure even within protected systems. This suggests that species-specific interactions may interact with environmental variables to shape assemblage patterns. These findings align with previous studies demonstrating the influence of environmental variables on fish assemblages; for example, research on the Dhansiri River in the Eastern Himalayas found significant relationships between fish community structure and ecological factors (Ongh et al., 2025), while a study in the Seti Gandaki River, Nepal, showed that variations in pH, dissolved oxygen, and temperature affected fish assemblage composition (Pokharel et al., 2018). Collectively, these results suggest that fish communities in protected areas are structured by both environmental gradients and species–specific associations, highlighting their ecological distinctiveness.

Our study also found that only one invasive fish species, *X. helleri*, was present across all surveyed sites, exclusively in the SANBI protected area. This limited occurrence highlights the combined influence of geographic isolation, habitat integrity, and restricted human access in reducing the establishment and spread of invasive fish within these protected areas. The surveyed protected areas, including Songimvelo, Barberton, Ohrigstad, Skertspruit, SANBI, and the SANParks site, are managed under provincial or national protection frameworks (such as NEMBA) that enforce strict regulations on fishing, stocking, aquaculture, and other activities known to facilitate the spread of non–native species. Such regulatory control reduces invasion pathways and limits propagule pressure, particularly in remote or well–managed reserves (Foxcroft et al., 2013).

Geographic location and hydrological connectivity are key factors influencing the presence of fish species (Hirschfeld et al., 2021; Zare–Shahraki et al., 2022). Ohrigstad and Skertspruit protected areas are situated in upper catchment areas with limited connections to downstream or neighboring water bodies, which restricts the spread of invasive species from typical sources such as urban waterways and recreational fishing areas. This finding is consistent with Acreman et al. (2020), who reported that protected areas located in headwater sections of rivers with instream barriers in the lower sections can prevent upstream invasion and establishment of non–native fish species. In contrast, the SANBI site at the Lowveld National Botanical Garden is situated at the confluence of the Crocodile and Nels Rivers, near the urban centre of Mbombela, which increases its vulnerability to the introduction of ornamental fish. Furthermore, as a publicly accessible conservation and recreational space that hosts numerous events and visitors, the botanical garden experiences frequent human activity that may unintentionally facilitate the introduction of species such as *X. helleri*.

Invasive species tend to be more prevalent in ecosystems experiencing multiple stressors, such as those in urbanised areas (Strayer, 2010; e.g., Quinn and van Klinken, 2011) or in highly regulated rivers (e.g., Robson and Mitchell, 2010). In contrast, the relatively intact ecological condition of protected river systems strengthens their resistance to invasion. Environmental variables, such as high-water quality, stable flow regimes, and dense native riparian vegetation, reduce the availability of ecological niches for potential invaders, a phenomenon well recognised in invasion ecology (Emery-Butcher et al., 2020). In degraded systems, altered habitats can provide opportunities for opportunistic non–native species to establish (IPBES, 2023), but such disturbance–driven openings are largely absent in these protected areas. Furthermore, the low propagule pressure characteristic of remote and well–protected sites further reduce invasion probability, as propagule pressure is a critical predictor of establishment success (Lockwood et al., 2005; Taylor et al., 2025). Furthermore, the observed distribution patterns of *X. helleri* can be explained by its species–specific traits. The *X. helleri* is a common aquarium species that can establish even under low introduction frequencies (D’Amore et al., 2019), a pattern also documented within the study region by Masina et al. (2025), who reported its presence and persistence in the Lowveld National Botanical Garden and adjacent water bodies. The absence of this species from other protected areas suggests that such introductions are highly localized and have not yet spread widely within the study region.

Despite our findings, it is essential to acknowledge the temporal limitations of this survey, as sampling was conducted across four periods: October 2023, April 2024, July 2024, and March 2025, covering spring, autumn, and winter at all six selected sites within the protected areas. Nevertheless, the data represent only a snapshot in time, and some invasions may occur outside these periods or at densities too low to detect. Consequently, long–term monitoring and early detection remain crucial, as rapid management responses are more cost–effective and ecologically successful when invasions are identified early (Martinez et al., 2020).

3.5 Conclusion

This study provides an updated and spatial assessment of freshwater fish species in the protected areas of Mpumalanga Province. The results show that invasions are currently limited in extent, with only *X. helleri* recorded, and both confined to a single, highly accessible site. The limited occurrence of invasive species in the surveyed protected areas suggests that factors such as geographic isolation, intact habitat conditions, and effective management contribute to reducing the risk of invasion. However, the presence of invasive species in areas with high public access and hydrological connectivity highlights potential entry points for future invasions. The research demonstrates that systematic biodiversity surveys can generate critical baseline data to guide conservation interventions even over a limited temporal scope. Early detection and rapid response measures should be prioritised in vulnerable sites, particularly those near urban areas or connected to other water bodies. Long–term monitoring is essential for tracking changes in invasion patterns and proactively adapting management strategies. By combining field–based monitoring with regulatory enforcement and public awareness, managers can enhance the resilience of freshwater ecosystems in protected areas against the growing global threat of aquatic invasive species.

CHAPTER 4: DEMOGRAPHICS, STATUS, AND DIETARY HABITS OF SWORDTAIL FISH XIPHOPHORUS HELLERI HECKEL, 1848 IN A PROTECTED BOTANICAL GARDEN AND SURROUNDING AREAS

Abstract

One of the major challenges faced by protected areas is the introduction and subsequent spread of invasive non–native species, which must be effectively managed to ensure the protected area's function. In protected freshwater systems, fish invasions pose a substantial threat through impact mechanisms such as predation and hybridisation. *Xiphophorus helleri* (Swordtail fish), a freshwater species native to northern Mexico and Central America, was introduced globally through the aquarium trade and has become established in various non–native habitats. The distribution of *X. helleri* in the Lowveld National Botanical Garden (LNBG) and the nearby Crocodile River system was assessed by investigating its growth, mortality rate, population structure, and diet composition. This study provides new insights, revealing that swordtail fish, which had not been previously recorded in the Crocodile River system, are now present in this area. Sampling conducted in October 2023 and March 2024 revealed a significant population of *X. helleri* in an LNBG pond and in the nearby Crocodile River downstream of the pond, accounting for 91.7% of the total fish caught. We found that *X. helleri* exhibited rapid growth and competitive superiority, contributing to its dominance over native species. Mortality rates were found to be low, suggesting that *X. helleri* is well–suited to the environmental conditions of the LNBG and Crocodile River systems. This spread indicates that the species' distribution was influenced by local hydrology, particularly the occasional flooding of the pond into the Crocodile River. The findings highlight the threat posed by *X. helleri*, which can potentially outcompete native species, underscoring the need for effective management strategies to control the spread of *X. helleri* and mitigate its ecological impacts.

Keywords: *Xiphophorus helleri*, growth, stomach contents, mortality, distribution.

4.1 Introduction

Protected areas are crucial for biodiversity conservation as they serve as sanctuaries that safeguard ecosystems and habitats from potential threats associated with human–induced disturbances (DeFries et al., 2007; Le Saout et al., 2013; Opuni–Frimpong et al., 2021). These areas can contribute to the conservation of rare and endangered species and the maintenance of ecological processes (Araújo et al., 2002; Kearney et al., 2020). Protected land and water on earth are expected to expand to 30% by 2030, necessitating increased investments and management actions under the Kunming–Montreal Global Biodiversity Framework (Target 3) (Convention on Biological Diversity, 2022). However, one of the major challenges faced by protected areas is the introduction and subsequent spread of invasive non–native species. Biological invasions must be more effectively managed to ensure the function of protected areas (Foxcroft et al., 2019; Wasserman et al., 2019; Carneiro et al., 2024). Indeed, under Target 6 of the Global Biodiversity Framework, impacts of invasive non–native species should be minimised and invasion rates reduced by 50% by 2030 (Convention on Biological Diversity 2022).

Biological invasion is one of the major drivers of global change worldwide, posing threats to biodiversity, ecosystem services, and human health (Simberloff et al., 2013; Early et al., 2016; Wasserman et al., 2019; IPBES, 2023). The introduction and subsequent establishment of non–native species are frequently linked to human activities, such as accidental releases from aquaculture facilities, intentional introductions, and/or escape from the ornamental fish trade in aquatic ecosystems (Chan et al., 2019; Wasserman et al., 2019; Weyl et al., 2020a). The escalating rates of species introductions (Seebens et al., 2017), coupled with other anthropogenic stressors such as climate change (Gallardo et al., 2018), globalization and habitat modifications (Didham et al., 2007; Hulme, 2021), can facilitate the establishment and proliferation of invasive alien species. While only a subset of non–native species may cause direct harm to native species, their individual and cumulative impacts on ecosystems can nonetheless be substantial (Gallardo et al., 2024).

In freshwater ecosystems, invasions by non–native fish species have caused deleterious effects on native aquatic communities (Weyl et al., 2010; Bernery et al., 2022; Dalu et al., 2022). Direct impacts include non–native species competing with and preying on native species (Bernery et al., 2022; Su et al., 2023), while indirect impacts include structural or physico–chemical modification of recipient ecosystems, which may render conditions unfavourable for native species (e.g., Zambrano et al., 2010; Pagnucco, 2015). These impacts can also lead to changes in nutrient cycling and energy budgets within native ecosystems, as well as alterations in habitats for various species (Wahl et al., 2011; Vilizzi et al., 2015). For example, invasive common carp (*Cyprinus carpio* Linnaeus, 1758) have been shown to increase phosphorus and nitrogen concentrations through sediment resuspension and bioturbation, thereby promoting algal blooms and reducing water clarity (Badiou et al., 2011; Huser et al., 2022). Moreover, these impacts can extend to human welfare, public health, and the economy (Tsiamis et al., 2020; Diagne et al., 2021a; Vaz et al., 2021). The impacts of fish invasions are particularly pernicious problems in freshwater ecosystems, due to top–down modifications of food webs, hybridisation, and other impact mechanisms (Bernery et al., 2022).

South Africa's aquatic ecosystems, like many regions globally, face a growing threat from the invasion by non–native fish species such as Nile tilapia *Oreochromis niloticus* (Linnaeus, 1758), common carp *Cyprinus carpio*, Florida bass *M. salmoides* (Lacepède, 1802), and smallmouth bass *Micropterus dolomieu* Lacepède, 1802 that present significant challenges to both the environment and local biodiversity (Cambray, 2003; Kadye and Booth, 2012; Ellender and Weyl, 2014; Ramoejane et al., 2020; Weyl et al., 2020b). The swordtail fish (*Xiphophorus helleri* Heckel, 1848) is a freshwater species belonging to the subfamily Poeciliinae, native to northern Mexico and Central America (Magalhães and Jacobi, 2017). They have been introduced to various regions worldwide, including the United States, Sri Lanka, Canada, and Africa, mainly through the aquarium trade (Skelton, 2001; Goldberg et al., 2019). These fish exhibit sexual dimorphism. Male swordtails have a modified anal fin called a gonopodium, which facilitates internal fertilisation of the female. They also feature an extended lower caudal fin ray, giving them the name "swordtail" (Magalhães and Jacobi, 2017). The species is tolerant to a wide range of environmental conditions while exhibiting trophic opportunism, high fecundity, and fast growth rates, enabling the species to successfully colonise and establish itself in many environments (Bomford and Glover, 2004). The species feeds on aquatic macroinvertebrates and can prey on fish larvae (Skelton, 2001), threatening co–occurring native fish species.

In South Africa, *X. helleri* was first introduced via the aquarium trade in 1974 (Figure 4.1; Ellender and Weyl, 2014). Since then, it has spread to various water bodies, particularly in the eastern and northeastern parts of the country (Ellender and Weyl, 2014). The species is known to inhabit a range of aquatic environments, including rivers, streams, and ponds (Ellender and

Weyl, 2014). The invasion of *X. helleri* in South Africa has raised concerns about its impact on local aquatic ecosystems, such as many non–native species, swordtails can outcompete native fish for resources and may alter the structure of the aquatic community (Ellender and Weyl, 2014). Despite this, the demographics and invasion status of *X. helleri* in aquatic ecosystems following its introduction in South Africa are poorly understood (Ellender and Weyl, 2014). This knowledge gap hinders effective risk assessment and management of this species and its potential impacts.

Figure 4.1. Images of the swordtail fish *Xiphophorus helleri* Heckel, 1848 caught in the Lowveld Botanical Garden, Nelspruit (South Africa). Photo credit: Tatenda Dalu.

The present study assessed the distribution of *X. helleri* in the Lowveld National Botanical Garden and the nearby Crocodile River systems (Gladdespruit and Shisanyama) by investigating its growth, mortality rate, population structure, and diet composition. The outcomes of this study provide insights that can guide environmental managers and policymakers regarding the invasiveness of this species in the region. This assists managers of protected areas by elucidating the characteristics and potential trophic interactions of *X. helleri*, which can inform effective strategies for its eradication or control.

4.2 Materials and methods

4.2.1 Study area

Sampling of *X. helleri* was done at a pond situated within the Lowveld National Botanical Garden (LNBG), Mbombela (25°26′42″S, 30°57′57″E), and the nearby Crocodile River systems, specifically at the Gladdespruit (site C1 – 25°27′44.4″S, 30°56′58.9″E) and Shisanyama (site C2 – 25°27′49.0″S, 30°58′24.0″E) sites in October 2023 and March 2024. The Gladdespruit River site was located upstream of the LNBG, whereas the Shisanyama River was located downstream of the LNBG (Figure 4.2). The LNBG is situated near the confluence of the Nels River and the Crocodile River in the Mpumalanga Province (Gozo, 2009). During wet seasons, the pond occasionally floods and spills into the Crocodile River just before the latter merges with the Nels River. This area receives an average annual precipitation of approximately 780 mm, with maximum average summer temperatures that reach 35°C, occasionally exceeding 40°C (McCracken, 2019). The garden features native plants and trees, with a few areas having manicured, native lawns (Mucina and Rutherford 2006). The garden thus serves as a crucial element in the conservation of rare and endangered plant species (Van der Walt, 2010; Thomas et al., 2022).

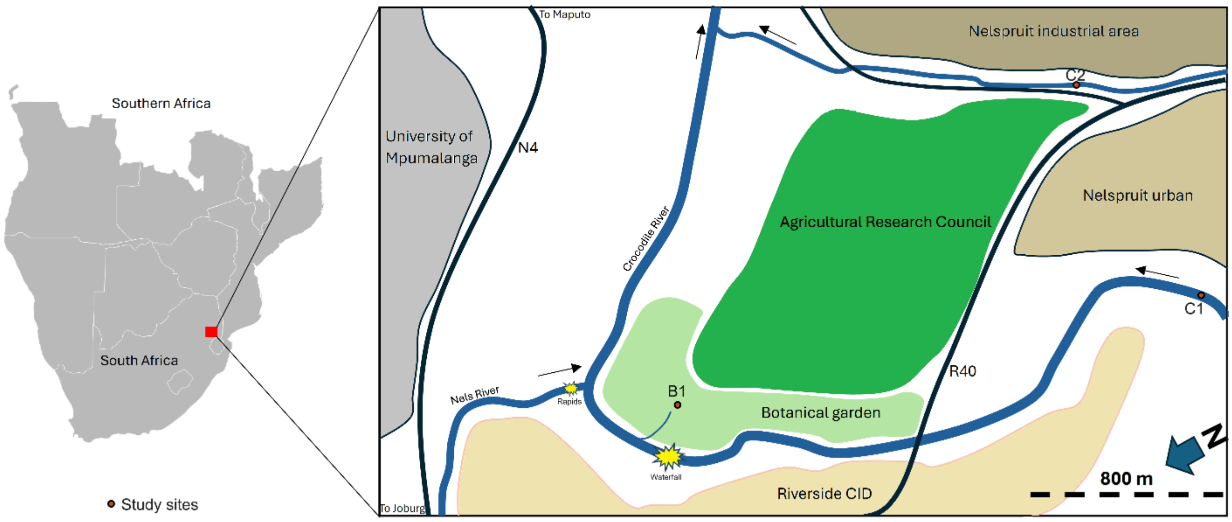

Figure 4.2. A map showing the location of the selected sites within the Nelspruit City region of Mpumalanga province, South Africa.

4.2.2 Water physicochemical variables

At each sampling event, water parameters including temperature (°C), salinity (ppt), pH, total dissolved solids (TDS) (mg L^{-1}), electrical conductivity (µS cm^{-1}), and oxidation–reduction potential (mV), were measured *in situ* using a portable handheld multiparameter Cyberscan Series meter (Eutech Instruments, Singapore). Measurements were taken from three different locations at each site, prior to fish collection. The pond depth was estimated by calculating the average of five measurements obtained using a graduated pole/rod.

4.2.3 Fish sampling

Fish sampling was conducted in October 2023 and March 2024 using a combination of seine nets, fyke nets, and an electrofisher. In October 2023, sampling involved the use of fyke and seine nets for two consecutive days in the pond. For seine netting, five seine hauls with a mesh size of 18 mm were performed (i.e., between 09:00–12:00). Two single–ended fyke nets with a net mesh of 24 mm connected by a 12.5 m long net, giving a total length of 18 m, were deployed overnight (i.e., from 1600–0800), with an average soak time of 14 hrs. In March 2024, sampling was carried out using a backpack electrofisher. Shocked fish were collected with a hand–held net (mesh size 500 µm) from the nearby Crocodile River system. All captured fish were identified to species level using identification keys by Skelton (2001). In addition, *X. helleri* were separated based on sex, counted, and measured to the nearest centimetre total length (TL). Captured native fish species (i.e., *Enteromius eutaenia*, *Micralestes acutidens*, *Oreochromis mossambicus*, *Pseudocrenilabrus philander*) were released back into the pond while 50 *X. helleri* were retained for stomach content analysis. This subsample comprised of 25 males and 25 females to maintain an equal sex ratio. The sizes of the individuals ranged from 5 cm to 10.5 cm in total length, encompassing both juveniles and adults, based on reported size–at–maturity thresholds for *X. helleri* (FishBase, 2024).

4.2.4 Fish stomach content

Fifty *X. helleri* fish were dissected and had their stomachs removed, which were placed in a petri dish. Thereafter, the stomachs were examined using an inverted microscope, following the methods by Zengeya and Marshall (2007). Each item in the diet (macroinvertebrates, fish, and organic matter) was sorted and identified to the lowest possible family level and counted. The frequency of occurrence method determines the diet, which records the percentage of stomachs containing a particular food item out of the total number of stomachs containing food (Zengeya and Marshall, 2007). Additionally, the percentage of non–food items (organic matter) that might have been ingested accidentally was recorded.

4.2.5 Data analysis

FAO–ICLARM (Food and Agriculture Organization–International Centre for Living Aquatic Resources Management) Stock Assessment Tools (FiSAT 2) computer software package was used to assess the growth parameters, mortality rate and virtual population analysis for *X. helleri*. The von Bertalanffy growth function (VBGF) was used to estimate the growth parameters using the formula:

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

where L_t is the predicted length in cm at the age *t*, $L\infty$ is the asymptotic length in cm, and *K* is the growth coefficient. The species having low K values have older ages and bigger sizes at maturity, lower reproduction, longer life spans high asymptotic length, and t_0 is the hypothetical age at which the length of the fish equals zero (usually negative).

The natural mortality rate (M) was calculated using Pauly’s empirical formula:

$$Log\ (M) - 0.0066 - 0.279 \log\ (L\infty) + 0.6543\ log\ (K) + 0.4634\ log\ (T)$$

where L∞ and K are the VBGF parameters, and T is the mean average habitat temperature taken in the degree Celsius (21.8 to 22.9 ° C in the pond). The total mortality (Z) was estimated using the length–converted catch curve analysis method. The exploitation rate (E) was calculated from equation: $E = F/Z$, where F is the fishing mortality calculated by $F = Z–M$. The virtual population analysis (VPA) for the *X. helleri* from the pond was estimated using input values of length structure, growth, and natural and fishing mortality into the FiSAT 2 computer software package.

The fish were divided into several total length (TL) size classes to assess changes in food composition across different size groups: 5–5.5, 5.6–6, 6.1–6.5, 6.6–7, 7.1–7.5, 7.6–8, 8.1–8.5, 8.6–9, 9.1–9.5, 9.6–10, and 10.1–10.5 cm. The size intervals (0.5 cm) were chosen to detect fine–scale ontogenetic dietary shifts, which are known to occur over small size differences in poeciliids (Zandonà et al., 2015). A χ^2 contingency table analysis was carried out to test the differences in stomach contents among fish sexes and size classes.

4.3 Results

4.3.1 Water physicochemical variables

The water pH at the pond site was generally alkaline, ranging from 8.06 to 8.08. In contrast, the Crocodiles River sites (i.e., Shiyanyma (C2) and Gladdespruit (C1)) exhibited slightly acidic conditions, with pH values ranging from 6.8 to 6.9. The mean water temperature across all sites ranged from 20.8°C to 22.3°C. Electrical conductivity varied, with mean values of 403.9 $\mu S\ cm^{-1}$ at the pond, 627.1 $\mu S\ cm^{-1}$ at Shiyanyma, and 189.4 $\mu S\ cm^{-1}$ at Gladdespruit. The mean TDS levels were high at Shiyanyma (276.6 ppm), followed by the pond site (175.5 ppm), with the lowest mean TDS values at Gladdespruit (78.6 ppm). Mean salinity was 19.5 ppt, 34.4 ppt, and 92.375 ppt at the pond, Shiyanyma, and Gladdespruit, respectively. Lastly, the ORP values were –62 mV, –10.7 mV, and –7.7 mV at the pond, Shisanyama, and Gladdespruit rivers, respectively.

4.3.2 Fish composition

A total of 2 963 fish, representing five species from four families – Alestidae (32 individuals, 1.1% of *Micralestes acutidens*), Cichlidae (154 individuals, 5.2% of *Pseudocrenilabrus philander* and 59 individuals, 2% of *Oreochromis mossambicus*), Cyprinidae (3 individuals, 0.1% of *Enteromius eutaenia*), and Poeciliidae (2 718 individuals, 91.7% of *Xiphophorus* *helleri*) were caught at the three sites (i.e., pond, Gladdespruit, and Shisanyama rivers). The pond site accounted for 99.6% of the *X. helleri* caught (2 707 individuals), while only 11 individuals (0.4%) were caught at the Shisanyama site, and no *X. helleri* were caught in the Gladdespruit River site (i.e., upstream of the pond).

4.3.3 Length frequency distribution

For length–frequency distribution data, a total of 2 716 *X. helleri* (1 863 female and 853 male) were measured during the present study. The ratio of males to females sampled was 1:2.2. The total length ranged from 3.0 to 10.5 cm, with the dominant length ranges being between 3.6 cm and 7.0 cm (Figure 4.3). The total length of *X. helleri* ranged from 3.6 to 10.5 cm in males and from 3.0 to 10.0 cm in females (Figure 4.3). We observed a significant difference ($p = 0.018$) in size class between sexes. The von Bertalanffy growth function (VBGF) parameters of *X. helleri* were estimated at $L\infty = 10.60$ cm (95% CI: 10.20–11.00 cm), $K = 0.01$ year^{-1} (95 % CI: 0.008–0.012 year^{-1}). The total mortality of *X. helleri* was $Z = 0.02$ year^{-1} at 95% confidence interval of the total mortality rate, showing a variation difference of (confidence interval = –0.02 to 0.05), whereas the natural mortality was $M = 0.11$ year^{-1} using a mean pond temperature of 22.3°C.

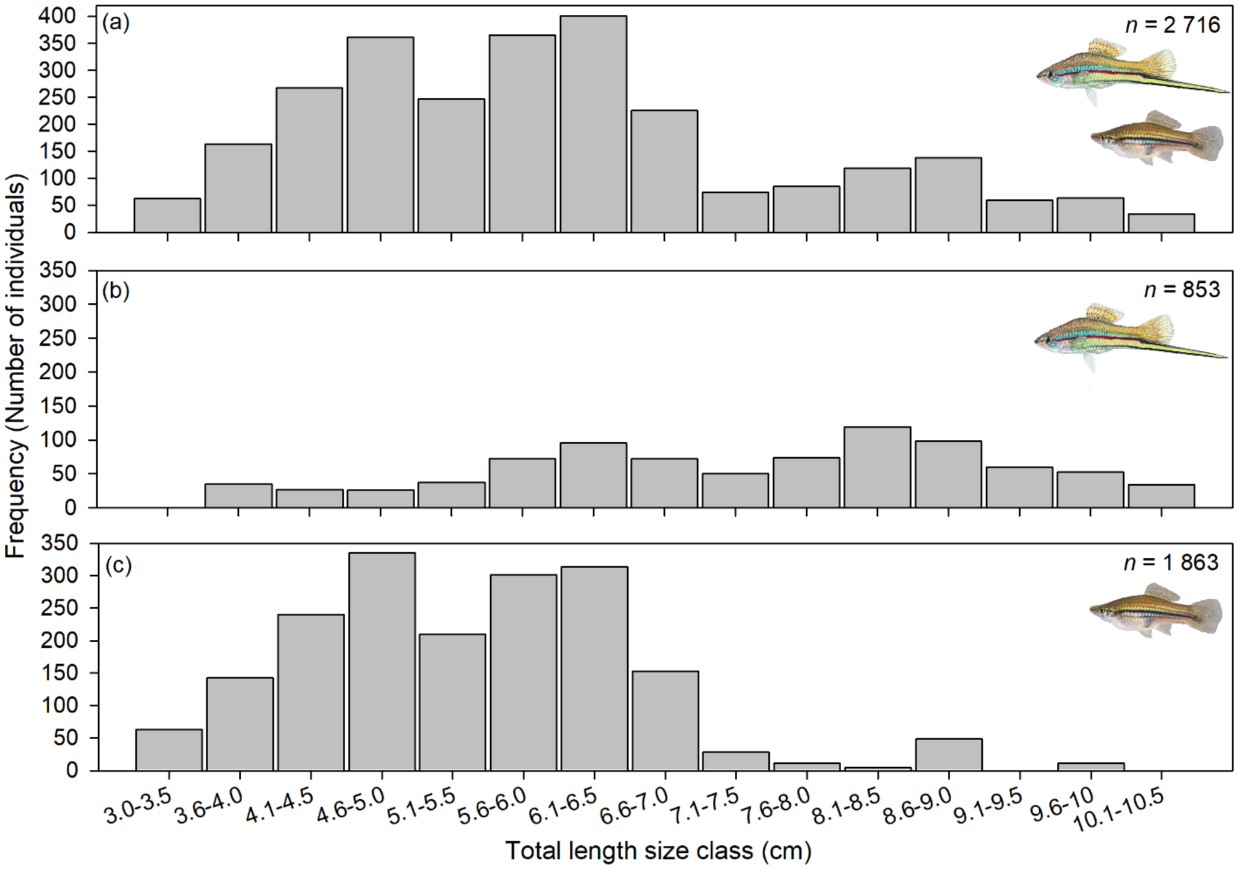

Figure 4.3. The length frequency distribution of *Xiphophorus helleri* population from the Lowveld National Botanical Garden Pond divided into fifteen total length (TL) size classes for (a) both sexes, (b) male only, and (c) female only.

4.3.4 Fish stomach content analysis

Out of the 50 stomachs examined, 8 (16% – females 12% and males 4%) had empty stomachs. The most frequent food recorded in both females and males was organic matter (OM), which was found in 14 (56%, OM range 10–100%) and 19 (76%, OM range 30–95%) individuals, respectively. Contingency table analysis revealed no significant difference among macroinvertebrates ($\chi^2 = 4.387$, $p = 0.356$), fish ($\chi^2 = 6.140$, $p = 0.189$), and OM ($\chi^2 = 15.067$, $p = 0.179$) occurrences between fish sexes. Female stomach fullness ranged from 0 to 100% (Table 4.1). Four (16%) female stomachs contained macroinvertebrates (range 5–30%), whereas 7 (28%) females contained fish particles in their stomachs (range 5–40%). For males, stomach fullness ranged from 0% to 95% (Table 4.1). Nine (36%) and eight (32%) males had macroinvertebrates (range, 5–20%) and fish particles (range, 5–10%) within their stomachs, respectively.

Table 4.1. Frequency range of occurrence (%) of different prey items by total length size class in stomachs of male and female *Xiphophorus helleri* sampled in the Lowveld National Botanical Garden Pond. Numbers in parenthesis represent mean values

Size class (cm TL)	Sex	*n*	Macroinvertebrates (%)	Fish (%)	Organic matter (%)	Stomach fullness (%)
5–5.5	Female	1	0 (0)	0 (0)	80 (80)	80 (80)
5.6–6	Female	7	0 (0)	0 (0)	0–95 (28.8)	0–95 (28.8)
6.1–6.5	Female	13	0–10 (1.5)	0–40 (8.1)	0–100 (32.3)	0–100 (41.9)
6.6–7	Female	4	0–5 (1.3)	0–10 (3.8)	0–90 (40)	0–90 (45)
7.1–7.5	Female	1	30 (0)	0 (0)	0 (0)	30 (30)
7.6–8	Female	2	0 (0)	0 (0)	0–90 (45)	0–90 (45)
6.6–7	Male	3	0–10 (3.3)	0–5 (1.7)	0 (0)	0–15 (5)
7.1–7.5	Male	4	0–5 (2.5)	0–5 (1.3)	0–90 (57.5)	10–90 (61.3)
7.6–8	Male	2	5–20 (12.5)	5–5 (5)	30–30 (30)	40–55 (47.5)
8.1–8.5	Male	4	0–10 (2.5)	0–5 (3.8)	30–95 (51.3)	40–95 (57.5)
8.6–9	Male	5	0–10 (2)	0 (0)	40–90 (74)	50–90 (76)
9.1–9.5	Male	2	0 (0)	0–5 (2.5)	70–90 (80)	75–90 (82.5)
9.6–10	Male	2	0 (0)	0 (0)	80–90 (85)	80–90 (85)
10.1–10.5	Male	3	0–10 (5)	0–5 (1.7)	0–50 (30)	5–55 (36.7)

4.4 Discussion

This study assessed the distribution of *X. helleri* in the Lowveld National Botanical Garden and Crocodile River in South Africa by investigating its growth, mortality rate, population structure, and diet composition. The study revealed that the population abundance of *X. helleri* in the LNBG pond was high compared to other co–occurring fish species such as *P. philander*, *O. mossambicus*, *M. acutidens*, and *E. eutaenia*. This suggests that *X. helleri* experiences low predation in the pond and/or its superior competitive abilities, and this could be due to its rapid development, which allows it to achieve enhanced swimming speeds quickly, and thus increase its chances of avoiding/escaping predators (Benson and Basolo, 2006; Royle et al., 2006). On the other hand, fast growth enables the species to outcompete other co–occurring species, thereby increasing their chances of survival relative to slow growing species. As a non–native species, *X. helleri* has adapted to the new environment and outcompeted native species for resources such as food, breeding sites, and habitat. These observations are similar to research from other parts of the world where it was found that high abundance of *X. helleri* in a system can negatively impact native aquatic biodiversity, with these impacts being exacerbated when *X. helleri* co–occurs with other introduced poeciliids such as *Gambusia affinis* and/or *Poecilia reticulata* (Goren and Galil, 2005; Mabrouki et al., 2020).

Furthermore, the study revealed that the distribution of *X. helleri* within the study area was influenced by the local hydrology and geography, particularly in relation to the pond within the LNBG and the nearby Crocodile River systems. One critical observation was that the pond, which occasionally floods and spills into the Crocodile River, empties downstream of a waterfall. This geographic feature explains the absence of *X. helleri* at the Gladdespruit River site. The waterfall acts as a physical barrier, preventing the species from moving upstream to the Gladdespruit River site, thus restricting their presence to areas below the waterfall. On the other hand, the Shisanyama River site, being downstream of the pond and the waterfall, serves as an accessible habitat for these fish. The pond's occasional overflow into the Crocodile River, coupled with the lack of significant barriers downstream, thus facilitates the incursion of *X. helleri* to the Shisanyama River site. Similar barrier effects have been observed in other *X. helleri* invasions. For instance, in the Irwin River in Western Australia, a weir was found to limit upstream dispersal, effectively restricting *X. helleri* to certain sections of the river (Morgan et al., 2004).

The population structure of fish, as depicted in length–frequency distributions, offers valuable insights that can assist in fisheries management. Understanding the size structure of fish populations is crucial for deciphering aspects such as growth, reproduction, and recruitment, with changes in size further serving as an early indicator of disturbance. The length–frequency distributions observed in this study provide snapshots of the size structure of the *X. helleri* found in the LNBG pond. A large portion of the catch fell within the range of 3.6 to 7.0 cm, and it was observed that sex affected the length frequency distribution. In this study, a significant difference in size class between sexes was observed. Male *X. helleri* were observed to have a more widely distributed length frequency compared to female *X. helleri*. Moreover, the longer lengths observed in male *X. helleri* may be attributed to their developing a distinctive 'sword' extending from the lower rays of their caudal fin (Magalhães and Jacobi 2017). In contrast, females grow more slowly and larger due to investing more energy in reproduction and egg incubation (Royle et al., 2006).

The growth rates in this study showed a faster growth curve, which can lead to earlier reproductive maturity, allowing individuals to reproduce at younger ages (Hixon et al., 2014). The findings in this study indicate that LNBG provides a suitable habitat for the growth of *X. helleri*. As an invasive fish species, *X. helleri* can have deleterious effects throughout competing with native fish species for resources and preying on native species, as has been observed elsewhere (Deacon and Magurran 2016). Significantly, while sampling *X. helleri* during the present study, other native fish species such as *P. Philander*, *O. mossambicus*, *E. eutaenia,* and *M. acutidens* were also sampled, albeit in lower abundance. This indicated that *X. helleri* may be outcompeting the native species for resources such as food, and/or they could be preying on them, resulting in their ability to grow faster. Hence, the low abundance of native species may be due to slow growth, which is subject to high mortality via starvation (little access to food resources) or predation (prolonged exposure to predation) (Grabowska and Przybylski, 2015). The latter appears more plausible, as evidenced by the presence of fish prey in the stomach of *X. helleri*. For example, stomach analyses indicated that the diet of *X. helleri* includes a significant amount of organic matter, along with smaller proportions of fish and macroinvertebrates. This dietary composition suggests that *X. helleri* functions as a generalist feeder, capable of utilizing a wide range of food resources (Kolar and Lodge, 2001). Specifically, 91.7% of the fish caught in this study were X. helleri, with only 8.3% being native species (*P. philander*, *O. mossambicus*, *E. eutaenia*, and *M. acutidens*). While this high percentage of *X. helleri* suggests their competitive presence in the LNBG pond, their impact on the low abundance of native species is due to a combination of factors, including competition for food resources and habitat, rather than primarily through direct predation.

The low value of mortality (F) in this study suggests that there were few negative factors affecting the *X. helleri* population in the pond. This may be attributed to favorable environmental conditions, as well as a potential absence or low abundance of natural predators in the system. Stoner (2004) noted that growth parameters may vary across different regions due to differences in ecological, fishing, feeding, and sampling methods. In the present study, the von Bertalanffy growth parameters for *X. helleri* were at $L\infty$ = 10.60 cm and K = 0.01

year^{-1}. In comparison, Miranda et al. (2018) reported $L\infty = 7.2$ cm and $K = 0.8$ year^{-1} for a population in Colombia, while Cunha et al. (2007) recorded $L\infty = 9.1$ cm and $K = 0.5$ year^{-1} in Brazilian waters. Bomford and Glover (2004) stated that *X. helleri* has proven invasive due to its wide environmental tolerances, which enable it to colonize anthropogenically modified habitats, as well as its high fecundity and fast growth rates. Based on the study's results, *X. helleri* demonstrated the ability to adapt to environmental conditions within the pond system, including competition pressures, with no evidence of predation by other fish in the system. As a result, they exhibited faster breeding and growth rates, enabling them to multiply rapidly and reach enhanced swimming speeds quickly (Stige et al., 2019).

In fish stocks, the exploitation rate should be lower than 0.5 to be considered sustainable, whereas stocks may be considered over–exploited if the rate is more than 0.5 (Rahman et al., 2024; Al–Beak, 2024). Our results showed that the exploitation rate was lower than that of biological reference points. Hence, the *X. helleri* in the LNBG pond is not threatened. However, the pond appears to be unfavourable for native species, and the low abundance of native species in the LNBG pond could be linked to the invasion of *X. helleri*, but more studies are required to confirm this.

4.5 Conclusion

This study highlights the invasive potential of *X. helleri* and the ability to establish and thrive in new environments, often at the expense of native species. The findings indicate that *X. helleri* swordtail fish capitalise on local resources and potentially outcompete native species for food, breeding sites, and habitat. This is concerning because the species is known to feed on macroinvertebrates and fish larvae and thus has the potential to negatively impact native species through predation. Recently, the authors of this study have made incidental catches of this species in the Crocodile River, suggesting that the species has already invaded this river system, possibly from the LNBG population. It is possible that this happened during the wet/rainy seasons, when the pond occasionally floods and drains. Given this, it is possible that the *X. helleri* was accidentally introduced to the LNBG pond, which may now act as a source population for the species' invasion into the Crocodile River. Further research is needed to fully understand the ecological impacts of *X. helleri* on other systems and to develop effective management strategies that mitigate the effects of the species on native biodiversity. While it may not be possible to completely eradicate this species from the LNBG pond, it may be possible to limit future introductions through public education and by removing this species from aquarium shops. Educational efforts could include awareness campaigns highlighting the ecological risks of releasing aquarium fish into natural or semi–natural water bodies, informative signage at botanical gardens and pet shops, and inclusion of invasive species topics in school environmental programs. Additionally, implementing or enforcing policies that restrict the sale or possession of *X. helleri*, such as mandatory labelling of potentially invasive species, public reporting hotlines, or trade bans in sensitive regions, could reduce the likelihood of future introductions.

CHAPTER 5: NO EVIDENCE FOR MULTIPLE PREDATOR EFFECTS BETWEEN A NON–NATIVE AND NATIVE WETLAND FISH

Abstract

Invasive predators may disrupt native predator–prey dynamics by modifying feeding rates and trophic interactions. Yet, the extent to which native and non–native predators jointly influence prey consumption remains insufficiently understood. Functional responses (FRs) provide a powerful framework for quantifying these dynamics and assessing the combined impacts of multiple predators during biological invasions. This study compared the FRs of the non–native swordtail fish (*Xiphophorus helleri*) and the native mouthbrooder (*Pseudocrenilabrus philander*) from a protected aquatic ecosystem in Mpumalanga, South Africa. Controlled experiments assessed prey consumption rates of both species, individually and in predator pairs, across six prey density levels using freeze–dried Chironomidae larvae as prey. Both fish species exhibited Type II FRs, with the mouthbrooder reaching higher maximum consumption rates (~14.5 prey items) compared to female swordtails (~8.1 prey items) and male swordtails (~3.6 prey items), despite having comparable attack rates. This reflects that the per capita effects of swordtails are relatively weak on native prey compared to those of mouthbrooders. Predator–predator interactions were primarily additive, with minimal non–trophic effects observed. Although swordtails exhibited weaker per capita effects compared to mouthbrooders, their invasion could still heighten overall predation pressure on prey communities if their population abundances increase. These findings underscore the importance of understanding trophic interactions in managing invasive species and maintaining ecological balance in protected areas.

Keywords: Attack rates; consumer–resource; feeding rate; functional responses; handling times; predator–prey interactions; *Pseudocrenilabrus philander*; *Xiphophorus helleri*

5.1 Introduction

Predator–prey interactions are fundamental to understanding ecosystem dynamics, as they regulate population sizes, influence community structures, and maintain ecological balance (Drossel et al., 2001; Lima, 2002). These interactions are shaped by various biotic and abiotic factors, including species–specific traits, prey availability, and environmental conditions (Laws, 2017; Luger et al., 2020; Cuthbert et al., 2021; Munyai et al., 2022). In aquatic ecosystems, predators play a critical role in regulating prey populations and maintaining ecosystem balance (Beauchamp, 2007). However, the direction (positive or negative) and strength of these effects can change significantly following biological invasion, as invasive predators may disrupt native predator–prey dynamics, leading to shifts in community structure and ecosystem functioning (Ricciardi and MacIsaac, 2000). The foraging strategies of predators further drive predator–prey dynamics, influencing the overall functioning of ecosystems (Embling et al., 2012; Singh et al., 2024).

Trophic interactions and food webs involve both density–mediated (consumptive) and trait–mediated (non–consumptive) processes, with the former often driven by waterborne cues in aquatic environments (Hughes, 2012; Alexander et al., 2013; Ng and Gaylord, 2020). Although density–mediated effects have received more attention in the literature (Werner and Peacor, 2003; Abrams, 2007; Munyai et al., 2022), trait–mediated effects are also important, especially when considering multiple predator effects (MPEs). Predator–predator interactions typically take three forms, including (i) additive, where predators act independently with predictable feeding rates and multiple predator feeding rates are predictable based on individuals (i.e., a lack of MPE); (ii) antagonistic, where interference reduces overall predation impact; and (iii) synergistic, where interactions between predators amplify their combined effect on prey (Soluk, 1993; Sih et al., 1998; Chase et al., 2002).

Functional response (FR) models provide a framework for quantifying predation impacts as a function of resource density (Solomon, 1949; Holling, 1959). These models describe the relationship between prey consumption rates and prey density, offering valuable insights into population regulation and stability in ecological systems (Hunsicker et al., 2011; Cuthbert et al., 2019a). Studies of FRs have identified three main types: linear (Type I), hyperbolic (Type II), and sigmoidal (Type III), each with implications for prey population stability (Holling, 1959; Buxton, 2020). Type II FRs, common in aquatic predators, suggest high consumption at low prey densities, which can destabilize prey populations (Joyce et al., 2019; Dick et al., 2014). Conversely, Type III FRs stabilize prey populations by reducing predation pressure at low densities (Hassell, 1978). These FR types are influenced by predator density, environmental variability, and interspecific or intraspecific interactions (Munyai et al., 2022; Gatto and Travis, 2024). FRs have been recently used to quantify the impacts of current and potential invasive species, benchmarked against trophically–analogous native species (Faria et al., 2023, 2025). These studies have generally shown that non–native species tend to display higher feeding rates than native comparators, especially in aquatic ecosystems, which are most vulnerable.

Assessments of the ecological impacts of invasive species are particularly important in protected areas, which are expected to expand substantially in the future under the targets of the Global Biodiversity Framework. Protected areas are vital for biodiversity conservation, serving as sanctuaries that safeguard ecosystems, species, and habitats from human–induced disturbances (DeFries et al., 2007; Kantharajan et al., 2022). Their primary objectives include preserving biodiversity, promoting the sustainable use of natural resources, and maintaining ecological balance (Margules and Pressey, 2000; Araújo et al., 2002; Barrios-O'Neill et al., 2015). Although multiple predatory species coexist in protected areas, biological invasions can modify their interactions, potentially altering predator–prey dynamics and ecosystem stability. This knowledge is particularly crucial in invaded protected areas, where effective management of invasive species and their potential predatory effects is essential to maintaining ecological balance.

The green swordtail *(Xiphophorus helleri* Heckel, 1848*)* is known for its active foraging behaviour and potentially high consumption rates (Pilakouta and Alonzo, 2014), while *Pseudocrenilabrus philander* (Weber, 1897) exhibits predation efficiency shaped by its reproductive and foraging adaptations (Weller et al., 2022). As a non–native species, the swordtail poses ecological challenges to freshwater ecosystems, including competition with and predation on native species, which can potentially disrupt ecosystem stability (Ellender and Weyl, 2014). In contrast, the native mouthbrooder has coevolved within its environment and exhibits behavioural traits such as lower aggression and specialized parental care, which contribute to stable community dynamics (Abecia et al., 2022; Weller et al., 2022).

This study, conducted in a pond located within the protected area of the Lowveld National Botanical Garden, aimed to examine the feeding interactions of the two co–occurring species, the native mouthbrooder (*P. philander*) and the non–native swordtail (*X. helleri*), towards a readily consumed prey (Chironomidae), under multi–predator scenarios using a comparative FR approach. Specifically, we investigated how conspecific and interspecific interactions influence prey consumption across varying prey densities. We hypothesized that the mouthbrooder, although potentially a generalist, would exhibit higher attack rates and efficiency at low prey densities, as native species are typically well adapted to local prey types and foraging conditions, giving them a competitive advantage over non–native species at lower resource levels. In contrast, the generalist swordtail would demonstrate higher overall consumption rates, potentially dampening the consumption rates of the native species. We also hypothesized that interspecific MPEs would be more noticeable than conspecific ones due to interference, resulting from potential competitive interactions between different predators.

5.2 Methods

5.2.1 Fish sampling

Swordtails (*X. helleri*) and mouthbrooders (*P. philander*) were collected in November 2024 from a single pond located within the protected area of the Lowveld National Botanical Garden (LNBG), Mbombela (25°26'42"S, 30°57'57"E). The garden functions as a key refuge for the conservation of rare and threatened plant species (Van der Walt 2010). As the study relied on a single–source population, caution should be exercised when generalizing the findings to other systems or populations. Fish were captured using three single–ended fyke nets (24 mm mesh size), deployed overnight (i.e., from 1600 to 0800), with an average soak time of 14 hrs at different points within the pond. A total of 270 Swordtails and mouthbrooders were retained and transported to the laboratory in 25–L buckets filled with source water over a short distance (1.4 km), without active aeration. All other fish species were released back into the pond. Experiments were conducted in a laboratory at the University of Mpumalanga, South Africa. Upon arrival, fish were housed in nine 25–L open buckets (30 individuals per bucket), separated by species and sex (male swordtails, female swordtails, and mouthbrooders). Buckets contained filtered source water and were continuously aerated using an air pump to maintain dissolved oxygen levels during the short acclimation period. Prior to the experiments, all fish were acclimatized for 2 days at 25°C under continuous light, approximating the conditions of their collection site. On the third day, fish were starved for 24 h in their respective buckets, separated by species and sex, prior to the experiments. The experiments were conducted in 168 individual 1–L open polyethylene buckets, each containing a single treatment and filled with 500 mL of filtered water sourced from a 50:50 mixture of stream and pond water. The buckets were arranged in a randomized design within the laboratory to minimize positional effects. To ensure accurate comparison of feeding rates, the fish used in the trials were size–matched based on total length (TL) (Swordtail female (mean ± SD) = 6.5 ± 0.4 cm TL; Swordtail male = 6.8 ± 0.5 cm TL; Mouthbrooder = 6.7 ± 0.3 cm TL), to minimize the effect of size between species.

5.2.2 Experimental design

The experimental treatments were (1) Swordtail female, (2) Swordtail male, (3) Mouthbrooder, (4) Swordtail female + Swordtail female, (5) Swordtail male + Swordtail male, (6) Swordtail female + Swordtail male, (7) Swordtail male + Mouthbrooder, and (8) Swordtail female + Mouthbrooder. For the functional response (FR) experiment, dead chironomid larvae (*Chironomus* sp.) were used as prey across all treatments. Each predator treatment included six prey density levels (2, 4, 8, 16, 32, and 64 individuals), with six randomized replicates for each fish group (i.e., 8 fish treatments × 6 prey densities × 6 replicates). After allowing the fish to acclimate for two hours, prey was introduced into the experimental buckets, and the fish were allowed to feed for four hours (13:00 to 17:00). Afterwards, the fish were removed from the arenas, and the remaining prey were counted to quantify numbers eaten. Predators were used once during the experimental trial to reduce the effects of intra–individual variation. Following the experiments, all fish were humanely euthanized according to the guidelines outlined by Weyl et al. (2016) and disposed of as biohazard material, in compliance with the University of Mpumalanga’s approved animal ethics protocol.

5.2.3 Statistical analyses

Generalized linear models (GLMs) were used to categorize functional response (FR) types for the three single predator treatments (Pritchard et al., 2017; Juliano, 2020). The GLM related the proportion of prey consumed to initial prey density using a binomial error distribution and logit link function:

$$\text{logit}\,(\frac{N_e}{N_0}) = \beta_0 + \beta_1 N_0 + \beta_2 N_0^2 \tag{1}$$

where $N_e$is the number of prey consumed, $N_0$is the initial prey density, and $\beta_1$and $\beta_2$indicate the direction of density dependence used to distinguish FR types. A significantly negative $\beta_1$indicates a Type II FR, whereas a significantly positive $\beta_1$coupled with a significantly negative $\beta_2$indicates a Type III FR. Prior to interpretation, GLM residuals were examined for overdispersion, independence, and appropriate model fit using dispersion statistics and diagnostic plots. Since prey were not replaced after consumption during the experiment, Rogers' random predator equation was used to model FRs (Rogers, 1972):

$$N_e = N_0(1 - \exp(a(N_e h - T))) \tag{2}$$

where 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 (Pritchard et al., 2017). Rogers' random predator equation is robust to prey depletion in parameter estimation (Cuthbert et al., 2020). The FR models were bootstrapped 2000 times to generate unbiased 95 % confidence intervals (Pritchard et al., 2017).

To estimate the feeding rates of multiple predators, we used the attack rate (a) and handling time (h) estimates derived from single predator feeding rates (FRs) in the absence of other predators (equation 2). These predicted values were then compared to the observed feeding rates in multiple predator groups. The comparison was conducted separately for conspecific and heterospecific groups using the respective single–predator FR parameters. Feeding rate predictions were made following the methods of McCoy et al. (2012) and Sentis and 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 FR estimates. This model assumes no emergent effects from multiple predators, and its predictions can be compared to observed multiple predator feeding trials to assess the direction and strength of these effects. To predict expected prey survival from the multiple predator experiments, initial values of N and P were set to the initial prey and predator densities used in the experimental treatments. For each predator treatment and prey density, equation 3 was integrated over the entire experimental duration to calculate the expected number of surviving prey.

We measured interaction strength (IS) as the proportion of prey killed at each predator density, water volume, and prey density by dividing the number of prey consumed by the initial prey density (Veselý et al., 2019).:

$$\mathrm{IS}(P, Z) = \frac{N_P - N_{P,Z}}{N_P} \tag{4}$$

where N_P and $N_{P,Z}$ are the numbers of live prey at the beginning and end of the experiment, respectively. The proportion of prey killed (IS) encompasses both trophic interactions (feeding on prey) and non–trophic interactions that can either enhance (e.g., facilitation among predators) or reduce (e.g., interference among predators) trophic interactions. Multiple predator effects, including interference effects (i.e., $\mathrm{IS}_{\mathrm{NT}}$), were calculated by subtracting the mean IS_{T} (predictions; equation 4) from the observed IS. Positive and negative values of $\mathrm{IS}_{\mathrm{NT}}$ indicate an increase or decrease in prey risk, respectively. All statistical analyses were performed in R v4.0.2 (R Core Team, 2020).

Multiple predator effects were analysed using linear models, separately for conspecific and heterospecific groups. Homogeneity of variances and residual normality were examined using simulation analyses (Hartig et al., 2022). To account for potential non–linear effects of prey density (Sentis et al., 2017), we compared models with the prey density covariate included as linear and quadratic terms via AIC, to select the model that minimised information loss. Model selection was conducted using Akaike's Information Criterion corrected for small sample sizes (AICc), which is recommended when the sample size is small relative to the number of model parameters (Burnham and Anderson, 2002).

5.3 Results

5.3.1 Single predator functional responses

Functional responses of single swordtails of both sexes and mouthbrooders were characterized as Type II, owing to significantly negative first–order terms (Table 5.1). Significant estimates of attack rates and handling times were returned for all treatment species, with attack rates and handling times tending to be highest (and maximum feeding rates lowest) in male swordtails, whereas handling times were lowest and maximum feeding rates were greatest in mouthbrooders (Table 5.1). The functional responses of all species had overlapping confidence intervals across all prey densities, indicating that while trends suggested greater consumption by mouthbrooders, these differences were not statistically significant (Figure 5.1).

Table 5.1. Functional response parameters of study species, from logistic regression (first–order terms) and Rogers' random predator equation (attack rate and handling time).

Species	**First–order term (*p*–value)**	**Attack rate (*p*–value)**	**Handling time (*p*–value)**	**Maximum feeding rate**
Swordtail (F)	–0.01 (0.02)	0.33 (0.01)	0.12 (0.01)	8.07
Swordtail (M)	–0.031 (< 0.001)	0.483 (0.04)	0.280 (< 0.001)	3.57
Mouthbrooder	–0.014 (0.01)	0.431 (< 0.001)	0.069 (0.001)	14.49

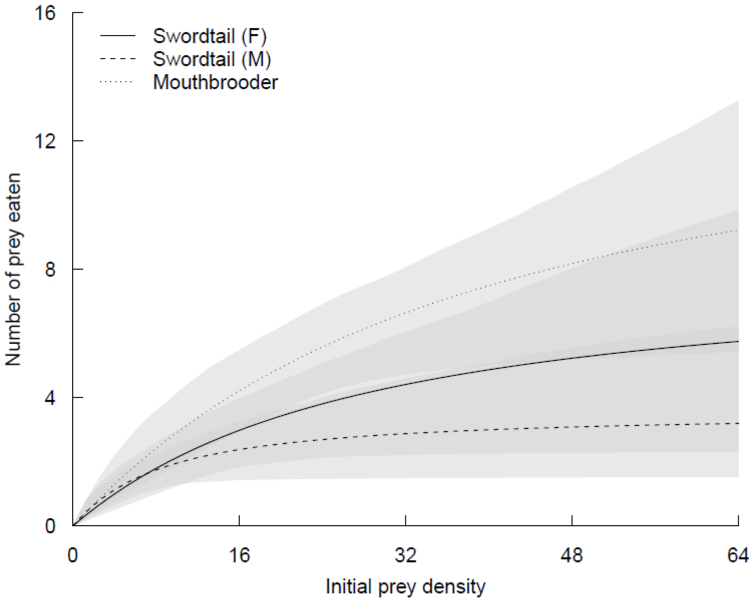

Figure 5.1. Functional response curves (with bootstrapped non–parametric 95% confidence intervals) of the study fish species. Fits are from Rogers' random predator equation (Rogers, 1972).

5.3.2 Multiple predator effects

Non–trophic interaction strengths from multiple predator treatments consistently overlapped zero, indicating that there were no substantive non–trophic interaction strengths between conspecific or heterospecific groups (Figure 5.2). Including prey supply as a linear term minimised information loss in both models compared to non–linear (quadratic) terms (dAIC > 2.0). There were no significant differences among study species in terms of non–trophic interaction strengths in both the conspecific ($F_{(4,11)}$ =1.62, p = 0.18) and heterospecific ($F_{(4,11)}$

=1.99, *p* = 0.10) groups. Prey supply always significantly decreased non–trophic interaction strengths (conspecific: *t* = 2.12, *p* = 0.04; heterospecific: *t* = 2.37, *p* = 0.02), suggesting that antagonisms were more to be detected at higher prey supplies (Figure 5.2).

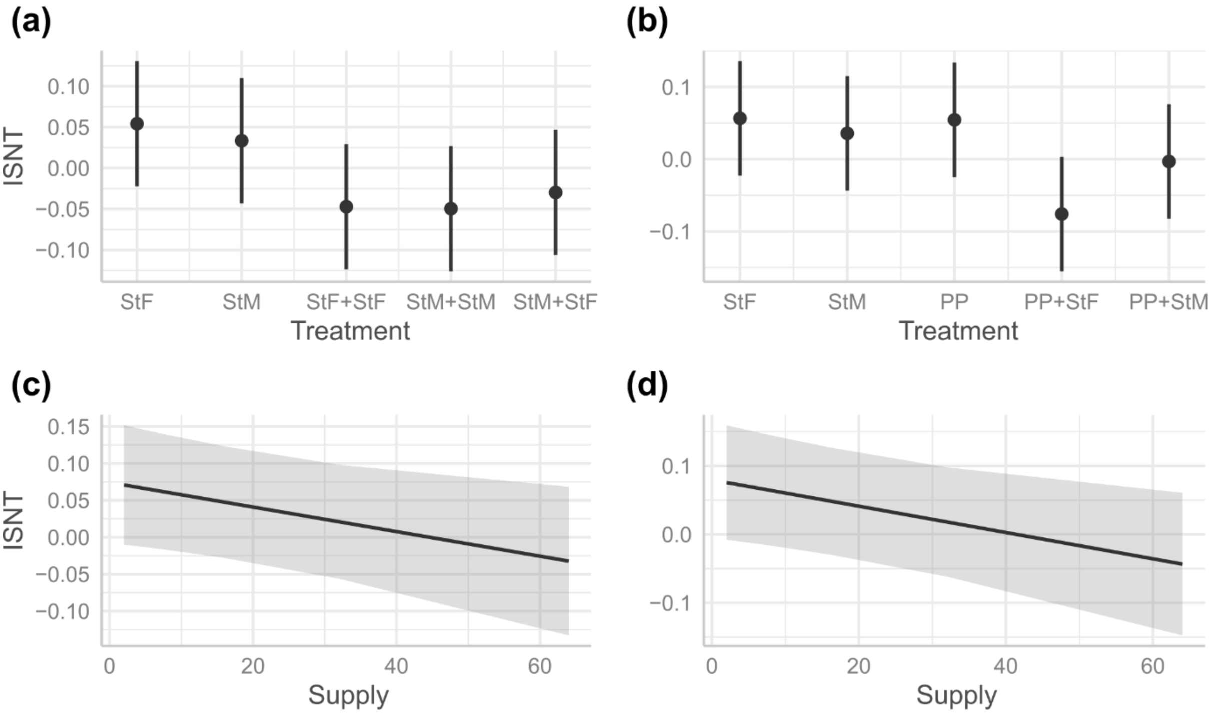

Figure 5.2. Non–trophic interaction strengths (ISNT) as a function of study species treatment (a, b) and prey supply (c, d), grouped into conspecific (a, c) and heterospecific (b, d) treatments. Outputs are from linear models, with 95% confidence intervals displayed. Zero y values indicate an absence of non–trophic interaction strength. Note that the y–axis scale differs among subplots. Abbreviations: StF (female swordtail), StM (male swordtail), PP (mouthbrooder).

5.4 Discussion

Predation plays an important role in ecosystem structuring and functioning of aquatic systems (Carpenter et al., 1985; Wasserman et al., 2013). Thus, it is crucial to understand predator–prey dynamics to accurately quantify interaction strengths between trophic levels, particularly in the context of biological invasions that can disrupt food webs. In this study, we explored these dynamics in non–native and native fish collected in a protected area using a comparative FR approach. In predator–prey interactions with single predators, our predictions that the mouthbrooder would exhibit higher attack rates and efficiency at low prey densities, while the swordtail would demonstrate higher overall consumption rate*s,* were not supported. In fact, the native species exhibited substantially higher feeding rates than non–natives, with much greater maximum feeding rates and similar attack rates. Our study further revealed additive effects for both interspecific (swordtail and mouthbrooder) and conspecific predator pairs, indicating that predator impacts were independent and predictable from their single–species effects. This means that, following invasion, consumption rates of natives are not impeded by non–natives, leading to a potential increase in total trophic interaction strengths from predators, depending on their population–level responses.

The study revealed that the feeding rates for both predators exhibited a significant decrease in the proportion of prey consumed as prey densities increased across treatments. Feeding rates increase with prey density, but at a decreasing rate, indicating a Type II functional response, where the proportion of prey consumed declines as prey density increases (Cuthbert et al., 2019b). This pattern suggests that, at higher prey densities, consumption rates were limited by handling time in all predator treatments (Holling, 1959; Cuthbert et al., 2021). The overall proportion of prey consumed by single predators was generally lower compared to that of multiple predators. These results suggest that predator effects are additive: increasing predator numbers raises total prey consumption but does not enhance individual predator efficiency. Despite this, the mouthbrooder exhibited a higher maximum feeding rate than the swordtail, which may be explained by differences in their morphology and feeding behaviour. As a cichlid, the mouthbrooder has a more robust jaw structure and a greater ability for oral manipulation, allowing it to handle and consume prey more efficiently (Wainwright et al., 2007). In contrast, the swordtail, with its less specialized jaw structure, is suited for more opportunistic feeding and may be less efficient at rapidly consuming prey (Zandona et al., 2011). Similarly, Munyai et al. (2022) observed higher attack rates and maximum feeding rates of native species, such as the Mozambique tilapia (*Oreochromis mossambicus*), which were linked to their jaw morphology and prey–handling strategies. Similarly, *P. philander* demonstrated greater feeding efficiency compared to the non–native *X. helleri*, which may contribute to its functional role within native food webs. However, it remains uncertain whether these feeding efficiencies translate into meaningful impacts on prey populations or community structure in natural ecosystems, given the controlled nature of the experiment and the complexity of in *situ* ecological dynamics.

The study further suggests that the behavioural differences between male and female swordtails were evident in their attack rates, handling times, and maximum feeding rates, suggesting potential sex–based ecological roles or energetic constraints. Male swordtails demonstrated a higher attack rate (0.483) than females (0.327), suggesting that they are more aggressive or efficient at detecting and pursuing prey. This may be a compensatory behaviour linked to their generally higher energy demands for mate competition and display structures, such as the elongated caudal fin, which increases hydrodynamic drag (Langerhans et al., 2005). However, their longer handling time (0.280) compared to females (0.124) suggests that, despite a higher initial prey capture rate, males may be less efficient at processing or consuming prey. This trade–off may reflect species–specific morphological or behavioural traits that influence prey capture and handling efficiency.

Moreover, female swordtails achieved a higher maximum feeding rate (8.065 prey items) than males (3.571 prey items), even though both sexes were closely size–matched. This suggests that females may have a greater capacity to process and consume prey, potentially due to their reproductive investment requiring higher energy intake. The relatively lower feeding rate observed in male swordtails may reflect a trade–off between foraging efficiency and the energetic or functional costs of maintaining sexually selected traits, such as body coloration and fin extensions. While beneficial for attracting mates, these traits can impair mobility or increase predation risk, thereby reducing foraging performance. Similar sex–specific differences in feeding behaviour have been reported in other poecilid fishes, such as *Poecilia reticulata*, where males and females differ in foraging strategies due to a combination of genetic, plastic, and social factors (Earl et al., 2024).

These results also suggest that combinations of similarly sized fish species may exhibit limited interference during prey foraging, potentially resulting in minimal predator–predator interactions. Regarding predator–predator interactions, the study found no significant non–trophic interaction strengths between conspecific and heterospecific predator pairings, indicating predominantly additive effects. This aligns with the findings of Sih et al. (1998), Vance–Chalcraft and Soluk (2005), Griffen (2006), McCoy et al. (2012), and Sentis and Boukal (2018), which indicate additive feeding rates in multiple predator scenarios, suggesting limited interference or facilitation among predators. This finding suggests that, under the conditions of this experiment, total predator impacts appear largely additive, which could simplify modelling in similar multi–predator systems. However, given the limitations of this study, caution is warranted when extrapolating these results. Furthermore, prey density was found to have a strong influence on predation rates. Previous studies on MPEs have reported a unimodal response, where predation rates peak at intermediate prey densities before declining at higher densities (Sentis et al., 2017). Prey availability thus plays a crucial role in shaping predator interactions, as emphasised by Sentis and Boukal (2018).

Interestingly, the lack of significant differences in non–trophic interaction strengths between conspecific and heterospecific groups might suggest that the swordtail and mouthbrooder share similar behavioural or foraging strategies, resulting in comparable interaction strengths. This contrasts with the hypothesis that interspecific pairings would exhibit greater complementarity in foraging strategy. Instead, the findings suggest that competition for shared prey resources may reduce synergistic effects (Chase et al., 2002). However, since only one prey type was tested, it is difficult to determine whether this outcome reflects actual behavioural similarity or simply results from the limited resource. Further research using a broader range of prey types is needed to explore potential differences in foraging behaviour and resource use.

Despite our findings, it is essential to acknowledge potential limitations in our methodology. While this study utilized thawed, frozen chironomid larvae as prey during the experiments, we recognize that using live prey might have produced different outcomes due to potential behavioural responses to varying predator or prey densities. However, our approach intentionally excluded prey behaviour to concentrate solely on the effects of predator–predator interactions on the functional response between these fish species. Additionally, the use of small experimental arenas with minimal habitat complexity could have introduced confinement effects, potentially amplifying or mitigating trophic (predator–prey) and non–trophic (predator–predator) interactions (Uiterwaal et al., 2018). Consequently, while extrapolating these results to the natural pond systems should be done cautiously, laboratory experiments under controlled conditions remain valuable for comparative analyses of species interactions. These controlled settings help identify interaction strengths without interfering with broader ecological mechanisms. Although no significant predator–predator interactions were detected in this study, it is possible that such interactions might manifest in larger, more complex ecosystems. As such, our results should be interpreted as suggestive rather than conclusive, highlighting potential patterns that warrant further investigation under natural conditions.

Understanding the biotic processes that influence the structure and functioning of ecosystems within protected areas is essential. Recent studies have highlighted the importance of examining individual consumer variability within populations in these habitats (Atkinson et al., 2017; Carneiro et al., 2024). While existing data on trophic interactions in single predator–

prey dynamics provide valuable insights into the strength of MPEs, further investigation into both interspecific and conspecific interactions is crucial. This is particularly important in the context of fish predation, a significant impact mechanism in invasive fish (Bernery et al., 2022), as fish play a key role in driving top–down trophic cascades and shaping the structure and functioning of invertebrate communities, including the presence of Chironomidae. Thus, although fish may often represent transient components of a community (Hastings et al., 2017), their influence cannot be excluded when examining factors that contribute to the functional ecology of protected area ecosystems.

5.5 Conclusion

Under the controlled conditions of this study, the native mouthbrooder demonstrated higher feeding efficiency and maximal consumption rates than the non–native swordtail, suggesting a potential advantage in prey exploitation within its native range. Both species exhibited Type II functional responses, indicating the potential for destabilizing effects on prey populations at low densities. Predator interactions, both conspecific and heterospecific, appeared largely additive, suggesting limited interference or facilitation among predators under the conditions tested. These findings underscore the important influence of prey density on predator dynamics and competition, as negative non–trophic interactions increased with higher prey availability. While these patterns may inform hypotheses about multi–predator dynamics in natural systems, caution is warranted when extrapolating to field conditions. Further research is needed to assess whether managing prey populations can influence predator impacts in more complex, ecologically realistic settings.

CHAPTER 6: EVALUATING THE EFFECTIVENESS OF CURRENT MANAGEMENT STRATEGIES FOR AQUATIC INVASIVE SPECIES IN PROTECTED AREAS IN MPUMALANGA PROVINCE, SOUTH AFRICA

Abstract

Aquatic invasive species pose a significant threat to biodiversity and ecosystem functioning wherever they occur, including in protected areas that are intended to conserve native and often endemic species. Despite increasing awareness of their ecological and economic impacts, the management of aquatic invasive species is still not fully integrated or consistently prioritised within broader conservation strategies. This study assessed the efficacy of current management strategies for aquatic invasive species in protected areas managed by the Mpumalanga Tourism and Parks Agency (MTPA), the South African National Biodiversity Institute (SANBI), and the South African National Parks (SANParks) in the Mpumalanga province of South Africa. A qualitative approach was employed, utilizing semi–structured interviews with eight senior conservation staff members from various protected areas. Thematic analysis was used to assess perspectives on management experience, species presence, perceived threats, and control measures. Results revealed significant gaps in aquatic invasive species management, including the absence of species checklists, inconsistent monitoring, limited formal training, and inadequate funding. While some participants reported collaborative efforts and the use of adaptive strategies, many reserves lacked baseline data and clear decision–making frameworks. The findings suggest that although awareness of aquatic invasive species threats exists, practical implementation of management strategies remains limited and fragmented. Constraints such as inadequate funding and insufficient targeted training impede the effective implementation of aquatic invasive species management strategies. Strengthening aquatic invasive species management in Mpumalanga’s protected areas requires long–term funding, targeted training, improved documentation of invasive species data and management strategies, and inter–agency collaboration. These steps are essential for enhancing proactive and science–based management of aquatic invasive species and safeguarding native freshwater biodiversity.

Keywords: Aquatic invasive species, protected areas, biodiversity conservation, management strategies, freshwater ecosystems

6.1 Introduction

In the Anthropocene, humans are widely regarded as the dominant influence on the planet, responsible for significant ecological changes and contributing to biodiversity loss (Vitousek et al., 1997; Folke et al., 2021). Although humans have altered the planet in numerous ways, the facilitated movement of species, whether accidental or intentional, has led to an ever–increasing number of new species introductions and their establishment in non–native areas (Seebens et al., 2017). Aquatic invasive species, typically non–native or alien species, represent one of the most pressing challenges to conserving biodiversity in protected areas. These species, often introduced through human activities such as shipping, aquaculture, and recreational activities, have the potential to drastically alter the ecosystems they invade (Chan et al., 2019; Wasserman et al., 2019; Weyl et al., 2020). Protected areas, which are critical for preserving native species and maintaining ecological balance, are not immune to the threats posed by aquatic invasive species (Rico–Sánchez et al., 2020). These areas serve as refuges for a diverse array of flora and fauna, many of which are already under pressure from other anthropogenic factors such as climate change, habitat destruction, and pollution (Mora and Sale, 2011; McNeely, 2020).

The introduction of aquatic invasive species can trigger a cascade of ecological changes at different scales, with the most severe consequences including the displacement or extinction of native species through mechanisms such as competition, predation, or hybridization (Jones et al., 2021; Adeniran–Obey et al., 2024; Sayer et al., 2025). They can also cause changes to abiotic factors, such as nutrient cycling, which lead to alterations in the diversity and fitness of plant and animal communities (Vilà et al., 2011). These effects are amplified by traits commonly associated with invasive alien species, such as rapid reproduction, broad environmental tolerance, and high dispersal potential (Whitney and Gabler, 2008; Havel et al., 2015). Certain aquatic plants, particularly invasive alien species, for example, have been shown to increase turbidity, organic matter, and greenhouse gas emissions while reducing the diversity of native macrophytes (Gallardo et al., 2016; Bezabih Beyene et al., 2022; Tasker et al., 2022). In freshwater environments, the rapid spread of aquatic invasive species is facilitated by the connectivity of water bodies, often leading to the displacement of sensitive or endangered species (Zedler and Kercher, 2004; Jones et al., 2021; Havel et al., 2015).

Invasive species not only drive significant and potentially long–lasting ecological changes but also cause substantial economic damage globally, with estimated costs exceeding USD 1.3

trillion between 1970 and 2017, comparable to those of natural disasters (Diagne et al., 2021b; Turbelin et al., 2023). Invasive alien species, including aquatic invasive species, contribute to these financial burdens, influencing various sectors of the economy (Cuthbert et al., 2021; Diagne et al., 2021b; Fantle–Lepczyk et al., 2022). These costs are further exacerbated when considering the expenses associated with management and control efforts (Jardine and Sanchirico, 2018). Therefore, effective management of aquatic invasive species is a crucial component of ecosystem management and conservation in freshwater systems.

Effective management of aquatic invasive species in protected areas requires a strategic approach to control and eradication (Otero et al., 2013). While preventing the introduction of invasive alien species is the most effective long–term strategy (Mack et al., 2000), many species establish undetected before intervention is possible, often through cryptic invasion that creates detection and management delays (Morais and Reichard, 2018). Once established, aquatic invasive species can be challenging to manage because their underwater habitats hinder early detection, often allowing them to spread rapidly and form persistent populations (Adeniran–Obey et al., 2024). Management options range from deliberate inaction, where intervention is deemed not cost–effective or ecologically unjustified, to implementing control or eradication measures (Simberloff, 2021). Resource managers have various control methods at their disposal, including biological, chemical, and mechanical techniques, each with varying levels of effectiveness depending on species–specific and environmental conditions (Hussner et al., 2017). The selection of an appropriate management strategy must consider not only the potential for successful control but also the risk of unintended ecological consequences, such as facilitating secondary invasions by other non–native species (Robichaud and Rooney, 2021).

Therefore, evaluating the effectiveness of current management strategies is crucial to determining which methods yield the best results in reducing aquatic invasive species populations while minimizing ecological disruptions in protected areas (Garcia–Lozano et al., 2025). Despite extensive research on specific invasive species, developing effective management strategies for aquatic invasive species in protected ecosystems remains a complex and ongoing challenge (Jones et al., 2021). This study assessed the effectiveness of existing management strategies for controlling aquatic invasive species in protected areas, with a focus on identifying the most successful approaches and potential areas for improvement. We hypothesized that limited budgets hinder the effectiveness of aquatic invasive species management strategies in protected areas. The findings of this study will provide valuable insights to enhance ecosystem management and inform future control efforts.

6.2 Methods

6.2.1 Research ethics

Ethical approval for this study was granted by the University of Mpumalanga Research Ethics Committee, with the reference number AS/TDalu 01–150322, and prior to conducting the research, permission was obtained from the Mpumalanga Tourism and Parks Agency (MTPA), the South African National Biodiversity Institute (SANBI), and South African National Parks (SANParks) to conduct interviews with personnel involved in invasive species management. The research proceeded after obtaining informed consent from the participants, ensuring their privacy and confidentiality by maintaining secrecy and anonymity. To protect the identity of participants and their affiliated institutions, the protected areas were anonymized using letter “A” to “H” (See Table 6.2).

6.2.2 Study area

The study was conducted in protected areas located within Mpumalanga Province, South Africa, and managed by three key conservation authorities: the Mpumalanga Tourism and Parks Agency (MTPA), the South African National Biodiversity Institute (SANBI), and South African National Parks (SANParks). The MTPA is a provincial body responsible for managing nature reserves and promoting tourism within Mpumalanga. In contrast, SANParks is a national agency responsible for overseeing South Africa’s national parks, including the Kruger National Park, which spans the Mpumalanga province. The SANBI, also a national institution established under the National Environmental Management: Biodiversity Act, focuses on biodiversity research and managing national botanical gardens, rather than direct protected area management. These organizations are responsible for managing a range of biodiversity–rich areas, including wetlands, rivers, grasslands, and forest ecosystems. The selected protected areas span various ecological zones and play a critical role in conserving endemic and threatened species. Mpumalanga is recognized for its high conservation value and includes nationally and internationally significant sites, such as Ramsar wetlands and parts of the Kruger to Canyons Biosphere Reserve.

6.2.3 Sampling and data collection

A qualitative approach involving in–depth, semi–structured interviews was used to assess and understand interviewees' perspectives on the effectiveness of management strategies for controlling aquatic invasive species in protected areas (Babbie, 2020; Table 6.1). A total of eight participants were interviewed, consisting of individuals actively engaged in invasive species management, including protected area managers, ecologists, conservation officers, and senior reserve rangers. Of these, six participants were from the MTPA, one from SANParks, and one from SANBI. Four participants were interviewed in person, while the remaining four completed a Google Forms questionnaire that included the same core questions used in the interviews. Interviews were conducted in either English or SiSwati, depending on the participant's preference, and each session lasted between 30 and 40 minutes.

6.2.4 Data analysis

The study applied a deductive thematic analysis approach to analyze and interpret the data (Dalu et al., 2020; Mabadahanye et al., 2025). Thematic analysis is a method used to identify recurring patterns or themes within qualitative data, thereby gaining a deeper understanding of a particular topic (Maguire and Delahunt, 2017). In this study, coding was conducted as part of the analytical process following data collection. Codes represent the smallest unit of analysis, highlighting relevant aspects of the data related to the study's focus. This method offers a structured process for extracting codes and organizing them into broader themes that reflect the key insights from the study (Mabadahanye et al., 2025). Codes represent the smallest unit of analysis, highlighting relevant elements within the data that align with the study's objectives. These codes were then systematically grouped into larger themes that reflected key patterns and insights emerging from the participants' responses (Mabadahanye et al., 2025).

Table 6.1. The study's interview questions were administered to MTPA, SANBI, and SANParks–protected areas in Mpumalanga Province.

Question No.	Questions	Theme
1	How long have you been involved in conservation and the management of aquatic invasive species?	1
2	What is your educational background, and any relevant training related to conservation and aquatic species management?	1
3	Do aquatic invasive species pose a threat to your protected area? If yes, why?	2
4	Does this protected area have documented checklists of aquatic invasive species (both plants and animals)? How frequently is it updated?	2
5	Which aquatic invasive species are currently the most problematic in your protected area, and why are they considered harmful?	3
6	What management strategies are currently in place to control aquatic invasive species?	4
7	How do you decide which management method to use for different aquatic invasive species?	4
8	What have been the most noticeable impacts of aquatic invasive species in your protected area?	3
9	What methods do you use to assess whether invasive species management strategies are effective?	4
10	What management strategies have been most effective in controlling aquatic invasive species? What factors contribute to their success or failure?	4
11	What are the key challenges you face in managing invasive species in this protected area?	3
12	Do you collaborate with other organizations, researchers, or government agencies to manage invasive species? If so, how?	5
13	What improvements or resources would help enhance the effectiveness of invasive species control efforts in your area?	5
14	Is there anything else you would like to add regarding invasive species management in your protected area?	5

The semi–structured interviews were structured into five research themes that covered a broad range of factors: (1) Experience and expertise (question 1 and 2), (2) Threats and species presence (question 3 and 4), (3) Species impact and management challenges (questions 5, 8, and 11), (4) Management strategies and decision–making (questions 6, 7, 9 and 10), and (5) Collaboration and resource availability (questions 12, 13 and 14). As part of the coding process, specific codes were allocated to each response based on the topics and interview questions. For example, the code T3/A/Q5 represents Theme 3 (Management Strategies and Decision–Making), Nature Reserve A, and Question 5 (Tables 6.1 and 6.2). This coding system helped to organize and analyze responses consistently across all participants.

Table 6.2. Positions of participants interviewed from MTPA, SANBI, and SANParks protected areas in Mpumalanga Province.

Protected area	**Reserve manager**	**Ecologist**	**Control scientist**	**Section ranger**
A	×			
B			×	
C				×
D	×			
E			×	
F		×		
G				×
H		×		

6.4 Results and discussion

6.4.1 Experience and expertise

Participants had various levels of experience in conservation, ranging from three to forty–two years. The most experienced participant, from nature reserve F, had forty–two years of experience, while the least experienced, from nature reserve H, had only three years (Figure 6.1). The participants' educational qualifications included PhD, MSc, BSc, and Diplomas in the fields of Zoology, Fisheries Sciences, Aquatic Health, Wildlife Management, and Forestry. While these qualifications demonstrate a strong foundation in biodiversity and environmental management, most participants lacked specialized training in aquatic invasive species.

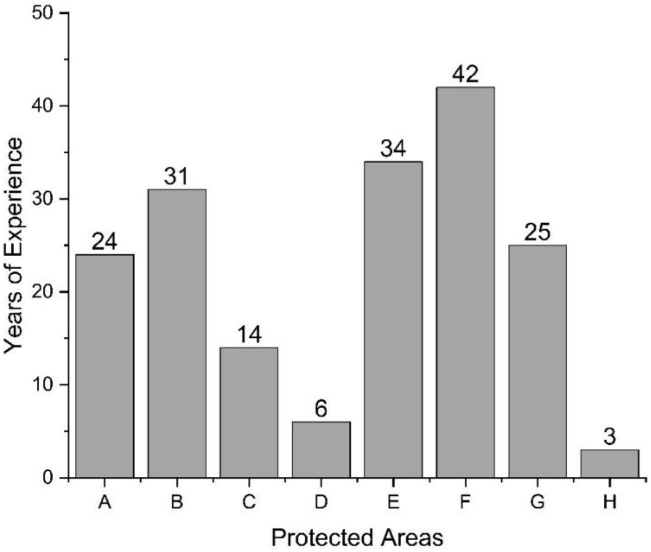

Figure 6.1. Years of experience of participants from MTPA, SANBI, and SANParks across protected areas.

Effective management of aquatic invasive species depends not only on awareness but also on technical expertise, specialized training, and ecological understanding. In this study, only one out of the eight participants indicated having formal training in aquatic health, while the remaining seven had educational backgrounds primarily focused on terrestrial ecosystems or general conservation. This highlights a significant knowledge gap in aquatic invasive species–specific expertise, which could contribute to the relatively low prioritization of aquatic invasive species within protected area management in Mpumalanga. While Hilton et al. (2023) emphasize that diverse expertise among practitioners can enhance adaptive management, this study highlights the absence of such diversity across protected areas, potentially limiting effective aquatic invasive species responses. To ensure that managers of protected areas have the necessary skills and knowledge of aquatic invasive species, they need to receive adequate training and information on aquatic invasive species.

The responses from participants indicated a significant gap in the availability of information and training specifically focused on aquatic invasive species. This lack of training is significant because detecting, identifying, and controlling aquatic invasives often requires a nuanced understanding of aquatic ecology, early warning systems, and species–specific responses to intervention (Jones et al., 2021; Kinsley et al., 2022; Britton et al., 2023). For example, species such as *Pontederia crassipes* and *Micropterus nigricans* can spread rapidly if early signs are overlooked, which typically occurs when staff are unfamiliar with aquatic systems (May *et al.,* 2022). Training also plays a critical role in improving adaptive management. As McGeoch et al. (2016) noted, capacity building in invasion biology can significantly increase the effectiveness of response strategies and reduce management delays. This point can be supported by comments from some of the interviewees:

> "*… I hold a diploma in nature conservation with thirty–one years of experience in conservation and have received training in biodiversity conservation. However, I haven't had specific training focused on aquatic invasive species management ...*" T1/B/Q2
> "*… Diploma in Conservation. No specific training in invasive aquatic species Management …*" T1/F/Q2

6.4.2 Aquatic invasive species presence and threats

Participant responses regarding the presence and threat of aquatic invasive species to protected areas in Mpumalanga revealed a mix of informed concern and uncertainty. None of the reserves maintained a documented checklist for aquatic invasive species, although some had records for terrestrial species.

> "*… No, only for terrestrial invasive species …*" T2/A/Q4
> "*… No, we don't have a checklist for aquatic invasive species …*" T2/D/Q4

This reflects the general trend in South African protected areas, where terrestrial species have historically received more management attention than aquatic species (Foxcroft et al., 2019). A documented checklist not only facilitates early detection but also informs the selection of appropriate control strategies and helps track the effectiveness of management interventions over time (McGeoch et al., 2012). Early detection enables managers to respond before invasive species become well established, thereby reducing management costs and ecological damage (Genovesi and Monaco, 2014). Without such documentation, management efforts are to remain reactive rather than proactive, limiting long–term success in ASI control. The absence of monitoring systems for aquatic species aligns with findings by Van Wilgen and Richardson. (2014), who reported that South African protected areas often lack formal monitoring systems for aquatic invasive species, making it difficult to track changes in species composition and their impact. This contrasts with trends at the European level, where 88% of surveyed managers undertook monitoring of biological invasions in terrestrial and marine systems (Garcia–Lozano et al., 2025).

Threats from aquatic invasive species are widely recognized as significant pressures on biodiversity and ecosystem functioning. According to Gallardo et al. (2016), aquatic invasive species can outcompete native species, alter food webs, and degrade habitat quality, thereby reducing overall ecosystem resilience. Five out of eight participants provided clear and direct acknowledgements of the ecological risks associated with aquatic invasive species.

> "*… Yes, impact on indigenous species …*" T2/E/Q3
> "*… Yes, there is a chance that ecosystem functioning may be affected by the introduction of a new species ...*" T2/H/Q3

In contrast, three participants indicated limited knowledge or focus on aquatic invasive species within their respective reserves. They noted that their conservation efforts are primarily directed toward terrestrial invasive species, while others admitted that they lacked sufficient information to comment on the presence or impact of aquatic invasive species. This point can be supported by comments from some of the interviewees:

> "*… Currently we do not have specific information on the presence or impact of aquatic invasive species in this protected area …*" T2/B/Q3
> "*… I don't know because we don't focus on aquatic invasive species that much, more attention is given to terrestrial invasive species …*" T2/C/Q3

6.4.3 Invasive alien species impact and management challenges

Five participants revealed that certain aquatic invasive species are recognized as problematic in specific protected areas within Mpumalanga, while in other areas, knowledge and monitoring remain limited. One participant pointed out that invasive species could increase management costs, an observation supported by Van Wilgen et al. (2017), who found that invasive species increase operational costs and divert funding from other conservation efforts. Participants identified several species of concern, including *M. salmoides* (Florida bass), *Pontederia crassipes* (water hyacinth), *Pistia stratiotes* (water lettuce), and *Cherax quadricarinatus* (Australian redclaw crayfish).

> "*… Florida bass (Micropterus salmoides) impact on indigenous small fish species …*" T3/E/Q5
> "*… Cherax quadricarinatus is the only aquatic animal that has established viable population in our rivers …*" T3/H/Q5

In contrast, three participants expressed uncertainty, indicating a lack of detailed information or monitoring frameworks. These findings are consistent with previous research (Van Wilgen and Richardson, 2014; Foxcroft et al., 2017), which reports that aquatic invasive species are frequently under–documented and overlooked within South African protected areas. The lack of consistent data hinders both the recognition of threats and the ability to prioritize species for control (Corrigan et al., 2016). Without this foundational knowledge, management efforts risk being delayed or misdirected.

> "… *We don't have any detailed information on aquatic invasive species in this reserve ...*" T3/A/Q5
> "… *I have no idea …*" T3/C/Q5

6.4.4 Management strategies and decision–making

Management strategies and decision–making approaches also varied. Three participants indicated that decision–making is guided by formal policy and regulatory frameworks.

> "… *According to species and NEMBA …*" T4/E/Q7
> "… *The management strategies are mostly adaptive and guided by relevant scientific recommendations ...*" T4/H/Q7

However, five participants admitted to not having implemented any aquatic invasive species management, explaining:

> "… *We haven't yet had to make decisions regarding management methods for aquatic invasives …*" T4/A/Q7
> "… *I have no information ...*" T4/D/Q7

The decision–making process for aquatic invasive species remains underdeveloped due to a lack of baseline data and established protocols. van Poorten and Beck (2021) similarly found that the lack of reliable data limits strategic decision–making for aquatic invasive species management. While some reserves apply informed, policy–aligned strategies, others lack the ecological data, species expertise, or institutional guidance necessary to implement targeted control. This echoes findings by Van Wilgen and Richardson. *(2014)* and Shackleton et al. (2019), who found that decision–making for invasive species management in South Africa is often constrained by limited capacity, inconsistent enforcement of policies, and underdeveloped monitoring systems.

In terms of effectiveness, participants shared mixed evaluations of available strategies. One noted that: "… *physical removal is effective but expensive and time consuming* …" (T4/F/Q10), highlighting the logistical burden of mechanical control. A broader, systems–level response was mentioned using a "… *permit system* …" (T4/F/Q10), suggesting formal oversight of control activities. Some participants noted that the overall effectiveness of aquatic invasive species strategies remains "… *yet to be quantified* …" (T4/H/Q10), which echoes concerns raised in earlier studies that found invasive species programs often proceed without consistent outcome monitoring (Van Wilgen and Richardson, 2014). Without systematic assessment, it becomes difficult to determine what works and what requires revision.

6.4.5 Collaboration and resource availability

Collaboration with external stakeholders emerged as an important element in the management of invasive species, particularly in areas where formal partnerships have been established. Five participants indicated active collaboration with external stakeholders (Figure 6.2), including forums, researchers, and government agencies. For example, participants mentioned that:

> "… *there is collaboration with different stakeholders, and the adaptive management strategies are guided by research done by different universities.*" T5/H/Q12
> "… *when plants get washed into the dam, the information is shared with strategic partners* …" T5/H/Q12

The establishment of forums and inter–agency communication channels suggests that collaborative platforms are present, but their intensity and consistency may vary across reserves. These responses align with findings by Shackleton et al. (2019) and Foxcroft et al. (2017), who emphasised the value of inter–organisational collaboration and knowledge exchange in strengthening invasive species management. Adaptive strategies informed by research, such as those reported here, offer a more responsive and evidence–based approach to the complex and shifting nature of biological invasions.

The other three participants reported no active partnerships with research institutions, government agencies, or other collaborations (Figure 6.2). The lack of collaboration contrasts with findings by Veeger and Westermann–Behaylo (2022), who noted that multi–stakeholder collaboration increases access to resources and knowledge sharing, resulting in better management outcomes. Workers may not have access to the most up–to–date information and recommended procedures for properly controlling aquatic invasive species if resources, such as funding and training, are limited. Because they may not be up to date on the newest techniques and technology. According to Rodriguez and Walter (2017), employee training and development are key tools for enhancing individual and organizational motivation, helping workers achieve their short–term and long–term goals and objectives.

> "… *No, we wish to* …" T5/A/12

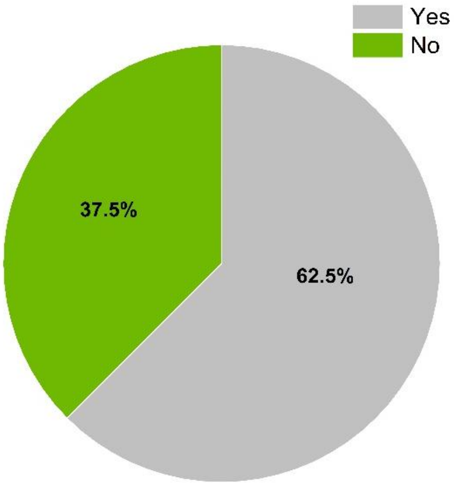

Figure 6.2. Collaboration with external stakeholders on invasive species management by MTPA, SANBI, and SANParks.

Furthermore, participants proposed several improvements to enhance management strategies, including increased funding, specialized training, and clearer government guidelines. These recommendations align with those by Foxcroft et al. (2017) and Lukey and Hall (2020), who advocated for stronger policy frameworks and better coordination between government agencies and conservation organizations to improve invasive species management in South African protected areas.

> "… *Long–term funding and government support are needed because without budget you cannot do anything* ..." T5/B/13
> "… *We need training on aquatic invasive species to gain more knowledge about them and help manage their population within our reserve*…" T5/C/13
> "… *strategies are prioritized around budget season rather than invasive plant season* …" (T5/G/Q13)

6.5 Conclusion

The findings of this study demonstrate that while some progress has been made in managing aquatic invasive species in protected areas of Mpumalanga, major challenges persist. Interviewees reported a lack of formal aquatic invasive species checklists, inadequate species–specific training, limited funding, and inconsistent monitoring. These gaps and challenges hinder proactive management, contributing to reactive responses that are often ineffective or delayed. Although collaboration with external stakeholders and adaptive management approaches exist in some reserves, their implementation is uneven. To improve aquatic invasive species management, protected areas require sustained funding, targeted training programs, clear policy guidance, comprehensive monitoring systems, and collaboration with researchers from various institutions. Strengthening these elements will enable conservation managers to make informed decisions, improve ecological outcomes, and better protect freshwater ecosystems from the impacts of invasive species.

CHAPTER 7: GENERAL SYNTHESIS

7.1 General discussion and conclusions

This study demonstrates that aquatic invasive species are not yet widespread across protected areas in Mpumalanga; however, where present, their ecological influence can be substantial. Only one invasive species, *Xiphophorus helleri*, was recorded, occurring exclusively at the SANBI–Lowveld National Botanical Garden, where it was also the most abundant species. Its rapid growth, competitive superiority, and low mortality rates suggest favourable environmental conditions and limited biotic resistance within this system. Experimental findings further indicated predominantly additive predator interactions, implying that the invasion of *X. helleri* may intensify predation pressure on prey communities if overall predator abundance increases. Together, these results highlight that even a single invasive species, when established within a protected ecosystem, can influence community structure, species interactions, and trophic dynamics.

To address the knowledge gaps, this study assessed the extent, effects, and management for aquatic invasive species in protected areas in the Mpumalanga Province, South Africa. The research was structured into data chapters, each exploring a distinct yet interconnected aspect of aquatic invasions, ranging from their distribution and demographic characteristics to their ecological impacts and management effectiveness. Together, these chapters provide a comprehensive understanding of how aquatic invasive species establish, interact with, and are managed within protected freshwater ecosystems.

The distribution analysis revealed that only one invasive fish species, *X. helleri*, was detected across the six protected areas surveyed, and its occurrence was restricted to the Lowveld National Botanical Garden (LNBG) (Chapter 1). This uneven distribution supports the hypothesis that the occurrence of aquatic invasive species differs among protected areas, likely reflecting variation in human activity, hydrological connectivity, and habitat conditions. The absence of invasive fish in the remaining protected areas suggests that some protected areas may currently exhibit resistance to invasion, potentially due to limited anthropogenic disturbance or geographical isolation. The presence of *X. helleri* at the LNBG indicates that most protected areas surveyed were still primarily dominated by native fish communities. This finding is encouraging and suggests that protected areas with restricted public access and geographical isolation remain resilient to aquatic invasions.

However, the recording of *X. helleri* in the LNBG pond and nearby river systems underscores that even well–managed protected areas are not immune to introductions. The location of the garden at a river confluence and its high level of visitor activity facilitated the species' introduction, possibly through aquarium releases or unintentional transfers during water management operations. These findings align with global studies that identify ornamental fish trade and recreational activities as major pathways for aquatic invasions (Bernery et al., 2022; Vezi et al., 2024). The study also examined the population dynamics, demographic status, and dietary habits of *X. helleri* within the LNBG and nearby Crocodile River systems. In Chapter 4, the results revealed that *X. helleri* displayed a rapid population growth and dominance, accounting for approximately 91.7% of all species captured during the sampling period. This dominance reflects both favourable environmental conditions and high reproductive capacity, characteristics that are typical of successful invasive fish species. The population structure was skewed towards younger individuals (between 3.6 cm and 7.0 cm), suggesting ongoing recruitment and a stable breeding population within the LNBG pond. Additionally, low mortality rates indicated that the species is well–adapted to the physicochemical conditions of these systems.

Dietary analysis further revealed that *X. helleri* is a trophic generalist, consuming a wide range of food resources, including detritus and small invertebrates. Such feeding enables the species to exploit multiple trophic niches, reducing its dependence on specific food sources and thereby enhancing its survival in variable environments. The swordtail diet also suggests potential competition with native fish species that occupy similar feeding niches, potentially altering local food web dynamics. Hydrological connectivity between the LNBG pond and adjacent Crocodile River systems proved to be a key factor influencing the spread of the species. Occasional flooding events facilitated the downstream dispersal of individuals, effectively linking the confined garden pond to the broader river system. This underscores how even small artificial water bodies within protected areas can serve as an invasion source when hydrological connections allow for dispersal beyond their initial introduction site.

Using a controlled laboratory–based approach, we investigated the feeding interactions of the two co–occurring species, the native mouthbrooder (*Pseudocrenilabrus philander*) and the non–native swordtail (*Xiphophorus helleri*), towards a readily consumed prey (Chironomidae), under multi–predator scenarios using a comparative FR approach (Chapter 5). This chapter advanced the understanding of how non–native species integrate into existing trophic networks and how their presence may influence the strength and direction of native predator–prey interactions. The results demonstrated that both *X. helleri* and *P. philander* exhibited Type II functional responses, characterised by a decelerating rate of prey consumption with increasing prey density. However, native mouthbrooders displayed substantially higher maximum consumption rates (~14.5 prey items) compared to female swordtails (~8.1) and male swordtails (~3.6), suggesting that the native species exerts a stronger per capita predation pressure on prey populations. The findings from this chapter offer insights into the ecological functioning and resilience of protected aquatic ecosystems in the face of non–native fish invasions. The lack of substantial interference between native and non–native predators suggests that native species may retain their ecological roles despite the presence of invaders, at least in the early stages of invasion. However, continued coexistence could alter prey community structure and resource dynamics in the long term, especially under conditions of environmental stress such as eutrophication or reduced habitat complexity.

Regarding the evaluation of current management strategies for aquatic invasive species within protected areas, the study employed social components through semi–structured interviews (Chapter 6). The results revealed several systemic shortcomings in the management of aquatic invasive species, including the absence of species checklists, inconsistent monitoring, limited formal training, and inadequate funding. Chapter 6 emphasises that effective management of aquatic invasive species requires a shift from passive awareness to active prevention, early detection, and rapid response systems. Integrating aquatic invasive species management into broader biodiversity and water resource frameworks is essential to ensure that interventions are prioritised and adequately resourced.

7.2 Future research

Future research on aquatic invasive species in South African protected areas should focus on long–term and multidisciplinary approaches to better understand invasion dynamics and improve management control. Establishing long–term monitoring programs across various aquatic systems would enable the detection of temporal patterns in the spread of aquatic invasive species and help evaluate the effectiveness of current management approaches. Incorporating molecular tools, such as environmental DNA (eDNA), would enhance early detection, enabling the rapid identification of non–native species even at low population densities. Furthermore, ecosystem–level investigations that incorporate food–web modeling, stable isotope research, and functional response experiments are crucial for assessing the extensive ecological impacts of invaders on community structure and ecosystem processes.

Future research should also investigate the hydrological connectivity between artificial and natural water systems to understand the pathways that enable species spread within and beyond protected areas. Research on the social and institutional aspects of aquatic invasive species management is equally essential, encompassing stakeholder understanding, policy implementation, and community involvement in prevention efforts. Finally, ultimately applied studies testing the effectiveness of integrated management approaches that combine biological control, mechanical removal, and ecological restoration would yield critical evidence for developing adaptive, cost–effective, and sustainable strategies to mitigate the impacts of aquatic invasive species in South Africa’s protected freshwater ecosystems.

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