Monitoring the efficacy of a lowland instream barrier on the lower uThukela River and the importance of river connectivity

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ABSTRACT

Freshwater is the key to life on earth, with rivers being the pathway that allows it to run from mountains to the ocean, performing many important functions along its way. Humans rely on the many ecosystem services that freshwater provides, such as water quantity provision for domestic, industrial, and agricultural processes, food supply, water purification, and recreation and tourism, to name a few. Water-scarce countries, such as South Africa, are particularly vulnerable to water shortage issues and require many water supply solutions, like dams, weirs, and transfer schemes, to harvest the available rainfall. The uThukela River in KwaZulu-Natal is not only an important resource within its catchment but also to external catchments through inter-basin water transfer schemes, including that of the Thukela-Vaal transfer, which feeds the economically important hub of South Africa, the Gauteng Province.

The lower uThukela River is a highly stressed system, with synergistic effects from multiple stressors relating to water quality, water quantity, habitat alterations, and wildlife disturbance affecting it. Additionally, the Lower Thukela Bulk Water Supply Scheme (LTBWSS) weir was recently constructed in its lower reaches, approximately 20 km upstream of the uThukela Mouth to the Indian Ocean, to provide bulk water to surrounding local municipalities. Due to the rich diversity of fish species in the region, particularly those with marine, estuarine, and freshwater migratory patterns, a fishway was incorporated into the design of the weir to facilitate fish movements over the weir.

This study evaluated the impact that the LTBWSS weir has on fish community structures in the region and additionally assessed the efficacy of the fishway in allowing fish movements through it. Various sites were selected upstream, downstream, and on the tributary Mandeni

Stream to assess environmental variables driving fish community structures, with passive and active sampling methods used to assess the fishway's functionality.

Fish collection occurred at three sites upstream of the LTBWSS weir, four sites downstream of it on the uThukela River, and two sites on the Mandeni Stream. Abiotic variables relating to water quality, velocity, depth, and habitat were collected along with fish to determine which environmental variables were driving the fish communities at these sites. Multivariate analyses indicated that available substrate and cover, the average depth, and temperature were drivers of the fish communities in the study. Upstream sites showed lower species richness compared with downstream sites, with fish communities largely made of freshwater species and few euryhaline species. Additionally, individual species showed different responses to different environmental variables. Furthermore, since the construction of the LTBWSS, the loss of previously highly abundant cichlid species has occurred in the region. This is likely because of the synergistic effects of stressors created by it, such as the disruption of fine sediment transport, water abstraction, and pollution.

Passive assessment of the fishway's efficacy in catering for migratory species used PIT telemetry. Budget constraints only allowed the installation of a single PIT antenna at the upstream entrance of the fishway, which was able to assess the upstream migration of fish from downstream. The results found that only eight individuals representing three species managed to navigate the fishway during the study successfully. This included *Oreochromis mossambicus*, *Labeo molybdinus*, and *Clarias gariepinus*. Active sampling involved electrofishing three key locations in the fishway on a monthly basis. Results showed that small-size classes of fish largely dominated the fishway and that the downstream entrance had the highest abundances and species richness. Further research on the role of the fishway in maintaining river connectivity is recommended.

The outcomes of this study showed the importance that water resource managers have in maintaining the resource for humans and the environment. Knowing individual species' responses to environmental variables allows their populations to be better managed. Additionally, the outcomes of this study showed the importance of river connectivity past a barrier and highlighted the need for effective fish passage solutions in South Africa. It emphasised the need to better understand the migratory requirements of local fish to build better fish passage structures. Major stressors to be addressed include the impacts caused by barriers relating to flow releases, migration blocks, and habitat alteration upstream and downstream of them. Furthermore, the proper management of fish passage structures is essential to their functionality, which includes regular monitoring of the fishway for issues such as debris blockages and swiftly finding solutions to them to ensure that no undue delays or stress may occur for migratory fish.

PREFACE

The data described in this thesis were collected in KwaZulu-Natal, Republic of South Africa, from May 2021 to August 2022. Experimental work was carried out while registered at the School of Life Sciences, University of KwaZulu-Natal, Pietermaritzburg, under the supervision of Prof Colleen T. Downs and co-supervision of Dr Celine Hanzen and Dr Matthew Burnett.

This thesis, submitted for the degree of Master of Science in the College of Agriculture, Engineering and Science, University of KwaZulu-Natal, School of Life Sciences, Pietermaritzburg campus, represents original work by the author and has not otherwise been submitted in any form for any degree or diploma to any University. Where use has been made of the work of others, it is duly acknowledged in the text.

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Bradley van Zyl

May 2023

I certify that the above statement is correct, and as the candidate's main supervisor, I have approved this thesis for submission.

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Prof Colleen T Downs

Supervisor

May 2023

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DECLARATION 1 - PLAGIARISM

I, Bradley Van Zyl, declare that

1. The research reported in this thesis, except where otherwise indicated, is my original research.
2. This thesis has not been submitted for any degree or examination at any other university.
3. This thesis does not contain other persons' data, pictures, graphs, or other information, unless specifically acknowledged as being sourced from other persons.
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DECLARATION 2 - PUBLICATIONS

DETAILS OF CONTRIBUTION TO DRAFT PUBLICATIONS that form part and/or include research presented in this thesis. (Note: These have not been submitted yet).

Publication 1- not submitted

Van Zyl, B., Burnett, M., Hanzen, C., Downs, CT

A fish community assessment of the lower uThukela River, KwaZulu-Natal, South Africa

Author contributions:

BVZ conceived the paper with CTD, MB and CH. MB, CH and CTD sought funding. BVZ collected the data with assistance from CH and MB. BVZ analysed the data with input from MB and CH. BVZ wrote the draft paper. MB, CH and CTD contributed valuable comments to the manuscript.

Publication 2- not submitted

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Floods, riots, load shedding: Does the Lower Thukela Bulk Water Supply Scheme work in the uThukela River, KwaZulu-Natal, South Africa

Author contributions:

BVZ conceived the paper with CTD, MB and CH. MB, CH and CTD sought funding. BVZ collected the data with assistance from CH and MB. BVZ analysed the data with input from MB and CH. BVZ wrote the draft paper. MB, CH and CTD contributed valuable comments to the manuscript.

Signed: [redacted] ....

Bradley Van Zyl

May 2023

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"For I know the plans I have for you," declares the Lord, "plans to prosper you and not harm you, plans to give you hope and a future."

~ Jeremiah 29:11

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CHAPTER 1

Introduction

The state of freshwater ecosystems as water resources in developing countries is essential for the livelihoods of vulnerable human communities (King and Pienaar, 2011), with developments in these resources significantly threatening water quality, flow, and habitat-altering stressors (Fouchy et al., 2019). Developing countries face water insecurity, environmental degradation, and pollution issues (Department of Environmental Affairs, 2012; Capps et al., 2016). This is exacerbated in water-scarce countries with highly seasonal and variable rainfall distributions and can be unsustainable when meeting the needs of a growing population (Department of Environmental Affairs, 2012; DeNicola et al., 2015). Many African countries, including southern African ones, are considered water scarce. Consequently, the water quantity problem is aggravated by the development of water resource-dependent sectors (e.g., agriculture, mining, urbanisation, and industry) and places pressure on the freshwater ecosystem functioning (Department of Environmental Affairs, 2012; Dickens et al., 2019; Thirion and Jafta, 2019).

Freshwater ecosystems provide important ecosystem services that are often irreplaceable (Postel and Carpenter, 1997), such as water supply, the control of water quality, recreation and tourism, habitat facilitation, food provision, and climate regulation, to name a few (Hanna et al., 2018; Kaval, 2019). Despite this, they are heavily modified and among the most endangered ecosystems globally (Dudgeon et al., 2006; Rodell et al., 2018; du Plessis, 2019). Globally the development of artificial instream barriers can negatively affect the well-being of freshwater ecosystems (Rodell et al., 2018); however, its impact is largely under-studied in the African context (du Plessis, 2019). Despite known negative impacts of anthropogenic activities on freshwater ecosystems (Tickner et al., 2020), African freshwater ecosystems continue to degrade from increasing anthropogenic developments, especially for water security and hydropower (Hsu et al., 2013; Dube et al., 2015). In South Africa, the high demand for water by the agriculture, urban communities, mining, and industry sectors increases pressure on an already strained water resource and can have a negative impact on freshwater ecosystems (Rivers-Moore et al., 2011; du Plessis, 2019).

The flow of water in terrestrial and aquatic ecosystems, through surface and subsurface flows, wetlands, rivers, lakes and floodplains, indicates the importance of connected aquatic ecosystems (O'Brien et al., 2019). The health of terrestrial and aquatic ecosystems is inherently linked to healthy water resources, which requires that human-dependent ecosystem services do not leave the water resources in a worse state after using them (Dugan et al., 2010). Terrestrial and aquatic wildlife stressors, such as land-use change and changes in water quality, flow and habitat, are known threats to river ecosystem health in South Africa (Jewitt et al., 2015; O'Brien et al., 2019). Despite South Africa's commitment to achieving the internationally recognised Sustainable Development Goals (SDGs) that aim to achieve a balance between the protection and the use of water resources (Dickens et al., 2019) by established management policies and legislation (King and Pienaar, 2011), the aforementioned stressors are still considered poorly managed (Hsu et al., 2013; Schreiner, 2013).

1.1 River connectivity and the impact of instream barriers on fish populations

One compounding stressor in freshwater ecosystems is anthropogenic instream barriers that fragment rivers and fish populations (Carpenter et al., 2011). The use of weirs and barriers across streams and rivers has been around for several centuries. Without these impoundments, weirs and other instream structures, the essential services they provide for society, such as water storage for abstraction, hydropower generation, flood control, and waterway crossings, would be difficult to achieve (Belletti et al., 2020). These practices, unfortunately, almost always involve fragmenting river ecosystems and disrupting the natural river connectivity, negatively impacting the migratory pathways of fish (D'Enno et al., 2002; Carpenter et al., 2011; Barbarossa et al., 2020).

The ecological need for fish to migrate upstream and downstream past a barrier, allowing river connectivity, can be necessitated through a fish passage structure (Fouché and Heath, 2013; Wilkes et al., 2019). A fishway, as described by Clay (1995), is "*essentially a water passage around or through an obstruction, designed to dissipate the energy in the water in such a manner as to enable fish to ascend without undue stress*". Although the term describes a fishway, the terms fish pass and fish ladder are commonly used throughout the literature describing structures which perform a similar function (Beach, 1984; D'Enno et al., 2002; Baki et al., 2016; Celestino et al., 2019). Literature suggests that the term fish passage speaks more to the science and movement of fish past a barrier via a structure that allows it, with terms such as a fish ladder, fishway, and fish pass, referring to the physical structure with this function or similar function. Here onwards, the term fishway will be used for the structure, with fish passage referring to the science and successful movement of fish through it. More broadly, a fishway can be described as a natural or artificial structure that allows fish migration to occur by enabling them to overcome impassable obstructions in the river (Bok et al., 2007).

In South Africa, fish passage science is influenced by a water research commission report by Bok et al. (2007), where the three most common fishway types were the pool and weir, vertical slots, and natural-like fishways with rock ramps. They all have advantages and disadvantages and are used according to the types of fish species designed for, often with modifications to accommodate specific migratory fish or freshwater ecosystems (Bok et al., 2007). The pool and weir-type fishway design consists of a number of pools produced by a series of small weirs, where water flows over the weirs from one pool to the next at a slope of 8% to 10% (Ead et al., 2004). The pool and weir type fishway is generally implemented in situations where the migratory fish species under consideration are those that exhibit strong swimming burst speeds or jumping capabilities, such as the anadromous salmonid species (Ead et al., 2004). The vertical slot fishway is suitable for situations where several fish species need to be catered for, whose range of hydraulic and biological requirements differ (Katopodis and Williams, 2012). The vertical slot fishway is better suited to migratory fish that are weak jumpers with strong swimming or climbing capabilities (Bok et al., 2007). Their design incorporates a series of baffles on a moderately sloped bed (5% to 10%) which release water to the next through either a single or double narrow vertical slot (Baudoin et al., 2015). Natural-like fishways are alternatives to technical fishways, and they are shown to pass a wide variety of species at low-head dams (Baudoin et al., 2015) and generally have low bed slopes varying from 1% to a maximum of 5% (Baki and Azimi, 2021). Generally, they are designed to simulate riverine habitats by incorporating large natural elements (e.g., rocks, boulders and tree logs) which dissipate energy, reduce flow velocities and create greater flow complexities than technical fishways, providing attractive cues to passing fish (Franklin et al., 2012; Baki et al., 2016).

The successful operation of a fishway requires two fundamental stages of fish passage to be accomplished. Firstly, the entrance of the fishway is successfully located by fish species (Clay, 1995). Secondly, the hydraulic conditions in the fishway must suit the intended fish species to navigate the facility successfully (Porcher and Travade, 2002). Suitable hydraulic conditions are controlled by the design of the fishway, with considerations being made for both the largest and smallest migrators. A successful fishway design caters to the requirements of the intended species', whereby considerations are made for the size ranges of fish, the swimming, jumping and crawling abilities of the species, the migratory behaviour of the species and the flow conditions inside it, which allow them to pass (Bok et al., 2007).

Several challenges to fishway design exist, primarily catering for multiple species with various swimming capabilities and migratory requirements (Zielinski et al., 2020).

Additionally, the spread of non-native fish can often be controlled through the use of instream fish barriers (McLaughlin et al., 2013; Burnett et al., 2023). Fish passage solutions tend to cater for upstream migration with little to no consideration for downstream migration (McLaughlin et al., 2013; Silva et al., 2018). An innovative program in North America is examining the design of a selective fishway to address these challenges, primarily to restrict the movement of sea lamprey (*Petromyzon marinus*) upstream while allowing desirable fish to pass (Zielinski et al., 2020; Zielinski and Freiburger, 2021). Fish passage solutions and implementation are primarily championed in the Northern hemisphere (Roscoe and Hinch, 2010; Silva et al., 2018; Zielinski and Freiburger, 2021), with little development in the Southern hemisphere, including southern Africa (Silva et al., 2018). It is understood that fish passage solutions must cater to local conditions and consider local fish species migration requirements, as Northern hemisphere fishway designs cannot be accepted as a universal practice (Kemp, 2016). However, behavioural knowledge of local species outside the Northern hemisphere is often lacking (Silva et al., 2018; Burnett et al., 2021b).

1.2 Fish migration

Migratory fish patterns in freshwater systems are commonly understood by the salmonid species ascending waterfalls as they return from the ocean, but importantly also include many other species that have migratory requirements to a lesser or greater extent (McIntyre et al., 2016). Fish migration can be defined as those movements which result in an alteration between two or more separate habitats, occurs with periodicity in an individual's lifetime, and involves a large part of the population and a directed movement at some stage of the lifecycle (Northcote, 1978, 1984). Potamodromous migrations occur entirely in freshwater, whereas diadromous migrations occur between freshwater and marine environments (Lucas and Baras, 2008). Diadromy can be further classified into three categories according to the response to changing salinity at a particular life stage as well as the direction of movement, namely, anadromy, catadromy, and amphidromy (Lucas and Baras, 2008). McDowall (1997) defines them as follows:

- **Anadromy:** Diadromous fish in which most feeding and growth are at sea before the migration of fully grown, adult fish into fresh water to reproduce; either there is no subsequent feeding in fresh water, or any feeding is accompanied by little somatic growth; the principal feeding and growing biome (the sea) differs from the reproductive biome (freshwater).
- **Catadromy**: Diadromous fish in which most feeding and growth are in freshwater before fully grown adult fish migrate to the sea to reproduce. There is no subsequent feeding at sea or any feeding accompanied by little somatic growth. The principal feeding and growing biome (freshwater) differs from the reproductive biome (the sea)
- **Amphidromy:** Diadromous fish in which there is the migration of larval fish to sea soon after hatching, followed by early feeding and growth at sea, and then a migration of small post-larval to juvenile fish from the sea back into fresh water. There is further, prolonged feeding in freshwater during which most somatic growth from juvenile to adult stages occurs, as well as sexual maturation and reproduction. The principal feeding biome is the same as the reproductive biome (freshwater).

Migratory fish move for various reasons, such as to access breeding sites and feeding areas, to evade predators or because of changing water quality or temperature conditions (Lucas and Baras, 2008; McIntyre et al., 2016). All individuals do not have to move, and their yearly timings may vary in consecutive years; however, in most cases, migration is critical for individual health and, ultimately, the persistence of the population (McIntyre et al., 2016). The migratory behaviour of fish means that they occupy different ecological niches throughout their lifecycles (Lucas and Baras, 2008). As components of river ecosystems, fish will contribute to the functioning of these ecosystems through the roles they perform within them (Fausch et al., 2002; Dugan et al., 2010). Through fish migration, the circulation of nutrients and energy between aquatic ecosystems, including between saltwater and freshwater ecosystems, can be achieved (McIntyre et al., 2016).

Migratory fish depend on ecological connectivity, exposing them to various ecosystems (Lucas and Baras, 2008). Instream barriers are some of the biggest stressors on migratory fish as they delay or even completely impede the passage of fish upstream or downstream of them, depriving these fish of the ecological connectivity that they require (Lucas and Baras, 2008; McIntyre et al., 2016; Barbarossa et al., 2020). These barriers greatly reduce river connectivity, with the average range connectivity of non-diadromous species being less than that of diadromous species (Barbarossa et al., 2020). Migratory fish, therefore, act as significant environmental and social indicators as they are susceptible to multiple stressors and resource degradation and generally have specific habitat requirements (Harris, 1995; Dugan et al., 2010). As a result, they are useful ecosystem well-being indicators as they are long-lived, highly mobile organisms that perform functions within ecosystems, they are relatively easily monitored and have a socioeconomic value (Chovanec et al., 2003; Baumgartner et al., 2014; O'Brien et al., 2018). Additionally, freshwater migratory fish play an important role in people's livelihoods globally (Cooke et al., 2016b), particularly in developing countries where their migrations are capitalised on by subsistence and small-scale commercial fisheries (Bruton, 1978; Plug et al., 2010; Coetzee et al., 2015).

1.3 Fish migrations in South Africa

The study of migratory fish for South Africa is largely lacking despite it being estimated that more than 100 species have migratory requirements to different extents (Whitfield, 1990; Bok et al., 2007). Many local fish species in inland waters of South Africa can have migratory behaviour, including potamodromous and diadromous behaviours (Darwall et al., 2009). In South Africa, potamodromous and diadromous species are good indicators of connectivity and river health at a localised and catchment scale (O'Brien et al., 2019; Burnett et al., 2021b; Hanzen et al., 2022). Potamodromous species such as the yellowfishes *Labeobarbus* spp. and the minnows *Enteromius* spp. are good indicators of physical, chemical, and ecological connectivity on a localised scale (O'Brien et al., 2019; Burnett et al., 2021b). Catadromous species such as the *Anguilla* spp. provide a distinct understanding of the physical, chemical, and hydrological connectivity at a catchment scale since they move across the catchment twice in their life cycle (O'Brien et al., 2019; Hanzen et al., 2021; Hanzen et al., 2022). Due to the nature of their lifecycles, migratory fish, compared with non-migratory fish, are twice as susceptible to becoming endangered (Riede, 2004) and are more vulnerable to the growing impacts of anthropogenic stressors such as river fragmentation, habitat loss and water pollution (O'Brien et al., 2019).

Over 165 000 instream barriers have been built in South Africa (Mantel et al., 2017). These developments and anthropogenic structures disconnect the river systems and can disrupt the migrations of local fishes such as the anguillid eels, mudfishes and yellowfishes (Paxton, 2004; Impson et al., 2007). The large-scale migrations, particularly for the anguillid eels (Hanzen et al., 2022), are often for spawning reasons, and thus altered natural conditions threaten the reproduction and survival of the species (Baras et al., 2002). Although it is known on a catchment scale for anguillid eels, they are the only long-distance catadromous migrators in southern Africa (O'Brien et al., 2019; Hanzen et al., 2022), so fragmented natural conditions on a localised scale can also impact the species dependent on smaller migrations. The native yellowfishes, *Labeobarbus* spp., are facultative migrators. They move between the lotic and lentic freshwater environments depending on responses to changing water quality and temperatures, feeding times, seeking of habitat features and seasonal spawning (O'Brien and

De Villiers, 2008; Burnett et al., 2018; Ramesh et al., 2018; Burnett et al., 2021b). The impediment of these facultative migrations, because of natural or anthropogenic stressors, could also adversely affect the presence or even survival of these species in impacted stretches of rivers. Amphidromous migrators, such as some of the *Eleotridae* spp. and *Gobiidae* spp., are also susceptible to the effects of barriers as their life cycles depend on upstream migrations of juveniles into freshwater to grow and reproduce and the downstream drift of larvae into the marine environment (Maeda and Tachihara, 2005; Franklin and Gee, 2019). Therefore, an impassable barrier in the lower reaches of a river where amphidromous migrators are present can significantly impact the survival of these species.

Freshwater migratory fish are important to people's livelihoods (Cooke et al., 2016b). This is evident in South African subsistence fisheries, where fishers have capitalised on the seasonal migrations of catfish (*Clarias* spp.) (Bruton, 1978), cichlid, and cyprinid species throughout history (Plug et al., 2010; Coetzee et al., 2015). Additionally, migratory fish, for example, the *Labeobarbus* spp., *Hydrocynus vittatus*, and *Clarias gariepinus* in southern Africa (Brand et al., 2009; Potts et al., 2022), have been important from a socioeconomic perspective as they are targeted by recreational angling industries (Brand et al., 2009; Potts et al., 2022). Whereas other migratory fish, such as that of the *Anguilla spp*., provide an important cultural and spiritual role for the Zulu and Xhosa cultures of South Africa (Impey, 2011).

The migrations of South African fish species are linked to maintaining the sustainability of ecosystems and require adequate management of instream barriers (O’Brien et al., 2019). However, the failure of water resource managers in South Africa to make this link has not been addressed, and the lack of management regarding these processes may be the reason why the region is not meeting their SDG’s (O’Brien et al., 2019). Additionally, non-native invasive fish add to the list of stressors to the well-being of native fish species as they predate on them as well as compete for food and habitat requirements (Weyl and Lewis, 2006).

1.4 Fish passage development in South Africa

In water-scarce areas globally, impoundments or dams are seen as a necessity to meet the need for water security, subsequently aiding in economic development and poverty alleviation (Briscoe, 2009). However, contrary to the increased water supply provided by these dams, the agricultural, industrial, and urban expansion sectors are promoted, resulting in increased competition for water resources (Kallis, 2010; Scarrow, 2014). Whilst economically beneficial, this creates a long-term supply-demand cycle, where water demand becomes higher than initially planned for and which can negate the initial water supply benefits of dams (Di Baldassarre et al., 2018). Secondly, an extended period of abundant water supply because of dams may generate an increased dependence on water infrastructure, which increases social and economic vulnerability when eventual water shortages occur (Di Baldassarre et al., 2018). In developing and water-scarce countries, these two long-term water supply issues may result in dams being largened or more dams being constructed, often without consideration, and effective solutions, to the environmental impacts they present (Todd et al., 2017). In particular, including fish passage solutions on larger dams is not feasible as the need for one is outweighed by the costs of building it, or the height that it would need to provide fish passage is too much (Bok et al., 2007).

In a water-scarce country like South Africa, dams of all sizes are used to maximise water storage for sectors such as agriculture, urban communities, mining, and industry on various scales (Rivers-Moore et al., 2011; Mantel et al., 2017; du Plessis, 2019). However, this excessive water use aggravates the water-scarce situation in South Africa because of the high demand for the resource, which affects the welfare of the aquatic ecosystems (Rivers-Moore et al., 2011; du Plessis, 2019). Despite this, there are over 165 000 dams on or off-stream in the country (Mantel et al., 2017), with over 600 being formal dams with impoundments which serve as migration barriers, accompanied by ~1430 gauging weirs which can be partial barriers to migrations (O'Brien et al., 2019). These barriers interfere with the natural river connectivity when they are encountered in-stream. Barriers can incorporate a fish passage structure, such as a fishway, to help restore longitudinal river connectivity for migratory fish (Bok et al., 2007).

In South Africa, fish passage structures on instream barriers date back to 1948, with the first fishway being constructed on the Eerste River in the Western Cape (Bok et al., 2007). Despite a large number of dams and gauging weirs in the country, there are approximately only 60 fish passage facilities that have been implemented (O'Brien et al., 2019), which is less than 1% of all the instream barriers in South Africa. The lack of fish passage solutions demonstrates a low priority for river connectivity in the country (Bok et al., 2007). According to Bok et al. (2007), of the existing fishways, only about 20% are functional, 33% are ineffective, and the rest are unevaluated; however, this may differ slightly if a more recent evaluation is done. The lack of fishway construction on many instream barriers has contributed excessively to habitat fragmentation across the country (Bok et al., 2007; Mantel et al., 2017; O'Brien et al., 2019), ultimately affecting the general conservation of fish and their distributions (Dugan et al., 2010; Nel et al., 2011). This negates target 6.6 (to protect and restore water-related ecosystems) of sustainable development goal (SDG) 6 set for 2020, and it is questionable whether this was achieved for South Africa's water resources (Dickens et al., 2019). In addition, the draft of the National Water Resources Strategy 3 (NWRS-3) states that one of the thirteen priority focus areas for the water sector between 2020 and 2030 is *"Protecting and restoring ecological infrastructure for the green economy"* (Department of Water and Sanitation, 2022). Once gazetted, this would emphasise the need for barriers across the country to maintain ecological connectivity of the freshwater biota through adequate fish passage solutions. It is therefore critical that fish passage solutions which are included in the design/restoration of all South

African instream barriers are effective in passing local migratory species (Kemp, 2016; Silva et al., 2018).

On a national level in South Africa, little has been done to mitigate the generally well-known negative effects of barriers on freshwater ecosystems (Bourne et al., 2011; O'Brien et al., 2019). Successful fishway design requires combined inputs from engineers, aquatic scientists, and water resource managers (Silva et al., 2018; O'Brien et al., 2019; Twardek et al., 2022). However, in South Africa, the design processes for the required infrastructure are dominated by the engineering sector (Bok et al., 2007; Silva et al., 2018), with little to no input from experienced freshwater biologists for these structures to meet the migratory requirements of local species (Dugan et al., 2010; O'Brien et al., 2019). Collaborative work between freshwater biologists, water resource managers and engineers is necessary to address the limitations imposed on fish passage solutions and would allow for more effective fishways to be implemented (Roscoe and Hinch, 2010). Although the development of fish passage science is ongoing, with continued research, a fishway constructed on newly developed instream barriers will help reduce river fragmentation (Silva et al., 2018). Where topography and site conditions permit it, a bypass channel-rock ramp combination tends to be the preferred alternative over the more formal vertical slot and pool and weir-type fishways (Bok et al., 2007; O'Brien et al., 2019).

In designing an effective solution for fish passage, knowledge of when fish are migrating along with their direction of travel is key (Franklin and Gee, 2019). Knowing what species need to be catered for, their size when encountering the fishway, and the timing of their migration can help optimise the flow conditions in the fishway (Bok et al., 2007; Franklin and Gee, 2019). The type of fishway, however, is determined by the targeted species and whether its design flows function within the boundaries of the hydrographs of the natural river or the artificial hydrographs produced by the developed infrastructure (Bok et al., 2007; O'Brien et al., 2019).

1.5 KwaZulu-Natal Rivers

South Africa's water resources are presently divided into nine water management areas (WMA's) for national water resource management purposes (Department of Water and Sanitation, 2016). In KwaZulu-Natal, the ten major river systems (from north to south: Pongola, Mkuze, Mfolozi, Mhlatuze, Thukela, Mvoti, Umgeni, Umkomazi, Umzimkulu, Mtamvuna) fall under the Pongola-Mtamvuna WMA (Department of Water and Sanitation, 2016). Formerly, the country was divided into 19 WMA's, whereby the uThukela River catchment was managed as its own WMA, and the combined northern and combined southern KwaZulu-Natal systems were managed as two other WMA's in the province (Kleynhans and Louw, 2007). The uThukela system falls under the primary drainage region 'V' in South Africa (Department of Water Affairs and Forestry, 2004). The uThukela River is one of the major rivers in South Africa and the largest in KwaZulu-Natal Province, with a length of ~500 km and a catchment area of ~30,000 km^2 in extent (Department of Water Affairs and Forestry, 2004). Its source is in the Drakensberg Mountains, where it flows east through central KwaZulu-Natal before discharging through the uThukela Estuary into the Indian Ocean (Department of Water Affairs and Forestry, 2004).

Along its length, but more so in the lower reaches, the uThukela River is impacted by human settlements, wastewater treatment works, factories, mills, and different forms of agriculture, whose processes either abstract water, discharge effluent, do both, or act as sources of pollutants into its main stem or smaller tributaries (Department of Water Affairs, 2013; Umgeni Water, 2017). The stressors imparted by these individual or combined sources onto the lower uThukela River contribute to various water quality, water quantity, habitat altering, and disturbance to wildlife stressors (Wade et al., 2021). The water quality stressors in this system are because of anthropogenic activities. These include the Sappi Tugela Pulp and Paper Mill, which is responsible for elevated salts, organics, and altered system variables. The localised industrial, urban, and peri-urban centres are responsible for toxicants, while localised agricultural activities, which are dominantly sugarcane (*Saccharum officinarum*) farming, are responsible for nutrient enrichment and organic contaminants, as are livestock farming, municipal wastewater treatment works and upstream sources (Wade et al., 2021, Evans et al., 2022). The water quantity stressors are because of upstream diversions and dams for water abstraction (Wade et al., 2021), which alter the natural timing, volume, duration, and frequency of flows in the river (World Commission on Dams, 2000). Habitat stressors have been linked to sand mining operations in the area, which is indirectly associated with reduced flows (Wade et al., 2021), resulting in the natural movement and deposition processes of the riverine sediments being altered (Koehnken et al., 2020). Wildlife disturbing stressors are associated with the unrestrained harvesting of fish stocks, recreational activities which disturb wildlife, and the establishment of non-native fauna which out-compete and predate on indigenous species (Wade et al., 2021).

The water supply of the uThukela system is important to the communities within its catchment as well as other areas in South Africa that benefit from its inter-basin water transfer schemes (Department of Water Affairs, 2013). The four major water supply schemes within the system are shown in Figure 1.1 (Department of Water Affairs, 2013). Nationally, the Thukela-Vaal transfer scheme aids in supplying the economically important hub of South Africa, Gauteng Province, with water augmented through transfer schemes into the Wilge catchment just outside Harrismith, which eventually feeds into the Vaal River (Van Vuuren, 2008; Department of Water Affairs, 2013). Provincially, the Mooi-Umgeni transfer scheme supplies the Pietermaritzburg to Durban region via water transfers into the Umgeni system, which is further south, the Thukela-Mhlathuze transfer scheme supplies the Richards Bay region via water transfers into the Mhlathuze system which is further north, and the Lower Thukela Bulk Water Supply Scheme (LTBWSS) supplies areas in the KwaDukuza and Mandeni Local Municipalities (Department of Water Affairs, 2013; Umgeni Water, 2017). The LTBWSS is an abstraction weir built across the uThukela River, presently abstracting 55ML/d of water, with the potential of abstracting 110ML/d of water, and supplies places within the municipality such as the Sappi Tugela Pulp and Paper Mill in Mandeni (Umgeni Water, 2017).

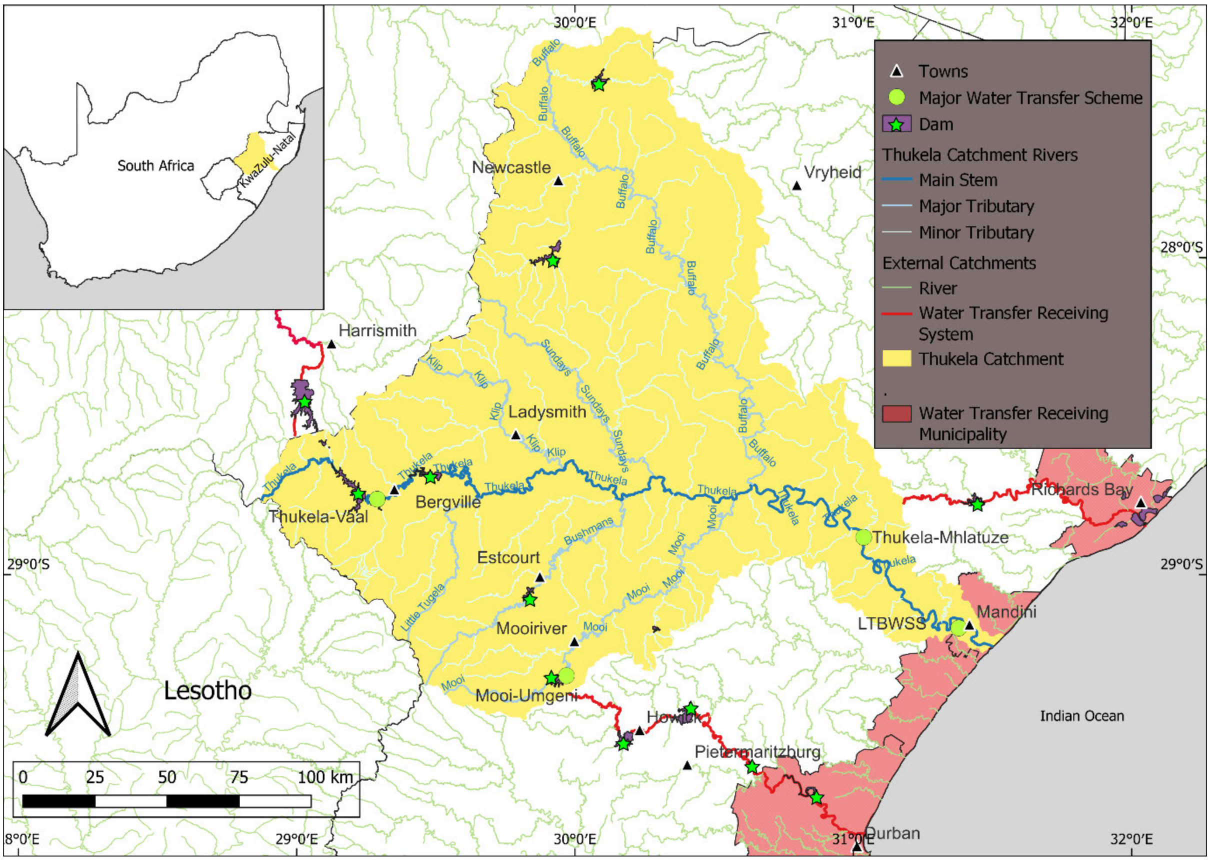

Figure 1.1: The uThukela catchment showing major water transfer schemes in South Africa.

The rivers of KwaZulu-Natal have a total of 59 freshwater fish species, where there is a decreasing gradient of fish species richness from the tropical north-eastern rivers (uPhongolo River, n = 40 species) to the temperate south-western rivers (Mtamvuna River, n = 18 species) of the province (Skelton, 2001; Darwall et al., 2009; Evans et al., 2022). Additionally, species richness increases with decreasing altitude, with the lower reaches of each river having a higher species richness (Skelton, 2001; Evans et al., 2022). According to available Present Ecological State, Ecological Importance and Ecological Sensitivity (PESEIS) data (Department of Water and Sanitation, 2014), Freshwater Biodiversity Information System (FBIS) data (FBIS, 2022), and other studies (Skelton, 2001; Kleynhans, 2007; Evans et al., 2022), the uThukela River catchment has 40 species of fish, of which 31 are native, and nine are non-native (Table 1.1). Additional information related to the preferred habitat, flow types, and migratory behaviour of these species may be important considerations in fish community assessments and migration studies and are therefore listed in Table 1.1. Although there is some uncertainty with the migratory behaviour of some species, particularly with the extent of upstream potamodromy of the lesser studied species, their accuracy comes from the best available literature in the SA Migratory Biota Index (Bok et al., 2007) and other recent literature.

Table 1.1: A list showing the preferred habitats and flow types, migratory behaviour, and IUCN status of native and non-native fish species found in the uThukela River catchment, KwaZulu-Natal Province, South Africa

	Species	**Abbr.**	**Preferred habitat and flow types**	**Migratory behaviour**	**IUCN Status**
1	*Awaous aeneofuscus* **Freshwater Goby** (Peters, 1852)	AAEN	Benthopelagic, Rivers and estuaries. Quiet swift water, also lagoons. (Skelton, 2001)	Anadromous (Bok et al., 2007), possibly Amphidromous (Whitfield, 2019)	LC
2	*Acanthopagrus berda* **River bream** (Forskall, 1775)	ABER	Demersal. Marine, Freshwater, Brackish. Spawn in estuaries (Garratt, 1993).	Oceonodromous (Riede, 2004), Amphidromous (Bok et al., 2007)	LC
3	*Anguilla bengalensis labiata* **African mottled eel** (Peters. 1852)	ABEN	Benthopelagic, rock pools. Streams, pools and reservoirs (Skelton, 2001).	Catadromous.	NT
4	*Anguilla bicolor bicolor* **Shortfin eel** (McClelland, 1844)	ABIC	Demersal. Freshwater as an adult, estuaries and seas as young. Rocky bottoms and deep pools, prefers marshes. Predominantly lowland	Catadromous	NT

			rivers. Freshwater streams and pools. (Skelton, 2001)		
5	*Anguilla marmorata* **Giant mottled eel** (Quoy & Gaimard, 1824)	AMAR	Demersal, freshwater as adults, estuaries and seas as young, rocky bottoms and deep pools, throughout the river into upland tributaries. Freshwater streams and pools. (Skelton, 2001)	Catadromous	LC
6	*Anguilla mossambica* **African longfin eel** (Peters, 1852)	AMOS	Demersal, freshwater as adults, estuaries and seas as young, rocky bottoms and deep pools, throughout the river into upland tributaries. Streams and pools. (Skelton, 2001).	Catadromous	NT
7	*Amphilius natalensis* **Natal mountain catfish** (Boulenger, 1917)	ANAT	Demersal, freshwater. Cobbles and rocks of swiftly flowing streams. Common in upland streams. (Skelton, 2001)	Potamodromous	LC
8	*Amphilius uranoscopus* **Stargazer mountain catfish** (Pfeffer, 1889)	AURA	Demersal, freshwater. Rocky habitats. Clear, flowing water. (Skelton, 2001)	Potamodromous	LC
9	*Ambassis dussumieri* **Bald glassy** (Cuvier, 1828)		Demersal, marine to freshwater. Tolerant of freshwater within a narrow temperature range (23 – 26 C)	Unknown, possibly diadromous of sorts	LC
10	*Ambassis natalensis* **Slender glassy** (Gilchrist & Thompson, 1908)		Demersal, marine to freshwater. Tolerates freshwater within a temperature range of 19 – 27 C.	Unknown, possibly diadromous of sorts	LC
11	**Cyprinus carpio* **Common carp** (Linnaeus, 1758)	CCAR	Benthopelagic, freshwater, brackish. Well-vegetated lakes. Soft bottom sediments. Warm, deep, slow-flowing waters. Vulnerable in its native range, considered an invasive elsewhere. (Kottelat and Freyhof, 2007)	Potamodromous. Considerable spawning migrations to backwaters and flooded meadows. (Kottelat and Freyhof, 2007)	VU
12	*Clarias gariepinus* **Sharptooth catfish** (Burchell, 1822)	CGAR	Benthopelagic, freshwater. Prefer shallow and swampy areas with a soft muddy substrate. May also occur in fast-flowing rivers and rapids. Quiet waters, lakes and pools. (Teugels, 1986, Skelton, 2001)	Potamodromous. Migrate to rivers and temporary streams to spawn.	LC
13	*Coptodon rendalli* **Redbreast tilapia** (Boulenger, 1897)	CREN	Benthopelagic, freshwater, brackish. Prefers quiet, well-vegetated water along river banks. Backwaters, floodplains and swamps. (Skelton, 2001)	Potamodromous	LC
14	*Eleotris fusca* **Dusky sleeper** (Forster, 1801)	EFUS	Demersal, marine, freshwater, brackish. Lagoons, estuaries and lower reaches of freshwater streams and prefer muddy bottoms (Skelton, 2001). Juveniles are mainly found in more saline environments of lagoons and estuaries, with adults also found in freshwater (Pethiyagoda, 1991).	Amphidromous	LC
15	*Eleotris melanosoma* **Broadhead sleeper**	EMEL	Demersal, marine to freshwater. Muddy reaches of estuaries and	Amphidromous	LC

	(Bleeker, 1852)		mangrove swamps, sometimes entering freshwater in medium to large rivers. Also found amongst bank vegetation of freshwater streams. (Skelton, 2001)		
16	*Enteromius anoplus* **Chubbyhead barb** (Weber, 1897)	EANO	Benthopelagic. Freshwater, brackish. Favours cooler waters. Various habitats, from small streams to large rivers and lakes. Associated with fallen logs, brushwood, or marginal vegetation habitats. (Skelton, 2001)	Potamodromous. Lateral migrations to flooded banks after rains for breeding purposes. (Skelton, 2001)	LC
17	*Enteromius gurneyi* **Redtail barb** (Gunther, 1868)	EGUR	Benthopelagic. Freshwater. Small streams in the sandstone belt. Favours pools, where it is frequently the only other fish species besides freshwater eels. (Skelton, 2001)	Potamodromous	VU
18	*Enteromius paludinosus* **Straightfin barb** (Peters, 1852)	EPAU	Benthopelagic. Freshwater. Prefers quiet, well-vegetated waters in lakes, swamps, and marshes or marginal areas of large rivers or slow-flowing streams. (Skelton, 2001)	Potamodromous. Moving into flooded vegetation and influent rivers during the rainy season for spawning. (Skelton, 2001)	LC
19	*Enteromius trimaculatus* **Threespot barb** (Peters, 1852)	ETRI	Benthopelagic. Freshwater. Found in shallow waters near river outlets, also close to swampy areas. Various habitats, especially where there is vegetation (Skelton, 2001). Thrives in sand and rock-bottomed streams and can tolerate degraded habitats and streams.	Potamodromous. Upstream movements in flooded rivers after rains for breeding (Skelton, 2001).	LC
20	*Enteromius viviparus* **Bowstripe barb** (Weber, 1897)	EVIV	Benthopelagic. Freshwater. Vegetated pools of streams and rivers and lake margins, usually in the Lowveld, coastal plains (Skelton, 2001). Relies on submerged roots and vegetation to lay eggs on.	Potamodromous	LC
21	*Gilchristella aestuaria* **Gilchrist's round herring** (Gilchrist, 1913)	GAES	Pelagic-neritic. Marine, freshwater, brackish. Mostly found in estuaries, and also rivers and lakes (Whitfield, 1998).	Unknown	LC
22	**Gambusia affinis* **Mosquitofish** (Baird & Girard, 1853)	GAFF	Benthopelagic. Freshwater, brackish. Most abundant in lower reaches of streams. Adults inhabit standing to slow-flowing water, most common in vegetated lakes, backwaters, and quiet pools of streams. (Page and Burr, 2011)	Potamodromous	LC
23	*Glossogobius callidus* **River goby** (Smith, 1937)	GCAL	Benthopelagic. Freshwater, brackish. Inhabits rivers and the upper reaches of estuaries. Lives in pools, on the bottom amongst cobbles or vegetation (Whitfield, 1998). Although found in estuaries, larvae were most abundant in	Unknown, although literature may suggest amphidromous with larvae found in estuaries (Strydom and Neira, 2006), most likely from larval drift by river	LC

			mesohaline regions (Strydom and Neira, 2006).	currents similar to *G. giuris*	
24	*Glossogobius giuris* **Tank goby** (Hamilton, 1822)	GGIU	Benthopelagic. Marine, freshwater, brackish. Mainly freshwater and estuaries. Found in clear to turbid streams, usually with rock, gravel, or sand bottoms (Allen, 1991).	Amphidromous. Spawning in freshwater, relies on larval drift by river currents to wash eggs and larvae into the sea (Allen, 1991).	LC
25	*Hypseleotris cyprinoides* **Golden sleeper** (Valenciennes. 1837)	HCYP	Demersal, marine to freshwater. Favours shallow vegetated margins in freshwater streams that enter estuaries. Threatened by coastal development and habitat destruction (Skelton, 2001).	Amphidromous	DD
26	**Lepomis macrochirus* **Bluegill** (Rafinesque, 1819)	LMAC	Benthopelagic. Freshwater. Frequently found in lakes, ponds, reservoirs and sluggish streams. Prefers deep weed beds. (Page and Burr, 2011)	Unknown.	LC
27	*Labeo molybdinus* **Leaden labeo** (du Plessis, 1963)	LMOL	Benthopelagic. Freshwater. Prefers rapids but is absent from the coldest streams. Often in large permanent pools of large rivers and will enter rapids. Rocky habitats of the main river channel (Skelton, 2001).	Potamodromous. Upstream migrations for breeding in swollen rivers after rains (Skelton, 2001).	LC
28	*Labeobarbus natalensis* **KwaZulu-Natal yellowfish** (Castelnau, 1861)	LNAT	Benthopelagic. Freshwater. Wide variety of habitats, from pools and rapids of clear streams to deep turbid waters of rivers and impoundments (Burnett et al., 2021b)). Prefers warmer areas of rivers, often congregating at inlets of small tributaries. Spawns in fast-flowing stretches of river, over algae-free gravel beds (Skelton, 2001).	Potamodromous. Upstream migrations in spring and summer for feeding and breeding purposes (Skelton, 2001). Downstream migration to deep pools in winter (Burnett et al., 2021b).	LC
29	*Labeo rubromaculatus* **Tugela labeo** (Gilchrist & Thompson, 1913)	LRUB	Benthopelagic. Freshwater. Endemic to the uThukela catchment. Occurs from sea level up to an elevation of 1520m. Prefers deep pools and slow-flowing rivers and also occurs in rocky rapids (Skelton, 2001).	Potamodromous. Upstream spring and summer migration for breeding (Skelton, 2001).	VU
30	*Monodactylus argenteus* **Round moony** (Linnaeus, 1758)	MARG	Pelagic-neritic. Marine, freshwater, brackish. Found in bays, tidal creeks, mangrove estuaries, and lower freshwater reaches of rivers (Allen, 1991). Often frequenting vegetation with juveniles entering freshwater (Skelton, 2001).	Unknown.	LC
31	*Monodactylus falciformis* **Oval moony** (Lacepede, 1801)	MFAL	Marine, freshwater, brackish. Coastal waters, as well as estuaries and lagoons for juveniles. Associated with reefs. Often frequenting vegetation (Skelton, 2001).	Catadromous (Bok et al., 2007)	LC
32	*Microphis brachyurus* **Short-tailed pipefish**	MBRA	Demersal. Marine, freshwater, brackish. Relatively shallow, still to	Anadromous.	LC

	(Bleeker, 1854)		slow-flowing water (Pethiyagoda, 1991). Juveniles and subadults are usually found in estuaries, while adults are found upstream in freshwater.		
33	*Microphis fluviatilis* **Freshwater pipefish** (Peters, 1852)	MFLU	Demersal. Marine, freshwater, brackish. Coastal rivers and streams in quiet water amongst vegetation or logs at river edges (Okeyo, 1998).	Unknown, possibly anadromous like *M. brachyurus*	DD
34	**Micropterus dolomieu* **Smallmouth bass** (Lacepede, 1802)	MDOL	Benthopelagic. Freshwater. Shallow rocky areas of lakes and clear, gravel-bottom runs and flowing pools of rivers. Shallow sand, gravel, or rocky bottoms for nesting. (Page and Burr, 2011)	Potamodromous	LC
35	**Micropterus punctulatus* **Spotted bass** (Rafinesque, 1819)	MPUN	Demersal. Freshwater. Clear to slightly turbid, gravel-bottomed and flowing pools. Runs and creeks and small to medium rivers. Also inhabits lakes and reservoirs. (Page and Burr, 2011)	Potamodromous.	LC
36	**Micropterus salmoides* **Largemouth bass** (Lacepede, 1802)	MSAL	Benthopelagic. Freshwater. Inhabit lakes, ponds, swamps, backwaters, pools of creeks, and small to large rivers. Prefers quiet or slow-flowing, clear water with submerged and floating vegetation and overgrown banks (Page and Burr, 2011).	Potamodromous.	LC
37	*Oreochromis mossambicus* **Mozambique tilapia** (Peters, 1852)	OMOS	Benthopelagic. Freshwater, brackish. Thrives in standing waters. Commonly over mud bottoms, often in well-vegetated areas (Skelton, 2001). Common in blind estuaries and coastal lakes but usually absent from permanently open estuaries, and fast-flowing water, as well as at high altitudes (De Moor and Bruton, 1988). Can grow and reproduce in fresh and brackish water.	Amphidromous in estuarine and coastal lakes. Potamodromous in freshwater (Riede, 2004; Bok et al., 2007).	VU
38	**Oncorhynchus mykiss* **Rainbow trout** (Walbaum, 1792)	OMYK	Benthopelagic. Freshwater only in South Africa. Inhabit clear, cold headwaters, high-altitude rivers and lakes. Stocked in lakes. Cool (<21 C), well-aerated water is necessary. Needs gravel-bottomed beds for breeding (Skelton, 2001, Page and Burr, 2011).	Potamodromous in South Africa. Upstream migration to clear headwaters for breeding (Skelton, 2001).	NE
39	*Pseudomyxus capensis* **Freshwater mullet** (Valenciennes, 1836)	PCAP	Demersal. Marine, freshwater, brackish. Found as far upriver as 135km from the mouth in South Africa (Bok, 1979).	Catadromous. Breeding at sea, juveniles move into estuaries and rivers for growth and maturing (Skelton, 2001).	LC
40	*Pseudocrenilabrus philander*	PPHI	Benthopelagic. Freshwater. From flowing waters to lakes, usually prefers vegetated zones where the	Potamodromous. Upstream migrations during heavy rains.	LC

	Southern mouthbrooder (Weber, 1897)		current is not too strong (Skelton, 2001).		
41	**Poecilia reticulata* **Guppy** (Peters, 1859)	PRET	Benthopelagic. Freshwater, brackish. Inhabits warm springs, weedy ditches and canals. Various habitats from turbid water in ponds, canals, and ditches at low elevation to high altitude mountain streams. Vegetation is essential. (Page and Burr, 2011)	Non-migratory.	LC
42	**Salmo trutta* **Brown trout** (Linnaeus, 1758)	STRU	Pelagic-neritic. Freshwater only in South Africa. Inhabit clear, cold headwaters, high-altitude rivers and lakes. Stocked in lakes. Cool (<21 C), well-aerated water is necessary. Needs gravel-bottomed beds for breeding (Skelton, 2001, Page and Burr, 2011).	Potamodromous. Upstream migration to clear, flowing headwaters for breeding. (Skelton, 2001)	LC
43	*Tilapia sparmanii* **Banded tilapia** (Smith, 1840)	TSPA	Benthopelagic. Freshwater. Found in various habitats, favours areas with submerged or emergent vegetation along edges of rivers, lakes, and swamps (Skelton, 2001). Tends to be confined to shallow weedy areas. Spawns on substrate or branches of aquatic weeds.	Potamodromous. Seasonal upstream migrations, breeding before and during them.	LC

*Non-native species

1.6 Monitoring Freshwater environments in South Africa

Biotic indices monitor the ecological state, health, and integrity of aquatic ecosystems by using the biological characteristics of living organisms found in and around rivers (Kleynhans, 2007; Dickens et al., 2019; Evans et al., 2022). It is globally accepted that fish are good indicator species to monitor aquatic ecosystem health because of their sensitivity to water quality and ability to accumulate toxins (Holmlund and Hammer, 1999). Fish biological indices can be developed and used by understanding the characteristics of the biology and ecology of fish species and their tolerance to environmental variables (Karr, 1981; Kleynhans, 1999; Kleynhans, 2007). In 1999, the Fish Assemblage Integrity Index (FAII) was developed for use specifically in southern African freshwater environments (Kleynhans, 1999), where it was then further upgraded to the Fish Response Assessment Index (FRAI) in 2007 (Kleynhans, 2007). Although the FRAI is broadly used as a tool for fish community assessments in southern Africa, its approach relies on ecological knowledge of indigenous fish and historical data for river systems, which is limited in South Africa (Kleynhans, 2007). This, coupled with the rapid techniques used to collect data, the lack of species richness in some systems and sites, and the broad category indications for each score creating low confidence scores, suggests the FRAI approach has some shortcomings (Avenant, 2010). However, it is still a useful tool widely adopted in southern Africa to communicate the ecological state of freshwater ecosystems based on fish as indicators (Evans et al., 2022).

Biological indices, using statistical methods, such as redundancy analyses, are available as additional lines of evidence to evaluate the ecosystem's integrity with an acceptable level of certainty (O'Brien et al., 2018), and where their use in the FRAI approach can evaluate the response of fish communities to multiple stressors (Avenant, 2010; Malherbe et al., 2016). Furthermore, by understanding the overall integrity of the fish community and the river in which it occurs, the understanding of the response of those fish to their environmental stressors can be improved (Malherbe et al., 2016; Evans et al., 2022). This can all contribute to assessing and providing solutions to the present state and the potential drivers of the fish communities (Evans et al., 2022).

1.7 Fish telemetry globally and in South Africa

Understanding fish movements is important when managing key ecologically and economically important fish species (Cooke et al., 2016a). To accomplish management objectives for aquatic ecosystems, the behaviour of fish and their spatial requirements in the ecosystem need to be considered (Dickens et al., 2019; Lynch et al., 2019; Lynch et al., 2020). Different techniques that are used to observe the individual movements of fish include trapping, Capture-Mark-Recapture (CMR), and telemetry (Lucas and Baras, 2000; Cooke et al., 2013). Traditional monitoring methods to assess fish behaviour, such as snorkelling, camera traps, and

CMR, have limitations when applied in Africa because of the unpredictable and turbid nature of the continent's rivers (Hocutt et al., 1994; Lucas and Baras, 2000; Cowley and Naesje, 2004). These limitations, coupled with a struggling African economy, lead to numerous African freshwater ecosystems and fish species being understudied (Hocutt et al., 1994; Cowley and Naesje, 2004). Fish telemetry techniques have been used globally to study the movement of fish in their environment (Lucas and Baras, 2000; Hussey et al., 2015; Cooke et al., 2016a; Brownscombe et al., 2019; Burnett et al., 2021b).

Fish telemetry can assist water resource managers in characterising fish behaviour (Lucas and Baras, 2000), identifying migration routes (Melnychuk, 2009; Trancart et al., 2018), insight into fishery capacities (Crossin et al., 2017; Brooks et al., 2019), effects of invasive species (Bacheler et al., 2015), the use of habitat and the biological response of fish to changing environmental factors (Koster and Crook, 2017; Thiem et al., 2018), detection of their activity patterns (Fuchs and Caudill, 2019), and can be used as a tool to corroborate established fish assessment methods (Cooke et al., 2016a; Koster and Crook, 2017). It does, however, have limitations in addressing all fish behavioural questions and should be used alongside suitable techniques when assessing its compatibility (Lucas and Baras, 2000; Cooke et al., 2013; Thorstad et al., 2013; Roberts et al., 2017).

Despite the many applications of fish telemetry, its use is generally lacking in developing regions such as Africa (Lennox et al., 2017; Burnett et al., 2021a). The lack of implementing fish telemetry in Africa can be attributed to the cost of the methods, misunderstanding of its benefits, and the lack of skills associated with its application (Hocutt et al., 1994; Baras et al., 2002; Grubich and Odenkirk, 2014). Despite the cost-benefit that using fish telemetry for inland water and resource management has, its adoption in Africa continues to fall behind that of developed regions (Hocutt et al., 1994; Baras et al., 2002). The Burnett et al. (2021a) literature review showed that out of the 54 African countries, only eight countries had published studies on fish telemetry and only concerned 27 fish species. Nguyen et al. (2018) noted that a failure to clearly understand the information requirements or failure to match telemetry methods to conservation outcomes is a downfall of any effective fish telemetry study. In developing countries, where resources for research are limited, fish telemetry projects have a higher chance of success when closely associated with water resource management questions (Dube et al., 2015; Nguyen et al., 2018). However, it is increasingly becoming evident that African fish telemetry is considered worth the cost despite struggling economies, with 57% of studies taking place in the last 10 years (Burnett et al., 2021a). This could result from technological advancements and the realisation of the importance of fish behaviour for water resource managers to help reach sustainable development goals (Cooper et al., 2014; Burnett et al., 2020). To date, the passive integrated transponders (PIT) method, a commonly used fish telemetry method globally, has not been used for African inland fish telemetry studies (Burnett et al., 2021a).

1.8 PIT telemetry and its application

The use of PIT telemetry in fisheries research dates to the mid-1980s, when its biological feasibility was first tested on two salmonoid species (Prentice and Park, 1984). The survival, tag retention and tissue response data results showed that PIT tags were biologically feasible to use in freshwater and saltwater applications if injected into the fish's dorsal musculature or body cavities (Prentice and Park, 1984; Prentice et al., 1990). Consequently, the technology gained traction in fisheries research and has become a popular fish identification system used globally (Prentice et al., 1990; Lucas and Baras, 2000; Cooke et al., 2013; Burnett et al., 2021a). Bond et al. (2007) and Baker et al. (2017) list several benefits of using a PIT system. These include: small tag sizes (down to 8 mm) allow juveniles to be tagged; unique tag numbers, so an almost infinite range allowing large sample sizes; handling of the fish is not required to decode the tag as the information can be obtained electronically using a reader placed a short distance away from the fish; tags are relatively inexpensive compared with other telemetry technologies; tags do not have a battery and therefore have an unlimited life expectancy making it suitable for long term studies; tags are completely passive and therefore pose no risk to the fish; and lastly the tagging system can be used without specialised licenses or training.

Passive integrated transponder technology consists of two components, the PIT tag and the PIT tag reading system. The PIT tag is passive and comprises an integrated circuit chip, capacitor, and antenna coil enclosed in a glass cylinder. Its operation requires it to be energised by an external energy source. The PIT tag reader is the external energy source. It generates an electromagnetic field that induces a current in the antenna coil and energises the integrated circuit, which sends a signal back to the reader. Reader technologies include handheld readers, backpack-mounted manual tracking systems (Roussel et al., 2000) and stationary monitoring systems (Castro-Santos et al., 1996). Handheld readers are useful during fish sampling techniques whereby fish are physically caught and handled, usually to gather data relating to physical characteristics. Manual tracking systems are useful when understanding the fine-scale movements and habitat uses of tagged individuals in a river reach (Morhardt et al., 2000; Roussel et al., 2000). Stationary monitoring systems are useful when trying to understand the movements of fish through or around a strategic site, such as fishways (Castro-Santos et al., 1996; Thiem et al., 2011; Hodge et al., 2017)).

Tag detection efficiencies may be from the biotic and abiotic factors influencing the type of PIT reading system, or from factors associated with the PIT tag itself. Complex habitat structures such as undercut banks, debris accumulations, and deep pools have been shown to negatively affect manual tracking detection efficiencies in PIT telemetry (Cucherousset et al., 2008; Burnett et al., 2013). Fast-travelling fish or large groups moving through or past stationary monitoring systems show decreased detection efficiencies as a result of missed detections from code collisions (Castro-Santos et al., 1996; Morhardt et al., 2000). Reading antennas may also be influenced by interference from external sources, which disrupt the electromagnetic field (Bond et al., 2007; Fetherman et al., 2014; Morris et al., 2018), and may also result in negative detection efficiencies. Tag detection efficiencies are also a result of tag size and its orientation with respect to the antenna, as these factors impact the read range (Bond et al., 2007; Burnett et al., 2013). A study on the detection efficiency of half-duplex (HDX) PIT tags by (Burnett et al., 2013) showed that the read range increased as tag size increased when looking at 12, 23, and 32 mm sized tags. This study also showed that larger tags (23 and 32 mm) produced a greater vertical and horizontal read range when oriented parallel, with only the 32 mm tags being successfully read in the horizontal perpendicular plane of orientation. Parallel orientation refers to a tag with its long axis parallel to the stream flow, while perpendicular orientation refers to the tag being at a right angle to the stream flow (Burnett et al., 2013). This positively coincides with preferred tagging practices to obtain optimal detection efficiencies, whereby a tag is aligned to the long axis of the fish's sagittal plane and would usually be moving parallel to the stream flow (Burnett et al., 2013). It is, however, crucial to note that a fish will not always move parallel to the stream flow and may, at times, change its orientation perpendicularly to it, which may impact tag detection efficiency (Burnett et al., 2013; Bond et al., 2007). In the case of an antenna system placed perpendicular to the flow in a vertical slot fishway, a fish moving through it directly against the flow would have the tag in the optimal detection position, parallel to stream flow and perpendicular to the antenna (Bond et al., 2007; Burnett et al., 2013). The maximised read range of a PIT antenna is made and orientation-to-the-tag specific, as well as dependant on whether the tag is full-duplex (FDX) or HDX (Bond et al., 2007), and would need to be tested before use.

Studies on small-bodied fish became feasible with the implantation of small PIT tags (12 mm or smaller) into their body cavity (Dixon and Mesa, 2011; Musselman et al., 2017).

However, care should be taken as small individuals below a certain size may be susceptible to slow growth rates and higher mortalities after being intracoelomically tagged (Prentice et al., 1990). PIT tag retention is well understood for salmonid species and shows that tag retention is fish size dependent (Acolas et al., 2007), and species-specific (Jepsen et al., 2005); however, it is lacking for warm water fish (Cooke et al., 2011; Musselman et al., 2017). In a review of the literature on PIT tag retention and survival studies on non-salmonid fishes from 1989 to 2015, Musselman et al. (2017) noted that of the 29 studies which met the criteria, tag retention was greater than 89% in 85% of them, with fish survival greater than 89% in 57% of them although the median was 92%. An experimental component of the Musselman et al. (2017) study on six different North American warm water fishes agreed with the tag retention and survival percentages of the literature, with the majority of mortalities being recorded in a single species whose average sizes were the smallest in the sample group. This suggests that although the general tag retention efficiencies are high, the target species and size should be tested under laboratory conditions before field tests are conducted so as not to introduce any bias into the data analyses.

1.9 Aims and objectives

The study's primary aim was to determine the impact of the newly constructed LTBWSS as a barrier for migratory fish and the impact this may have on the local fish community structures in the lower uThukela River, KwaZulu-Natal, South Africa. The secondary aim of the study was to assess the efficacy of the fishway incorporated into the LTBWSS weirs design.

The following objectives were set to achieve the aims:

- Conduct four seasonal surveys to sample fish communities at ten sites in the lower uThukela catchment.

- Conduct a Fish Response Assessment Index (FRAI) to evaluate the ecological state of fish communities at each site.
- Perform the first PIT tag study of its type in Africa to determine if upstream migration by fish through the fishway is achieved.
- Conduct monthly samples in the fishway to assess which species and size classes are using it each month.

1.10 Structure of the thesis

This thesis is structured with the data chapters prepared as draft manuscripts for submission to international peer review journals for publication. These are preceded by an introduction chapter and then followed by a final conclusions and recommendation chapter. Therefore, minor duplication was unavoidable.

The chapters include:

Chapter 1: Introduction. This chapter reviews the available literature on river connectivity and fish passage solutions globally and within the context of South Africa. Included is the use of telemetry in monitoring fishway efficacy. Lastly, this chapter serves as a rationale for the study, providing the aims and objectives and thesis format.

Chapter 2: A fish community assessment of the lower uThukela River, KwaZulu-Natal, South Africa. This chapter assesses the environmental variables in the region that are driving overall fish community structures, and the environmental drivers of individual species. Furthermore, the impact that the LTBWSS weir has on fish community structures is determined.

Chapter 3: Monitoring the efficacy of the Lower Thukela Bulk Water Supply Scheme (LTBWSS) weir fishway, uThukela River, KwaZulu-Natal, South Africa. This chapter assesses the functionality of the LTBWSS fishway using two techniques, PIT telemetry and monthly sampling of the fishway by electrofishing.

Chapter 4: Conclusions and recommendations. This chapter provides a summary of the previous chapters, highlighting findings, and providing suggestions for future similar studies. Some repetition was unavoidable because of the manuscript format.

1.11 References

Acolas, M., Roussel, J. & Bagliniere, J. 2007. Laboratory experiment on survival, growth and tag retention following PIT injection into the body cavity of juvenile brown trout (*Salmo trutta*). *Fisheries Research,* 86, 280 - 284.

Allen, G. R. 1991. Field guide to the freshwater fishes of New Guinea. Christensen Research Institute, Lexington, MA.

Avenant, M. 2010. Challenges in using fish communities for assessing the ecological integrity of non-perennial rivers. *Water SA,* 36, 397-406.

Bacheler, N. M., Whitfield, P. E., Muñoz, R. C., Harrison, B. B., Harms, C. A. & Buckel, C. A. 2015. Movement of invasive adult lionfish *Pterois volitans* using telemetry: importance of controls to estimate and explain variable detection probabilities. *Marine Ecology Progress Series,* 527, 205-220.

Baker, C. F., Reeve, K., Baars, D., Jellyman, D. & Franklin, P. 2017. Efficacy of 12-mm half-duplex Passive Integrated Transponder tags in monitoring fish movements through stationary antenna systems. *North American Journal of Fisheries Management,* 37, 1289-1298.

Baki, A. B. M. & Azimi, A. H. 2021. Hydraulics and design of fishways II: vertical-slot and rock-weir fishways. *Journal of Ecohydraulics*, 1-13.

Baki, A. B. M., Zhu, D. Z. & Rajaratnam, N. 2016. Flow simulation in a rock-ramp fish pass. *Journal of Hydraulic Engineering,* 142, 04016031.

Baras, E., Benech, V. & Marmulla, G. 2002. Outcomes of a pilot fish telemetry workshop for developing countries. *Hydrobiologia,* 483, 9-11.

Barbarossa, V., Schmitt, R. J., Huijbregts, M. A., Zarfl, C., King, H. & Schipper, A. M. 2020. Impacts of current and future large dams on the geographic range connectivity of freshwater fish worldwide. *Proceedings of the National Academy of Sciences,* 117, 3648-3655.

Baudoin, J.-M., Burgun, V., Chanseau, M., Larinier, M., Ovidio, M., Sremski, W., Steinbach, P. & Voegtle, B. 2015. Assessing the passage of obstacles by fish. Concepts, design and application. *Comprendre pour agir-Collection de l'Onema,* French National Agency for Water and Aquatic Environments.

Baumgartner, L. J., Conallin, J., Wooden, I., Campbell, B., Gee, R., Robinson, W. A. & Mallen-Cooper, M. 2014. Using flow guilds of freshwater fish in an adaptive management framework to simplify environmental flow delivery for semi-arid riverine systems. *Fish and Fisheries,* 15, 410-427.

Beach, M. 1984. Fish pass design-criteria for the design and approval of fish passes and other structures to facilitate the passage of migratory fish in rivers. Fisheries Research Technical Report 78. Ministry of Agriculture, Fisheries and Food, UK.

Belletti, B., De Leaniz, C. G., Jones, J., Bizzi, S., Börger, L., Segura, G., Castelletti, A., Van De Bund, W., Aarestrup, K. & Barry, J. 2020. More than one million barriers fragment Europe's rivers. *Nature,* 588, 436-441.

Bok, A. 1979. The distribution and ecology of two mullet species in some fresh water rivers in the Eastern Cape, South Africa. *Journal of the Limnological Society of Southern Africa,* 5, 97-102.

Bok, A., Kotze, P. & Heath, R. 2007. *Guidelines for the planning, design and operation of fishways in South Africa*, Water Research Commission, Pretoria.

Bond, M. H., Hanson, C. V., Baertsch, R., Hayes, S. A. & Macfarlane, R. B. 2007. A new low-cost instream antenna system for tracking passive integrated transponder (PIT)-tagged fish in small streams. *Transactions of the American Fisheries Society,* 136, 562-566.

Bourne, C. M., Kehler, D. G., Wiersma, Y. F. & Cote, D. 2011. Barriers to fish passage and barriers to fish passage assessments: the impact of assessment methods and assumptions on barrier identification and quantification of watershed connectivity. *Aquatic Ecology,* 45, 389-403.

Brand, M., Maina, J., Mander, M. & O'Brien, G. 2009. Characterisation of the social and economic value of the use and associated conservation of the yellowfishes in the Vaal River. Water Research Commission Report, Pretoria.

Briscoe, J. 2009. Water security: Why it matters and what to do about it. *Innovations: Technology, Governance, Globalization,* 4, 3-28.

Brooks, J. L., Chapman, J. M., Barkley, A., Kessel, S. T., Hussey, N. E., Hinch, S. G., Patterson, D. A., Hedges, K. J., Cooke, S. J. & Fisk, A. T. 2019. Biotelemetry informing management: Case studies exploring successful integration of biotelemetry data into fisheries and habitat management. *Canadian Journal of Fisheries and Aquatic Sciences,* 76, 1238-1252.

Brownscombe, J. W., Lédée, E. J., Raby, G. D., Struthers, D. P., Gutowsky, L. F., Nguyen, V. M., Young, N., Stokesbury, M. J., Holbrook, C. M. & Brenden, T. O. 2019. Conducting and interpreting fish telemetry studies: considerations for researchers and resource managers. *Reviews in Fish Biology and Fisheries,* 29, 369-400.

Bruton, M. 1978. The habitats and habitat preferences of *Clarias gariepinus* (Pisces: Clariidae) in a clear coastal lake (Lake Sibaya, South Africa). *Journal of the Limnological Society of Southern Africa,* 4, 81-88.

Burnett, M. J., Hanzen, C., Whitehead, A., O'Brien, G. C. & Downs, C. T. 2023. The lesser of two evils: the role of an instream barrier to control the distribution and invasive potential of non-native fish species in the Mooi River, South Africa. [In Review].

Burnett, M. J., O'Brien, G. C., Jacobs, F. J., Botha, F., Jewitt, G. & Downs, C. T. 2020. The southern African inland fish tracking programme (FISHTRAC): An evaluation of the approach for monitoring ecological consequences of multiple water resource stressors, remotely and in real-time. *Ecological Indicators,* 111, 106001.

Burnett, M. J., O'Brien, G., Wepener, V. & Pienaar, D. 2018. The spatial ecology of adult Labeobarbus marequensis and their response to flow and habitat variability in the Crocodile River, Kruger National Park. *African Journal of Aquatic Science,* 43, 375-384.

Burnett, M. J., O'Brien, G. C., Jacobs, F. J., Jewitt, G. & Downs, C. T. 2021a. Fish telemetry in African inland waters and its use in management: a review. *Reviews in Fish Biology and Fisheries*, 31, 337–357.

Burnett, M. J., O'Brien, G. C., Jewitt, G. & Downs, C. T. 2021b. Temporal and spatial ecology of an iconic *Labeobarbus* spp. in a socio-economically important river. *Environmental Biology of Fishes,* 104, 1103-1119.

Burnett, N. J., Stamplecoskie, K. M., Thiem, J. D. & Cooke, S. J. 2013. Comparison of detection efficiency among three sizes of half-duplex passive integrated transponders using manual tracking and fixed antenna arrays. *North American Journal of Fisheries Management,* 33, 7-13.

Capps, K. A., Bentsen, C. N. & Ramírez, A. 2016. Poverty, urbanization, and environmental degradation: urban streams in the developing world. *Freshwater Science,* 35, 429-435.
Carpenter, S. R., Stanley, E. H. & Vander Zanden, M. J. 2011. State of the world's freshwater ecosystems: physical, chemical, and biological changes. *Annual Review of Environment and Resources,* 36, 75-99.
Castro-Santos, T., Haro, A. & Walk, S. 1996. A passive integrated transponder (PIT) tag system for monitoring fishways. *Fisheries Research,* 28, 253-261.
Celestino, L. F., Sanz-Ronda, F. J., Miranda, L. E., Makrakis, M. C., Dias, J. H. P. & Makrakis, S. 2019. Bidirectional connectivity via fish ladders in a large Neotropical river. *River Research and Applications,* 35, 236-246.
Chovanec, A., Hofer, R. & Schiemer, F. 2003. Fish as bioindicators. In: Markett, B. A., Breure, A. M., Zechmeister, H. G. (Eds), *Trace metals and other contaminants in the environment.* Elsevier, New York, pp. 639-676.
Clay, C. H. 1995. *Design of Fishways and Other Fish Facilities,* Lewis Publishers, London.
Coetzee, H. C., Nell, W., Van Eeden, E. S. & De Crom, E. P. 2015. Artisanal fisheries in the Ndumo area of the lower Phongolo River floodplain, South Africa. *Koedoe: African Protected Area Conservation and Science,* 57, 1-6.
Cooke, S. J., Brownscombe, J. W., Raby, G. D., Broell, F., Hinch, S. G., Clark, T. D. & Semmens, J. M. 2016a. Remote bioenergetics measurements in wild fish: opportunities and challenges. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology,* 202, 23-37.
Cooke, S. J., Midwood, J. D., Thiem, J. D., Klimley, P., Lucas, M. C., Thorstad, E. B., Eiler, J., Holbrook, C. & Ebner, B. C. 2013. Tracking animals in freshwater with electronic tags: past, present and future. *Animal Biotelemetry,* 1, 1-19.
Cooke, S. J., Nguyen, V. M., Dettmers, J. M., Arlinghaus, R., Quist, M. C., Tweddle, D., Weyl, O. L., Raghavan, R., Portocarrero-Aya, M. & Cordoba, E. A. 2016b. Sustainable inland fisheries–perspectives from the recreational, commercial and subsistence sectors from around the globe. *Conservation Biology,* 20, 467-505.
Cooke, S. J., Woodley, C. M., Brad Eppard, M., Brown, R. S. & Nielsen, J. L. 2011. Advancing the surgical implantation of electronic tags in fish: a gap analysis and research agenda based on a review of trends in intracoelomic tagging effects studies. *Reviews in Fish Biology and Fisheries,* 21, 127-151.
Cooper, N., Swan, A. & Townend, D. 2014. A confluence of new technology and the right to water: Experience and potential from South Africa’s constitution and commons. *Ethics and Information Technology,* 16, 119-134.
Cowley, P. & Naesje, T. 2004. Telemetry–a means to investigate the lives of fishes underwater. *Ichthos,* 72, 1-3.
Crossin, G. T., Heupel, M. R., Holbrook, C. M., Hussey, N. E., Lowerre-Barbieri, S. K., Nguyen, V. M., Raby, G. D. & Cooke, S. J. 2017. Acoustic telemetry and fisheries management. *Ecological Applications,* 27, 1031-1049.
Cucherousset, J., Marty, P., Pelozuelo, L. & Roussel, J.-M. 2008. Portable PIT detector as a new tool for non-disruptively locating individually tagged amphibians in the field: A case study with Pyrenean brook salamanders (*Calotriton asper*). *Wildlife Research,* 35, 780-787.
D'enno, D., Marmulla, G. & Welcomme, R. 2002. *Fish passes: design, dimensions and monitoring*. Food and Agriculture Organization of the United Nations, Rome, Italy.
Darwall, W., Tweddle, D., Smith, K. & Skelton, P. 2009. *The status and distribution of freshwater biodiversity in southern Africa*, IUCN, Gland, Switzerland.
De Moor, I. J. & Bruton, M. N. 1988. *Atlas of alien and translocated indigenous aquatic animals in southern Africa*. National Scientific Programmes Unit: CSIR, Pretoria.

Denicola, E., Aburizaiza, O. S., Siddique, A., Khwaja, H. & Carpenter, D. O. 2015. Climate change and water scarcity: The case of Saudi Arabia. *Annals of Global Health,* 81, 342-353.

Department of Environmental Affairs 2012. 2nd South Africa environment outlook. A report on the state of the environment. Pretoria, South Africa.

Department of Water Affairs 2013. National Water Resource Strategy 2: Water for an equitable and sustainable future. 2 ed. Pretoria, South Africa.

Department of Water Affairs and Forestry 2004. Thukela WMA: Internal Strategic Perspective. *National Water Resource Planning.* Pretoria, South Africa.

Department of Water and Sanitation 2014. A Desktop Assessment of the Present Ecological State, Ecological Importance and Ecological Sensitivity per Sub Quaternary Reaches for Secondary Catchments in South Africa. Compiled by RQIS-RDM.

Department of Water and Sanitation 2016. New nine (9) Water Management Areas of South Africa (Notice 1056). 40279 ed. South Africa: *Government Gazette*, 40279.

Department of Water and Sanitation 2022. National Water Act, 1998 (Act no. 36 of 1998): Review of the National Water Resource Strategy. (Notice 2327). Pretoria (South Africa): *Government Gazette*, 47133.

Di Baldassarre, G., Wanders, N., Aghakouchak, A., Kuil, L., Rangecroft, S., Veldkamp, T. I., Garcia, M., Van Oel, P. R., Breinl, K. & Van Loon, A. F. 2018. Water shortages worsened by reservoir effects. *Nature Sustainability,* 1, 617-622.

Dickens, C., Smakhtin, V., Mccartney, M., O'Brien, G. & Dahir, L. 2019. Defining and quantifying national-level targets, indicators and benchmarks for management of natural resources to achieve the sustainable development goals. *Sustainability,* 11, 462.

Dixon, C. J. & Mesa, M. G. 2011. Survival and tag loss in Moapa White River Springfish implanted with passive integrated transponder tags. *Transactions of the American Fisheries Society,* 140, 1375-1379.

Du Plessis, A. 2019. Evaluation of Southern and South Africa's freshwater resources. In: Du Plessis, A. (Ed), *Water as an inescapable risk.* Springer, Switzerland, pp. 147-172.

Dube, T., Mutanga, O., Seutloali, K., Adelabu, S. & Shoko, C. 2015. Water quality monitoring in sub-Saharan African lakes: A review of remote sensing applications. *African Journal of Aquatic Science,* 40, 1-7.

Dudgeon, D., Arthington, A. H., Gessner, M. O., Kawabata, Z.-I., Knowler, D. J., Lévêque, C., Naiman, R. J., Prieur-Richard, A.-H., Soto, D. & Stiassny, M. L. 2006. Freshwater biodiversity: Importance, threats, status and conservation challenges. *Biological Reviews,* 81, 163-182.

Dugan, P. J., Barlow, C., Agostinho, A. A., Baran, E., Cada, G. F., Chen, D., Cowx, I. G., Ferguson, J. W., Jutagate, T. & Mallen-Cooper, M. 2010. Fish migration, dams, and loss of ecosystem services in the Mekong Basin. *Ambio,* 39, 344-348.

Ead, S., Katopodis, C., Sikora, G. & Rajaratnam, N. 2004. Flow regimes and structure in pool and weir fishways. *Journal of Environmental Engineering and Science,* 3, 379-390.

Evans, W., Downs, C. T., Burnett, M. J. & O'Brien, G. C. 2022. Assessing fish community response to water quality and habitat stressors in KwaZulu-Natal, South Africa. *African Journal of Aquatic Science,* 47, 47-65.

Fausch, K. D., Torgersen, C. E., Baxter, C. V. & Li, H. W. 2002. Landscapes to riverscapes: bridging the gap between research and conservation of stream fishes: A continuous view of the river is needed to understand how processes interacting among scales set the context for stream fishes and their habitat. *BioScience,* 52, 483-498.

[FBIS], Freshwater Biodiversity Information System. 2022. Downloaded from https://freshwaterbiodiversity.org on 20 October 2022.

Fetherman, E. R., Avila, B. W. & Winkelman, D. L. 2014. Raft and floating radio frequency identification (RFID) antenna systems for detecting and estimating abundance of PIT-tagged fish in rivers. *North American Journal of Fisheries Management,* 34, 1065-1077.
Fouché, P. & Heath, R. 2013. Functionality evaluation of the Xikundu fishway, Luvuvhu River, South Africa. *African Journal of Aquatic Science,* 38, 69-84.
Fouchy, K., Mcclain, M. E., Conallin, J. & O'Brien, G. 2019. Multiple stressors in African freshwater systems. In: Sabater, S., Elosegi, G., Ludwig, R. (Eds), *Multiple stressors in river ecosystems.* Elsevier, pp. 179-191.
Franklin, A. E., Haro, A., Castro-Santos, T. & Noreika, J. 2012. Evaluation of nature-like and technical fishways for the passage of alewives at two coastal streams in New England. *Transactions of the American Fisheries Society,* 141, 624-637.
Franklin, P. & Gee, E. 2019. Living in an amphidromous world: Perspectives on the management of fish passage from an island nation. *Aquatic Conservation: Marine and Freshwater Ecosystems,* 29, 1424-1437.
Fuchs, N. T. & Caudill, C. C. 2019. Classifying and inferring behaviors using real-time acceleration biotelemetry in reproductive steelhead trout (*Oncorhynchus mykiss*). *Ecology and Evolution,* 9, 11329-11343.
Garratt, P. 1993. Spawning of riverbream, *Acanthopagrus berda*, in Kosi estuary. *African Zoology,* 28, 26-31.
Grubich, J. R. & Odenkirk, J. 2014. Initial observations of movement patterns in the apex fish predator, the Nile perch (Lates niloticus), in Lake Nasser, Egypt. *Egyptian Journal of Aquatic Research,* 40, 65-69.
Hanna, D. E., Tomscha, S. A., Ouellet Dallaire, C. & Bennett, E. M. 2018. A review of riverine ecosystem service quantification: Research gaps and recommendations. *Journal of Applied Ecology,* 55, 1299-1311.
Hanzen, C., Lucas, M. C., O'Brien, G., Calverley, P. & Downs, C. T. 2021. Spatial ecology of freshwater eels in South Africa: implications for conservation. *Hydrobiologia,* 848, 2579-2593.
Hanzen, C. C., Lucas, M. C., Weyl, O. L., Marr, S. M., O'Brien, G. & Downs, C. T. 2022. Slippery customers for conservation: Distribution and decline of anguillid eels in South Africa. *Aquatic Conservation: Marine and Freshwater Ecosystems,* 32, 1277– 1290.
Harris, J. H. 1995. The use of fish in ecological assessments. *Australian Journal of Ecology,* 20, 65-80.
Hocutt, C., Seibold, S. & Jesien, R. 1994. Potential use of biotelemetry in tropical continental waters. *Revue d'hydrobiologie Tropicale,* 27, 77-95.
Hodge, B. W., Fetherman, E. R., Rogers, K. B. & Henderson, R. 2017. Effectiveness of a fishway for restoring passage of Colorado River Cutthroat Trout. *North American Journal of Fisheries Management,* 37, 1332-1340.
Holmlund, C. M. & Hammer, M. 1999. Ecosystem services generated by fish populations. *Ecological Economics,* 29, 253-268.
Hsu, A., Lloyd, A. & Emerson, J. W. 2013. What progress have we made since Rio? Results from the 2012 Environmental Performance Index (EPI) and Pilot Trend EPI. *Environmental Science & Policy,* 33, 171-185.
Hussey, N., Kessel, S., Aarestrup, K., Cooke, S., Cowley, P. & Fisk, A. 2015. Aquatic animal telemetry: A panoramic window into the underwater world. *Science,* 348, 1-10.
Impey, A. 2011. Songs of the in-between: remembering in the land that memory forgot. In: Peddie, I. (Ed), *Popular music and human rights*, Ashgate, London, pp. 39-52
Impson, N. D., Bills, I. R. & Wolhuter, L. E. 2007. *Technical report on the state of yellowfishes in South Africa 2007,* KV 212/08, Water Research Commission, Pretoria.

Jepsen, N., Schreck, C., Clements, S. & Thorstad, E. 2005. A brief discussion on the 2% tag/bodymass rule of thumb. In: Spedicato, M. T., Lembo, G., Marmulla, G. (Eds), *Aquatic telemetry: Advances and Applications Proceedings of the Fifth Conference on Fish Telemetry held in Europe*, pp. 255-259.

Jewitt, D., Goodman, P. S., Erasmus, B. F., O'Connor, T. G. & Witkowski, E. T. 2015. Systematic land-cover change in KwaZulu-Natal, South Africa: Implications for biodiversity. *South African Journal of Science,* 111, 01-09.

Kallis, G. 2010. Coevolution in water resource development: The vicious cycle of water supply and demand in Athens, Greece. *Ecological Economics,* 69, 796-809.

Karr, J. R. 1981. Assessment of biotic integrity using fish communities. *Fisheries,* 6, 21-27.

Katopodis, C. & Williams, J. G. 2012. The development of fish passage research in a historical context. *Ecological Engineering,* 48, 8-18.

Kaval, P. 2019. Integrated catchment management and ecosystem services: A twenty-five year overview. *Ecosystem Services,* 37, 100912.

Kemp, P. S. 2016. Meta-analyses, metrics and motivation: Mixed messages in the fish passage debate. *River Research and Applications,* 32, 2116-2124.

King, J. & Pienaar, H. 2011. Sustainable use of South Africa's inland waters: a situation assessment of resource directed measures 12 years after the 1998 National Water Act. *Water Research Commission Report No. TT,* 491, 1-245, Pretoria.

Kleynhans, C. 1999. The development of a fish index to assess the biological integrity of South African rivers. *WATER SA,* 25, 265-278.

Kleynhans, C. 2007. Module D: Fish response assessment index (FRAI). *River ecoclassification manual for ecostatus determination (Version 2):* Report produced for the Department of Water Affairs and Forestry (Resource Quality Services) and the Water Research Commission, WRC Report No. TT330/08, Pretoria.

Koehnken, L., Rintoul, M. S., Goichot, M., Tickner, D., Loftus, A. C. & Acreman, M. C. 2020. Impacts of riverine sand mining on freshwater ecosystems: A review of the scientific evidence and guidance for future research. *River Research and Applications,* 36, 362-370.

Koster, W. & Crook, D. 2017. Using telemetry data to develop conceptual models of movement to support the management of riverine fishes. *Marine and Freshwater Research,* 68, 1567-1575.

Kottelat, M. & Freyhof, J. 2007. *Handbook of European freshwater fishes*, Publications Kottelat.

Lennox, R. J., Aarestrup, K., Cooke, S. J., Cowley, P. D., Deng, Z. D., Fisk, A. T., Harcourt, R. G., Heupel, M., Hinch, S. G. & Holland, K. N. 2017. Envisioning the future of aquatic animal tracking: technology, science, and application. *BioScience,* 67, 884-896.

Lucas, M. C. & Baras, E. 2000. Methods for studying spatial behaviour of freshwater fishes in the natural environment. *Fish and Fisheries,* 1, 283-316.

Lucas, M. C. & Baras, E. 2008. *Migration of freshwater fishes*, Blackwell Science, Oxford, UK.

Lynch, A. J., Bartley, D. M., Beard Jr, T. D., Cowx, I. G., Funge-Smith, S., Taylor, W. W. & Cooke, S. J. 2020. Examining progress towards achieving the ten steps of the Rome declaration on responsible inland fisheries. *Fish and Fisheries,* 21, 190-203.

Lynch, A. J., Baumgartner, L. J., Boys, C. A., Conallin, J., Cowx, I. G., Finlayson, C. M., Franklin, P. A., Hogan, Z., Koehn, J. D. & Mccartney, M. P. 2019. Speaking the same language: Can the sustainable development goals translate the needs of inland fisheries into irrigation decisions? *Marine and Freshwater Research,* 70, 1211-1228.

Maeda, K. & Tachihara, K. 2005. Recruitment of amphidromous sleepers *Eleotris acanthopoma, Eleotris melanosoma*, and *Eleotris fusca* into the Teima River, Okinawa Island. *Ichthyological Research,* 52, 325.

Malherbe, W., Wepener, V. & Van Vuren, J. 2016. The effect of a large-scale irrigation scheme on the fish community structure and integrity of a subtropical river system in South Africa. *Ecological Indicators,* 69, 533-539.

Mantel, S. K., Rivers-Moore, N. & Ramulifho, P. 2017. Small dams need consideration in riverscape conservation assessments. *Aquatic Conservation: Marine and Freshwater Ecosystems,* 27, 748-754.

McDowall, R. M. 1997. The evolution of diadromy in fishes (revisited) and its place in phylogenetic analysis. *Reviews in Fish Biology and Fisheries,* 7, 443-462.

McIntyre, P. B., Reidy Liermann, C., Childress, E., Hamann, E. J., Hogan, J. D., Januchowski-Hartley, S. R., Koning, A. A., Neeson, T. M., Oele, D. L. & Pracheil, B. M. 2016. Conservation of migratory fishes in freshwater ecosystems. In: Closs, G. P. (Ed), *Conservation of freshwater fishes*, Cambridge University Press, Cambridge, pp. 324-360.

Mclaughlin, R. L., Smyth, E. R., Castro-Santos, T., Jones, M. L., Koops, M. A., Pratt, T. C. & Vélez-Espino, L. A. 2013. Unintended consequences and trade-offs of fish passage. *Fish and Fisheries,* 14, 580-604.

Melnychuk, M. C. 2009. Estimation of survival and detection probabilities for multiple tagged salmon stocks with nested migration routes, using a large-scale telemetry array. *Marine and Freshwater Research,* 60, 1231-1243.

Morhardt, J. E., Bishir, D., Handlin, C. I. & Mulder, S. D. 2000. A portable system for reading large passive integrated transponder tags from wild trout. *North American Journal of Fisheries Management,* 20, 276-283.

Morris, M. S., Holcombe, E. F., Borsky, A. J., Bentley, P. J. & Sandford, B. P. 2018. Detection of PIT-tagged juvenile salmonids migrating in the Columbia River Estuary, 2017. *National Oceanic and Atmospheric Administration, Northwest Fisheries Science Center, Seattle. Report to US Department of Energy, Contract,* 46273.

Musselman, W. C., Worthington, T. A., Mouser, J., Williams, D. M. & Brewer, S. K. 2017. Passive integrated transponder tags: review of studies on warmwater fishes with notes on additional species. *Journal of Fish and Wildlife Management,* 8, 353-364.

Nel, J., Murray, K., Maherry, A., Petersen, C., Roux, D., Driver, A., Hill, L., Van Deventer, H., Funke, N. & Swartz, E. 2011. Technical report for the national freshwater ecosystem priority areas project. *Water Research Commission Report*, 11, Pretoria.

Nguyen, V. M., Young, N. & Cooke, S. J. 2018. Applying a knowledge–action framework for navigating barriers to incorporating telemetry science into fisheries management and conservation: a qualitative study. *Canadian Journal of Fisheries and Aquatic Sciences,* 75, 1733-1743.

Northcote, T. 1978. Migratory strategies and production in freshwater fishes. In: Gerking, S. (Ed), *Ecology of freshwater fish production*, John Wiley & Sons, NewYork, pp. 326-359.

Northcote, T. 1984. Mechanisms of fish migration in rivers. In: McLeave, J. D., Arnold, G. P., Dodson, J. J., Neill, W. (Eds), *Mechanisms of migration in fishes.* PlenumPress, New York, pp. 317-356.

O'Brien, G. & De Villiers, P. 2008. *Biology and Ecology of the Orange-Vaal Largemouth and Smallmouth Yellowfishes in the Vaal River*, Water Research Commission, Pretoria.

O'Brien, G. C., Dickens, C., Hines, E., Wepener, V., Stassen, R., Quayle, L., Fouchy, K., Mackenzie, J., Graham, P. M. & Landis, W. G. 2018. A regional-scale ecological risk

framework for environmental flow evaluations. *Hydrology and Earth System Sciences,* 22, 957-975.
O'Brien, G. C., Ross, M., Hanzen, C., Dlamini, V., Petersen, R., Diedericks, G. J. & Burnett, M. J. 2019. River connectivity and fish migration considerations in the management of multiple stressors in South Africa. *Marine and Freshwater Research,* 70, 1254-1264.
Okeyo, D. O. 1998. Updating names, distribution and ecology of riverine fish of Kenya in the Athi-Galana-Sabaki River drainage system. *Naga, ICLARM Quarterly*, Jan-Mar, 44-53.
Page, L. M. & Burr, B. M. 2011. *Peterson field guide to freshwater fishes of North America north of Mexico*, Houghton Mifflin Harcourt.
Paxton, B. R. 2004. *Catchment-wide movement patterns and habitat utilisation of freshwater fish in rivers: implications for dam location, design and operation: a review and methods development for South Africa,* KV145/04, Water Research Commission, Pretoria.
Pethiyagoda, R. 1991. *Freshwater fishes of Sri Lanka*. Wildlife Heritage Trust of Sri Lanka.
Plug, I., Mitchell, P. & Bailey, G. 2010. Late Holocene fishing strategies in southern Africa as seen from Likoaeng, highland Lesotho. *Journal of Archaeological Science,* 37, 3111-3123.
Porcher, J. & Travade, F. 2002. Fishways: biological basis, limits and legal considerations. *Bulletin Français de la Pêche et de la Pisciculture*, 364, 9-20.
Postel, S. & Carpenter, S. 1997. Freshwater ecosystem services. In: Daily, G.C. (Ed), *Nature's services: Societal dependence on natural ecosystems*. Island Press, Washington DC, USA, 195.
Potts, W. M., Saayman, M., Saayman, A., Mann, B. Q., Van Der Merwe, P., Britz, P. & Bova, C. S. 2022. Understanding the economic activity generated by recreational fishing in South Africa provides insights on the role of recreational fisheries for social development. *Fisheries Management and Ecology,* 29, 29-43.
Prentice, E. F., Flagg, T. & McCutcheon, C. 1990. Feasibility of using implantable passive integrated transponder (PIT) tags in salmonids. *American Fisheries Society Symposium*
Prentice, E. F. & Park, D. L. 1984. A study to determine the biological feasibility of a new fish tagging system. *Annual Report of Research (1983 - 1984).* Northwest and Alaska Fisheries Center.
Ramesh, T., Downs, C. T. & O'Brien, G. C. 2018. Movement response of Orange-Vaal largemouth yellowfish (*Labeobarbus kimberleyensis*) to water quality and habitat features in the Vaal River, South Africa. *Environmental Biology of Fishes,* 101, 997-1009.
Riede, K. 2004. *Global register of migratory species: from global to regional scales: final report of the R&D-Projekt 808 05 081*, Federal Agency for Nature Conservation.
Rivers-Moore, N., Goodman, P. & Nel, J. 2011. Scale-based freshwater conservation planning: towards protecting freshwater biodiversity in KwaZulu-Natal, South Africa. *Freshwater Biology,* 56, 125-141.
Roberts, D., Udyawer, V., Franklin, C., Dwyer, R. & Campbell, H. 2017. Using an acoustic telemetry array to assess fish volumetric space use: a case study on impoundments, hypoxia and an air-breathing species (*Neoceratodus forsteri*). *Marine and Freshwater Research,* 68, 1532-1543.
Rodell, M., Famiglietti, J. S., Wiese, D. N., Reager, J., Beaudoing, H. K., Landerer, F. W. & Lo, M.-H. 2018. Emerging trends in global freshwater availability. *Nature,* 557, 651-659.

Roscoe, D. W. & Hinch, S. G. 2010. Effectiveness monitoring of fish passage facilities: historical trends, geographic patterns and future directions. *Fish and Fisheries,* 11, 12-33.

Roussel, J., Haro, A. & Cunjak, R. 2000. Field test of a new method for tracking small fishes in shallow rivers using passive integrated transponder (PIT) technology. *Canadian Journal of Fisheries and Aquatic Sciences,* 57, 1326-1329.

Scarrow, R. M. 2014. Sustainable migration to the urban west: Environment and growth in an uncertain future. *International Journal of Sociology,* 44, 34-53.

Schreiner, B. 2013. Viewpoint—Why has the South African National Water Act been so difficult to implement? *Water Alternatives,* 6, 239-245.

Silva, A. T., Lucas, M. C., Castro-Santos, T., Katopodis, C., Baumgartner, L. J., Thiem, J. D., Aarestrup, K., Pompeu, P. S., O'Brien, G. C. & Braun, D. C. 2018. The future of fish passage science, engineering, and practice. *Fish and Fisheries,* 19, 340-362.

Skelton, P. 2001. *A Complete Guide to the Freshwater Fishes of Southern Africa.* Struik Publishers, Cape Town (ZA).

Strydom, N. A. & Neira, F. J. 2006. Description and ecology of larvae of *Glossogobius callidus* and *Redigobius dewaali* (Gobiidae) from temperate South African estuaries. *African Zoology,* 41, 240-251.

Teugels, G. G. 1986. A systematic revision of the African species of the genus *Clarias* (Pisces; Clariidae). *Annales-Musee Royal de l'Afrique Centrale. Sciences Zoologiques (Belgium)*.

Thiem, J., Binder, T., Dawson, J., Dumont, P., Hatin, D., Katopodis, C., Zhu, D. & Cooke, S. 2011. Behaviour and passage success of upriver-migrating lake sturgeon *Acipenser fulvescens* in a vertical slot fishway on the Richelieu River, Quebec, Canada. *Endangered Species Research,* 15, 1-11.

Thiem, J. D., Wooden, I. J., Baumgartner, L. J., Butler, G. L., Forbes, J., Taylor, M. D. & Watts, R. J. 2018. Abiotic drivers of activity in a large, free-ranging, freshwater teleost, Murray cod (*Maccullochella peelii*). *PLoS One,* 13, e0198972.

Thirion, C. & Jafta, N. 2019. State of Rivers Report: River Ecostatus Monitoring Programme 2017 - 2018.: Department of Water and Sanitation.

Thorstad, E. B., Rikardsen, A. H., Alp, A. & Økland, F. 2013. The use of electronic tags in fish research–an overview of fish telemetry methods. *Turkish Journal of Fisheries and Aquatic Sciences,* 13, 881-896.

Tickner, D., Opperman, J. J., Abell, R., Acreman, M., Arthington, A. H., Bunn, S. E., Cooke, S. J., Dalton, J., Darwall, W. & Edwards, G. 2020. Bending the curve of global freshwater biodiversity loss: an emergency recovery plan. *BioScience,* 70, 330-342.

Todd, C. R., Lintermans, M., Raymond, S. & Ryall, J. 2017. Assessing the impacts of reservoir expansion using a population model for a threatened riverine fish. *Ecological Indicators,* 80, 204-214.

Trancart, T., Tétard, S., Acou, A., Feunteun, E., Schaeffer, F. & De Oliveira, E. 2018. Silver eel downstream migration in the River Rhine, route choice, and its impacts on escapement: a 6-year telemetry study in a highly anthropized system. *Ecological Engineering,* 123, 202-211.

Twardek, W. M., Landsman, S. J. & Cooke, S. J. 2022. Collaboration between fish passage scientists and engineers: Insights from an international questionnaire. *Journal of Environmental Management,* 323, 116268.

Umgeni Water 2017. Infrastructure Master Plan 2017/2018 - 2047/2048. Pietermaritzburg, KwaZulu-Natal, South Africa: Umgeni Water.

Van Vuuren, L. 2008. Thukela-Vaal Transfer scheme. *Water Wheel,* Nov-Dec, 14-21.

Wade, M., O'Brien, G. C., Wepener, V. & Jewitt, G. 2021. Risk assessment of water quantity and quality stressors to balance the use and protection of vulnerable water resources. *Integrated Environmental Assessment and Management,* 17, 110-130.
Weyl, O. L. & Lewis, H. 2006. First record of predation by the alien invasive freshwater fish *Micropterus salmoides* L.(Centrarchidae) on migrating estuarine fishes in South Africa. *African Zoology,* 41, 294-296.
Whitfield, A. K. 1990. Life-history styles of fishes in South African estuaries. *Environmental Biology of Fishes,* 28, 295-308.
Whitfield, A. K. 1998. *Biology and Ecology of Fishes in South African Estuaries.* Ichthyological Monograph, no. 2, J.L.B. Smith Institute of Ichthyology, Grahamstown.
Wilkes, M. A., Webb, J. A., Pompeu, P. S., Silva, L. G., Vowles, A. S., Baker, C. F., Franklin, P., Link, O., Habit, E. & Kemp, P. S. 2019. Not just a migration problem: Metapopulations, habitat shifts, and gene flow are also important for fishway science and management. *River Research and Applications,* 35, 1688-1696.
World Commission on Dams 2000. *Dams and development: A new framework for decision-making: The report of the world commission on dams*, Earthscan.
Zielinski, D. & Freiburger, C. 2021. Advances in fish passage in the Great Lakes basin. *Journal of Great Lakes Research,* 47, S439-S447.
Zielinski, D. P., Mclaughlin, R. L., Pratt, T. C., Goodwin, R. A. & Muir, A. M. 2020. Single-stream recycling inspires selective fish passage solutions for the connectivity conundrum in aquatic ecosystems. *BioScience,* 70, 871-886.

CHAPTER 2

A fish community assessment of the lower uThukela River, KwaZulu-Natal, South Africa

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Running header: Lower uThukela River fish community assessment

2.1 Abstract

In South Africa, a water-scarce country, dams and weir construction are on the rise to ensure water security for a growing nation. The human need for this infrastructure is generally prioritised over their environmental impact, particularly for aquatic fauna with migratory needs. Such infrastructure can block migratory pathways of fish, trap sediment, and alter flows in the river. The Lower Thukela Bulk Water Supply Scheme (LTBWSS) abstraction weir was built on the lower uThukela River, KwaZulu-Natal Province, South Africa, in 2017, near the town of Mandeni. The riverine stretch where it is constructed is at a critical point for marine, estuarine, and freshwater migrant local fish species, and as such, a vertical slot fishway was incorporated into its design to help facilitate the movement of fish over the weir. This study used data collected from field surveys at three sites upstream of the weir, four sites downstream of it, and two sites on the Mandeni Stream, a tributary of the uThukela, to assess the impact that the weir has on local fish community structures. Multivariate statistical analyses were used to determine the environmental variables driving fish community structures in the region. The results showed that the dominant cover, dominant substrate, average depth, and temperature significantly affected fish communities in the study. Individual species were driven by different habitats, velocity-depth, and physical water quality variables. Furthermore, the presence of the LTBWSS has influenced three cichlid species, particularly *T. sparrmanii,* which was previously shown to favour silt substrate. The resulting loss in downstream sedimentation because of the LTBWSS weir has caused the absence of the species, along with synergistic effects of water quality and quantity on the downstream sections of the uThukela River because of the weir.

Keywords: instream barrier, freshwater ecology, environmental variables, fish community

2.2 Introduction

Freshwater ecosystems provide essential ecosystem services important for human livelihoods and maintain environmental integrity (Hanna et al., 2018). They provide ecosystem services such as drinking water, controlling natural water quality, supplying food, facilitating habitat for organisms, regulating the climate, and creating recreation and tourism options, to name a few, but are often irreplaceable (Postel and Carpenter, 1997; Hanna et al., 2018; Kaval, 2019). Their societal and ecological value is high, particularly in developing regions where the sustenance of many human populations depends on these services (King and Pienaar, 2011; Fouchy et al., 2019). As a result of this dependence, freshwater ecosystems are among the most threatened ecosystems on the planet because they are often severely modified through anthropogenic development to sustain the growing human population's needs (Dudgeon et al., 2006; Rodell et al., 2018; du Plessis, 2019). Such developments often excessively use water resources to support essential societal services, contributing to biodiversity loss worldwide (Dudgeon, 2010; Dugan et al., 2010). This tends to be brought on by dams, weirs and other instream barriers created for water quantity provision for various economic sectors, flood control, and hydropower generation (Belletti et al., 2020), which contribute to river fragmentation and associated habitat loss and habitat alterations (World Commission on Dams, 2000; Carpenter et al., 2011; Fouchy et al., 2019; Barbarossa et al., 2020), shifts in hydrological dynamics (World Commission on Dams, 2000; Zuo and Liang, 2015), and water quality and pollution issues from aggravated land-use and agricultural processes (Evans et al., 2019). Additionally, translocated invasive species threaten indigenous biodiversity by predating on, or competing with indigenous biota for resources, diminishing or completely eradicating resident populations (Ellender and Weyl, 2014; Gallardo et al., 2016). Climate change influences further increase these stressors' detrimental effects (DeNicola et al., 2015; Mittal et al., 2016).

Fish form essential constituents of river ecosystems, contributing to ecosystem well-being through the roles they play in it (Fausch et al., 2002; Dugan et al., 2010). Freshwater fish populations support various ecological functions, including the movement of nutrients between habitats, the management of pest species, the upkeep of sediment processes, and the generation of food (Holmlund and Hammer, 1999). Furthermore, most fish migrate to some degree, which means they can occupy several ecological niches throughout their lifetimes (Lucas and Baras, 2008), acting as agents for the cycling of nutrients and energy between the aquatic environments they occupy, including between saltwater and freshwater ecosystems (McIntyre et al., 2016). These migrations occur for various reasons, such as spawning, feeding, and evading predators or harmful environmental conditions, but are ultimately important to individual and population health (Northcote, 1978; Lucas and Baras, 2008; McIntyre et al., 2016). Through their various ecological functions, certain fish species are usually valuable indicators of ecosystem health (Chovanec et al., 2003), with migratory species generally being better indicators because of their mobility, unique habitat needs, and vulnerability to a variety of stressors and resource degradation (Harris, 1995; Dugan et al., 2010). Therefore, to effectively manage those fish populations and the system as a whole, it is important to understand the environmental drivers of fish species' community structure and distribution within a particular system (Desai et al., 2021; Evans et al., 2022).

The uThukela River is ~500 km long and has a catchment area of just under 30,000 km^2, and it is South Africa’s second-largest river and the largest catchment in KwaZulu-Natal Province (Department of Water Affairs and Forestry, 2004). Its source is in the Drakensberg Mountains, from whence it runs across central KwaZulu-Natal in an easterly direction until emptying into the Indian Ocean through the uThukela Estuary (Department of Water Affairs and Forestry, 2004). Throughout its catchment, as well as its reach into the Indian Ocean, the uThukela River provides important ecosystem services and resources to humans and the environment (Department of Water Affairs and Forestry, 2004; Department of Water Affairs, 2013). Its water supply is not only valued by communities in its catchment but also by other areas in the country which gain water from its inter-basin water transfer schemes, including Gauteng Province, the economic hub of South Africa (Van Vuuren, 2008; Department of Water Affairs, 2013). The nutrients provided by the uThukela River are important to the varying ecosystems within its catchment, as well as the offshore marine environment, particularly the Thukela Banks and uThukela Marine Protected Area (De Lecea and Cooper, 2016; Department of Environmental Affairs, 2019; Wade et al., 2021). However, several water quality, quantity, and habitat altering and wildlife disturbance stressors have been caused by the heavy use of the rivers in the uThukela catchment, impacting social and biological elements of the system (Department of Water Affairs and Forestry, 2004; Department of Water and Sanitation, 2022b).

The uThukela River main stem and tributaries, particularly the lower reaches, have been impacted by water abstraction, effluent discharge, and various other pollution sources from processes associated with human settlements, sewerage treatment plants, factories, processing plants, and agricultural practices (Department of Water Affairs, 2013; Umgeni Water, 2017). There are multiple stressors caused by the excessive use of the water and poor land practices in the uThukela catchment, impacting social and biological elements of the system (Department of Water Affairs and Forestry, 2004; Wade et al., 2021; Department of Water and Sanitation, 2022b). Water quality and quantity issues are major stressors in the lower uThukela catchment, with sources like the Sappi Tugela Pulp and Paper Mill responsible for elevated salts and organics, the localised industrial, urban, and peri-urban areas contributing to toxicants, and the stock farms, sewerage plants, upstream sources, and sugarcane (*Saccharum officinarum*) farms contributing to organic contaminants and nutrient enrichment (Wade et al., 2021; Evans et al., 2022). Due to the upstream extraction of water through dams and river diversions, the natural flow regimes of the river have been disrupted, which is the cause of the water quantity problems

(Wade et al., 2021). Sand mining operations, indirectly brought about by lower flows in the region, have been connected to habitat stressors (Wade et al., 2021), with these types of operations known to alter the natural transport and deposition processes of the riverine sediments (Koehnken et al., 2020). Unmanaged fish harvesting and the presence of non-native fauna in the area are wildlife-disturbing stressors on the lower uThukela River, especially in its mouth (Wade et al., 2021). Recent evaluations on the state of the lower uThukela River and estuary have established it as an ecological category C classification, meaning it is acceptable to be moderately modified (Wade et al., 2021; Evans et al., 2022). This shows managers that the fundamental ecosystem functions are predominantly unaltered, despite some loss of natural habitat and biota (Kleynhans and Louw, 2007). In 2017, the Lower Thukela Bulk Water Supply Scheme (LTBWSS) infrastructure in Mandeni, KwaZulu-Natal, was commissioned to abstract water from the uThukela River to supply the KwaDukuza and Mandini local municipalities (Department of Water and Sanitation, 2022a). Presently, it has the capacity to abstract 55 Ml/d of raw water, with a future phase ultimately allowing the abstraction of up to 110 Ml/d.

Our study aimed to determine the impact of the newly constructed LTBWSS as a barrier for migratory fish and the impact this may have on the local fish community structures in the lower uThukela River, KwaZulu-Natal, South Africa. Our objectives were to 1) determine the environmental drivers influencing fish community structures in the study area, using measured hydraulic variables and habitat characteristics and 2) determine the impact that the recently constructed LTBWSS weir has on the local fish community structures on the lower uThukela River. We predicted that the weir had negative impacts despite having a fishway.

2.3 Methods

2.3.1 Study area

The present study area focuses on the lower parts of the freshwater portion of the uThukela catchment in KwaZulu-Natal Province, South Africa, in the region of Mandeni town. The study occurred in quaternary catchment V50C and V50D of the Department of Water and Sanitation (DWS) catchment management areas of South Africa, from the Mdlebeni road bridge to the N2 road bridge (site EWR19; Fig. 2.1) on the uThukela River, which included the Mandeni Stream that flows into the uThukela River (Fig. 2.1). The upper tidal limit of the uThukela estuary penetrates approximately 8 km upstream from the mouth, located near site EWR19 (Fig 2.1). Despite the study being in the freshwater reaches, the presence of euryhaline fish was expected as some species in the region have dependencies on both freshwater and saltwater at different stages of their life cycles (Whitfield, 1998; Skelton, 2001; Whitfield, 2019).

Initially, four sites were selected to assess the fish community structures in the area surrounding the LTBWSS weir, with two sites upstream (sites EWR16 and UPSTR; Fig. 2.1) of the weir and two downstream of it (sites DWNSTR and EWR17; Fig. 2.1). One upstream and one downstream site were based on historical Environmental Water Requirements (EWR) sites. The other two were selected in the immediate upstream and downstream vicinity of the weir, with all sites having accessibility under consideration. The immediate upstream and downstream sites were deemed representative of a stretch of the river under the influence of the weir. Furthermore, additional ad hoc sites were included in the study to gain a comprehensive outlook on fish communities in the lower uThukela River. These were one site further upstream (site Mdlebeni; Fig. 2.1) and two sites further downstream on the uThukela River (sites EWR18 and EWR19; Fig. 2.1), and two sites situated on the Mandeni Stream (sites Mandini US and Mandini DS; Fig. 2.1), a tributary which enters the uThukela River downstream of the LTBWSS weir. The downstream site on the Mandeni (shown as Mandini

DS, Fig 2.1) is situated below a weir, approximately 200 m upstream of its confluence with the uThukela River (Wade et al., 2021).

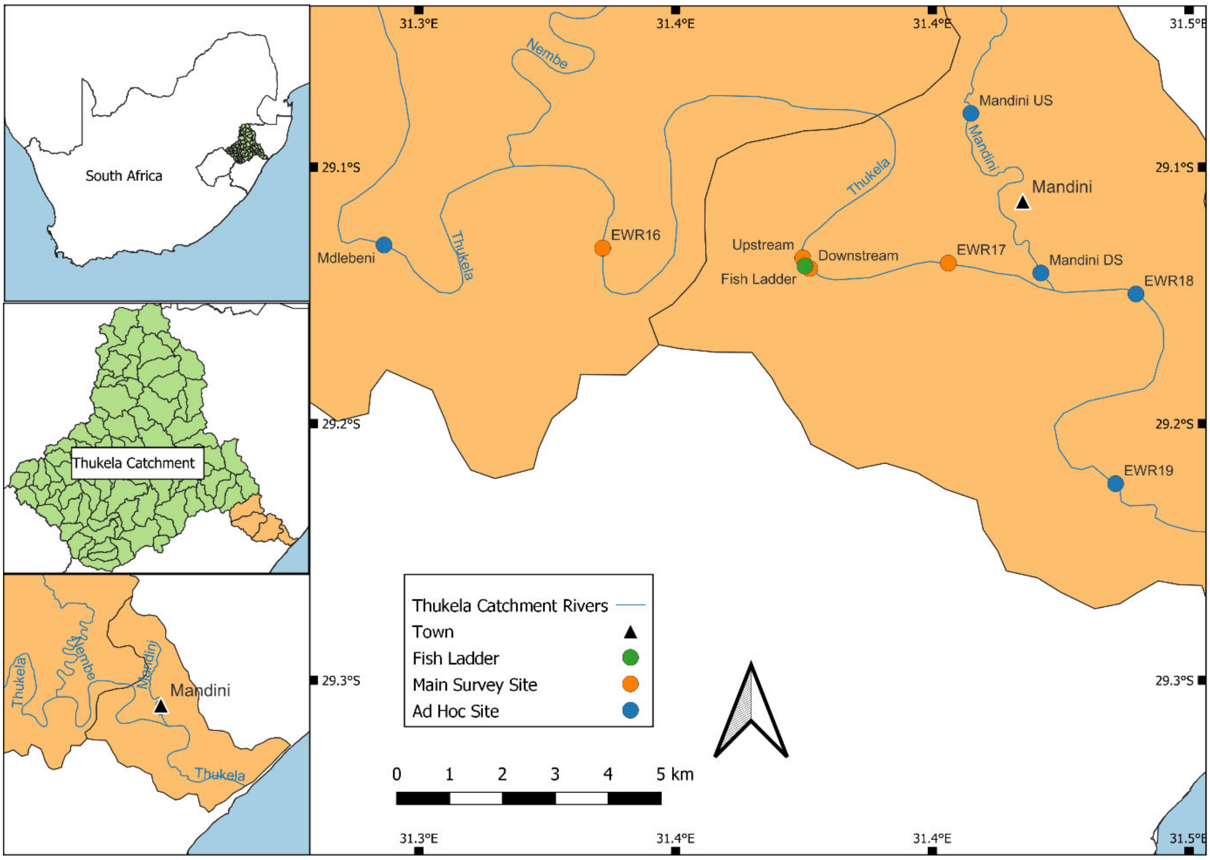

Figure 2.1: Map of the present study area, quaternary catchment V50C and V50D, with sampling sites, in the lower uThukela River, KwaZulu-Natal, South Africa. (Note: site Upstream and Downstream are referred to as INSTR and DWNSTR, respectively, in text).

2.3.2 Fish capture

Three fish collection surveys were conducted from May 2021 to December 2021 as the initial component of the fish community assessment at sites situated around the LTBWSS weir (Fig 2.1). Surveys took place seasonally and included two low-flow and one high-flow survey. A second high-flow survey in early 2022 could not be conducted because the uThukela River was in flood following a sustained high rainfall period from January to April 2022. Fish data obtained from additional ad hoc surveys in the lower uThukela basin was also used as part of the fish community assessment. Fish collection techniques included fyke nets, electrofishing, and seine netting. Approval to conduct these surveys was granted by the conservation authority Ezemvelo KZN Wildlife (permit numbers OP1060-2021 and OP1060-2022).

For the initial sites, a minimum of four small double-ended Dutch-type commercial fyke nets (T&L Netmaking, Mooroolbark, Australia) were used in a single overnight sample period at each site per survey. The fyke nets used were double-ended Dutch-type fyke nets with a 9.7 m leader net between the hoop nets which were 600 mm high x 800 mm wide. The netting material for the entire net had a stretched mesh size of 20 mm. Otter guards were placed at the entrances of all nets (Jefferies et al., 1984). We deployed nets using an inflatable boat powered by a small battery-operated sneaker motor (Watersnake Venom, Watersnake Electric Motors and Accessories, Australia). We first fastened the net to the bank and set the first fyke and moved into the river at ca. 30° to the bank in the direction of the water flow to set the other end of the fyke in the water. The fyke nets were set between 15:00 and 17:00 on the first day and were then checked and removed between 8:00 and 10:00 the following day. During the May 2021 survey, a minimum of 7 nets were used at the site immediately downstream of the weir to increase the sample size collected for another study that required fish for a catch-mark-recapture (CMR) study (Chapter 3). These nets were deployed for four days, whereby they were set between 17:00 and 17:30 on the first day and then checked in the morning between 10:00 and 11:00 and again in the afternoon between 17:00 and 18:00, until the end of the survey. On the day of removing nets at all sites, additional fish collection was conducted using electrofishing or seine netting methods where applicable. Through a combination of all three sampling techniques, an attempt was made to sample all accessible velocity depth classes (Kleynhans, 2007) at each site.

At all sites, except in the impoundment formed by the LTBWSS at the site directly upstream of the weir, we used a backpack-mounted SAMUS electrofisher (SAMUS 725MS Electrofisher, SAMUS Special Electronics, Poland). Electrofishing was conducted in flowing water less than a metre deep or slow-flowing water containing large amounts of debris or rocks that would make seine netting impossible. We adjusted the current strength of the electrofisher to the conditions of each sample area so it was optimised for the capture of a variety of species (Bohlin et al., 1989). We conducted the electrofishing in teams of three by walking in the water with insulated waders; one person operated the electrofisher, and two people handled the landing nets on either side of the operator. Each effort was approached from downstream, moving up, allowing stunned fish to drift downstream towards the samplers. The landing nets used had a minimum mesh size of 3 mm, and a maximum mesh size of 10 mm. Each effort consisted of a series of 5-s bursts of electricity over a 2-to-5-min period. A site was intermittently electrofished for no longer than 60 min.

We conducted seine netting in the slow to no-flowing sections of the river, which were generally deeper, or the sections containing large shallow sand banks. We used two different seine nets where appropriate. The small seine net (length = 12 m, depth = 1.5 m, mesh size = 3 mm; Eigevis Group of Companies, Cape Town, South Africa) was used in areas where the water was shallow, slow to no flowing and had a relatively smaller sample area. We used the large seine net (length = 32 m, depth = 2.5 m, mesh size = 25 mm; Eigevis Group of Companies, Cape Town, South Africa) in slightly faster-moving water where the small seine net had too much resistance or was more efficient in performing one large seine of an area. We performed a maximum of five seine net drags (each drag was recorded as an effort) per site. The ad hoc surveys used the same electrofishing or seine netting methods as described above.

Captured fish were immediately placed into buckets containing a minimum of 15 litres of river water, from which they could be processed. Processing included counting, identifying the individual to the species level, and measuring standard, fork, and total lengths to the nearest millimetre. Measurements of individually collected fish are useful in analysing population structures, as their size classes can be valuable indicators of the state of the fish populations (Evans et al., 2022). Once processed, we returned the fish to the river alive and as close to the capture point as possible. The time taken to process an individual fish was less than 30 s.

2.3.3 Habitat assessment

We collected i*n situ* physico-chemical characteristics at each site sampled. We measured water quality variables once for the entire site per sample using a calibrated XS Instruments PC 5 Tester multiparameter tool (XS Instruments, Italy). Measured water quality variables included temperature, pH, total dissolved solids (TDS), electrical conductivity (EC), and salinity. We assessed the available habitat and velocity/depth profiles at five points within each effort conducted at the study site. Habitat was visually assessed in terms of its substrate and cover features. We described substrate as either bedrock, boulders, cobbles, gravel, sand, mud, silt, or other (Kleynhans, 1999, 2007). Cover features were described as either the substrate itself, position in the water column, marginal vegetation, overhanging vegetation, instream/aquatic vegetation, root wads, wood-debris, undercut banks, depth, or rippled surface (Kleynhans, 1999, 2007). The velocity/depth profile for each of the five points per effort were measured using a transparent Velocity Head Rod (GroundTruth, Hilton, South Africa). Ecohydraulic (velocity-depth) flow classes for fish (Fig. 2.2), which represent suitability criteria for fish (Kleynhans, 2007; James and King, 2010), were also calculated using the average depth and average velocity of each effort.

Historical fish assemblages in the lower uThukela River were obtained through available literature on the area (Skelton, 2001; Wade et al., 2021; Evans et al., 2022), as well as databases such as the Present Ecological State, Ecological Importance & Ecological

Sensitivity (PESEIS) (Department of Water and Sanitation, 2014), and the Freshwater Biodiversity Information System (FBIS) (FBIS, 2022).

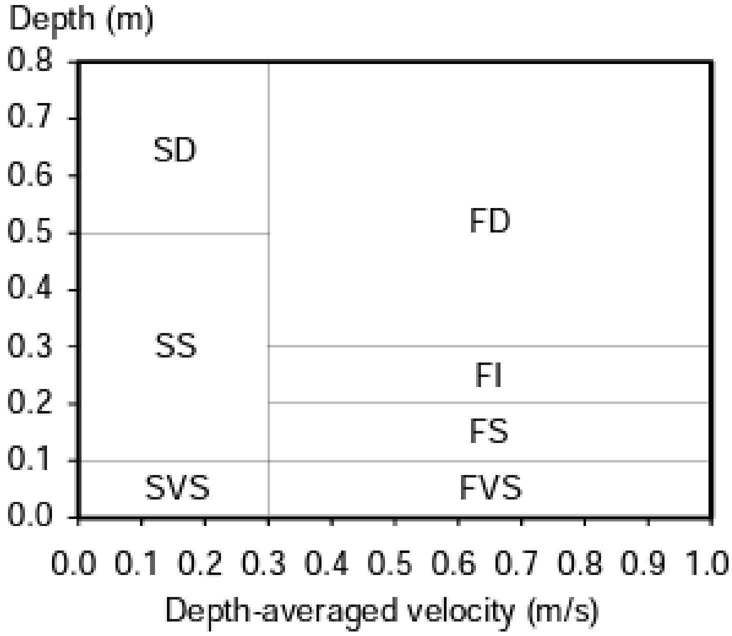

Figure 2.2: Ecohydraulic flow classes (velocity-depth classes) for fish as obtained from James and King (2010).

2.3.4 Analyses

To assess the relationships between the fish communities and environmental factors in the lower uThukela River, we used a variety of statistical methods. All statistical analyses were performed with R version 4.2.1 (R Core Team, 2022). A modelling approach using multivariate generalised linear models (GLM)(Warton, 2011) was used. Firstly, a collinearity check was performed on the environmental variables to ensure that the variables used in the model did not have high correlations that could influence the model's accuracy. We then fitted fish species presence data to environmental variables to determine the environmental factors influencing community structure in the lower uThukela River using the 'mvabund' package (Wang et al., 2012). We used the Wald Test with 250 resampling iterations through PIT-trap resampling (Warton et al., 2017). The effect of the tested environmental variables was considered to be significant at $P < 0.05$. An additional summary of the multivariate GLM with 999 PIT-trap resampling iterations using the Wald test and a significance when $P < 0.05$, allowed us to further analyse the levels of the tested environmental conditions.

2.4 Results

2.4.1 Habitat

The dominant habitat variables relating to ecohydraulic flow classes, substrate, and cover features for each site in our study area are summarised in Table 2.1 using the collated totals from all the efforts performed at them. For the seven sites on the lower uThukela River, the slow-deep ecohydraulic flow class was characteristic for all but site EWR16 which had a slow-shallow classification. Only sites EWR17 and EWR18 had dual dominant ecohydraulic flow classes, having an even proportion of slow-deep and slow-shallow classification. Sand was a dominant substrate throughout all sites on the lower uThukela besides the UPSTR site, which had a mud substrate dominance. Additional to sand, Mdlebeni and EWR17 had mud as a dual-dominant substrate, with EWR16 having cobble, and DWNSTR having boulders. Depth as a cover feature was dominant throughout all sites on the uThukela, with additional cover features for Mdlebeni and EWR17 being marginal vegetation, EWR16 being the cobble substrate, and the downstream site having boulder substrate. The two Mandeni sites were characterised by the slow-shallow ecohydraulic flow class. The Mandeni US site was dominated by bedrock and sand substrate features and overhanging vegetation as the dominant cover feature. The Mandeni DS site was dominated by mud and boulder substrate, with depth and the boulder substrate being the dominant cover features.

Table 2.1: Summary of the dominant ecohydraulic flow class, substrate, and cover features of the various sites used for sampling in the lower uThukela River, KwaZulu-Natal, South Africa. (See Fig. 2.1 for site locations).

Site	Ecohydraulic flow class	Substrate	Cover
Mdlebeni	Slow Deep	Mud/Sand	Depth/Marginal Vegetation
EWR16	Slow Shallow	Cobble/Sand	Depth/Cobble Substrate
UPSTR	Slow Deep	Mud	Depth
DWNSTR	Slow Deep	Boulder/Sand	Depth/Boulder Substrate
EWR17	Slow Deep/Slow Shallow	Mud/Sand	Depth/Marginal Vegetation
EWR18	Slow Deep/Slow Shallow	Sand	Depth
EWR19	Slow Deep	Sand	Depth
Mandeni US	Slow Shallow	Bedrock/Sand	Overhanging Vegetation
Mandeni DS	Slow Shallow	Mud/Boulder	Depth/Boulder Substrate

Table 2.2: A list of all fish species expected in the freshwater reaches of the study area, their historical occurrence, and presence/relative abundance in the lower uThukela River, KwaZulu-Natal, South Africa. (Note: * *Non-native*/invasive species).

Species	Falls in the distribution range	Historical presence	Presence (n) in the present study
Awaous aeneofuscus	X	X	7
Acanthopagrus berda	X	X	2
Anguilla bengalensis	X	X	
Anguilla marmorata	X	X	5
Anguilla mossambica	X	X	1
Amphilius natalensis	X	X	
Amphilius uranoscopus	X	X	
**Cyprinus carpio*	X	X	12
Clarias gariepinus	X	X	48
Coptodon rendalli	X	X	
Eleotris fusca	X	X	10
Enteromius gurneyi	X	X	
Enteromius paludinosus	X	X	40
Enteromius trimaculatus	X	X	172
Enteromius viviparus	X	X	58
Enteromius spp. (Fry)			38
Gilchristella aestuaria	X	X	
Glossogobius callidus	X	X	7
Glossogobius giuris	X	X	1
Labeo molybdinus	X	X	66
Labeo rubromaculatus	X	X	18
Labeobarbus natalensis	X	X	137
Oreochromis mossambicus	X	X	322
Pseudomyxus capensis	X	X	55
Pseudocrenilabrus philander	X	X	
**Poecilia reticulata*	X	X	244
Tilapia sparmanii	X	X	
Ambassis dussumieri	X		3
Ambassis natalensis	X		
Anguilla bicolor bicolor	X		
Eleotris melanosoma	X		
Hypseleotris cyprinoides	X		
Monodactylus argentus	X		
Monodactylus falciformis	X		
Microphis brachyurus	X		2
Microphis fluviatilis	X		1
**Micropterus salmoides*	X		1
Kuhlia rupestris	X		1

Table 2.3: Collected abundances of fish species at sample sites across the study area in the lower uThukela River, KwaZulu-Natal, South Africa.

	uThukela River Sites							Mandeni Stream Sites	
Species	Mdlebeni	EWR 16	UPSTR	DWNSTR	EWR 17	EWR1 8	EWR1 9	Mandeni US	Mandeni DS
Aaen		3		1	1		2		
Aber					1		1		
Adus					3				
Amar				3	2				
Amos									1
Ccar			2	8	1				1
Cgar	3		2	20	5	4	2	3	9
Efus				4	5				1
Epau	13			11	2		14		
ESpp		38							
Etri	111	18	25	7	1		6		4
Eviv	32	6		20					
Gcal		2		2	1		1		1
Ggiu							1		
Krup									1
Lmol		1	1	44	4				16
Lnat	12	9	1	33	7	42	1		32
Lrub		2	1	2	3		1		9
Mbra					2				
Mflu					1				
MFry				1					
Msal				1					
Omos		3		62	140	3	76	1	37
Pcap					7	13	33		1
Pret								180	64

(Note: Abbreviations for species*: Aaen – Awaous aeneofuscus, Aber – Acanthopagrus berda, Adus – Ambassis dussumieri, Amar – Anguilla marmorata, Amos – Anguilla mossambica, Ccar – Cyprinus carpio, Cgar -Clarias gariepinus, Efus – Eleotris fusca, Epau – Enteromius paludinosus, ESpp - unknown Enteromius species, classification could not be determined because of the small size (< 10 mm TL), Etri – Enteromius trimaculatus, Eviv – Enteromius viviparus, Gcal – Glossogobius callidus, Ggiu – Glossogobius giuris, Krup – Kuhlia rupestris, Lmol – Labeo molybdinus, Lnat – Labeobarbus natalensis, Lrub – Labeo rubromaculatus, Mbra – Microphis brachyurus, Mflu – Microphis fluviatilis, MFry – Mullet fry too small to identify species, Msal – Micropterus salmoides, Omos – Oreochromis mossambicus, Pcap – Pseudomyxus capensis, Pret – Poecilia reticulata*).

2.4.2 Fish species community composition

Historical survey data showed that a combined 24 indigenous freshwater fish species and two additional invasive species were present and collected in these quaternary catchments (Department of Water and Sanitation, 2014; Evans et al., 2022; FBIS, 2022) (Table 2.2). Historical data showed that of the 14 species found upstream of the weir, two were euryhaline and included *Awaous aeneofuscus* and *Eleotris fusca*. The distribution range of a further ten indigenous species and one invasive species were also expected to be present in the study area (Skelton, 2001). A total of 1251 fish from 23 species were collected in the study area (Table 2.2) using fyke nets, electrofishing, and seine netting methods where appropriate. These included 18 historically present species and five whose distribution ranges fall into the study area and could be expected to occur there. In terms of counts, the most abundant species collected were *Oreochromis mossambicus* (n = 322), *Poecilia reticulata* (n = 244), *Enteromius trimaculatus* (n = 172) and *Labeobarbus natalensis* (n = 137), which were responsible for 70 % of all individuals that were captured. However, *P. reticulata* were only captured in the Mandeni Stream, accounting for 68 % of the relative abundance caught in that stream (Table 2.3). Cyprinidae was the most species-rich family in the lower uThukela River, with six indigenous species (*Enteromius paludinosus*, *Enteromius viviparus*, *E. trimaculatus*, *Labeo molybdinus*, *Labeo rubromaculatus*, and *L. natalensis*) and one non-native species (*Cyprinus carpio*).

The proximity of the study area to the uThukela Estuary led to the detection of euryhaline species, with *A. aeneofuscus* and *Glossogobius callidus* being found as high up the system as site EWR16. Other euryhaline species, such as *Acanthopagrus berda*, *Ambassis dussumieri*, *E. fusca*, *Glossogobius giuris*, *K. rupestris*, *Microphis brachyurus*, *Microphis fluviatilis*, and *Pseudomyxus capensis* were only found at sites downstream of the LTBWSS weir. Four species (*Clarias gariepinus*, *E. trimaculatus*, *L. natalensis*, and *O. mossambicus*) were widespread across the sites in the study area, only missing from one or two sites (Table 2.3). *Clarias gariepinus* was only absent at site EWR16, whereas *E. trimaculatus* could not be found at sites EWR18 and the upstream Mandeni site. The only species present at all sites on the uThukela River was *L. natalensis*, only absent at the upstream site of the Mandeni Stream. *Oreochromis mossambicus*, one of the study's most abundant species (n = 322), was not found at two of the three sites upstream of the LTBWSS weir, sites Mdlebeni and UPSTR. The study sites showed varying degrees of species diversity with no clear pattern and had the following species counts on the uThukela; Mdlebeni (n = 5), EWR16 (n = 9), UPSTR (n = 6), DWNSTR (n = 15), EWR17 (n = 17), EWR18 (n = 4), EWR19 (n = 11). There is a large distinction between species diversity in the two sites of the Mandeni Stream, with the upstream site (n = 3) having less than a quarter of the species present at the downstream site (n = 13). The non-native, *P. reticulata*, was only found in the Mandeni Stream, where it was prolific at both sites, but more so at the upstream site, where it made up 98 % of the collected abundance (Table 2.3).

The preferred habitats, flow types, and migratory behaviours of the fish present and expected to be found in the study area can be found in Table 1.1 (Chapter 1). It is important to note that the migratory classification of some of the potamodromous, amphidromous, and anadromous species may not be entirely accurate, but is based off the best available literature from the SA Migratory Biota Index (Bok et al., 2007), along with any other recent literature.

2.4.3 Fish responses to environmental variables

The "mvabund" package allowed us to fit multivariate fish community data to a variety of environmental variables, such as mean water velocity, ecohydraulic flow classes, dominant substrate, dominant cover features, and water quality variables, to see which were driving fish communities in the study. The initial environmental variables included pH and electrical conductivity (EC); however, a collinearity check on the model found that there was a high correlation, above 60 %, between mean depth and velocity, EC and TDS, EC and pH, temperature and pH, and TDS and pH (Supplementary information Fig. S2.1). A decision was made to omit EC and pH from the model to ensure that the correlation of variables did not decrease its accuracy but kept depth and velocity as both can be important drivers of local fish community structures (Kleynhans, 2007). The full model was tested, which included eight environmental variables: ecohydraulic flow class, dominant substrate, dominant cover, mean velocity, mean depth, total dissolved solids, temperature, and salinity. Along with the main environmental variables, the levels within the environmental variables ecohydraulic flow classes (fast deep, fast intermediate, fast shallow, slow deep, slow shallow), dominant substrate (boulder, cobble, gravel, sand, mud, silt), and dominant cover (depth, marginal vegetation, overhanging vegetation, ripple surface, substrate, and woody debris), were also tested. According to the results, the main environmental factors affecting the composition of the fish communities in the lower uThukela River were dominant substrate ($P = 0.008$), dominant cover ($P = 0.028$), average depth ($P = 0.044$), and temperature ($P = 0.008$). Furthermore, the levels of the environmental variables showed that: for ecohydraulic flow classes, the fast deep ($P = 0.003$) and slow shallow ($P = 0.006$) were significant; the dominant substrate showed significance for boulders ($P = 0.008$), cobble ($P = 0.002$), gravel ($P = 0.001$), sand ($P = 0.001$), and silt ($P = 0.015$); and the dominant cover showed significance for depth ($P = 0.001$), marginal vegetation ($P = 0.003$), overhanging vegetation ($P = 0.001$), and substrate ($P = 0.011$).

Five indigenous species collected in the study (*O. mossambicus*, *E. trimaculatus*, *L. natalensis*, *L. molybdinus*, *L. rubromaculatus*) were considered because of relatively high abundances in the study and are known to be ecological indicators in the region. Here a GLM for each species against the environmental variables (ecohydraulic, dominant substrate, dominant cover, mean depth, mean velocity, temperature, TDS, and salinity), and the levels, as mentioned above, were run. Only four of these species (*O. mossambicus*, *L. molybdinus*, *L. rubromaculatus*, and *C. gariepinus*) showed significant relationships with some of the variables and are illustrated in Fig. 2.3. The probability of occurrence of *O. mossambicus* (GLM, P = 0.0298) was positively related to the temperature. The two mudfish species, *L. Molybdinus* (GLM, P = 0.0408) and *L. rubromaculatus* (GLM, P = 0.0126), substrate specialists, keyed into substrate conditions, with gravel as a dominant substrate positively influencing their probability of occurrence. Additionally, for *L. molybdinus* (GLM, P = 0.0335), higher velocity increased the likelihood of its presence. Increases in total dissolved solids showed to be a significant driver for both *L. rubromaculatus* (GLM, P = 0.0004) and *C. gariepinus* (GLM, P = 0.0004), with the probability of occurrence for the two species positively driven. The probability of occurrence decreased for both species, *L. rubromaculatus* (GLM, P = 0.0193) and *C. gariepinus* (GLM, P = 0.0058), when the salinity levels increased.

Less abundant species, but still of importance to the study, were also run using the same GLM model. These were *E. viviparus, E. palludinosus, G. callidus, A. aeneofuscus*, *E. fusca*, *A. marmorata*, and *A. mossambica*. Species that showed significance to tested environmental variables were *E. fusca, G. callidus* and *A. marmorata*. *Eleotris fusca* showed a significant relationship when environmental conditions for the ecohydraulic flow class fast intermediate (GLM, P = 0.0005) and fast shallow (GLM, P = 0.013) were present, as well as for the boulder substrate (GLM, P = 0.027) and the rippled surface as a cover feature (GLM, P = 0.0163). Similarly, *G. callidus* showed a significant relationship to the fast intermediate flow class (GLM, P = 0.0002) and silt substrate (GLM, P = 0.0003). The most abundant anguillid eel in the study, *A. marmorata*, showed a significant relationship to the boulder substrate (GLM, P = 0.0437).

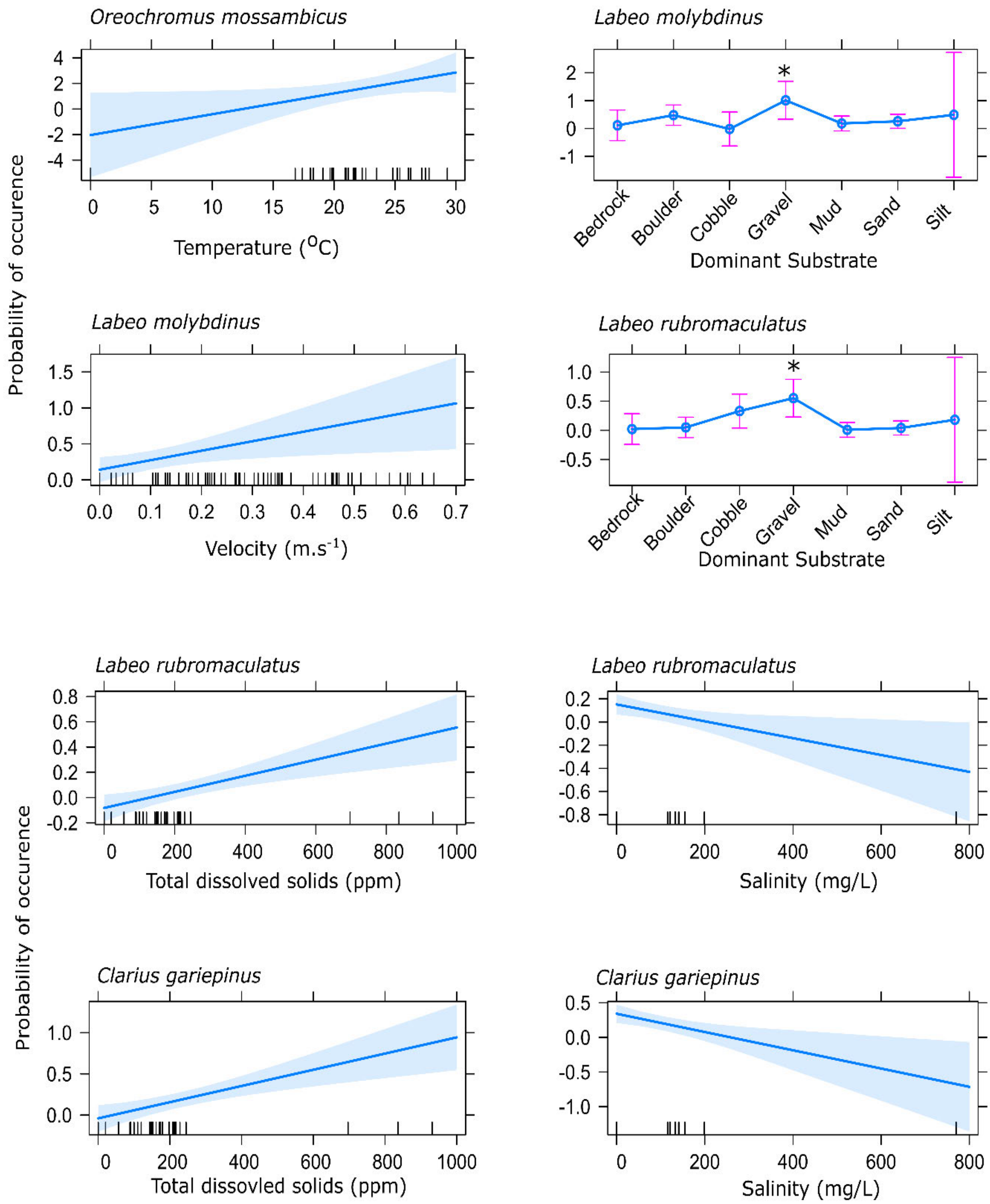

Figure 2.3: Generalised linear models showing the relationship where significant between the probability of occurrence (95% confidence intervals) of ecological indicator fish species when linked to environmental variables in the lower uThukela River, KwaZulu-Natal, South Africa.

2.5 Discussion

The composition of fish communities within the lotic environment is complex, with more than one environmental variable driving them (Carvalho and Tejerina-Garro, 2015). Different species react differently to factors associated with habitat conditions such as substrate and cover, hydraulic parameters such as depth and velocity, or conditions associated with physical, chemical, and biological stressors such as temperature and instream barriers, pollutants, and invasive species, respectively. According to statistical modelling, the fish communities in the present study were impacted by various environmental variables, with the main drivers being dominant cover, dominant substrate, depth, and temperature. Furthermore, individual species showed varying relationships to the levels of variables within these environmental drivers.

In other studies, geomorphic conditions such as dominant substrate and cover features significantly shape fish populations (Cheek and Taylor, 2016; Desai et al., 2021). Regarding the geomorphic conditions in this study, the uThukela River and Mandeni Stream differed greatly. The sites in the uThukela system were dominated by sand substrate, with a few sites having various other substrates, with the Mandeni Stream having a good combination of larger substrate types (boulders and bedrock) and small grain sediment (mud and sand). Cover features were also different, with all sites on the uThukela being dominated by the depth of the water column with various other cover features and the Mandeni by overhanging vegetation and boulders. The influence of cover and substrate was seen in the present study, whereby different species responded differently to the available habitat. Species with a demersal lifestyle have significant relationships to substrate conditions (Allen, 1991; Skelton, 2001). The two mudfish species, *L. molybdinus* and *L. rubromaculatus*, showed a high probability of occurrence with gravel substrate, among other variables, and is linked to their benthic feeding habits (Skelton, 2001). Similarly, silt was an important substrate condition for the presence of

G. callidus in the study and is appropriate as they live and feed on benthic organisms (Allen, 1991, Skelton, 2001). *Anguilla marmorata*, a species known for living in rock crevices (Skelton, 2001), had boulders as the main driver of their presence in the study. *Eleotris fusca* in this study showed a marked difference in their environmental drivers as compared with available literature. According to Skelton (2001), the species is relatively inactive and found in muddy substrate conditions with logs, stones and root wads as cover to hide under, yet in this study, they showed a preference for boulder substrate with fast intermediate and fast, shallow flow classes, an environment that creates a ripple surface cover feature. The majority of *E. fusca* individuals captured in the study were in their juvenile size class, likely in their young-of-the-year, amphidromous, upstream migration phase (Whitfield, 2019). The detection of juvenile *E. fusca* is likely the cause of our findings being different to the known literature, as the species is known to be cryptic, especially with regard to its life-history information. Such findings may prove valuable to the further understanding of the species.

Parameters linked to hydraulic conditions, such as depth and velocity, are also known to be influential drivers of fish communities in lotic systems (Bice et al., 2014; Chea et al., 2020; Magoulick et al., 2021). Furthermore, the depth and velocity relationship can create important ecohydraulic flow classes for fish (Kleynhans, 2007; James and King, 2010) as already seen with juvenile *E. fusca*. Another species in the study, *G. callidus*, with a similar demersal lifestyle to *E. fusca*, was also found with a preference for the fast intermediate flow class in this study, and again it was largely because of juvenile size classes of *G.callidus* individuals detected in the present study. The cyprinid, *L. molybdinus*, showed a positive relationship to velocity in this study, a known characteristic of this rheophilic species (Skelton, 2001; Desai et al., 2021). Although dominant substrate and temperature were the most significant drivers of fish communities in this study, the depth in the uThukela partly accounts for its species diversity. Depth in a system allows the availability of diverse microhabitats for fish, as seen in other studies (Carvalho and Tejerina-Garro, 2015; Desai et al., 2021), and is likely the reason why it is a driver for fish communities in the present study, but did not show as being significant for any individual species.

Physical water conditions such as temperature, dissolved solids, and salinity were found to be drivers of fish presence in the present study. Two species, *L. rubromaculatus* and *C. gariepinus*, showed similar preferences to TDS and salinity, with both having positive relationships to TDS and negative relationships to salinity, which is expected from these freshwater species (Skelton, 2001). *Oreochromis mossambicus* showed a positive relationship with water temperature in the study area.

Biological stressors, such as non-native fish, are known to have detrimental ecological impacts on indigenous fauna in South African freshwater ecosystems (Ellender and Weyl, 2014). Fortunately, in the present study and other recent ones performed in the same area as the present study (Jacobs, 2017; Evans et al., 2022), non-native fish impacts are low for the lower uThukela River. Non-native species, such as *C. carpio,* that are global invasive species known to destroy nests of indigenous fish and out-compete them for resources (Stuart and Jones, 2006) were caught in relatively low abundances in the present study. Furthermore, *M. salmoides*, an aggressive predatory fish that is dominant in the upper parts of the catchment (Evans et al., 2022; Burnett et al., 2023), where the water is not as turbid, only had one individual captured in this study. However, *P. reticulata*, a small growing fish (<10 cm), which is highly invasive in small rivers (Page and Burr, 2011), was one of the most abundant species in this study, which, fortunately, was limited to the Mandeni Stream. *Poecilia reticulata* is a small fish and is often predated on by large fish when present. The uThukela River still presented large piscivorous fish in the present study that would feed on *P. reticulata*. In addition, there is a physical barrier created by the weir located 200 m upstream of the Mandeni's confluence with the uThukela, as well as a chemical barrier created by the highly polluted Mandeni Stream (Wade et al., 2021). The impact of the weir on the Mandeni is clearly evident by the species diversity between the upstream and downstream sites on the Mandeni Stream (Table 2.3). The upstream site only had *O. mossambicus*, *C. gariepinus*, and *P. reticulata* present, of which the latter was the most abundant, compared with the downstream site, which had an additional ten species to these when it was back flooded by the high flows in the uThukela River in 2022 (pers. obs., B. van Zyl). The presence of these three species in the Mandeni is likely because it historically functioned as an ephemeral system that has recently been augmented into a perennial stream through return flows from industrial effluent and a local wastewater treatment works (Wade et al., 2021). As such, its fish assemblage reflects species with high tolerances to intermittent water supply (in its historical state) and those which can tolerate high pollution loads, with the ten additional species in 2022 being sensitive species that migrated from the uThukela River.

The impact that the LTBWSS weir has on the fish community composition may be seen by the comparison of euryhaline species captured at the different sites upstream and downstream of it, as well as the general species richness on either side of it. The three upstream sites (Mdlebeni, EWR16, UPSTR) were dominated by purely freshwater fish, with only two species of euryhaline fish (*A. aeneofuscus* and G. *callidus*) found at site EWR16, which also had the highest upstream diversity of nine species (Table 2.3). That is compared with the downstream sites, which had a combined total of 12 euryhaline species, which included five at the immediate downstream site (DWNSTR) and nine at site EWR17, which was also the most diverse site in the study with 17 species (Table 2.3). The difference in euryhaline species at these two sites is likely because of a partial barrier caused by the Sappi extraction point located between the two sites (Jacobs, 2017; Wade et al., 2021). Furthermore, a direct comparison between the sites immediately upstream (UPSTR) and downstream (DWNSTR) showed the weir's impacts on their fish communities. UPSTR is a deep impoundment with not much cover for fish, dominated by mud substrate and has a low species richness (n = 6). Unlike DWNSTR, which was dominated by boulders and sand substrate, it had various depth profiles and boulders as cover and demonstrated a much higher species richness (n = 15). Additionally, the long-term temporal effects that the LTBWSS may have had on the downstream fish communities were also shown compared with the study performed by Jacobs (2017). Their study was conducted on the 4 km stretch downstream from the weir location before it was constructed and included a fish collection component using similar sampling methods as the present study (seine netting, electrofishing and cast netting). Notably, their study collected all four expected cichlid species (*Coptodon rendalli*, *O. mossambicus*, *Pseudocrenilabrus philander*, *Tilapia sparrmanii*) in relatively high abundances, with *T. sparrmanii* being the species with the most individuals collected (n = 550). Subsequently, their study found that *T. sparrmanii* had a high correlation with silt substrate, particularly juveniles, with their community structures significantly changing when substrate conditions changed. Comparably, our study only detected *O. mossambicus*, despite sampling the same sites. Such a big shift in cichlid populations is worrying, especially considering that they are an important food source for many African subsistence fisheries (Coetzee et al., 2015). It is possible that the LTBWSS weir is acting as a sediment trap to suspended solids and not allowing the required downstream delivery of these important sediments (Casserly et al., 2021). Furthermore, compounded effects, because of the LTBWSS abstraction, may be affecting the downstream river environment. This includes the provision of downstream water quantity not being available to dilute the pollution from both the Mandeni Stream and the discharge from the Sappi Tugela Pulp and Paper Mill, which is 500 m downstream of the Mandeni confluence to uThukela, just above site EWR18 (Wade et al., 2021). Site EWR18 had the lowest species richness in the uThukela River (n = 4), as seen resulting from flow alteration and sediments behind the LTBWSS weir.

2.5.1 Conclusions and recommendations

Our findings provide baseline ecological information for fish of the lower uThukela catchment, and we identified significant environmental determinants linked to the fish community compositions in the region. The inclusion of ad hoc sites into the study helped gain a broader perspective of fish community structures and drivers of the entire lower uThukela system. Different environmental variables drive the different fish species' presence in the region, influencing the overall fish community composition at the different sites.

Through our study, it was shown that the LTBWSS weir has an impact on the fish communities up and downstream of it. Upstream communities are largely the predominantly freshwater species, with few euryhaline migratory fish present, which was similar to the fish community composition before the construction of the LTBWSS weir and fishway, albeit one historically present euryhaline species was not found and that one newly present euryhaline species was found in this study. Downstream communities are more diverse in terms of species and those that can tolerate wide salinity ranges. It is also likely that downstream of the weir does not receive transportation of the required fine sediments, which were crucial to the cichlid species *T. sparrmanii,* which was found in the region in very high abundances before the weir but were not recorded during this study despite extensive sampling. Additionally, the abstraction of water by the LTBWSS infrastructure likely worsens the impacts of compounded pollution sources from the Mandeni Stream and the Sappi Tugela Pulp and Paper Mill effluent on site EWR18.

Future research needs to specifically look at species with relatively unknown life histories by obtaining fish movement data which helps to get a better understanding of their habitat preferences, migratory behaviours, and life cycles, as these are important considerations for monitoring their well-being in a system. An in-depth search for the missing cichlids is important to determine if there are still some remnant populations whose populations, with better resource management and conservation practices, could be allowed to regenerate. Additionally, the exact stressors impacting the region need to be quantified, which will help water resource managers mitigate anthropogenic impacts on the lower uThukela River and its associated mouth.

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2.7 References

Allen, G. R. 1991. Field guide to the freshwater fishes of New Guinea. Christensen Research Institute, Lexington, MA.

Barbarossa, V., Schmitt, R. J., Huijbregts, M. A., Zarfl, C., King, H. & Schipper, A. M. 2020. Impacts of current and future large dams on the geographic range connectivity of freshwater fish worldwide. *Proceedings of the National Academy of Sciences,* 117, 3648-3655.

Belletti, B., De Leaniz, C. G., Jones, J., Bizzi, S., Börger, L., Segura, G., Castelletti, A., Van De Bund, W., Aarestrup, K. & Barry, J. 2020. More than one million barriers fragment Europe's rivers. *Nature,* 588, 436-441.

Bice, C., Gehrig, S., Zampatti, B., Nicol, J., Wilson, P., Leigh, S. & Marsland, K. 2014. Flow-induced alterations to fish assemblages, habitat and fish–habitat associations in a regulated lowland river. *Hydrobiologia,* 722, 205-222.

Bohlin, T., Hamrin, S., Heggberget, T. G., Rasmussen, G. & Saltveit, S. J. 1989. Electrofishing—theory and practice with special emphasis on salmonids. *Hydrobiologia,* 173, 9-43.

Burnett, M. J., Hanzen, C., Whitehead, A., O'Brien, G. C. & Downs, C. T. 2023. The lesser of two evils: the role of an instream barrier to control the distribution and invasive potential of non-native fish species in the Mooi River, South Africa. [In Review].

Carpenter, S. R., Stanley, E. H. & Vander Zanden, M. J. 2011. State of the world's freshwater ecosystems: physical, chemical, and biological changes. *Annual Review of Environment and Resources,* 36, 75-99.
Carvalho, R. A. & Tejerina-Garro, F. L. 2015. Environmental and spatial processes: what controls the functional structure of fish assemblages in tropical rivers and headwater streams? *Ecology of Freshwater Fish,* 24, 317-328.
Casserly, C. M., Turner, J. N., O'Sullivan, J. J., Bruen, M., Bullock, C., Atkinson, S. & Kelly-Quinn, M. 2021. Effect of low-head dams on reach-scale suspended sediment dynamics in coarse-bedded streams. *Journal of Environmental Management,* 277, 111452.
Chea, R., Pool, T. K., Chevalier, M., Ngor, P., So, N., Winemiller, K. O., Lek, S. & Grenouillet, G. 2020. Impact of seasonal hydrological variation on tropical fish assemblages: Abrupt shift following an extreme flood event. *Ecosphere,* 11, e03303.
Cheek, C. A. & Taylor, C. M. 2016. Salinity and geomorphology drive long-term changes to local and regional fish assemblage attributes in the lower Pecos River, Texas. *Ecology of Freshwater Fish,* 25, 340-351.
Chovanec, A., Hofer, R. & Schiemer, F. 2003. Fish as bioindicators. In: Markett, B. A., Breure, A. M., Zechmeister, H. G. (Eds), *Trace metals and other contaminants in the environment.* Elsevier, New York, pp. 639-676.
Coetzee, H. C., Nell, W., Van Eeden, E. S. & De Crom, E. P. 2015. Artisanal fisheries in the Ndumo area of the lower Phongolo River floodplain, South Africa. *Koedoe: African Protected Area Conservation and Science,* 57, 1-6.
De Lecea, A. M. & Cooper, R. 2016. The importance of the Thukela River Estuary, East Coast of South Africa, for the biology of the near-shore environment and associated human aspects: a review. In: Diop, S., Scheren, P., Machiwa, J. F. (Eds), *Estuaries: a lifeline of ecosystem services in the Western Indian Ocean*. Springer, Cham, pp. 53-65.
Denicola, E., Aburizaiza, O. S., Siddique, A., Khwaja, H. & Carpenter, D. O. 2015. Climate change and water scarcity: The case of Saudi Arabia. *Annals of Global Health,* 81, 342-353.
Department of Environmental Affairs 2019. Notice declaring the uThukela Marine Protected Area in terms of Section 22A of the National Environmental Management: Protected Areas Act, 2003 (Act No. 57 of 2003). *Government Gazette,* 42478, Pretoria, South Africa.
Department of Water Affairs 2013. National Water Resource Strategy 2: Water for an equitable and sustainable future. 2 ed. Pretoria, South Africa.
Department of Water Affairs and Forestry 2004. Thukela WMA: Internal Strategic Perspective. *National Water Resource Planning.* Pretoria, South Africa.
Department of Water and Sanitation 2014. A Desktop Assessment of the Present Ecological State, Ecological Importance and Ecological Sensitivity per Sub Quaternary Reaches for Secondary Catchments in South Africa. Compiled by RQIS-RDM.
Department of Water and Sanitation 2022a. National Water Act, 1998 (Act no. 36 of 1998): Review of the National Water Resource Strategy. (Notice 2327). *Government Gazette*, 47133. Pretoria, South Africa.
Department of Water and Sanitation 2022b. Proposed Water Resource Classes and Resource Quality Objectives for Thukela Catchments in the Pongola - Mtamvuna Water Management Area. *Government Gazette*, 46032. Pretoria, South Africa.
Desai, M., Hanzen, C., Downs, C. T. & O'Brien, G. C. 2021. Environmental drivers of ichthyofauna community composition of the river ecosystems draining the Lake St. Lucia basin, South Africa. *Hydrobiologia,* 848, 3539-3554.
Du Plessis, A. 2019. Evaluation of Southern and South Africa's freshwater resources. In: Du Plessis, A. (Ed), *Water as an inescapable risk.* Springer, Switzerland, pp. 147-172.

Dudgeon, D. 2010. Prospects for sustaining freshwater biodiversity in the 21st century: linking ecosystem structure and function. *Current Opinion in Environmental Sustainability,* 2, 422-430.

Dudgeon, D., Arthington, A. H., Gessner, M. O., Kawabata, Z.-I., Knowler, D. J., Lévêque, C., Naiman, R. J., Prieur-Richard, A.-H., Soto, D. & Stiassny, M. L. 2006. Freshwater biodiversity: importance, threats, status and conservation challenges. *Biological Reviews,* 81, 163-182.

Dugan, P. J., Barlow, C., Agostinho, A. A., Baran, E., Cada, G. F., Chen, D., Cowx, I. G., Ferguson, J. W., Jutagate, T. & Mallen-Cooper, M. 2010. Fish migration, dams, and loss of ecosystem services in the Mekong basin. *Ambio,* 39, 344-348.

Ellender, B. R. & Weyl, O. L. 2014. A review of current knowledge, risk and ecological impacts associated with non-native freshwater fish introductions in South Africa. *Aquatic Invasions,* 9, 117–132.

Evans, A. E., Mateo-Sagasta, J., Qadir, M., Boelee, E. & Ippolito, A. 2019. Agricultural water pollution: key knowledge gaps and research needs. *Current Opinion in Environmental Sustainability,* 36, 20-27.

Evans, W., Downs, C. T., Burnett, M. J. & O'Brien, G. C. 2022. Assessing fish community response to water quality and habitat stressors in KwaZulu-Natal, South Africa. *African Journal of Aquatic Science,* 47, 47-65.

Fausch, K. D., Torgersen, C. E., Baxter, C. V. & Li, H. W. 2002. Landscapes to riverscapes: bridging the gap between research and conservation of stream fishes: A continuous view of the river is needed to understand how processes interacting among scales set the context for stream fishes and their habitat. *BioScience,* 52, 483-498.

FBIS (Freshwater Biodiversity Information System). 2022. Downloaded from https://freshwaterbiodiversity.org on 20 October 2022.

Fouchy, K., Mcclain, M. E., Conallin, J. & O'Brien, G. 2019. Multiple stressors in African freshwater systems. In: Sabater, S., Elosegi, G., Ludwig, R. (Eds), *Multiple stressors in river ecosystems.* Elsevier, pp. 179-191.

Gallardo, B., Clavero, M., Sánchez, M. I. & Vilà, M. 2016. Global ecological impacts of invasive species in aquatic ecosystems. *Global Change Biology,* 22, 151-163.

Hanna, D. E., Tomscha, S. A., Ouellet Dallaire, C. & Bennett, E. M. 2018. A review of riverine ecosystem service quantification: Research gaps and recommendations. *Journal of Applied Ecology,* 55, 1299-1311.

Harris, J. H. 1995. The use of fish in ecological assessments. *Australian Journal of Ecology,* 20, 65-80.

Holmlund, C. M. & Hammer, M. 1999. Ecosystem services generated by fish populations. *Ecological Economics,* 29, 253-268.

Jacobs, P. G. 2017. *Hydrological assessment to predict velocity-flow classes in the lower Thukela River.* MSc, North-West University, Potchefstroom Campus.

James, C. & King, J. 2010. Ecohydraulics for South African rivers: A review and guide. *WRC Report*. Water Research Commission, Pretoria.

Jefferies, D., Green, J. & Green, R. 1984. *Commercial fish and crustacean traps*. Vincent Wildlife Trust.

Kaval, P. 2019. Integrated catchment management and ecosystem services: A twenty-five year overview. *Ecosystem Services,* 37, 100912.

King, J. & Pienaar, H. 2011. Sustainable use of South Africa's inland waters: a situation assessment of resource directed measures 12 years after the 1998 National Water Act. *Water Research Commission Report No. TT,* 491, Water Research Commission, Pretoria, pp. 1-245.

Kleynhans, C. 1999. The development of a fish index to assess the biological integrity of South African rivers. *Water SA,* 25, 265-278.

Kleynhans, C. 2007. Module D: Fish response assessment index (FRAI). *River ecoclassification manual for ecostatus determination (Version 2): Report produced for the Department of Water Affairs and Forestry (Resource Quality Services) and the Water Research Commission,* WRC Report No. TT330/08. Water Research Commission, Pretoria.

Kleynhans, C. & Louw, M. 2007. Module A: EcoClassification and EcoStatus determination. *River EcoClassification: Manual for EcoStatus Determination (version 2) Water Research Commission Report No. TT,* 333. Water Research Commission, Pretoria.

Koehnken, L., Rintoul, M. S., Goichot, M., Tickner, D., Loftus, A. C. & Acreman, M. C. 2020. Impacts of riverine sand mining on freshwater ecosystems: A review of the scientific evidence and guidance for future research. *River Research and Applications,* 36, 362-370.

Lucas, M. C. & Baras, E. 2008. *Migration of freshwater fishes*, Blackwell Science, Oxford, UK.

Magoulick, D. D., Dekar, M. P., Hodges, S. W., Scott, M. K., Rabalais, M. R. & Bare, C. M. 2021. Hydrologic variation influences stream fish assemblage dynamics through flow regime and drought. *Scientific Reports,* 11, 1-15.

McIntyre, P. B., Reidy Liermann, C., Childress, E., Hamann, E. J., Hogan, J. D., Januchowski-Hartley, S. R., Koning, A. A., Neeson, T. M., Oele, D. L. & Pracheil, B. M. 2016. Conservation of migratory fishes in freshwater ecosystems. In: Closs, G. P. (Ed), *Conservation of freshwater fishes*, Cambridge University Press, Cambridge, pp. 324-360.

Mittal, N., Bhave, A. G., Mishra, A. & Singh, R. 2016. Impact of human intervention and climate change on natural flow regime. *Water Resources Management,* 30, 685-699.

Northcote, T. 1978. Migratory strategies and production in freshwater fishes. In: Gerking, S. (Ed), *Ecology of freshwater fish production*, John Wiley & Sons, NewYork, pp. 326-359.

Page, L. M. & Burr, B. M. 2011. *Peterson field guide to freshwater fishes of North America north of Mexico*. Houghton Mifflin Harcourt.

Postel, S. & Carpenter, S. 1997. Freshwater ecosystem services. In: Daily, G.C. (Ed), *Nature's services: Societal dependence on natural ecosystems*. Island Press, Washington DC, USA, 195.

R Core Team 2022. R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.

Rodell, M., Famiglietti, J. S., Wiese, D. N., Reager, J., Beaudoing, H. K., Landerer, F. W. & Lo, M.-H. 2018. Emerging trends in global freshwater availability. *Nature,* 557, 651-659.

Skelton, P. 2001. *A Complete Guide to the Freshwater Fishes of Southern Africa,* Cape Town (ZA), Struik Publishers.

Stuart, I. & Jones, M. 2006. Movement of common carp, *Cyprinus carpio*, in a regulated lowland Australian river: implications for management. *Fisheries Management and Ecology,* 13, 213-219.

Umgeni Water 2017. Infrastructure Master Plan 2017/2018 - 2047/2048. Umgeni Water, Pietermaritzburg, KwaZulu-Natal, South Africa.

Van Vuuren, L. 2008. Thukela-Vaal Transfer scheme. *Water Wheel,* Nov-Dec, 14-21.

Wade, M., O'Brien, G. C., Wepener, V. & Jewitt, G. 2021. Risk assessment of water quantity and quality stressors to balance the use and protection of vulnerable water resources. *Integrated Environmental Assessment and Management,* 17, 110-130.

Wang, Y., Naumann, U., Wright, S. T. & Warton, D. I. 2012. mvabund–an R package for model-based analysis of multivariate abundance data. *Methods in Ecology and Evolution,* 3, 471-474.

Warton, D. I. 2011. Regularized sandwich estimators for analysis of high-dimensional data using generalized estimating equations. *Biometrics,* 67, 116-123.

Warton, D. I., Thibaut, L. & Wang, Y. A. 2017. The PIT-trap—A "model-free" bootstrap procedure for inference about regression models with discrete, multivariate responses. *PloS one,* 12, e0181790.

Whitfield, A. K. 1998. *Biology and Ecology of Fishes in South African Estuaries.* Ichthyological Monograph, no. 2, J.L.B. Smith Institute of Ichthyology, Grahamstown.

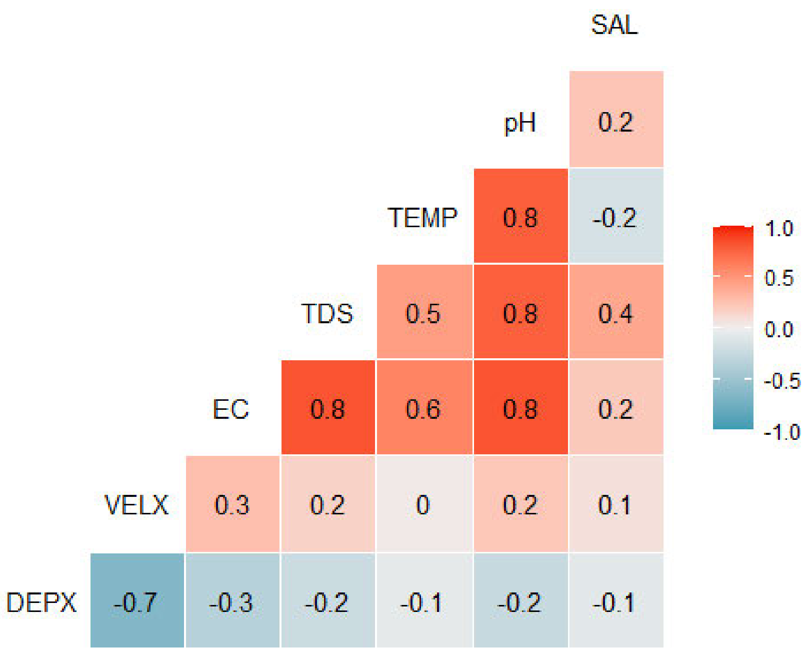
Whitfield, A. K. 2019. *Fishes of Southern African estuaries: From species to systems*, Smithiana Monograph No. 4, J.L.B. Smith Institute of Ichthyology, Grahamstown.

World Commission on Dams 2000. *Dams and development: A new framework for decision-making: The report of the world commission on dams*, Earthscan.

Zuo, Q. & Liang, S. 2015. Effects of dams on river flow regime based on IHA/RVA. *Proceedings of the International Association of Hydrological Sciences,* 368, 275-280.

2.8 Supplementary information

Supplementary information Fig. S2.1. Collinearity check for environmental variables assessed in the lower uThukela River catchment; SAL – salinity, TEMP – temperature, TDS – total dissolved solids, EC – electrical conductivity, VELX – mean velocity, DEPX – mean depth



CHAPTER 3

Floods, riots and load shedding: Does the Lower Thukela Bulk Water Supply Scheme Weir fishway work in the uThukela River, KwaZulu-Natal, South Africa

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Running header: Efficacy of the Lower Thukela Bulk Water Supply Scheme Weir fishway

3.1 Abstract

The development of dams and weirs in South Africa is to ensure water security for a growing population in a water-scarce country. Generally, such infrastructure disrupts river connectivity and threatens the well-being of migratory fish species in the region. The uThukela River is the second-largest river system in South Africa and the largest in KwaZulu-Natal. The Lower Thukela Bulk Water Supply Scheme (LTBWSS) is an abstraction weir located in the lower uThukela River, KwaZulu-Natal, South Africa. The presence of the LTBWSS impacts both the aquatic life of the river and the estuary and potentially disrupts the marine ecosystem, including the Thukela MPA. It is important that river connectivity is maintained over the LTBWSS for the movements of catadromous, amphidromous and potamodromous fish species. Therefore, a vertical slot fishway was designed to alleviate the effects of the impairment of ecological connectivity and required ecological monitoring. We studied the use of the vertical slot fishway by local fish species from May 2021 until August 2022. Electrofishing and PIT telemetry were used to study how the fishway was used for habitat and fish passage, respectively. Of the 107 PIT-tagged fish, eight individuals from three separate species ascended the fishway. From the tagged populations of the three species that ascended the fishway, the passage efficiency was 23% for sharptooth catfish (*Clarias gariepinus*), 9% for leaden labeo (*Labeo molybdinus*) and 3% for Mozambique tilapia (*Oreochromis mossambicus*). Additionally, various local species were shown to rely on the fishway at different times of the year. Further research on the role of the fishway in maintaining river connectivity is recommended.

Keywords: fishway, vertical slot, PIT telemetry, South Africa

3.2 Introduction

Terrestrial and aquatic ecosystems rely on healthy water resources for their proper functioning (Depledge and Galloway, 2005; Dudgeon, 2010; Dugan et al., 2010). In addition, human-dependent ecosystem services such as water supply, natural water quality control, food resources, climate regulation, and recreation and tourism require healthy aquatic ecosystems (Hanna et al., 2018; Kaval, 2019). Use of ecosystem services needs to operate sustainably so that the integrity of the ecosystem is maintained once they are done (Dugan et al., 2010). Threats to the health of South Africa's river ecosystems include shifts in land use, water quality, flow, and habitat, as well as stressors affecting both terrestrial and aquatic wildlife (Jewitt et al., 2015; O'Brien et al., 2019). Despite the country's commitment to the United Nations Sustainable Development Goals (SDGs), which seek to strike a balance between the preservation and use of water resources (Dickens et al., 2019) through established management policies and legislation (King and Pienaar, 2011), the aforementioned stressors continue to be regarded as being poorly handled (Hsu et al., 2013; Schreiner, 2013). Connectivity of freshwater ecosystems is demonstrated by the hydrological cycle between terrestrial and aquatic ecosystems, which includes surface and subsurface flows, wetlands, rivers, lakes, and floodplains (O'Brien et al., 2019). Connections between resource users, aquatic biota movement, and stressors and receptors in aquatic environments show the value of water resources (Silva et al., 2018).

Globally, dams and weirs have provided necessary services, including water storage for irrigation and drinking purposes and for their use in flood control (Belletti et al., 2020). Despite these necessary services, they come at a cost, as they often create short-term and long-term issues for the natural environment (World Commission on Dams, 2000; Tickner et al., 2020; Alla and Liu, 2021). These issues are often associated with the disruption of the natural river flow regimes (Mittal et al., 2016), fragmentation of longitudinal river connectivity (Carpenter et al., 2011, Barbarossa et al., 2020), and the alteration or disruption to sediment transfer (Simons and Şentürk, 1992; World Commission on Dams, 2000). The negative impact of these instream barriers on the health of freshwater ecosystems globally is well-known; however, it remains largely under-studied in Africa, and water security is prioritised (Rodell et al., 2018; du Plessis, 2019).

Although dams in Africa are seen as economically important, considering their water storage and hydropower capabilities (Briscoe, 2009), their impact on environmental processes is often ignored (Jackson and Marmulla, 2001; Elagib and Basheer, 2021). Of concern is that these physical instream barriers impede the movement of biota past them, fragment the river, and disrupt key natural processes such as fish migrations (Jackson and Marmulla, 2001; Carpenter et al., 2011; O'Brien et al., 2019). Migratory fish need to move for several reasons, including to access spawning areas, find foraging areas, evade predators, or avoid unfavourable water quality or temperature conditions (Lucas and Baras, 2008; McIntyre et al., 2016), with instream barriers blocking these movements.

Fish passage science may be referred to as the combined input from multiple research fields (i.e. biology, ecohydraulics, ecology, engineering, and physiology) to address the problems of river fragmentation caused by anthropogenic barriers through the design and implementation of fish passage facilities (Silva et al., 2018), which allow fish to move through or around the barrier (Clay, 1995; Wilkes et al., 2019). However, because of the high construction costs of fishways, their adoption into the design of instream barriers in economically disadvantaged countries has been historically questioned, including South Africa. Fortunately, present environmental law in South Africa, as a result of the country's commitment to sustainable development goals (SDGs) and, in particular, SDG 6.6 (*to protect and restore water-related ecosystems*), addresses the need for fishway provision on instream barriers as well as views a fishway as a suitable mitigation to ensure natural migrations of fish past anthropogenic structures (Bok et al., 2007). Although environmental law addresses the need for fishways in South Africa, their use on instream barriers is low, with approximately 60 in use, with varying degrees of functionality (Bok et al., 2007; O'Brien et al., 2019). Considering that the country has over 165 000 dams (Mantel et al., 2017), whereby more than 600 are large dams that block migration routes (Mantel et al., 2017; O'Brien et al., 2019), and approximately 1430 are gauging weirs which serve as partial migration barriers (O'Brien et al., 2019) that could potentially be impassable to many species and size classes of fish. This shows a relatively large number of disconnected freshwater ecosystems in South Africa, with many barriers impassable to migrating biota.

In South Africa, fish passage science is largely rudimentary, and its implementation into practice is mainly influenced by the Water Research Commission study conducted by Bok et al. (2007). Their work is relatively comprehensive and provides a platform to address river connectivity issues by providing a fishway. However, many fields of fish passage science and evaluation still need attention to ensure that better-functioning fish passage solutions are implemented. This is evident by the low effectiveness of existing fishway structures in the country (20 % are functional, 33 % are ineffective, and the remainder are unevaluated) (Bok et al., 2007). This is likely because the fine-scale biological information of local species, such as sizes, swimming performance, swimming behaviour, life cycle timing and reasons for migration, are not being accommodated in local fishway designs (Bok et al., 2007; Silva et al., 2018).

Of the various fishways used globally, Bok et al. (2007) suggest a vertical slot fishway in South Africa, which is easily fitted onto weirs, and caters for most migratory species in the region. The water in these fishways flows from one pool to the next through a vertical slit in the baffle, creating a water jet that dissipates energy in the centre while also leaving areas of significantly lower flow velocity on each side (Rajaratnam et al., 1986; Baudoin et al., 2015).

Any depth inside the slot allows the fish to migrate from one pool to the next without jumping, and low-velocity lateral zones allow them to rest (Rodríguez et al., 2006; Baudoin et al., 2015). They are better suited to local South African species, which mostly exhibit strong swimming capabilities (Bok et al., 2007), with species relying on their crawling behaviour, such as eels and gobies, generally being accommodated by other devices such as rock ramps or eel ladders (Porcher, 2002; Lagarde et al., 2021).

Fishway provision does not stop once it has been designed and constructed but requires further monitoring and assessment of various parameters and baseline conditions to determine and evaluate its functioning (Bok et al., 2007). Such monitoring data should include information on the number of fish present, their identity, size classification, biological characteristics, and information on hydraulic factors like water level, discharge patterns, and turbidity (D'Enno et al., 2002). Telemetry techniques on fish have been used globally to analyse fish movement in their environment (Lucas and Baras, 2000; Hussey et al., 2015; Brownscombe et al., 2019), with the passive integrated transponder (PIT) telemetry being a popular technique used globally in monitoring the movement of fish through fishways (Castro-Santos et al., 1996; Burnett et al., 2021a).

The uThukela River is the second-largest river in South Africa and the largest in the KwaZulu-Natal Province (Department of Water Affairs and Forestry, 2004). Its water is a valuable resource to many regions in the country, and as such its catchment has many instream barriers used for water storage and abstraction (Department of Water Affairs, 2013). Furthermore, it has a high diversity of fish species, with species richness increasing with a decreasing altitude (Skelton, 2001). The Lower Thukela Bulk Water Supply Scheme (LTBWSS) weir was recently built (commissioned in 2017) in the lower reaches of the uThukela River, KwaZulu-Natal, South Africa, to supply water to the surrounding municipalities with a present abstraction of 55 Ml/d, and ultimately a total of 110 Ml/d

(Department of Water and Sanitation, 2022). It is situated near the town of Mandeni and is approximately 20 km upstream of the uThukela Mouth to the Indian Ocean. Due to its proximity to the uThukela Estuary, the LTBWSS weir is located in a delicate zone where local fish from all migratory classes (potamodromy, amphidromy, catadromy, anadromy) are present and whose life cycles may depend on connectivity past the weir. The weir has a vertical slot fishway incorporated into its design to assist with the passage of local migratory species and was built according to the guidelines of Bok et al. (2007).

In this study, we aimed to conduct an infield efficacy test of the vertical slot fishway incorporated into the LTBWSS abstraction weir in coastal KwaZulu-Natal using passive integrated transponder (PIT) technology, a first for the region (Burnett et al., 2021a). Firstly, a literature search would need to be conducted to determine what species were expected in the area and their migratory behaviours. It was expected that the fishway design would not be suitable for passing all migratory species in the region effectively because required fish biological knowledge is still largely lacking and could not be adequately incorporated into the fishway design. In addition, the present study is the first to evaluate a fishway built to meet the migratory requirement of lowland freshwater South African fish. The results of this study aimed to guide future fish passage science and fishway design in the region.

3.3 Methods

3.3.1 Study area

We conducted the study in the lower reaches of the uThukela River catchment in KwaZulu-Natal Province, South Africa, centred around the LTBWSS weir near Mandeni town. The LTBWSS is ~12 km upstream of the uThukela Mouth's upper tidal or saline limit (roughly at sample site EWR19, Fig 3.1). The close proximity of the LTBWSS to the uThukela Mouth means that it needs to cater for all broad migratory groups of fish, namely amphidromous, catadromous, potamodromous, and possibly anadromous. Included are species with little-known migratory habits, such as those from the *Eleotridae* and *Gobiidae* families, which, elsewhere, are shown to be amphidromous (Maeda and Tachihara, 2005; Franklin and Gee, 2019; Lagarde et al., 2021). Such species (amphidromous) have been shown to rely on larval drift by freshwater flows to transport larvae into the nearby estuaries, which act as nurseries (McDowall, 1997). The study area falls under the Department of Water and Sanitation's quaternary catchment management area V50D, the lowest in the uThukela basin ending at the mouth to the Indian Ocean. The Mandeni Stream, a tributary of the uThukela River, which feeds into the study area downstream of the LTBWSS, was also sampled for taggable fish. The Mandeni stream has a weir just above the downstream Mandeni sample site (represented as Mandeni DS, Fig 3.1), disconnecting it from the upstream site (Wade et al., 2021). During high flows present in this study, the uThukela River backed up 200 m from its confluence with the Mandeni Stream, all the way to the downstream site on the Mandeni. Six sites formed part of the study area (Fig 3.1), including five downstream sites and the fishway. A natural cascading waterfall on the uThukela River forms part of the Sappi extraction point and acts as a partial instream barrier in the study area. It is situated upstream of site EWR17 and downstream of the LTBWSS.

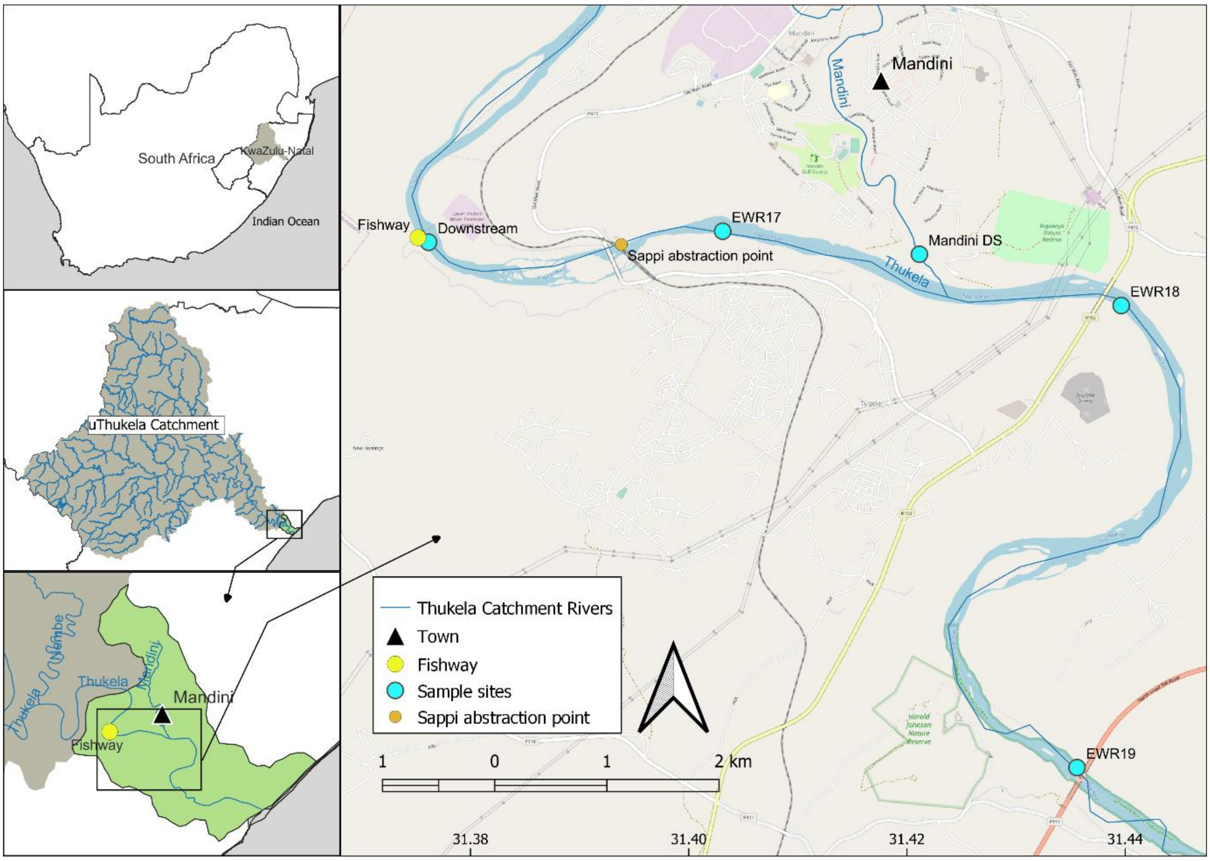

Figure 3.1: Map of the study area, quaternary catchment V50D, and the sampling sites in the lower uThukela River, KwaZulu-Natal, South Africa.

The fishway was one component of the LTBWSS infrastructure (29°10’08”S, 31°22’30”E) (Fig. 3.2) commissioned by Umgeni Water, the local water authority board and bulk water supplier in KwaZulu-Natal Province in 2017. The infrastructure consists of a water abstraction works facility on the southern bank, the fish ladder constructed next to the abstraction works facility, a 5 m wide creepy-crawly rock ramp on the southern end of a 170 m long weir spanning across the uThukela River, and a water treatment facility on the northern bank (Fig. 3.2). The fishway is a 45 m long concrete structure and has a floor height rise, from its downstream to upstream entrance, of 4.175 m at a gradient of 1:11. The design is of a vertical slot type fishway, consisting of 39 pools arranged in three connected zig-zag sections, with 15 pools in the upper section, an upper resting/turning basin, 11 pools in the middle section, a lower resting/turning basin, and 11 pools in the lower section before the downstream entrance (Fig. 3.2). The standard pools are 1.2 m long and 1.2 m wide, with baffle walls dividing the pools, each 2.5 m high and with a 0.15 m wide narrow vertical slot running the height of the wall (Fig. 3.2). The two pools which are resting/turning basins, are significantly larger than the others, and have horizontal (non-sloped) floors. The internal flooring throughout the fishway has a special surface finish made with 100 to 150 mm diameter boulders embedded into concrete, with the idea of assisting crawling species.

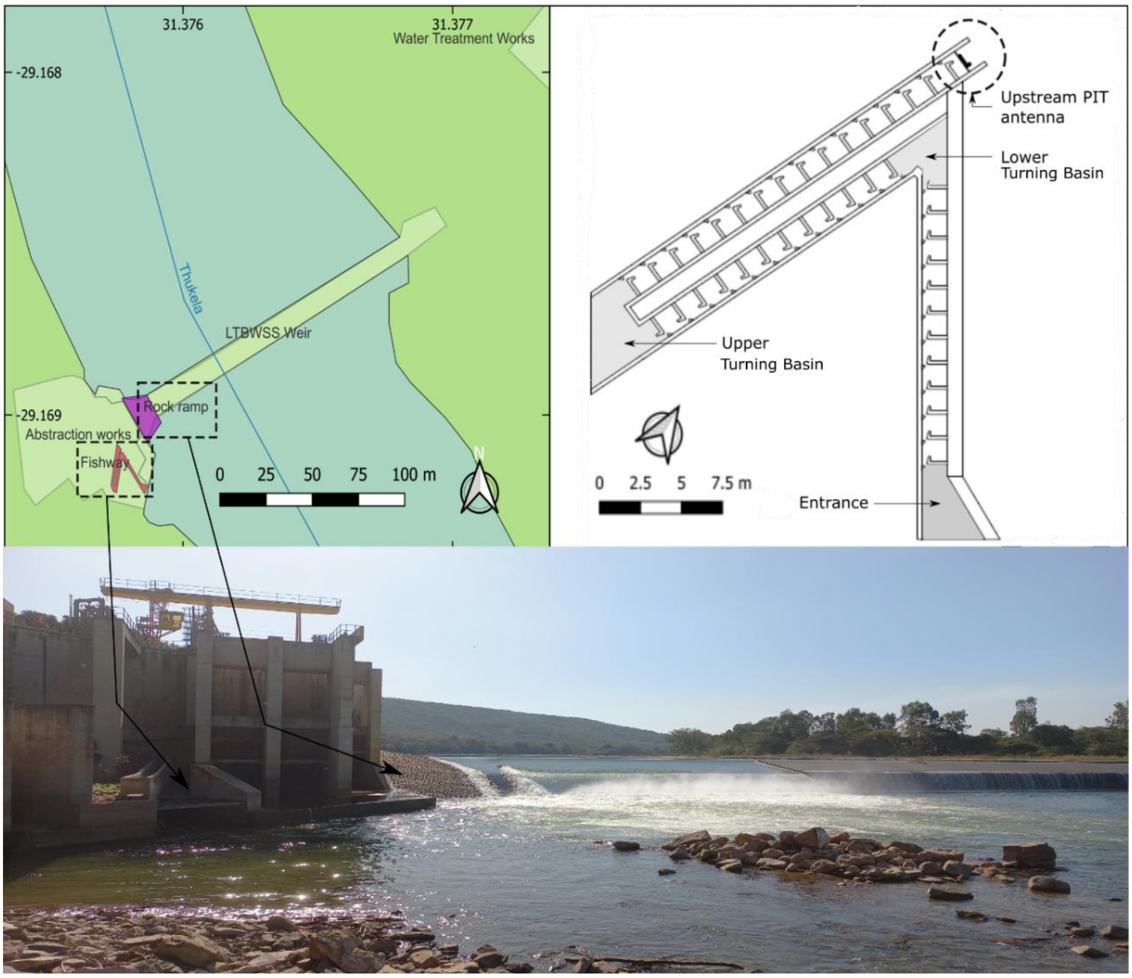

Figure 3.2: The weir and fishway in the lower uThukela River, KwaZulu-Natal, South Africa, where the top left shows the layout of the LTBWSS infrastructure, the top right shows a diagram of the LTBWSS fishway, and the bottom shows a photographic image of the LTBWSS weir and infrastructure as viewed from the south.

Using fish as indicators, two different methods were used to monitor the efficacy of the Lower Thukela Bulk Water Supply Scheme (LTBWSS) weir fishway. Firstly, we used the voluntary movement of Passive Integrated Transponder (PIT) tagged fish through the fishway, which a stationary PIT-tag monitoring system observed. Secondly, we sampled the fishway monthly to determine fish species and numbers using the fishway at the time.

3.3.2 Expected fish species

We undertook a literature search to determine which fish species were historically found in the study area to determine which fish species were expected to be found there. Furthermore, evidence of migration for the respective fish species was collated from the available literature. Migration of fish can be attributed to breeding, feeding, or survival strategies (Lucas and Baras 2008; McIntyre et al. 2016) and may occur over a catchment scale, between reaches, or within a reach. Catadromous migrations occur over great distances on a catchment scale, with the principal feeding and growing biome being freshwater and reproduction being in the ocean (McDowall 1997). Amphidromous migrations occur between freshwater and saltwater reaches and include the downstream movement of hatched larval fish to saltwater, followed by upstream movement into freshwater of juvenile fish for growth, feeding, and reproduction (McDowall 1997). Anadromous migrations can occur over large spatial ranges whereby the main feeding and growth occur in the ocean and breeding in freshwater (McDowall 1997). Potamodromous migrations occur only in freshwater reaches and can occur between reaches or in a reach (Northcote, 1978, 1984).

3.3.3 PIT tagging

We installed and incorporated a custom-designed pass-through PIT-tag monitoring antenna (Biomark Products, USA) in the upstream entrance of the fishway in the LTBWSS weir in the lower uThukela River, as shown in Fig 3.2. The antenna had an opening of 1930 mm x 460 mm and was installed and submerged in an upright position perpendicular to the direction of water flow (Fig. 3.2 and 3.3). A 25 mm diameter cable connected the PIT antenna to the PIT tag reader (Biomark IS1001 stationary PIT tag reader, Biomark Products, USA) to read passing PIT tags. The system was powered by two battery banks (each 24V and containing two 12V 105 Ah Deltec Sealed Single Post Lead Acid batteries connected in series) (Fig 3.3). The battery banks were controlled by a battery switcher (Biomark Products, USA) and set to alternate at 2 h intervals, allowing for the battery bank, not in use, to be charged by a smart battery charger (Victron Blue Smart IP65 24V 8A, Victron Energy, Netherlands), which was connected to the main electricity supply at the LTBWSS facility (Fig 3.3). Together these components constituted the PIT monitoring system. The PIT monitoring system was installed on the 9th of April 2021, with further adjustments to the settings on the 18th and 19th of May 2021 to get it functioning optimally for the location. The tagging of fish then commenced on the 19th of May 2021. The monitoring system ran uninterrupted from this date until 12 January 2022, when the cable connecting the antenna and reader was damaged by flood debris. The uThukela catchment experienced extreme water levels, including severe flood events, from December 2021 to June 2022 (Supplementary information Fig. S3.1). The floods during this period were the highest sustained recorded floods in KwaZulu-Natal since the cut-off low period of 26 – 29 September 1987, which followed the highest-ever recorded floods of Cyclone Demoina in January 1984 (Letsatsi and Kruger, 2022).

Additionally, South Africa experienced major electricity supply issues over the study period, with various stages of load-shedding being implemented. The severe stages of load-shedding impacted the charging of the batteries, not allowing them to reach full charge capacity and, over time, running them flat. Furthermore, after the floods in January 2022, the main electricity supply for the monitoring system was unplugged, by unknown individuals, at the Umgeni Water facility. Again, this allowed for the batteries to run flat. The continual drainage of the batteries to empty, with insufficient charge time afterwards, resulted in the batteries being damaged and not functioning with recommended outputs after January 2022, impacting the PIT study results. Due to the novelty of this PIT tag study and the cost implication of equipment, a single PIT antenna was used and placed in the upstream entrance of the fishway. This determined the complete passage of tagged fish through the fishway. The PIT antenna was removed from the fishway on 29 August 2022, 467 calendar days after its installation, because of power supply issues and the need to fix them.

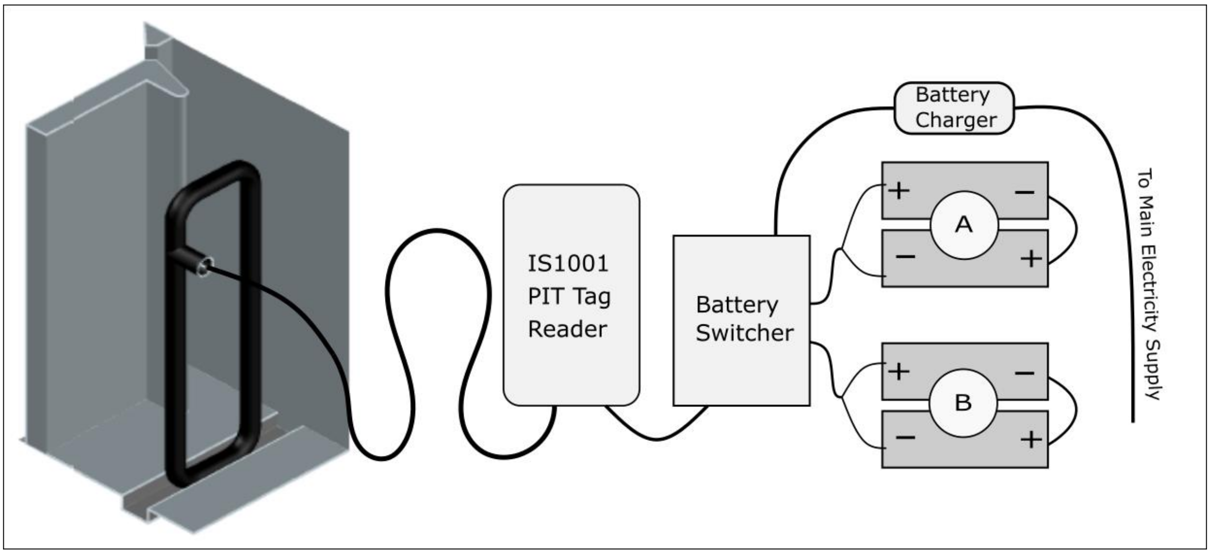

Figure 3.3: The PIT antenna and PIT tag reader setup arrangement used in the present study, constituting the PIT monitoring system.

We undertook fish collection surveys to PIT tag suitable fish for the study, which aligned with three major fish community assessment surveys of sites not part of the present study from May 2021 to December 2022 (Chapter 2). These included one high- and two low-flow surveys, with a second high-flow survey planned for early 2022 not taking place because the uThukela River was in flood and unsafe for sampling. We used fish captured at all sites in the study area (Fig 3.1), which met the tagging requirements. We used various sampling techniques for fish collection, including fyke nets, electrofishing, and seine nets. Surveys were conducted with the approval of Ezemvelo KZN Wildlife, the local conservation authority (permit numbers OP1060-2021 and OP1060-2022).

For fyke net sampling methods, we used small double-ended Dutch-type commercial fyke nets consisting of a central leader 9.7 m long, two internal funnels, a stretched mesh size of 20 mm, and an opening D-hoop height of 60 cm (T&L Netmaking, Mooroolbark, Australia). These nets were deployed for 24 h and checked every 12 h before being removed. We conducted electrofishing using a backpack-mounted SAMUS electrofisher (SAMUS 725MS Electrofisher, SAMUS Special Electronics, Poland) in shallow (< 1 m deep) flowing water. Electrofishing efforts were approached from downstream, whereby an effort consisted of short 5 s electrical bursts over a 2-to-5 min period. Seine netting was conducted in slow to no-flowing portions of the river. We used two different-sized seine nets (Eigevis Group of Companies, Cape Town, South Africa), with the smaller (length = 12 m, depth = 1.5 m, mesh size = 3mm) being preferred and the larger (length ~ 32 m, depth ~ 2.5 m, mesh size = 20 mm) only being used where the small seine net was inappropriate. We performed a maximum of five drags of a seine net at each site. We collected all fish suitable for PIT tagging from these efforts to tag.

We placed captured fish for tagging in an anaesthetic bath which was a bucket containing a minimum of 15 L of river water with a 2-Phenoxyethanol (0.2 mL/L) or clove oil (0.4 mL/L) mix to anaesthetise fish for tagging (Burnett et al., 2021b). Before tagging, we scanned each fish caught with a handheld PIT tag reader (Biomark HPR Lite, Biomark Products, USA) for any existing PIT tags. If no PIT tag was present, the fish was placed in the anaesthetic bath until loss of equilibrium was evident. We then identified each fish to the species level, made morphological measurements (length- total, fork, standard) to the nearest millimetre, and body mass measurements to the nearest 5 g before implanting it with a PIT tag. In this study, the ability to tag a fish largely depended on the size and morphology of the fish, and primarily the size and weight of the PIT tag. We used full duplex (FDX) PIT tags (12.5 mm x 2.03 mm, 0.106 g, Biomark APT12 Pre-Loaded PIT Tag, Biomark Products, USA). Additionally, the relatively small mass of the PIT tags required that a fish weighed more than 5.3 g to be tagged to not exceed the 2 % body mass rule of thumb for tagging applications (Jepsen et al., 2005, Winter, 1983). However, the 2 % body mass rule cannot be solely applied, with the fish's morphology and space for internal tags also needing to be considered as limiting factors (Jepsen et al., 2005; Hanzen et al., 2020).

In-field assessment of fish in this study found that those with fusiform, compressed, and depressed body shapes with a standard length greater than 100 mm were suitable for tagging, and those with elongated body shapes, such as the *Anguilla* spp. and *Microphis* spp. that were greater than 390 mm were suitable for tagging as in Hirt-Chabbert and Young (2012). All species of fish that met the minimum tagging requirements, including those reported as not migratory, were implanted with a PIT tag. We implanted a PIT tag into the peritoneal cavity underneath the fish's pectoral fin (Prentice et al., 1990) using a needle tag injector (Biomark MK25 PIT Tag Implanter, Biomark Products, USA). The insertion site of the tag was not closed by stitches or adhesives. The tags came pre-loaded in individual, single-use needles, which helped eliminate the need for disinfecting between implants, making the tagging process efficient and safer for the fish. The handling process was no longer than 60 s, after which fish were placed into a bucket with fresh river water to recover from the anaesthesia before being released as close as possible to the place of capture.

During biotic sampling, physico-chemical characteristics were measured once for the whole site and taken *in situ*. The water quality variables included temperature, pH, total dissolved solids (TDS) and conductivity using an XS Instruments PC 5 Tester multiparameter tool (XS Instruments, Italy). Habitat assessments were classified into cover features, substrate type, and velocity/depth, with five readings taken per effort. We visually assessed the cover features and described them as either substrate, water column, marginal vegetation, overhanging vegetation, aquatic vegetation, root wads, woody debris, undercut banks, depth, or ripple surface (Kleynhans, 1999). We assessed substrate visually or by feel and described it as either bedrock, boulders, cobbles, gravel, sand, mud, silt (Kleynhans, 1999), or other (being of anthropogenic origin). We measured velocity and depth using a Transparent Velocity Head Rod (GroundTruth, South Africa), with these readings used to place each effort into a velocity/depth class as suggested in (Kleynhans, 2007).

3.3.4 Monthly sampling

We conducted monthly sampling of the fishway from May 2021 to August 2022 to determine what fish species and abundances were using it. The July 2021 survey was incomplete because of political unrest that locked the KwaZulu-Natal Province down for several weeks (Vhumbunu, 2021). The fishway could also not be sampled from January 2022 to June 2022 because of extended high-water levels inundating the entire fishway from the uThukela River.

The same backpack-mounted electrofisher from the PIT tag study was used to sample the fish ladder at three accessible locations: the downstream entrance and the two resting/turning basins (Fig 3.2 and 3.3). The downstream exits of each turning basin sampled in the fishway were blocked using a seine net with a 3 mm mesh size. We performed one effort at each location, consisting of a series of timed 5 s electricity bursts and sweeping through the entire location twice.

Captured fish were contained in buckets containing fresh river water. We identified fish to species level and took standard morphological measurements (e.g., fork, standard and total length) to the nearest millimetre. We also included suitable fish caught in the fishway in the PIT tag study. Identification and measurements for each fish took no longer than 30 s. We released all fish at their place of capture in the fishway.

The fishway was additionally assessed using the presence/absence of species in it, as well as their abundances and size classes. This helped determine the different life stages of the species using it, an important consideration for fishway design (Bok et al., 2007). Catch per unit effort (CPUE) in the fishway was assessed as actual catches for each sampling location since only one effort was performed per location on a sample day.

3.4 Results

3.4.1 Fish species present

A comprehensive search of the literature revealed that 23 indigenous freshwater fish species had been historically identified in the river reach where the weir was situated, quaternary catchment V50D, with an additional two invasive species (Skelton, 2001; Department of Water and Sanitation, 2014; Wade et al., 2021; Evans et al., 2022; FBIS, 2022) (Table 3.1). The distribution range of a further eleven indigenous fish species and one invasive fish species were also expected to occur in the study area (Skelton, 2001; Table 3.1).

A total of 1225 fish were collected in 205 efforts at six sites in the study area, including the fishway, using fyke nets, electrofishing, and seine netting methods where appropriate (Table 3.2). The fish captured in the present study comprised of 23 identifiable species, and a single mullet fry too small to identify to species level was most likely *P. capensis* (Table 3.2). Of the 23 species captured in the study, 20 were indigenous, and three were non-native.

Furthermore, 18 species were from the historically identified list, with five species being confirmation of their expected distribution ranges in the uThukela River.

The migratory behaviour, IUCN status, importance of migration and the extent of this for each fish species are shown in Table 3.1. Expected catadromous migratory species in the study area were *Anguilla bengalensis*, *A. bicolor*, *A. marmorata*, *A. mossambica*, *Pseudomyxus capensis*, *Kuhlia rupestris*, and *Monodactylus falciformis,* with the only local species' fitting anadromous migratory behaviour being *Awaous aeneofuscus* and *Microphis brachyurus* (Table 3.1). Amphidromous fish in the study area include *Acanthopagrus berda*, *Eleotris fusca*, *Glossogobius giuris*, *Eleotris melanosoma*, *Hypseleotris cyprinoides,* as well as estuarine living *Oreochromis mossambicus.* Potamodromous migratory fish was the largest migratory group in the study area, with 16 species falling into this category, including the highly mobile species such as *Clarias gariepinus*, *Enteromius paludinosus*, *Enteromius trimaculatus*, *Labeo molybdinus*, *Labeo rubromaculatus*, *Labeobarbus natalensis*, and *Oreochromis mossambicus* (Table 3.1). Only one species has been classified as non-migratory, *Poecilia reticulata*, with the rest of the species in the region, *Glossogobius callidus*, *Gilchristella aestuaria*, *Ambassis dussumieri*, *Ambassis natalensis*, *Monodactylus argentus*, and *Michrophis fluviatilis*, having unknown migratory classifications (Table 3.1). Furthermore, 17 species had a critical migratory importance, of which the *Anguilla* spp.*,* *C. gariepinus*, the *Labeo* spp., *L. natalensis*, estuarine *O. mossambicus*, *P. capensis*, and *M. falciformis* had the highest importance. Most species have a spatial range between reaches, with six species having catchment-wide spatial requirements, including the *Anguilla* spp., *P. capensis*, and *M. falciformis*. However, much of the migratory information pertaining to euryhaline species is lacking.

Table 3.1: Historical and present fish species biodiversity of the lower uThukela River, quaternary catchment V50D, where the LTBWSS weir is situated, and their associated migratory information. (Note: Information obtained from (Skelton, 2001; Bok et al., 2007; Department of Water and Sanitation, 2014; Wade et al., 2021, FBIS, 2022; Evans et al., 2022). Importance of migration: 4-5 = critical, 3 = moderate, 1-2 = not important (Bok et al., 2007; Fouché and Heath, 2013); spatial range: 5 = catchment-wide, 3 = between reaches, 1 = within reaches (Bok et al., 2007, Fouché and Heath, 2013). Expected distribution used (Skelton, 2001; Whitfield, 2019). Historically used, the known distribution of databases such as (Department of Water and Sanitation, 2014; FBIS, 2022), and literature for the area such as (Wade et al., 2021; Evans et al., 2022). Present study is what was found in this study.)

Species	**Migratory pattern**	**Migratory reference (Bok et al., 2007) unless otherwise stated**	**IUCN Status****	**Expected distribution**	**Historical**	**Present study**	**Migratory importance**	**Spatial range**
Awaous aeneofuscus	Anadromous		LC	X	X	X	1	1
Acanthopagrus berda	Amphidromous		LC	X	X	X	3	3
Anguilla bengalensis	Catadromous		NT	X	X		5	5
Anguilla marmorata	Catadromous		LC	X	X	X	5	5
Anguilla mossambica	Catadromous		NT	X	X	X	5	5
Amphilius natalensis	Potamodromous		LC	X	X		1 - 3	3
Amphilius uranoscopus	Potamodromous		LC	X	X		1	3
**Cyprinus carpio*	Potamodromous	(Stuart and Jones, 2006)		X	X	X		
Clarias gariepinus	Potamodromous		LC	X	X	X	5	3
Coptodon rendalli	Potamodromous		LC	X	X		4	3
Eleotris fusca	Amphidromous	(Maeda and Tachihara, 2005)	LC	X	X	X		
Enteromius paludinosus	Potamodromous		LC	X	X	X	4	3

Enteromius trimaculatus	Potamodromous		LC	X	X	X	4	3
Enteromius viviparus	Potamodromous		LC	X	X	X	3 - 4	3
Gilchristella aestuaria	Unknown	-	LC	X	X			
Glossogobius callidus	Unknown	-	LC	X	X	X	2	DD
Glossogobius giuris	Amphidromous	(Riede, 2004)	LC	X	X	X	4	1
Labeo molybdinus	Potamodromous		LC	X	X	X	5	3
Labeo rubromaculatus	Potamodromous		VU	X	X	X	5	3
Labeobarbus natalensis	Potamodromous		LC	X	X	X	5	3
Oreochromis mossambicus	Amphidromous/ Potamodromous		VU	X	X	X	5/ 1-3	3
Pseudomyxus capensis	Catadromous		LC	X	X	X	5	5
Pseudocrenilabrus philander	Potamodromous		LC	X	X		1	1
**Poecilia reticulata*	Non-migratory	(Page and Burr, 2011)		X	X	X		
Tilapia sparmanii	Potamodromous		LC	X	X		2	3
Anguilla bicolor	Catadromous		NT	X			5	3 - 5
Ambassis dussumieri	Unknown	-	LC	X		X		
Ambassis natalensis	Unknown	-	LC	X				
Eleotris melanosoma	Amphidromous	(Maeda and Tachihara, 2005)	LC	X				
Enteromius gurneyi	Potamodromous		VU	X			4	DD
Hypseleotris cyprinoides	Amphidromous	(Whitfield, 2019)	DD	X				
Monodactylus argentus	Unknown	-	LC	X				
Monodactylus falciformis	Catadromous (facultative)		LC	X			5	5
Microphis brachyurus	Anadromous	(Riede, 2004)	LC	X		X		
Microphis fluviatilis	Unknown	-	DD	X		X		
**Micropterus salmoides*	Potamodromous	(Page and Burr, 2011)		X		X		
Kuhlia rupestris	Catadromous	(Feutry et al., 2013)	LC	X		X		

* Non-native/Invasive Species, ** NE - Not Evaluated, DD - Data Deficient, LC - Least Concern, NT - Near Threatened, VU – Vulnerable

Table 3.2: Relative abundances of fish per species captured using different sampling techniques, number of them PIT tagged, and those which successfully navigated the LTBWSS fishway in the lower uThukela River. (Note: * Non-native/Invasive species).

Species	Sampling Method				Total Sampled Abundance	PIT tagged	Passage Success
	Electrofishing	Fyke Net	Seine Net Small	Seine Net Large			
Acanthopagrus berda		1	1		2	1	
Ambassis dussumieri			3		3		
Anguilla marmorata	4	3			7	3	
Anguilla mossambica	2				2		
Awaous aeneofuscus	1	1	2	1	5	1	
Clarias gariepinus	10	24	2	5	41	22	5
**Cyprinus carpio*	2	2	6		10	1	
Eleotris fusca	16	1			17	2	
Enteromius paludinosus	51		27		78	1	
Enteromius trimaculatus	302	2	11		315	1	
Enteromius viviparus	60		20		80		
Glossogobius callidus	6		2		8		
Glossogobius giurus	1		1		2		
Kuhlia rupestris	2				2		
Labeo molybdinus	53	9	3		65	23	2
Labeo rubromaculatus	14		1		15	5	
Labeobarbus natalensis	47	6	30	40	123	14	
Microphis brachyurus			2		2		
Microphis fluviatilis			1		1		
**Micropterus salmoides*			1		1		
Mullet Fry			1		1		
Oreochromis mossambicus	56	36	226	9	327	33	1
**Poecilia reticulata*	64				64		
Pseudomyxus capensis	1		20	33	54		

Table 3.3: Data relating to PIT-tagged individuals which successfully navigated the LTBWSS fishway in this study.

Species	PIT Tag No.	Site	Capture and release location (GPS)		SL (mm)	Body mass (g)	Date tagged	Date detected	Time Detected	Time at liberty (days)
Labeo molybdinus	989.001038**16134**	DS	-29.169474	31.375757	140	110	23-May-21	14-Sep-21	15:21	114
Oreochromis mossambicus	989.001038**16152**	FW	-29.169351	31.375297	100	35	16-Jun-21	16-Sep-21	15:22	92
Clarias gariepinus	989.001038**17639**	DS	-29.168431	31.376787	320	160	4-Dec-21	10-Dec-21	17:04	6
Clarias gariepinus	989.001038**17607**	DS	-29.168431	31.376787	465	1210	4-Dec-21	10-Dec-21	5:43	6
Clarias gariepinus	989.001038**17664**	DS	-29.169014	31.375981	275	155	4-Dec-21	11-Dec-21	5:27	7
								16-Dec-21	21:43	5
								19-Dec-21	16:08	3
								13-Feb-22	18:16	56
Clarias gariepinus	989.001038**17632**	DS	-29.169129	31.376318	670	3940	4-Dec-21	22-Dec-21	18:39	18
								29-Dec-21	21:25	7
Clarias gariepinus	989.001038**16115**	DS	-29.169106	31.376503	192	60	21-May-21	22-Dec-21	20:56	215
Labeo molybdinus	989.001038**16295**	EWR 17	-29.168911	31.402079	280		6-Dec-21	30-Dec-21	23:47	24

3.4.2 PIT tag study

The connection between the PIT antenna and the reading system failed on the 12th of January, 2022 during a flood event. The issue was fixed on the 2nd of February 2022, and other tagged fish may have attempted the passage during the duration between. However, it is unlikely that passage may have been possible anyways because of large amounts of debris found blocking the upstream and downstream entrances, as well as some of the vertical slots, on-site visits from 02 February 2022 – 18 July 2022 (Supplementary information Fig. S3.2).

Of the 1225 fish collected, a total of 107 fish from 12 species were tagged as they met the minimum tagging requirements (Table 3.2). This included one indigenous catadromous species *A. marmorata,* one indigenous anadromous species *A. aeneofuscus*, two indigenous amphidromous species *E. fusca* and *A. berda*, seven indigenous potamodromous species *C. gariepinus*, *E. trimaculatus*, *E. paludinosus*, *L. molybdinus*, *L. rubromaculatus*, *L. natalensis*, *O. mossambicus*, and the non-native potamodromous migrator *C. carpio* (Tables 3.1 and 3.2). Only one individual of the non-native species, *C. carpio*, was tagged in the initial stages of the study. A decision was made to rather remove all non-native species captured after that during surveys, and as such, the further tagging of *C. carpio* ceased, and the species was not included in analyses. Of the sampling methods used, fyke nets produced the largest number of taggable fish with 58%, electrofishing with 32%, and the small and large seine nets accounting for 9% and 1%, respectively, of the taggable fish catches (Table 3.2). Only three species, *C. gariepinus*, *L. molybdinus*, and *O. mossambicus* had more than 20 tagged individuals (Tables 3.1 and 3.2).

Eight of the 107 fish (7,4%) tagged in this study successfully navigated and ascended the fishway, being picked up by the stationary PIT antenna. These eight fish comprised of three different species, *C. gariepinus* (n = 5), *L. molybdinus* (n = 2), and *O. mossambicus* (n = 1). Two distinct migration periods occurred between these fish, the early spring migration between

14 and 16 September 2021 and the summer migration between 10 and 30 December 2021 (Table 3.3). Both migration periods occurred at the onset of increased water level events recorded during anecdotal observations during field surveys and verified by DWS flow gauging weir data (Department of Water and Sanitation, 2023), albeit stations situated higher up in the uThukela catchment because of the Mandeni station being dysfunctional (Supplementary information Fig. S3.1).

A total of 41 *C. gariepinus* individuals were caught during the sampling period, of which 22 (54%) were of a taggable size. Five of the 22 (23%) tagged individuals managed to move through the fishway successfully after they were tagged and released at the downstream site immediately below the weir (Tables 3.2 and 3.3). Additionally, all five *C. gariepinus* individuals were initially detected by the PIT antenna between 10 December 2021 and 22 December 2021 during the late afternoon and through the night from 17:04 to 05:43. These individuals ranged in size (192 mm SL, 60 g body mass to 670 mm SL and 3940 g body mass on the day of tagging, Table 3.3). Time at liberty (days between tagging and detection) for the initial tag detection of an individual on the PIT antenna ranged from 6 to 215 days. Two individuals with PIT tag numbers 17664 and 17632 (the last five digits of the tag number were unique in this study) were picked up four and two times, respectively, by the PIT antenna. However, after the first detection, it was difficult to determine if these additional detections were up and downstream movements or whether the fish stayed in the abstraction facility before moving away from the PIT antenna.

A total of 65 *L. molybdinus* individuals were caught during the sampling period, of which 23 (35%) were of a taggable size (Table 3.2). Two of the 23 (9%) tagged individuals successfully moved through the fishway. Individual 16134 was tagged and released, measuring 140 mm SL, and weighing 110 g, at the immediate downstream site, where it was at liberty for 114 days before migrating during the early spring migration period (Table 3.3). This individual moved through the PIT antenna during the afternoon at 15:21. The largest distance covered by a single migration during the PIT tag study was that of individual 16295, which was tagged and released, measuring 280 mm SL, at site EWR17 (Table 3.3). After individual 16295's release, it successfully navigated the fish ladder 24 days later, and this included swimming the 2.8 km stretch between its release location and the top of the fishway, which included navigating a natural waterfall-type barrier (Fig 3.1). This individual moved through the PIT antenna at 23:47, showing a nocturnal movement.

A total of 327 *O. mossambicus* individuals were caught during the sampling period, of which 33 (10%) were of a taggable size (Table 3.2). Individual 16152 was the only *O. mossambicus* out of the 33 (3%) tagged individuals which successfully ascended the fishway. This individual was initially captured and tagged at the entrance to the fishway, having a standard length of 100 mm and weighing 35 g (Table 3.3). It was then recaptured during monthly sampling at the entrance of the fishway 76 days later, with a standard length of 105 mm. The same individual was then detected on the PIT antenna 16 days after the recapture. Like the *L. molybdinus* individual 16134, which moved during this study's early spring migration period, *O. mossambicus* individual 16152 also moved during the afternoon at 15:22.

3.4.3 Monthly sampling

During the monthly sampling of the fishway, a total of 443 fish were caught in 33 efforts over 11 sampling periods (Table 3.4). Of the expected 34 indigenous freshwater fish species in the quaternary catchment, 14 were caught in the fishway. None of the non-native fish species which occur in the study area were captured in the fishway. Species richness and abundance were greatest at the fishway entrance, with 304 individuals from 13 species captured, and the least at the lower middle section, with 20 individuals from 5 species captured (Table 3.4). The three *Enteromius* spp. captured in the study accounted for the majority of fish present in the fishway (n = 408) and were present in all surveys besides the two conducted in November 2021. *Enteromius trimaculatus* was the most abundant of all species present in the fishway (n = 297), with six species (*A. mossambica*, *A. aeneofuscus*, *C. gariepinus*, *G. giuris*, *K. rupestris*, and *L. molybdinus*) only having one individual present throughout the study period within the fishway. Only two species, *E. trimaculatus* and *L. natalensis* were found at all positions in the fishway, with the latter only being found in the fishway during the December 2021 survey.

Comparing the abundances and species composition at the three sample locations in the fishway, in all surveys besides the June 2021 and August 2022 surveys, the entrance had the highest catch rates (Fig 3.4). The highest abundances were recorded at the entrance (Fig. 3.4) in July 2022, with 168 individuals captured in one effort. Both the lower middle and upper middle sample locations were devoid of fish in both the August 2021 surveys (survey C and D, Fig 3.4 and Table 3.4) and both the November 2021 surveys (survey G and H, Fig 3.4 and Table 3.4), with the lower middle section also having no catches in the September 2021 and August 2022 surveys. There is disproportionality between the fishway catch rates of 2021 and 2022, with only 128 fish captured from nine surveys (27 efforts) in 2021, whereas from two surveys (six efforts) in 2022, 315 fish were captured. Of the 315 fish caught in the 2022 surveys, only two were caught in the lower middle sample location, compared with 217 from the entrance and 97 from the upper middle section.

Of the 443 fish captured in the fishway, 437 (98.6%) were smaller than 100 mm SL (Table 3.5). This result was skewed towards the abundant minnow species' *Enteromius* spp., seldom larger than 100 mm, accounting for 92% of fish abundance in the fishway. Without considering the *Enteromius spp*., the abundance of fish larger than 100 mm was still less than 18%.

Table 3.4: Abundance of fish per species caught in the three sample sections of the LTBWSS fishway during monthly sampling from May 2021 to August 2022.

(Note: Survey codes: A – 21 May 2021, B – 16 June 2021, C – 24 August 2021, D – 31 August 2021, E – 01 September 2021, F – 13 October 2021, G – 03 November 2021, H – 22 November 2021, I – 04 December 2021, J – 19 July 2022, K – 29 August 2022).

Fishway Entrance

Species	Survey										
	A	B	C	D	E	F	G	H	I	J	K
Anguilla marmorata				1							
Anguilla mossambica			1								
Awaous aeneofuscus						1					
Eleotris fusca				1			2	1	3		
Enteromius paludinosus					4				6	12	7
Enteromius trimaculatus	10			23	1				1	142	23
Enteromius viviparus			2	4	12	4			4	13	16
Glossogobius callidus											2
Glossogobius giurus											1
Kuhlia rupestris										1	
Labeo molybdinus						1					
Labeobarbus natalensis									2		
Oreochromis mossambicus				3							

Fishway Lower Middle

Species	Survey										
	A	B	C	D	E	F	G	H	I	J	K
Enteromius trimaculatus	2								5	2	
Enteromius viviparus		2									
Glossogobius callidus		1									
Labeobarbus natalensis									2		
Oreochromis mossambicus		5				1					

Fishway Upper Middle

Species	Survey										
	A	B	C	D	E	F	G	H	I	J	K
Anguilla marmorata		1									
Clarias gariepinus										1	
Enteromius paludinosus					6	1				4	11
Enteromius trimaculatus	1	1			4				4	40	38
Enteromius viviparus		1								2	
Labeobarbus natalensis	2								2		

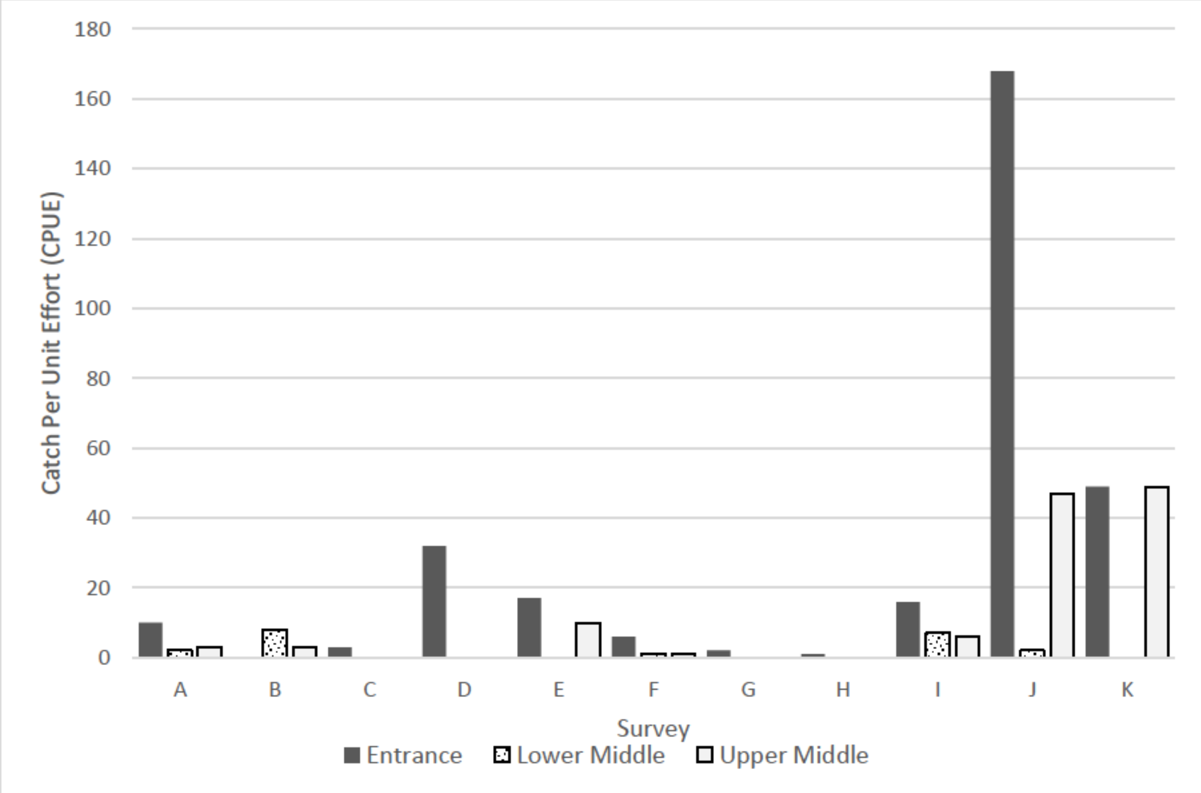

Figure 3.4: Combined abundances per for all fish in the LTBWSS throughout the study period during sampling from May 2021 to August 2022.

(Note: Survey codes: A – 21 May 2021, B – 16 June 2021, C – 24 August 2021, D – 31 August 2021, E – 01 September 2021, F – 13 October 2021, G – 03 November 2021, H – 22 November 2021, I – 04 December 2021, J – 19 July 2022, K – 29 August 2022).

Four catadromous individuals representing three species were present in the fishway, with three individuals from two anguillid species (*A. marmorata* and *A. mossambica*) and an individual rock flagtail, *K. rupestris* (Tables 3.4 and 3.5). They were all present in juvenile sizes for their species, with the anguillids in the 90 – 149 mm size class and the rock flagtail in the 60 – 69 mm size class (Table 3.5). Only one catadromous individual from the four captured, an *A. marmorata*, was found higher up in the fishway, beyond the downstream entrance, which was during the lowest flow period (June 2021).

Similarly, for the amphidromous and anadromous fish of the *Eleotridae* and *Gobiidae* families (*E. fusca*, *A. aeneofuscus*, *G. callidus*, and *G. giuris*), only one out of 12 individuals caught was not at the fishway's downstream entrance (Tables 3.4 and 3.5). However, this individual *G. callidus*, assuming it shares similar migratory behaviour to G. giuris, was found at the lower middle section fishway and during the June 2021 low-flow period. All these individuals were small-size classes for their species (30 – 59 mm) (Table 3.5).

A total of 427 fish individuals with potamodromous migratory behaviour were captured in the fishway, represented by five species of Cyprinidae (*E. paludinosus*, *E. trimaculatus*, *E. viviparus*, *L. molybdinus*, and *L. natalensis*), one Claroteidae species (*C. gariepinus*) and one Cichlidae species (*O. mossambicus*) (Tables 3.4 and 3.5). *Enteromius spp*. were the most abundant species in the fishway (n = 408), with all individuals in the 30 – 99 mm size range (Table 3.5). Of the indigenous cyprinids in the study area, the KwaZulu-Natal yellowfish (*Labeobarbus natalensis*), the endemic Tugela labeo (*Labeo rubromaculatus*), and the leaden labeo (*Labeo molybdinus*), are all species with known upstream migratory behaviour during warmer and higher flow periods (Table 3.1). Only *L. natalensis* (n = 8) and *L. molybdinus* (n = 1) were captured inside the fishway, of which all individuals were smaller than 100 mm (Table 3.5). The single *C. gariepinus* caught in the fishway was also the largest fish captured here (260 mm SL, Table 3.5). It was captured in the upper middle section of the fishway during the July 2022 survey. Of the four expected Cichlidae species in the quaternary catchment, only *O. mossambicus* was present in the fishway. Individuals were found at the entrance and the lower middle section of the fishway during alternate surveys between June 2021 and October 2021, with most found in the lower middle section. The individuals ranged in the size classes of 60 – 149 mm, with four in the larger 100 – 149 mm size class (Table 3.5).

Table 3.5: Size classes of species captured in the LTBWSS fishway in this study.

Species	Size Class SL (mm)													Fishway Position		
	0-19	20-29	30-39	40-49	50-59	60-69	70-79	80-89	90-99	100-149	150-199	200-249	250-299	Entrance	Lower Middle	Upper Middle
Anguilla marmorata									1	1				1		1
Anguilla mossambica									1					1		
Awaous aeneofuscus			1											1		
Clarias gariepinus													1			1
Eleotris fusca				5	2									7		
Enteromius paludinosus				9	28	11	3							29		22
Enteromius trimaculatus				92	94	96	12	2	1					200	9	88
Enteromius viviparus			1	44	4	2								55	2	3
Glossogobius callidus			2	1										2	1	
Glossogobius giurus				1										1		
Kuhlia rupestris						1								1		
Labeo molybdinus							1							1		
Labeobarbus natalensis				3		3			2					2	2	4
Oreochromis mossambicus						1	1	3		4				3	6	

3.5 Discussion

Rivers are vital to ecosystem functioning, allowing the dispersion of energy, water, sediments, nutrients and biota through their longitudinal, lateral and vertical connections to the environment (Freeman et al., 2007; Fullerton et al., 2010). These connections are necessary to many freshwater fish species, whose natural life history processes rely on migratory movements in the river environment (Dudgeon et al., 2006). These migrations in the three spatial directions form key ecological functions that address fish's spawning, feeding, dispersal, recolonisation, and predatory evasion needs (Northcote, 1978, 1984). Moving between habitats is now recognised across numerous species of freshwater fish as a common practice rather than an unusual occurrence (Lucas and Baras, 2008), frequently coordinated to take benefit of, or avoid, geographically and temporally changeable factors such as temperature, flow, nutritional resources, or other aspects of the environment. Changing water levels, such as floods or increases in flow, may provide the cues for fish to migrate for spawning with large and small flow increases being shown to stimulate movement in many species in an Australian fishway study (Northcote, 1984; Mallen-Cooper and Brand, 2007). Obstructing these connections and processes with artificial instream barriers can be detrimental to a fish's life cycle and ecosystem health (O'Brien et al., 2019). It is important to ensure fishway designs cater for the unique migratory needs of the target species' (Bok et al., 2007; Silva et al., 2018).

A successful fishway design allows the entrance to be located, allowing fish to move through it without delay (Clay, 1995; Porcher and Travade, 2002; Hodge et al., 2017). Fishway design has several difficulties, chiefly accommodating a variety of species with varying swimming abilities and migration needs (Zielinski and Freiburger, 2021). Additionally, whether the design flows function within the bounds of the natural river's hydrographs, or the artificial hydrographs produced by the developed infrastructure decide the type of fishway to be built (Bok et al., 2007; O'Brien et al., 2019). Solutions for fish passage often address upstream migration with minimal or no regard for downstream migration (McLaughlin et al., 2013; Silva et al., 2018), with the spillway overflows of impoundments often being considered adequate for downstream passage (Bok et al., 2007). Knowing when fish migrate and their direction of movement is essential for designing an efficient fish passage solution (Franklin and Gee, 2019). Fishways that accommodate the size and timing of considered species by optimising the flow conditions in the fishway when they use it can be effective in their function (Bok et al., 2007; Franklin and Gee, 2019). As a result, these considerations are also important variables in monitoring a fishway's efficacy (Bok et al., 2007).

This study was able to monitor the efficacy of the LTBWSS fishway using PIT telemetry, a first of its kind in Africa (Burnett et al., 2021a). However, there were many technical errors that prevented the present study from achieving a comprehensive assessment. These included the uThukela River flooding from January 2022 to June 2022 (Letsatsi and Kruger, 2022), political unrest in July 2021 (Vhumbunu, 2021), and increased planned national wide electricity cuts to conserve power usage, including staff at the LTBWSS facility unplugging the PIT antenna. All these factors accounted for downtime of the PIT antenna in 2022, restricted access to the site and reduced planned field surveys. In addition to this was delays caused by the COVID-19 pandemic. Applying telemetry techniques in Africa have technical issues, for example, erratic seasonal flows, poor infrastructure, and lack of skills and political will (Hocutt et al., 1994; Burnett et al., 2021a), as expressed in the present study. Despite these technical issues, results from the present study are informative and can provide guidance on the vertical slot fish ladder efficacy and potentially provide future recommendations to assist with fishway design and monitoring in the region.

The predominance of indigenous fish species found in the present study is favourable for the welfare of species biodiversity in the region and indicates that the well-known negative impacts of non-native fauna on indigenous ecosystems (Ellender and Weyl, 2014) are limited in the lower reaches of the uThukela River. The movement of non-native fish within their introduced environments can be detrimental (Koehn and MacKenzie, 2004; Bacheler et al., 2015) while limiting their movements through fish passage facilities are an important consideration for water resource managers (Stuart and Jones, 2006). Fishways do, however, provide a collection point within a river system where the selective removal of unwanted migratory pest species could be achieved (Stuart et al., 2006). Although they were present in low abundance, the non-native fish, *C. carpio* and *M. salmoides*, were not detected in the fishway in the present study.

3.5.1 Findings on migratory species

Seven of the 11 tagged indigenous species were represented by fish displaying potamodromous migratory behaviour (*C. gariepinus*, *E. trimaculatus*, *E. paludinosus*, *L. molybdinus*, *L. rubromaculatus*, *L. natalensis*, and *O. mossambicus*), with four species being of various diadromous behaviours, of which one was catadromous (*A. marmorata*), one was anadromous (*A. aeneofuscus*), and two were amphidromous (*A. berda* and *E. fusca*). However, the migratory classification of diadromous species in the region is sometimes questionable and often based on historical presence/absence data of different life stages of these species in various reaches of South African low-lying and estuarine rivers (Skelton, 2001; Whitfield, 2019). For example, *A. berda* (river bream) is classified as an oceonodromous migrator (migration within saltwater) by Riede (2004) despite being found in river systems, this fits Bok et al. (2007) definition as an amphidromous migrator. However, Bok et al. (2007) also classify *A. aeneofuscus* (freshwater goby) as anadromous, yet Whitfield (2019) suspects it to be amphidromous. Such confusion, especially when the classifications have vastly different meanings, including that of species with unknown migratory behaviours such as *G.callidus*, *Gilchristella aestuaria*, and *Microphis fluviatilis* in this study, may lead to fishway structures that do not accommodate the unique migratory needs of these species. Considering the different migratory behaviours and the size classes of species at the different stages of them, fish in their adult sizes or bigger than 100 mm standard length were most likely those with potamodromous or anadromous behaviour, with the euryhaline species that have catadromous and amphidromous behaviour more likely to be in their juvenile, upstream migration size so close to the estuary (Franklin and Gee, 2019; Lagarde et al., 2021). Therefore, the study results showing high abundances of tagged potamodromous species and few diadromous species are expected as the study area falls in the freshwater stretch of the lower uThukela River.

3.5.2 PIT tag study

The PIT telemetry monitoring of fish is a form of the capture-mark-recapture technique, whereby once fish have been marked, in this case, tagged, their 'recapture' is by passive means, through a receiving antenna detecting their uniquely coded tag (Castro-Santos et al., 1996; Roussel et al., 2000; Bond et al., 2007; Cucherousset et al., 2008; Morris et al., 2018). In the present study, a relatively great sampling effort still resulted in a low number of taggable fish, with fyke nets the most effective in capturing fish large enough to PIT tag, as demonstrated in another fish population sampling study (Portt et al., 2006). The low number of fish caught throughout the present study, with even lower suitable fish for tagging, suggests that the freshwater ecosystem in the lower uThuekla River is already highly stressed, as seen in other studies for the present study area (Wade et al., 2021; Evans et al., 2022). The poor fish abundances are primarily from other stressors in the present study area, such as the Sundumbili wastewater treatment works, the Sappi Tugela pulp and paper mill, surrounding industrial areas, and extensive agricultural activities altering flow in the uThukela River (Wade et al., 2021). These are potentially compounded by the instream barrier of the LTBWSS that limits the movement of fish, as seen in the present study.

The three species of fish that successfully navigated the fishway in this study were those with a tagging sample size greater than 20 individuals. This indicates that higher sample sizes will improve results providing a higher probability for detecting tagged fish migrations through the antenna as in similar studies (Castro-Santos et al., 1996; Roussel et al., 2000; Morris et al., 2018). However, these studies focused on selected species with well-documented migratory needs and resources available to assess these. In the present study, the first application of a PIT antenna to monitor a fishway in Africa to assess the migratory needs that are met in fishways for multiple species with limited knowledge of their migratory requirements is challenging.

Biotic and abiotic factors influence a PIT tag detection in fish studies. Biotic factors relating to the feasibility of PIT tags are dependent on the species under consideration (Baras et al., 2002; Jepsen et al., 2005; Musselman et al., 2017) as well as the size of the fish (Prentice et al., 1990; Acolas et al., 2007). Results drawn from this study suggest that the movement of tagged fish through the antenna gives us an idea that PIT tagging, and its retention, are suitable for *O. mossambicus*, *L. molybdinus*, and *C. gariepinus*. Abiotic factors influencing tag detection efficiency are complex habitat structures (Cucherousset et al., 2008; Burnett et al., 2013), code collisions from multiple tagged fish moving at the same time (Castro-Santos et al., 1996; Morhardt et al., 2000), electromagnetic field interference of the antenna from external sources (Fetherman et al., 2014; Morris et al., 2018), and tag size and orientation in the fish (Bond et al., 2007; Burnett et al., 2013). In this study, complex habitat structures (unless during the debris blockages of the floods), electromagnetic field interference, and the size of the tags, were unlikely to have affected the tag detection as these were accounted for in the design of the present study. The detection of tagged fish on the PIT antenna suggests that tag placement in this study (aligned to the long axis of the fish sagittal plane) is in line with international practice for optimal tag detection (Bond et al., 2007; Burnett et al., 2013). However, the collision of tag codes was unavoidable if multiple fish decided to move simultaneously. However, considering the low abundances and temporal detections of tags in the study, it was unlikely, although not impossible, that this could have affected the results.

Tagged fish that moved through the fishway indicated to do so in close succession during two periods, September and December, possibly indicating migration periods for these species. *Clarius gariepinus,* a seasonal migrator (Bruton, 1978), was the most successful PIT-tagged migrator, with five individuals successfully navigating the fishway. The results showed that a relatively good size range of fish species is dependent on the fishway to provide upstream passage. One individual, with tag number 17664 was detected four times by the PIT antenna, which suggests that it frequented the area, which could have included multiple downstream and upstream movements in the fishway or that it frequented the area of the antenna, likely feeding on debris gathered around it (as observed in other places in the abstraction hull; Personal observations by authors), before moving upstream into the impoundment. However, it is uncertain to state this specifically because of the single antenna used in the study. Although the last PIT-tagged fish migrated through the fishway on 31 December 2021, subsequent migrations during the summer period when the PIT monitoring system was not operational could have happened, despite excessive blockage from flood debris in the fish ladder, which may have hindered these movements.

The novelty of this study, in the African context (Burnett et al., 2021a), exposed the paucity of knowledge on our inland aquatic ecosystems and the organisms that inhabit them, especially when evaluating the efficacy of fishways already constructed. The present study highlights some challenges of applying this technology while providing valuable data relating to PIT telemetry use in the region. The application of PIT telemetry in the present study showed some interesting findings that justify the technique's continual use for efficacy evaluations of fishways in Africa. For example, the movement of a singular *L. molybdinus* from 2.5 km downstream successfully moved upstream in the natural river and then navigated the fishway. The fishway does allow fish to pass through it; however, its efficacy is still questionable because of the low number of successful navigations from tagged fish. Here, tagged *L. natalensis*, a highly mobile fish (Burnett et al., 2021b), was not detected navigating through the fishway. Similarly, for other species, such as *L. rubromaculatus,* and those of the Eleotridae and Gobiidae families. The PIT telemetry data applied alongside the monthly fishway sampling provided valuable insight into the LTBWSS fishway and how fish use it.

Furthermore, the technical design aspects of the fishway may have affected its efficacy in providing passage for all tagged fish of differing sizes and species. The choice of a vertical slot fishway with a 1:11 slope may be reason for this. Firstly, vertical slot fishways are known to have poor passage efficiency for species with climbing and crawling behaviours (such as elvers, prawns and gobiods) (Bok et al., 2007; Bernard et al., 2007). Secondly, Bernard et al. (2007) suggests that the highest allowable gradient for fishways is 1:10, and although the LTBWSS fishway was designed as 1:11 and therefore allowable, it is considered steep and likely only passable for strong swimming fish, since vertical slot fishways with gentle slopes (>1:15) are recommended for weaker swimmers (Bok et al., 2007; Bernard et al., 2007). Additionally, and although not measured, visual inspection of the facility shows that the fishway passes a small proportion of the total flow, likely making it difficult for fish to locate its downstream entrance.

3.5.3 Monthly sampling

Fishways can provide a habitat for fish rather than facilitate movement through the fishway for fish species present in the fishway (Castro-Santos et al., 2009). In the present study, the monthly sampling survey does not provide a fish's direction of movement in the fishway but rather its use of the fishway. Presence may, however, indicate a preference and absence of disfavour to specific conditions in those parts of the fishway that a fish moving through has to navigate through. For example, the lower middle section had considerably low abundances, which is of concern as it functions as a turning point in the fishway design and a resting basin for migratory fish in the fishway. The low fish abundance in the turning basins may indicate that the design conditions are not conducive for fish to stay or rest in these sections or that they could not easily reach this section from either the upstream or downstream directions. Many factors determine the ability of a fish to hold its position in a fishway as it attempts to move up; these are the relative depths, flows, turbulence, substrate, or cover (Castro-Santos et al., 2009; Calluaud et al., 2014). The limited size class, low abundances and low diversity of species indicated that the fishway provides habitat for a select few species, predominantly rheophilic or semi-rheophilic species, for example, *L. molybdinus* and *L. natalensis* and may limit full passage through the fishway.

Based on the monthly sampling, the LTBWSS fishway provides habitat and possible passage through the facility for smaller individuals of potamodromous migratory fish species, such as the *Enteromius* spp. and *L. natalensis*. The high proportion of small fish, less than 100 mm SL, caught in the fishway was skewed towards the abundant *Enteromius* spp., species that do not grow greater than 15 cm, and which accounted for 92% of fish abundance in the fishway. The *Enteromius* spp. are part of the cyprinid family and are highly mobile fishes needing to move to meet biological requirements (Skelton, 2001; Bok et al., 2007). Conditions within the fishway are likely favourable for them, as high debris loads create ideal micro-habitats and spawning areas (Skelton, 2001), which they may seek. Coupled with the lack of larger predatory species, the fishway may be acting as a refuge rather than providing passage through the LTBWSS structure for these smaller species. Like the *Enteromius* spp., *L. natalensis* is another highly mobile cyprinid which has potamodromous migratory behaviour and is known for its upstream migrations during spring and summer months (Skelton, 2001; Burnett et al., 2021b). This was likely observed in the study during the December 2021 survey, whereby small individuals from the species were found throughout the fishway, indicating a key movement period for the species in the region into the fishway. Furthermore, the amphidromous migrators *G. giuris* and *E. fusca*, and the catadromous migrators *A. marmorata*, *A. mossambica*, and *K. rupestris*, were found in small size classes for their species in the fishway, which is expected at this stage of their life cycle in the lower reaches of rivers (Franklin and Gee, 2019; Lagarde et al., 2021). Considering that multispecies fishways require design flows that accommodate the weakest swimmers (Bok et al., 2007), if small amphidromous and catadromous migrators were found throughout the fishway, upstream from its downstream entrance, it would be an indication that the fishway, in the hydraulic conditions at the time of sampling, allows them to move upstream and gives an idea of the fishways functionality for those species. However, in the present study, only one of the 11 amphidromous or catadromous migrators, an *A. marmorata*, was found past the fishway downstream entrance during the lowest flow period, suggesting that the LTBWSS fishway provides partial connectivity.

Fish abundances in the fishway drastically differed between the 2021 and 2022 surveys. The region experienced a sustained period of flooding from January 2022 until June 2022 (Supplementary information Fig. S3.1; Letsatsi and Kruger, 2022). High flows perform crucial tasks for riverine habitats, including cleaning channels, transporting sediment, bringing in new woody debris, and maintaining riparian and floodplain habitats (Schultz et al., 2003; Wald, 2009). Many of these are necessary to open up gravel or cobble beds for species that are substrate spawners or provide roots, reed clumps or other structures for those species which are vegetative spawners (Wald, 2009). The uThukela River likely experienced the benefits of such a system flush, as evident in the increased fish abundances encountered in the fishway in 2022. However, these high abundances were only found at the downstream entrance and upper middle section of the fishway, with almost no fish being found in two surveys in the lower middle section. Although this same phenomenon trended throughout the study period, it would have been expected that the lower middle section would follow the increased abundance trend of the other two sample sections in 2022. This may further support the idea that conditions in the lower middle section are not conducive for fish to stay or rest there. It is important to note that both the downstream entrance and upper middle section had high debris loads in them after the 2022 floods, and the lower middle section had nothing (pers. obs. B. van Zyl; Supplementary information Fig. S3.2), a factor that could be driving the high fish abundances after the flooding as habitat this provides habitat in the downstream entrance to the fishway (Wald, 2009).

3.5.4 Recommendations

Assessing the efficacy of a fishway requires that appropriate methods are employed. These methods should align with the target fish species' behaviours, morphometrics, and life cycles to achieve the best results (Porcher and Travade, 2002; Mallen-Cooper and Brand, 2007; Lagarde et al., 2021). PIT telemetry for the region is presently most suited for larger fish (SL > 100 mm), and its application in fishway efficiency surveys should require a minimum of two PIT antennas, with one positioned at the downstream entrance of the fishway, and the other at the upstream entrance as with international practices (Castro-Santos et al., 1996; Franklin et al., 2012). Although this is not always possible because of financial constraints, as in the present study, a single PIT antenna placed at the top of the fishway can only test one-way upstream migration pathways and does not account for downstream movement, which is increasingly becoming a requirement elsewhere in the world (Silva et al., 2018). Multiple PIT antennae on a single fishway structure would provide more details about the functioning of the fishway design, the successful upstream and downstream navigation of fish, the time tagged fish spend in the fishway, and fish migration timing for that region (Castro-Santos et al., 1996; Franklin et al., 2012). When applied successfully, a multi-PIT antenna, a long-term monitoring program, would greatly contribute to our understanding of the migratory behaviour of fish in the region.

To cater for upstream fish migration, the continual use of the vertical slot fishways in South African weir design needs to incorporate a more extensive monitoring design, along with multiple PIT antennae. Vertical slot fishways also need to consider the weaker swimming species by being designed at gentler gradients. The present study was conducted using limited resources and determined the upstream passage of fish through a vertical slot fishway over a single season. It is also important to evaluate downstream migrations in South Africa. Bok et al. (2007) indicated that weir crests, such as on the LTBWSS weir, provide for downstream passage through over-the-top spillage. This may work for adults (Bok et al., 2007) but has been shown to prevent larvae drift from amphidromous species such as gobies (Franklin and Gee, 2019). The cost of using multiple antennas, along with a capable reader and cables, may make it unsuitable for studies where the research equipment budget is limited, especially in the Southern hemisphere (Burnett et al., 2021a). In addition, fish >100 mm standard length required for a PIT study limits its use. However, regulations and the need to meet migratory requirements of fish in South Africa should make this cost-effective, especially because of the paucity of knowledge on fish passage efficacy in South Africa. PIT telemetry can be beneficial in long-term surveys (Thorstad et al., 2013; Burnett et al., 2021a). It can provide a better understanding of the fishway use by fish and potential migratory patterns of fish using fishways to migrate, removing sampling bias.

This study suggests that the use of present PIT telemetry technology in South African fishway efficacy studies is best suited for potamodromous upstream migrators and possibly downstream migrations of adult amphidromous and catadromous migrators, although these may use the crests of weirs and dams during their downstream migration, rather than the fishway (Bok et al., 2007). However, as PIT technology advances and smaller PIT tag sizes become available, smaller fish can be tagged and evaluated in South Africa. This could potentially include the smaller size classes of catadromous and amphidromous migrators, as well as species such as the *Enteromius* spp. and minnows, which were highly abundant in the fishway during this study. A reliable electricity supply must also be considered for such a PIT telemetry study. In the present situation in South Africa, load-shedding has become a regular occurrence, whereby it seriously affected this study by damaging the batteries, so we would recommend "off-the-grid" electricity supply options to be considered as backup power supplies. These options are not always viable as standard solar panels are a commodity that is highly sort after and often stolen, even in relatively secure areas.

As suggested by Bok, each fishway design implemented in the country should have a monitoring plan associated with it that evaluates its performance in terms of its designed function. Combining PIT telemetry and traditional techniques allows a holistic monitoring program and the detection of small and different size classes of fish to be sampled, as done in this study. Using conventional methods like trapping fish at the top and bottom entrances of the fishway can further aid in assessing the functionality of the fishway in terms of species use, migration patterns, and whether or not upstream and downstream migration is achievable by different species for the fishways design (Fouché and Heath, 2013).

As seen in the present study, high water levels and flood debris produced major challenges to assessing the fishway's functionality, especially in high flows. These issues may persist in future fishways built on the same design as the LTBWSS and highlight important considerations that need to be made. For example, on rivers where high rainfall and flooding can be expected, it is important that the sampling method used to assess the fishways functionality accounts for these high-water events. Methods that allow passive monitoring, such as PIT telemetry, are favourable in these conditions, provided they remain intact and uninterrupted. To ensure minimal damage, future fishway designs should provide space to place monitoring equipment, such as PIT telemetry equipment, to ensure that flood damage to this is minimised. Furthermore, the presence of flood debris blockages in fish passage facilities, and the accumulation of debris as a result of regular inspection of the facility not being performed, are major hindrances to the connectivity function they serve (Larinier, 2002; Moore and Rutherfurd, 2017). Solutions to minimising the high debris loads entering the fishway during floods need to be considered, along with regular inspection of the fishway to detect such issues early on. In the case of debris blockages in the fishway, it is paramount that managers timeously attend to these to ensure that connectivity through the fishway is quickly restored.

In response to expected species not having been detected in the fishway, it may be that the fish did not move upstream but rather into neighbouring environments. Additional work may be required to understand better fish movements in the region, particularly in other environments such as into tributaries or the nearby estuarine environment.

3.5.5 Conclusions

Despite challenges such as flooding and power supply to the PIT antenna in the study, PIT telemetry was a valuable technique to passively monitor the seasonal movement of fish in the region and through the fishway. Our results showed that larger fish used the fishway during the high flows, a period when active sampling of the fishway was unfeasible, and monitoring fish movements in it required an effective passive solution, such as PIT telemetry. However, despite its success in monitoring fish movements through the fishway, PIT telemetry cannot be solely used, especially where smaller size classes of fish are concerned, and therefore this requires additional suitable monitoring methods. Furthermore, the results showed that various local species rely on the LTBWSS fishway at different times of the year and that it did allow certain migratory fish to pass through, but not all. This suggests that some key migratory requirements of species may not be met by the fishways design. These complex requirements for the concerned species may not yet be fully understood, but this suggests that effective solutions will require further research into their needs.

Our study showed that fish from the broad migratory classes in the region relied on the LTBWSS fishway to provide connectivity between upstream and downstream habitats. The presence of amphidromous and catadromous species in juvenile-size classes in the study area indicated the need for effective fish passage solutions at lowland barriers, which cater for these stages of their lifecycle. Additionally, with potamodromous species present in a range of size classes, designing a multispecies fishway for a range of size classes presents a challenge, with a crucial understanding of the migratory requirements of species needing to be understood.

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3.7 References

Acolas, M., Roussel, J. & Bagliniere, J. 2007. Laboratory experiment on survival, growth and tag retention following PIT injection into the body cavity of juvenile brown trout (*Salmo trutta*). *Fisheries Research,* 86, 280 - 284.

Alla, Y. M. K. & Liu, L. 2021. Impacts of dams on the environment: a review. *International Journal of Environment, Agriculture and Biotechnology,* 6, 64-74.

Bacheler, N. M., Whitfield, P. E., Muñoz, R. C., Harrison, B. B., Harms, C. A. & Buckel, C. A. 2015. Movement of invasive adult lionfish *Pterois volitans* using telemetry: Importance of controls to estimate and explain variable detection probabilities. *Marine Ecology Progress Series,* 527, 205-220.

Baras, E., Benech, V. & Marmulla, G. 2002. Outcomes of a pilot fish telemetry workshop for developing countries. *Hydrobiologia,* 483, 9-11.

Barbarossa, V., Schmitt, R. J., Huijbregts, M. A., Zarfl, C., King, H. & Schipper, A. M. 2020. Impacts of current and future large dams on the geographic range connectivity of freshwater fish worldwide. *Proceedings of the National Academy of Sciences,* 117, 3648-3655.

Baudoin, J.-M., Burgun, V., Chanseau, M., Larinier, M., Ovidio, M., Sremski, W., Steinbach, P. & Voegtle, B. 2015. Assessing the passage of obstacles by fish. Concepts, design and application. *Comprendre pour agir-Collection de l'Onema,* French National Agency for Water and Aquatic Environments.

Belletti, B., De Leaniz, C. G., Jones, J., Bizzi, S., Börger, L., Segura, G., Castelletti, A., Van De Bund, W., Aarestrup, K. & Barry, J. 2020. More than one million barriers fragment Europe's rivers. *Nature,* 588, 436-441.

Bernard, J. M., Fripp, J., & Robinson, K. 2007. Stream Restoration Design Handbook (National Engineering Handbook, 210VI, part 654). *Technical Supplement 14N: Fish Passage and Screening Design*. US Department of Agriculture, Natural Resources Conservation Service: http://directives. sc. egov. usda. gov/viewerFS. aspx.

Bok, A., Kotze, P. & Heath, R. 2007. *Guidelines for the planning, design and operation of fishways in South Africa*, Water Research Commission, Pretoria.

Bond, M. H., Hanson, C. V., Baertsch, R., Hayes, S. A. & Macfarlane, R. B. 2007. A new low-cost instream antenna system for tracking passive integrated transponder (PIT)-tagged fish in small streams. *Transactions of the American Fisheries Society,* 136, 562-566.

Briscoe, J. 2009. Water security: Why it matters and what to do about it. *Innovations: Technology, Governance, Globalization,* 4, 3-28.

Brownscombe, J. W., Lédée, E. J., Raby, G. D., Struthers, D. P., Gutowsky, L. F., Nguyen, V. M., Young, N., Stokesbury, M. J., Holbrook, C. M. & Brenden, T. O. 2019. Conducting and interpreting fish telemetry studies: considerations for researchers and resource managers. *Reviews in Fish Biology and Fisheries,* 29, 369-400.

Bruton, M. 1978. The habitats and habitat preferences of *Clarias gariepinus* (Pisces: Clariidae) in a clear coastal lake (Lake Sibaya, South Africa). *Journal of the Limnological Society of Southern Africa,* 4, 81-88.

Burnett, M. J., O'Brien, G. C., Jacobs, F. J., Jewitt, G. & Downs, C. T. 2021a. Fish telemetry in African inland waters and its use in management: a review. *Reviews in Fish Biology and Fisheries*, 31, 337–357.

Burnett, M. J., O'Brien, G. C., Jewitt, G. & Downs, C. T. 2021b. Temporal and spatial ecology of an iconic *Labeobarbus* spp. in a socio-economically important river. *Environmental Biology of Fishes,* 104, 1103-1119.

Burnett, N. J., Stamplecoskie, K. M., Thiem, J. D. & Cooke, S. J. 2013. Comparison of detection efficiency among three sizes of half-duplex passive integrated transponders using manual tracking and fixed antenna arrays. *North American Journal of Fisheries Management,* 33, 7-13.

Calluaud, D., Cornu, V., Baran, P. & David, L. 2014. Relationship between fish behaviour, turbulence and unsteady flow in experimental vertical slot fishways. 10th International Symposium on Ecohydraulics, Trondheim, Norway, pp. 1-4.

Carpenter, S. R., Stanley, E. H. & Vander Zanden, M. J. 2011. State of the world's freshwater ecosystems: Physical, chemical, and biological changes. *Annual Review of Environment and Resources,* 36, 75-99.

Castro-Santos, T., Cotel, A. & Webb, P. 2009. Fishway evaluations for better bioengineering: an integrative approach. Challenges for diadromous fishes in a dynamic global environment. American Fisheries Society, Symposium. pp. 557-575.

Castro-Santos, T., Haro, A. & Walk, S. 1996. A passive integrated transponder (PIT) tag system for monitoring fishways. *Fisheries Research,* 28, 253-261.

Clay, C. H. 1995. *Design of Fishways and Other Fish Facilities.* Lewis Publishers, London.

Cucherousset, J., Marty, P., Pelozuelo, L. & Roussel, J.-M. 2008. Portable PIT detector as a new tool for non-disruptively locating individually tagged amphibians in the field: A case study with Pyrenean brook salamanders (*Calotriton asper*). *Wildlife Research,* 35, 780-787.

D'enno, D., Marmulla, G. & Welcomme, R. 2002. *Fish passes: Design, dimensions and monitoring*. Food and Agriculture Organization of the United Nations, Rome, Italy.

Department of Water Affairs 2013. National Water Resource Strategy 2: Water for an equitable and sustainable future. 2 ed. Pretoria (South Africa).

Department of Water Affairs and Forestry 2004. Thukela WMA: Internal Strategic Perspective. *National Water Resource Planning.* Pretoria (South Africa): .

Department of Water and Sanitation 2023. (DWS) Hydrology Verified Data Sets - 01 May 2021 to 29 June 2022. Pretoria, South Africa

Department of Water and Sanitation 2022. Proposed Water Resource Classes and Resource Quality Objectives for Thukela Catchments in the Pongola - Mtamvuna Water Management Area. *Government Gazette*, 46032, Pretoria, South Africa.

Department of Water and Sanitation 2014. A Desktop Assessment of the Present Ecological State, Ecological Importance and Ecological Sensitivity per Sub Quaternary Reaches for Secondary Catchments in South Africa. Compiled by RQIS-RDM.

Depledge, M. H. & Galloway, T. S. 2005. Healthy animals, healthy ecosystems. *Frontiers in Ecology and the Environment,* 3, 251-258.

Dickens, C., Smakhtin, V., Mccartney, M., O'Brien, G. & Dahir, L. 2019. Defining and quantifying national-level targets, indicators and benchmarks for management of natural resources to achieve the sustainable development goals. *Sustainability,* 11, 462.

Du Plessis, A. 2019. Evaluation of Southern and South Africa's freshwater resources. In: Du Plessis, A. (Ed), *Water as an inescapable risk.* Springer, Switzerland, pp. 147-172.

Dudgeon, D. 2010. Prospects for sustaining freshwater biodiversity in the 21st century: linking ecosystem structure and function. *Current Opinion in Environmental Sustainability,* 2, 422-430.

Dugan, P. J., Barlow, C., Agostinho, A. A., Baran, E., Cada, G. F., Chen, D., Cowx, I. G., Ferguson, J. W., Jutagate, T. & Mallen-Cooper, M. 2010. Fish migration, dams, and loss of ecosystem services in the Mekong Basin. *Ambio,* 39, 344-348.

Elagib, N. A. & Basheer, M. 2021. Would Africa's largest hydropower dam have profound environmental impacts? *Environmental Science and Pollution Research,* 28, 8936-8944.

Ellender, B. R. & Weyl, O. L. 2014. A review of current knowledge, risk and ecological impacts associated with non-native freshwater fish introductions in South Africa. *Aquatic Invasions,* 9, 117–132.

Evans, W., Downs, C. T., Burnett, M. J. & O'Brien, G. C. 2022. Assessing fish community response to water quality and habitat stressors in KwaZulu-Natal, South Africa. *African Journal of Aquatic Science,* 47, 47-65.

FBIS (Freshwater Biodiversity Information System). 2022. Downloaded from https://freshwaterbiodiversity.org on 20 October 2022.

Fetherman, E. R., Avila, B. W. & Winkelman, D. L. 2014. Raft and floating radio frequency identification (RFID) antenna systems for detecting and estimating abundance of PIT-tagged fish in rivers. *North American Journal of Fisheries Management,* 34, 1065-1077.

Feutry, P., Castelin, M., Ovenden, J. R., Dettai, A., Robinet, T., Cruaud, C. & Keith, P. 2013. Evolution of diadromy in fish: Insights from a tropical genus (*Kuhlia* species). *American Naturalist,* 181, 52-63.

Fouché, P. & Heath, R. 2013. Functionality evaluation of the Xikundu fishway, Luvuvhu River, South Africa. *African Journal of Aquatic Science,* 38, 69-84.

Franklin, P. & Gee, E. 2019. Living in an amphidromous world: Perspectives on the management of fish passage from an island nation. *Aquatic Conservation: Marine and Freshwater Ecosystems,* 29, 1424-1437.

Franklin, A. E., Haro, A., Castro-Santos, T. & Noreika, J. 2012. Evaluation of nature-like and technical fishways for the passage of alewives at two coastal streams in New England. *Transactions of the American Fisheries Society,* 141, 624-637.

Freeman, M. C., Pringle, C. M. & Jackson, C. R. 2007. Hydrologic connectivity and the contribution of stream headwaters to ecological integrity at regional scales. *Journal of the American Water Resources Association,* 43, 5-14.

Fullerton, A. H., Burnett, K. M., Steel, E. A., Flitcroft, R. L., Pess, G. R., Feist, B. E., Torgersen, C. E., Miller, D. J. & Sanderson, B. L. 2010. Hydrological connectivity for riverine fish: Measurement challenges and research opportunities. *Freshwater Biology,* 55, 2215-2237.

Hanna, D. E., Tomscha, S. A., Ouellet Dallaire, C. & Bennett, E. M. 2018. A review of riverine ecosystem service quantification: Research gaps and recommendations. *Journal of Applied Ecology,* 55, 1299-1311.

Hanzen, C., Lucas, M. C., O'Brien, G., Calverley, P. & Downs, C. T. 2020. Surgical implantation of radio tags in three eel species (*Anguilla* spp.) in South Africa. *Journal of Fish Biology,* 96, 847-852.

Hirt-Chabbert, J. & Young, O. 2012. Effects of surgically implanted PIT tags on growth, survival and tag retention of yellow shortfin eels *Anguilla australis* under laboratory conditions. *Journal of Fish Biology,* 81, 314-319.

Hocutt, C., Seibold, S. & Jesien, R. 1994. Potential use of biotelemetry in tropical continental waters. *Revue d'hydrobiologie Tropicale,* 27, 77-95.

Hodge, B. W., Fetherman, E. R., Rogers, K. B. & Henderson, R. 2017. Effectiveness of a fishway for restoring passage of Colorado River Cutthroat Trout. *North American Journal of Fisheries Management,* 37, 1332-1340.

Hsu, A., Lloyd, A. & Emerson, J. W. 2013. What progress have we made since Rio? Results from the 2012 Environmental Performance Index (EPI) and Pilot Trend EPI. *Environmental Science & Policy,* 33, 171-185.

Hussey, N., Kessel, S., Aarestrup, K., Cooke, S., Cowley, P. & Fisk, A. 2015. Aquatic animal telemetry: a panoramic window into the underwater world. *Science,* 348, 1-10.

Jackson, D. C. & Marmulla, G. 2001. The influence of dams on river fisheries. *FAO Fisheries Technical Paper*, 1-44.

Jepsen, N., Schreck, C., Clements, S. & Thorstad, E. 2005. A brief discussion on the 2% tag/bodymass rule of thumb. In: Spedicato, M. T., Lembo, G., Marmulla, G. (Eds), *Aquatic telemetry: Advances and Applications Proceedings of the Fifth Conference on Fish Telemetry held in Europe*, pp. 255-259.

Jewitt, D., Goodman, P. S., Erasmus, B. F., O'Connor, T. G. & Witkowski, E. T. 2015. Systematic land-cover change in KwaZulu-Natal, South Africa: Implications for biodiversity. *South African Journal of Science,* 111, 01-09.

Kaval, P. 2019. Integrated catchment management and ecosystem services: A twenty-five year overview. *Ecosystem Services,* 37, 100912.

King, J. & Pienaar, H. 2011. Sustainable use of South Africa's inland waters: a situation assessment of resource directed measures 12 years after the 1998 National Water Act. *Water Research Commission Report No. TT,* 491, Water Research Commission, Pretoria, pp. 1-245.

Kleynhans, C. 1999. The development of a fish index to assess the biological integrity of South African rivers. *Water SA,* 25, 265-278.

Kleynhans, C. 2007. Module D: Fish response assessment index (FRAI). *River ecoclassification manual for ecostatus determination (Version 2): Report produced for the Department of Water Affairs and Forestry (Resource Quality Services) and the*

Water Research Commission, WRC Report No. TT330/08, Water Research Commission, Pretoria.

Koehn, J. D. & Mackenzie, R. F. 2004. Priority management actions for alien freshwater fish species in Australia. *New Zealand Journal of Marine and Freshwater Research,* 38, 457-472.

Lagarde, R., Courret, D., Grondin, H., Faivre, L. & Ponton, D. 2021. Climbing for dummies: Recommendation for multi-specific fishways for the conservation of tropical eels and gobies. *Animal Conservation,* 24, 970-981.

Larinier, M. 2002. Fishways-general considerations. *Bulletin Français de la Pêche et de la Pisciculture*, 364, 21-27.

Letsatsi, N. & Kruger, A. 2022. The April 2022 floods in comparison with other recent flooding events in KwaZulu-Natal. *Weathersmart, WeatherSA*, 5.

Lucas, M. C. & Baras, E. 2000. Methods for studying spatial behaviour of freshwater fishes in the natural environment. *Fish and Fisheries,* 1, 283-316.

Lucas, M. C. & Baras, E. 2008. *Migration of freshwater fishes*, Blackwell Science, Oxford, UK.

Maeda, K. & Tachihara, K. 2005. Recruitment of amphidromous sleepers *Eleotris acanthopoma, Eleotris melanosoma*, and *Eleotris fusca* into the Teima River, Okinawa Island. *Ichthyological Research,* 52, 325.

Mallen-Cooper, M. & Brand, D. 2007. Non-salmonids in a salmonid fishway: What do 50 years of data tell us about past and future fish passage? *Fisheries Management and Ecology,* 14, 319-332.

Mantel, S. K., Rivers-Moore, N. & Ramulifho, P. 2017. Small dams need consideration in riverscape conservation assessments. *Aquatic Conservation: Marine and Freshwater Ecosystems,* 27, 748-754.

McDowall, R. M. 1997. The evolution of diadromy in fishes (revisited) and its place in phylogenetic analysis. *Reviews in Fish Biology and Fisheries,* 7, 443-462.

McIntyre, P. B., Reidy Liermann, C., Childress, E., Hamann, E. J., Hogan, J. D., Januchowski-Hartley, S. R., Koning, A. A., Neeson, T. M., Oele, D. L. & Pracheil, B. M. 2016. Conservation of migratory fishes in freshwater ecosystems. In: Closs, G. P. (Ed), *Conservation of freshwater fishes*, Cambridge University Press, Cambridge, pp. 324-360.

Mclaughlin, R. L., Smyth, E. R., Castro-Santos, T., Jones, M. L., Koops, M. A., Pratt, T. C. & Vélez-Espino, L. A. 2013. Unintended consequences and trade-offs of fish passage. *Fish and Fisheries,* 14, 580-604.

Mittal, N., Bhave, A. G., Mishra, A. & Singh, R. 2016. Impact of human intervention and climate change on natural flow regime. *Water Resources Management,* 30, 685-699.

Moore, H. E. & Rutherfurd, I. D. 2017. Lack of maintenance is a major challenge for stream restoration projects. *River Research and Applications,* 33, 1387-1399.

Morhardt, J. E., Bishir, D., Handlin, C. I. & Mulder, S. D. 2000. A portable system for reading large passive integrated transponder tags from wild trout. *North American Journal of Fisheries Management,* 20, 276-283.

Morris, M. S., Holcombe, E. F., Borsky, A. J., Bentley, P. J. & Sandford, B. P. 2018. Detection of PIT-tagged juvenile salmonids migrating in the Columbia River Estuary, 2017. *National Oceanic and Atmospheric Administration, Northwest Fisheries Science Center, Seattle. Report to US Department of Energy, Contract,* 46273.

Musselman, W. C., Worthington, T. A., Mouser, J., Williams, D. M. & Brewer, S. K. 2017. Passive integrated transponder tags: Review of studies on warmwater fishes with notes on additional species. *Journal of Fish and Wildlife Management,* 8, 353-364.

Northcote, T. 1978. Migratory strategies and production in freshwater fishes. In: Gerking, S. (Ed), *Ecology of freshwater fish production*, John Wiley & Sons, NewYork, pp. 326-359.
Northcote, T. 1984. Mechanisms of fish migration in rivers. In: McLeave, J. D., Arnold, G. P., Dodson, J. J., Neill, W. (Eds), *Mechanisms of migration in fishes.* PlenumPress, New York, pp. 317-356.
O'Brien, G. C., Ross, M., Hanzen, C., Dlamini, V., Petersen, R., Diedericks, G. J. & Burnett, M. J. 2019. River connectivity and fish migration considerations in the management of multiple stressors in South Africa. *Marine and Freshwater Research,* 70, 1254-1264.
Page, L. M. & Burr, B. M. 2011. *Peterson field guide to freshwater fishes of North America north of Mexico*, Houghton Mifflin Harcourt.
Porcher, J. 2002. Fishways for eels. *Bulletin Français de la Pêche et de la Pisciculture*, 364, 147-155.
Portt, C. B., Coker, G., Ming, D. & Randall, R. G. 2006. A review of fish sampling methods commonly used in Canadian freshwater habitats. Canadian Technical Report of Fisheries and Aquatic Sciences, pp. 2604.
Prentice, E. F., Flagg, T. & Mccutcheon, C. 1990. Feasibility of using implantable passive integrated transponder (PIT) tags in salmonids. *American Fisheries Society Symposium*
Rajaratnam, N., Van Der Vinne, G. & Katopodis, C. 1986. Hydraulics of vertical slot fishways. *Journal of Hydraulic Engineering,* 112, 909-927.
Riede, K. 2004. *Global register of migratory species: from global to regional scales: final report of the R&D-Projekt 808 05 081*, Federal Agency for Nature Conservation.
Rodell, M., Famiglietti, J. S., Wiese, D. N., Reager, J., Beaudoing, H. K., Landerer, F. W. & Lo, M.-H. 2018. Emerging trends in global freshwater availability. *Nature,* 557, 651-659.
Rodríguez, T. T., Agudo, J. P., Mosquera, L. P. & González, E. P. 2006. Evaluating vertical-slot fishway designs in terms of fish swimming capabilities. *Ecological Engineering,* 27, 37-48.
Roussel, J., Haro, A. & Cunjak, R. 2000. Field test of a new method for tracking small fishes in shallow rivers using passive integrated transponder (PIT) technology. *Canadian Journal of Fisheries and Aquatic Sciences,* 57, 1326-1329.
Schreiner, B. 2013. Viewpoint—Why has the South African National Water Act been so difficult to implement. *Water Alternatives,* 6, 239-245.
Schultz, A. A., Maughan, O. E., Bonar, S. A. & Matter, W. J. 2003. Effects of flooding on abundance of native and nonnative fishes downstream from a small impoundment. *North American Journal of Fisheries Management,* 23, 503-511.
Silva, A. T., Lucas, M. C., Castro-Santos, T., Katopodis, C., Baumgartner, L. J., Thiem, J. D., Aarestrup, K., Pompeu, P. S., O'Brien, G. C. & Braun, D. C. 2018. The future of fish passage science, engineering, and practice. *Fish and Fisheries,* 19, 340-362.
Simons, D. B. & Şentürk, F. 1992. *Sediment transport technology: water and sediment dynamics*, Water Resources Publication.
Skelton, P. 2001. *A Complete Guide to the Freshwater Fishes of Southern Africa*. Struik Publishers, Cape Town (ZA).
Stuart, I. & Jones, M. 2006. Movement of common carp, *Cyprinus carpio*, in a regulated lowland Australian river: Implications for management. *Fisheries Management and Ecology,* 13, 213-219.
Stuart, I. G., Williams, A., Mckenzie, J. & Holt, T. 2006. Managing a migratory pest species: a selective trap for common carp. *North American Journal of Fisheries Management,* 26, 888-893.

Thorstad, E. B., Rikardsen, A. H., Alp, A. & Økland, F. 2013. The use of electronic tags in fish research–an overview of fish telemetry methods. *Turkish Journal of Fisheries and Aquatic Sciences,* 13, 881-896.

Tickner, D., Opperman, J. J., Abell, R., Acreman, M., Arthington, A. H., Bunn, S. E., Cooke, S. J., Dalton, J., Darwall, W. & Edwards, G. 2020. Bending the curve of global freshwater biodiversity loss: an emergency recovery plan. *BioScience,* 70, 330-342.

Vhumbunu, C. H. 2021. The July 2021 Protests and socio-political unrest in South Africa: Reflecting on the causes, consequences and future lessons. *Conflict Trends,* 2021, 3-13.

Wade, M., O'Brien, G. C., Wepener, V. & Jewitt, G. 2021. Risk assessment of water quantity and quality stressors to balance the use and protection of vulnerable water resources. *Integrated Environmental Assessment and Management,* 17, 110-130.

Wald, A. R. 2009. *High flows for fish and wildlife in Washington*. State of Washington, Department of Fish and Wildlife, Washington, USA.

Whitfield, A. K. 2019. *Fishes of Southern African estuaries: From species to systems*, Smithiana Monograph No. 4, J.L.B. Smith Institute of Ichthyology, Grahamstown.

Wilkes, M. A., Webb, J. A., Pompeu, P. S., Silva, L. G., Vowles, A. S., Baker, C. F., Franklin, P., Link, O., Habit, E. & Kemp, P. S. 2019. Not just a migration problem: Metapopulations, habitat shifts, and gene flow are also important for fishway science and management. *River Research and Applications,* 35, 1688-1696.

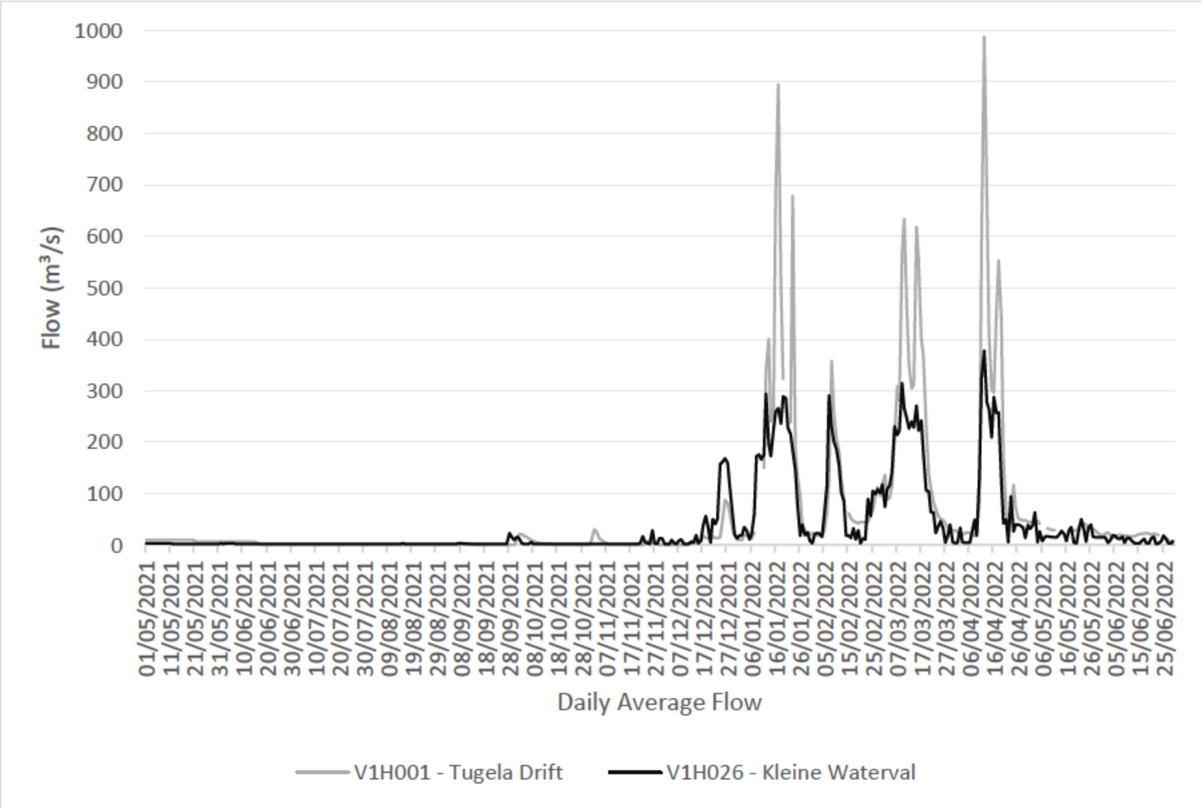
Winter, J. 1983. Underwater biotelemetry. In: Nielsen, L., Johnsen, J. (Eds) *Fisheries techniques.* American Fisheries Society, Bethseda, MD.

World Commission on Dams 2000. *Dams and development: A new framework for decision-making: The report of the world commission on dams*, Earthscan.

Zielinski, D. & Freiburger, C. 2021. Advances in fish passage in the Great Lakes basin. *Journal of Great Lakes Research,* 47, S439-S447.

3.8 Supplementary information

Supplementary information Fig. S3.1: Daily average flow rate at two upstream flow gauging sites on the uThukela River from 01 May 2021 to 29 June 2022 (Department of Water and Sanitation, 2023). Station locations: V1H026 (28°43’19”S, 29°22’32”E) and V1H001 (28°44’09”S, 29°49’16”E)



Supplementary information Fig. S3.2: Images of flood debris blockages in the LTBWSS fishway taken on 18/07/2022. Top left – debris blockages at the upstream entrance to the fishway, Top right – upstream entrance free of debris, Bottom – debris blockages at the downstream entrance of the fishway. In this case, it was the stainless steel grids used to cover the top of the fishway channel.

CHAPTER 4

Conclusions and recommendations

4.1 Background

Globally, instream barriers are known to have various impacts on the river environment, especially leading to river fragmentation, habitat loss, and habitat changes (World Commission on Dams, 2000; Fouchy et al., 2019; Barbarossa et al., 2020), changes in hydraulic conditions (World Commission on Dams, 2000; Zuo and Liang, 2015), and problems with water quality and pollution from intense land-use and agricultural processes (Evans et al., 2019).

The Lower Thukela Bulk Water Supply Scheme (LTBWSS) weir is an instream barrier in the lowland reaches of the uThukela River, KwaZulu-Natal, South Africa. It was built to alleviate the water supply problems faced by the KwaDukuza and Mandeni Local Municipalities in KwaZulu-Natal, officially commissioned in 2017. The infrastructure can abstract 55 Ml/d of bulk water, with plans to upgrade it to 110 Ml/d (Department of Water and Sanitation, 2022).

The design of the LTBWSS fishway is that of a vertical slot fishway and is based on best practices for South African conditions as developed by Bok et al. (2007). The efficacy of existing fishways in South Africa is poor (Bok et al., 2007; O'Brien et al., 2019), and as such, the confidence in their functionality, especially when multiple species require passage through them, is low. The lower uThukela River is home to unique marine, estuarine, and freshwater migrant fish species, and as such, its functionality in allowing migratory processes through it is important for many species, especially the anguillid eels (*Anguilla* spp.), which require catchment wide connectivity, from the ocean to the upland reaches (Hanzen et al., 2021, 2022).

The key research results are outlined and discussed in this chapter concerning the study's goals and objectives. Management and conservation suggestions are given based on the study's findings.

4.2 Summary of results

The following aims were set up to evaluate the efficacy of the LTBWSS weir and its importance to river connectivity in the lower uThukela River:

Firstly, the drivers of fish community structures in the lower uThukela River were assessed using various statistical analyses on data gathered from field work in the region (Chapter 2). Using R programming software, multivariate generalised linear models were used to assess important environmental variables that drive fish community structures (R Core Team, 2022). It was determined that overall fish community composition was driven by dominant substrate, dominant cover, temperature, and depth. Furthermore, it was found that different environmental variables influence the presence of species differently, linking to unique habitat preferences for species. The study area was dominated by indigenous fish species, with the known effects of non-native fish in South Africa (Ellender and Weyl, 2014) not affecting their community (Chapter 2).

Secondly, the LTBWSS weir's impact on local fish communities was assessed (Chapter 2). The use of presence/absence data at sites helped infer these results. The results found that upstream sites were less species-rich than downstream sites, particularly with euryhaline species. Additionally, there was a notable absence of three cichlid species in this study compared with a study conducted in the downstream reaches before the construction of the weir (Jacobs, 2017). Notably was the absence of *T. sparrmanii*, the most abundant species in the previous study, and which had shown a high correlation to silt substrate, which was hardly found in the present study. The synergistic effects of the LTBWSS's water abstraction and the barrier blocking fine sediment transport are likely the cause of the absence of the cichlid species.

Thirdly, the assessment of the fishway's efficacy was tested using two different methods (Chapter 3). Passive Integrated Transponder (PIT) telemetry was used to passively monitor the upstream movements of tagged fish through an antenna placed at the upstream entrance of the fishway. This study was only able to tag 107 fish from 12 species. Of these, eight individuals from three species successfully navigated the fishway. The second method of monitoring the fishway involved one day each month, where three key locations were sampled. The results showed that there was generally a higher concentration of fish at the fishways downstream entrance, with few fish caught in its lower middle section. Both studies were impacted by the severe flood events that hit the system from January 2022 until June 2022 (Letsatsi and Kruger, 2022), which brought down high loads of debris which damaged the PIT telemetry equipment and completely blocked the fishway for six months. The PIT study was also hampered by electricity problems relating to national power cuts and staff at the facility unplugging the equipment (Chapter 3).

4.3 Recommendations

Future research might focus on species whose life histories are poorly understood to understand better their habitat preferences, migratory patterns, and life cycles—as these factors are crucial for assessing how well-off they are in a system. A thorough investigation is necessary to find out if there are any remaining residual populations of the lost cichlids. These populations may be allowed to rebuild with better resource management and conservation techniques. Additionally, it is necessary to quantify the precise stresses affecting the area since doing so would aid water resource managers in their work.

Future PIT telemetry studies should use a minimum of two PIT antennas to test the fishway's true efficacy by seeing which migrators enter, how many successfully move through it, and the time taken for such movement. This would also allow two-way movement through the fishway to be tested, a requirement that is increasingly becoming a necessity globally. Furthermore, companies or organisations managing the country's fishways must constantly assess their performance through fishway monitoring protocols. Most important, is the early detection of issues inside the fishway, which can delay or disrupt fish migrations, such as debris blockages.

4.5 Conclusions

The study demonstrated that the LTBWSS weir impacts the fish communities up and downstream of it. This has restricted the presence of many euryhaline migratory fish to below the LTBWSS, likely disrupting river connectivity despite the fishway provided on the weir structure. The flow of sediments and increased abstraction have altered habitat, reducing certain species' occurrence, for example, *T. sparrmanii.* Reduce flows into the uThukela River estuary compounds pollution sources from the Mandeni Stream and the Sappi Tugela Pulp and Paper Mill effluent, reducing fish abundance. Investigating the life histories, habitat preferences, migratory behaviours, and life cycles of lesser-known migratory fish species in the region is crucial to inform fishway design and improve river connectivity. Various species rely on the LTBWSS fishway at different times of the year, showing some ability to pass certain fish. Present knowledge of migratory fish, importantly diadromous species, is sparse and, at times, out-dated or contrary in literature. A refreshed look into these species is needed, for example, *K. rupestris*.

Using telemetry techniques in parallel to traditional methods of fish sampling can prove useful in understanding the efficacy of fishways. Telemetry use to monitor fishways in the region is still in its infancy stages, and adequately assessing fishway implementation in the region remains a challenge that needs to be addressed. This can greatly contribute to accurately measuring the success of fishway construction and design for local species. This is particularly important as dam development is required to meet water security needs.

4.6 References

Barbarossa, V., Schmitt, R. J., Huijbregts, M. A., Zarfl, C., King, H. & Schipper, A. M. 2020. Impacts of current and future large dams on the geographic range connectivity of freshwater fish worldwide. *Proceedings of the National Academy of Sciences,* 117, 3648-3655.

Bok, A., Kotze, P. & Heath, R. 2007. *Guidelines for the planning, design and operation of fishways in South Africa*, Water Research Commission.

Department of Water and Sanitation 2022. National Water Act, 1998 (Act no. 36 of 1998): Review of the National Water Resource Strategy. (Notice 2327). Pretoria (South Africa): *Government Gazette*, 47133.

Ellender, B. R. & Weyl, O. L. 2014. A review of current knowledge, risk and ecological impacts associated with non-native freshwater fish introductions in South Africa. *Aquatic Invasions,* 9, 117–132.

Evans, A. E., Mateo-Sagasta, J., Qadir, M., Boelee, E. & Ippolito, A. 2019. Agricultural water pollution: key knowledge gaps and research needs. *Current Opinion in Environmental Sustainability,* 36, 20-27.

Fouchy, K., Mcclain, M. E., Conallin, J. & O'Brien, G. 2019. Multiple stressors in African freshwater systems. *Multiple stressors in river ecosystems.* Elsevier.

Hanzen, C., Lucas, M. C., O'Brien, G., Calverley, P. & Downs, C. T. 2021. Spatial ecology of freshwater eels in South Africa: implications for conservation. *Hydrobiologia,* 848, 2579-2593.

Hanzen, C. C., Lucas, M. C., Weyl, O. L., Marr, S. M., O'Brien, G. & Downs, C. T. 2022. Slippery customers for conservation: Distribution and decline of anguillid eels in South Africa. *Aquatic Conservation: Marine and Freshwater Ecosystems,* 32, 1277– 1290.

Jacobs, P. G. 2017. *Hydrological assessment to predict velocity-flow classes in the lower Thukela River.* MSc, North-West University, Potchefstroom Campus.

Letsatsi, N. & Kruger, A. 2022. The April 2022 floods in comparison with other recent flooding events in KwaZulu-Natal. *Weathersmart, WeatherSA*, 5.

O'Brien, G. C., Ross, M., Hanzen, C., Dlamini, V., Petersen, R., Diedericks, G. J. & Burnett, M. J. 2019. River connectivity and fish migration considerations in the management of multiple stressors in South Africa. *Marine and Freshwater Research,* 70, 1254-1264.

R Core Team 2022. R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.

World Commission on Dams 2000. *Dams and development: A new framework for decision-making: The report of the world commission on dams*, Earthscan.

Zuo, Q. & Liang, S. 2015. Effects of dams on river flow regime based on IHA/RVA. *Proceedings of the International Association of Hydrological Sciences,* 368, 275-280.