Aquatic highways: understanding the importance of habitat connectivity for migratory fish species, especially anguillid eels

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ABSTRACT

Connectivity among freshwater, estuarine, and marine ecosystems is crucial, facilitating the transfer of biomass among them and providing pathways for migratory aquatic species. This thesis focused on the importance of connectivity in these ecosystems and the impacts that impaired connectivity had on migratory species and fish communities residing within them.

The first objective of this study was to evaluate the impact of four instream barriers (weirs) on fish species movement and migration in the uMkhomazi River, KwaZulu-Natal, South Africa. The second was to determine which factors influenced anguillid eel recruitment into the uThukela, uMkhomazi and uMtamvuna estuaries in KwaZulu-Natal, South Africa. The third and final objective was to assess the factors shaping fish community structures within the uThukela, uMkhomazi, and uMtamvuna estuaries in KwaZulu-Natal, South Africa.

To achieve the first objective, sampling was conducted during the rainy season (March–April) and the dry season (June) in the Mkhomazi River. Sampling was conducted above and below four weirs along the river using electronarcosis to catch the individual fish. The KwaZulu-Natal yellowfish *Labeobarbus natalensis* was the most abundant fish species caught, and species abundance and diversity decreased with increasing altitude. Significant differences in species unevenness were present between communities in the respective river fragments, separated by the existing weirs, which potentially restricted the longitudinal movement of fish. Furthermore, eels were found present in all river fragments except the most upstream river fragment. It is suggested that all existing weirs be retrofitted with suitable and effective fishways, and that the proposed weirs and dams for the river include fishways to maintain a strong level of connectivity and better protect and conserve migratory fish within the system.

For the second objective, sampling was conducted from October 2024 to May 2025 in the three estuaries, namely uThukela, uMkhomazi, and uMtamvuna estuaries, along the KwaZulu-Natal Coast. Eight glass eel nets were placed in each estuary for a duration of three nights per month. Nets were checked every 12 hours. *Anguilla* spp. in the glass eel life cycle stage were only recorded in the uThukela Estuary during the study. In the uThukela Estuary, connectivity between the marine and estuarine environments, high tides, moon phases with lower light intensity and increases in certain water quality variables, namely dissolved oxygen, oxygen percentage and electrical conductivity (when related to nutrient concentration), were found to positively influence anguillid glass eel recruitment. The outcomes of this study provided insights into the cues that trigger anguillid eel recruitment from the ocean into estuaries along the east coast of South Africa, which improved our understanding of the recruitment of four globally important eels. It is suggested that conservation efforts aimed at maintaining the natural degree of connectivity between marine and estuarine systems would allow the continued recruitment of these eels into these estuaries. Additionally, management practices tailored to preserve naturally occurring water quality would help protect and conserve these ecologically and economically important eel species.

For the third objective, sampling was conducted from October 2024 to May 2025, during which eight glass eel nets were deployed in each estuary for three nights per month. The nets were checked every 12 hours. The degree of connectivity present in the uThukela was found to be greater than that of the uMkhomazi and uMtamvuna, as it contained the most diverse and abundant migratory species. The fish communities residing within the three selected estuaries were found to be shaped by numerous abiotic variables, including connectivity, water temperature, salinity, and dissolved oxygen. A combination of these factors

and suitable habitat is required to maintain the fish community structures in the selected estuaries. Factors shaping estuarine fish community structures along the east coast of South Africa are complex, but increased temperatures and longer estuary closure times have an impact and thus affect the conservation of these fish communities as the climate changes.

This thesis highlights the importance of connectivity for four globally important freshwater eel species and other migratory fish species that form part of the estuarine fish communities. It is evident from these findings that conservation interventions aimed at restoring connectivity are necessary to protect and preserve migratory fish species, including economically and ecologically important species such as anguillids.

PREFACE

The data described in this thesis were collected in KwaZulu-Natal, Republic of South Africa, from March 2024 to May 2025. Experimental work was conducted while I was registered in the Discipline of Biological Sciences at the University of KwaZulu-Natal, Pietermaritzburg, under the supervision of Prof Colleen T. Downs and Dr Matthew J. Burnett.

This thesis, submitted for the degree of Master of Science in the College of Agriculture, Engineering and Science, University of KwaZulu-Natal, 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.



Zain Armien

November 2025

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



……..

Prof Colleen T. Downs

Supervisor

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DECLARATION 1 - PLAGIARISM

I, Zain Armien, 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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    a. Their words have been re-written, but the general information attributed to them has been referenced
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DECLARATION 2 - PUBLICATIONS

DETAILS OF CONTRIBUTION TO PUBLICATIONS that form part and/or include research presented in this thesis.

PUBLICATION 1- not submitted

An assessment of anthropogenic instream structures' effects on fish presence and assemblages in the uMkhomazi River, South Africa

Zain Armien, Matthew J. Burnett, Justin Pringle & Colleen T. Downs

Author contributions:

ZA conceived the paper with CTD, MJB and JP. ZA collected and analysed data, and wrote the paper. CTD, MJB and JP contributed valuable comments to the manuscript.

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Evaluating eel recruitment into selected estuaries along the coast of the KwaZulu-Natal Province, South Africa

Zain Armien, Matthew J. Burnett & Colleen T. Downs

Author contributions:

ZA conceived the paper with CTD and MJB. ZA collected and analysed data, and wrote the paper. CTD contributed valuable comments to the manuscript.

PUBLICATION 3- not submitted

Assessing drivers of estuarine fish community structures on the KwaZulu-Natal coast of South Africa

Zain Armien, Matthew J. Burnett & Colleen T. Downs

Author contributions:

ZA conceived the paper with CTD and MJB. ZA collected and analysed data, and wrote the paper. CTD contributed valuable comments to the manuscript.

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CHAPTER 1

INTRODUCTION

1.1 Background

Connectivity between freshwater, estuarine, and marine systems is an important function that facilitates numerous processes (Whitfield et al., 2017). Natural connectivity enables the transport of biomass, including aquatic organisms, nutrient-rich organic waste, and other organic matter, between different types of aquatic ecosystems (Acou et al., 2000; Izegaegbe et al., 2020). This biomass supports the fauna and flora found in all three ecosystems and aids their functioning (Acou et al., 2000; Izegaegbe et al., 2020). Aquatic connectivity provides pathways for migratory fauna to move between freshwater, estuarine and marine systems, facilitating different biologically important processes (Havn et al., 2020).

When aquatic connectivity is hindered by instream structures constructed to support anthropogenic activities, the consequences are often dire for these ecosystems and the organisms that inhabit them (Righton et al., 2021; Hanzen et al., 2022). Instream structures alter the flow regimes of these systems (Marcinkowski and Grygoruk, 2017; Havn et al., 2020). Changes in flow regimes can have significant effects on both the aquatic communities and the riparian zones found along these systems (Belmar et al., 2013). The effects of these changes in flow regimes on aquatic communities are evident in the loss and degradation of habitat used by fish as refugia, which can have adverse effects on these communities (Belmar et al., 2013; Palmer and Ruhi, 2019).

It is evident that aquatic connectivity should be preserved whenever possible, as doing so greatly benefits ecosystem functioning (Acou et al., 2000; Izegaegbe et al., 2020). Where barriers to connectivity are present, intervention is necessary to restore the natural degree of connectivity that was historically present, allowing these ecosystems to function optimally and

allow the movement of aquatic fauna (Havn et al., 2020; Hanzen et al., 2021; Righton et al., 2021).

1.2 Types of barriers

Several anthropogenic practices hinder connectivity by constructing various structures that facilitate water use, whether for freshwater provisioning, agriculture, or industry (Baggio et al., 2021; Mishra, 2023). Instream structures such as dams, weirs, and hydropower stations, which store or regulate water, are often constructed across entire river sections, significantly altering natural connectivity (Marcinkowski and Grygoruk, 2017; Havn et al., 2020). These structures then fragment aquatic faunal communities by hindering the naturally occurring connectivity (Das et al., 2013; Cocan et al., 2020). This fragmentation may prevent migratory species from moving between specific areas within the system, which is crucial to their life cycles (Righton et al., 2021; Hanzen et al., 2022).

In addition to the permanent instream structures, periodic barriers are also constructed in some instances (Righton et al., 2021; Hanzen et al., 2022). These periodic barriers are often constructed in certain estuaries to facilitate anthropogenic activities such as fish farming and water storage (Woodridge and Adams 2020). By periodically opening and closing estuaries, organisms which are wanting to move between the estuarine and marine systems are prevented from doing so (Righton et al., 2021; Hanzen et al., 2022).

There are existing solutions to maintain connectivity; however, mismanagement and poor planning often prevent their implementation (Righton et al., 2021; Hanzen et al., 2022). One such solution is known as a fishway or fish ladder (Burnett et al., 2023; Fuentes-Pérez et al., 2024). These are artificial passages created within or around instream structures which

restore connectivity for aquatic fauna by allowing their movement through the instream barrier ladder (Burnett et al., 2023; Fuentes-Pérez et al., 2024).

1.3 Migratory aquatic fauna

Restricted connectivity hinders the migration of migratory aquatic fauna (Havn et al., 2020; Verhelst et al., 2021). Fish migrations are processes in which fish move to different parts of an ecosystem, or an entirely different ecosystem, to feed, reproduce or seek shelter (Brönmark et al., 2014). These migrations occur because of different factors like seasons – often related to thermal tolerances, flow changes, ontogenetic cues, competition, and food availability (Il'ichev, 2012; Taylor and Cook, 2012; O'Boyle et al., 2016; Hanzen et al., 2019; Righton et al., 2021)

When the potamodromous species are considered, such as the KwaZulu-Natal yellowfish (*Labeobarbus natalensis*), which are species that migrate to different areas of the freshwater system in which they reside, to carry out processes like spawning and feeding, the negative implications resulting from instream structures become more evident (Righton et al., 2021; Hanzen et al., 2022). *Labeobarbus natalensis* is not only ecologically important but also serves as a food source for some subsistence fishermen in South Africa (Karssing, 2008). Therefore, it is essential for these species to persist, and for solutions to be implemented to protect their migrations and facilitate their continued presence within these systems.

While all migratory aquatic fauna may experience adverse effects resulting from impaired connectivity, the effects become increasingly evident when diadromous species are considered (Havn et al., 2020; Verhelst et al., 2021). Diadromous species are categorised as such because of a particular migratory pathway, in which part of their life cycle occurs within the freshwater system and the other within the marine system (Havn et al., 2020). Diadromous

species are further subdivided into distinct categories based on their specific migratory pathways (Miles et al., 2014). Anadromous migratory species (a South African example is the evileye blaasop (*Amblyrhynchotes honckenii*)) are species that spawn in freshwater and mature in the marine environment (Chakraborty et al., 2020). Catadromous migratory species (e.g., anguillid eels) spawn in marine environments and mature in freshwater environments (Hanzen et al., 2019; Righton et al., 2021). The final diadromous migratory category is the amphidromous migratory species (a South African example is the slender glassy (*Ambassis natalensis*)), where the juvenile stage occurs in the marine environment, but spawning and maturation occur in freshwater systems (Havn et al., 2020; Verhelst et al., 2021).

The anguillid species are examples of a catadromous migrator (Tsukamoto and Aoyama, 1998; Hanzen et al., 2019; Havn et al., 2020; Righton et al., 2021). Globally, there are 19 anguillid species, many of which are currently declining because of anthropogenic pressures such as exploitation of the species and habitat loss (Tsukamoto and Aoyama, 1998; Hanzen et al., 2022). Thus, there is a growing need for better conservation efforts for these species to prevent further decline (Tsukamoto and Aoyama, 1998; Hanzen et al., 2022). Four species of anguillid eels occur on the east coast of Africa, namely, *Anguilla bengalensis, A. bicolor, A. marmorata* and *A. mossambica* (O'Brien et al., 2025). Compared with Anguilla spp. in the Northern Hemisphere, the four African examples are relatively understudied (Hanzen et al., 2019). These species spawn in the Indian Ocean east of Madagascar, where leptocephalus larvae develop from eggs laid by mature individuals (Tsukamoto and Aoyama, 1998; Cresci, 2020). These larvae migrate towards the East African and Madagascan coastline, where they undergo a morphological change into glass eels, which are recruited into certain estuaries where they proceed to morph into elvers (Hanzen et al., 2019; Cresci, 2020; Righton et al., 2021). The elvers are then categorised as yellow eels once they have migrated into the

freshwater system, where they will remain for several years as they grow (Tsukamoto and Aoyama, 1998; Hanzen et al., 2019; Righton et al., 2021). Following the yellow eel stage is the silver eel stage, during which their reproductive organs develop (Hanzen et al., 2019; Righton et al., 2021). These silver eel individuals then migrate from the freshwater system back to the east coast of Madagascar, where they will breed and die (Hanzen et al., 2019; Righton et al., 2021).

Due to the vast migrations undertaken by these species, they are particularly susceptible to impaired connectivity (Tsukamoto and Aoyama, 1998; Hanzen et al., 2022). Inhibiting the movement of diadromous migrants, such as the African freshwater eels, would prevent them from completing their life cycles and, in turn, from breeding (Righton et al., 2021; Hanzen et al., 2022). Importantly, in areas of South Africa, such as the Eastern Cape, anguillid eels are the top fish predators in many river systems (Parker et al., 2011). This further highlights the importance of protecting and conserving these species, particularly in the South African context (Parker et al., 2011; Righton et al., 2021; Hanzen et al., 2022).

1.4 Estuarine communities

Estuarine systems are uniquely positioned to connect marine and freshwater systems (Dias et al., 2016; Izegaegbe et al., 2020). This connection provides an important pathway for diadromous organisms (Havn et al., 2020; Whitfield et al., 2023). Estuarine systems are reliant on connectivity to maintain their functioning and community structures (Dias et al., 2016; Havn et al., 2020).

Estuarine systems are complex because they receive nutrients and aquatic fauna from both freshwater and marine systems (Acou et al., 2000; Dias et al., 2016; Izegaegbe et al., 2020). However, this means that estuarine systems are also susceptible to pollution entering

from both the marine and freshwater systems (Acou et al., 2000; Dias et al., 2016; Izegaegbe et al., 2020). Anthropogenic activities such as agriculture often generate chemical runoff from sources such as fertilisers and pesticides, which may either enter the estuary directly or be transported to the estuary via the freshwater system to which it is connected (Izegaegbe et al., 2020; Xiao et al., 2024). Furthermore, when connectivity to the estuary is hindered, an imbalance may occur, whereby the estuary may become hypersaline if connectivity is impaired at the freshwater ecotone, or the salinity of the estuary decreases significantly if connectivity is hindered at the marine ecotone (Adams and Van Niekerk, 2020; Wooldridge and Adams, 2020). The factors shaping fish community structure within estuaries are intricate, and their combination creates complex challenges for conservation (Amorim et al., 2017; Asha et al., 2015; Duque et al., 2020; Molina et al., 2020).

1.5 Study area

The study assessing the effects of anthropogenic instream structures on fish presence and assemblages was conducted in the uMkhomazi River, KwaZulu-Natal, South Africa, at ten selected sampling locations along the river. The uMkhomazi River is one of the few relatively free-flowing rivers in South Africa. The glass eel recruitment and estuarine fish community structure studies were conducted in three estuaries along the east coast of KwaZulu-Natal Province, South Africa. These estuaries were the uThukela, uMkhomazi, and uMtamvuna estuaries. The uThukela Estuary is located 98 km north of the city of Durban. The uMkhomazi Estuary is located 52 km south of Durban, while the uMtamvuna Estuary is situated on the border of the KwaZulu-Natal and Eastern Cape Provinces, 157 km south of Durban. Further details are presented in the respective data chapters.

1.6 Problem statement

Estuaries are unique ecosystems that provide a link between freshwater and marine ecosystems (Acou et al., 2000; Izegaegbe et al., 2020). Estuarine systems receive migratory aquatic fauna from both the marine and freshwater systems when natural connectivity is present (Acou et al., 2000; Izegaegbe et al., 2020). Numerous anthropogenic activities have adverse effects on these ecosystems, ranging from pollution to physical alterations in connectivity between estuaries and adjacent aquatic ecosystems (Izegaegbe et al., 2020; Xiao et al., 2024). When connectivity to the estuary is disrupted, migratory aquatic fauna, which comprise a large portion of the estuary's fish community, are prevented from migrating (Izegaegbe et al., 2020; Xiao et al., 2024). Determining which factors shape these fish community structures would indicate where intervention is most needed to protect and conserve the fish species that form these complex communities.

Connectivity at both estuary ends is particularly important for catadromous species, such as African freshwater eels (*Anguilla* spp.). The literature available on the recruitment of *Anguilla* spp. from the ocean into African estuaries is limited (McNeill et al., 2025). There are four *Anguilla* spp. found in South Africa. These species are globally important, but numerous knowledge gaps exist regarding them (Hanzen et al., 2022; McNeill et al., 2025). Determining the cues that recruit these eels into estuaries would provide information that would benefit their conservation in South Africa (Tsukamoto and Aoyama, 1998; Hanzen et al., 2022).

Connectivity remains equally important as the migration of fauna, such as *Anguilla* spp., continue from the estuary into the adjacent freshwater system (Havn et al., 2020; Hanzen et al., 2022). The uMkhomazi River is one of the few relatively free-flowing rivers in South Africa (Nel et al., 2018). Despite this, instream structures are present, which may hinder connectivity between the respective barriers and impede the inland penetration of aquatic

fauna, such as *Anguilla* spp., and the migration of potamodromous faunal species (Righton et al., 2021; Hanzen et al., 2022). If connectivity is being impaired by these structures, it may have significant drawbacks, particularly for migratory fish species residing within the river (Havn et al., 2020; Righton et al., 2021; Hanzen et al., 2022). Assessing the impact of these in-stream barriers would provide evidence to advocate for connectivity restoration (Havn et al., 2020).

1.7 Aims and objectives

This thesis aimed to assess factors that may be negatively impacting migratory aquatic fauna and those that may be shaping their communities, with a particular focus on connectivity. Therefore, the following three objectives were chosen:

1. To assess the impact of four instream barriers (weirs) on fish species movement and migration in the uMkhomazi River, KwaZulu-Natal, South Africa
2. To determine which factors influenced anguillid eel recruitment into the uThukela, uMkhomazi and uMtamvuna Estuaries in KwaZulu-Natal, South Africa, and
3. To assess which factors were shaping fish community structures within the uThukela, uMkhomazi and uMtamvuna Estuaries in Kwa-Zulu-Natal, South Africa.

1.8 Structure of the thesis

The main body of this thesis is organised as manuscripts prepared for publication in peer-reviewed journal articles. The first chapter (Chapter 1) is the Introduction, which provides the literature review of the concepts covered in this study. The next three chapters (2, 3, and 4) are empirical chapters, each addressing a specific objective. Each chapter is formatted according to the journal it is intended to be (or has been) submitted to. Because of this thesis format, a

certain degree of repetition, particularly in the methods section, was unavoidable. However, this is deemed of little concern, as this format allows the reader to read each chapter separately without losing the overall context of the thesis. Chapter 2 investigated the effects of anthropogenic in-stream structures on fish presence and assemblages in the uMkhomazi River, South Africa. Chapter 3 investigated eel recruitment into selected estuaries along the coast of the KwaZulu-Natal Province, South Africa. Chapter 4 investigated the drivers of estuarine fish community structures on the KwaZulu-Natal coast in South Africa. Chapter 5 presents the general discussion, overall conclusions for each chapter, and the recommendations made based on the findings.

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CHAPTER 2

An assessment of anthropogenic instream structures' effects on fish presence and assemblages in the uMkhomazi River, South Africa

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Running header: Impact of instream barriers on fish

2.1 Abstract

Anthropogenic instream barriers, such as weirs and dams, can significantly hinder the migration of large-scale migratory aquatic species. Here, we assessed the effect of four weirs and their impact on fish communities, especially migratory African freshwater eels (*Anguilla* spp.). Our study was conducted along the uMkhomazi River in KwaZulu-Natal, South Africa, during the rainy season (March - April) and the dry season (June). We sampled above and below four weirs along the river in the low and high flow seasons using electronarcosis to catch individual fish. The KwaZulu-Natal yellowfish *Labeobarbus natalensis* was the most abundant fish species caught, and species abundance and diversity decreased with increasing altitude. There was a significant difference in the species unevenness between communities in the respective river fragments separated by the existing weirs, potentially restricting the longitudinal movement of fish. In addition, we found that the eels were present in all river fragments except for the most upstream one. We suggest that all existing weirs be retrofitted with suitable (as the design differs according to the fish species which it is intended for) and effective fishways, and that the proposed weirs and dams for the river include fishways to maintain a strong level of connectivity and better protect and conserve migratory fish within the system.

Keywords: River connectivity; longitudinal movement; weirs, dams, anguillid; fishway; migration; fragmentation

2.2 Introduction

As human populations grow, there is an ever-growing need for access to freshwater, whether for direct consumption, industry, or agricultural use (Baggio et al., 2021; Mishra, 2023). Water storage facilities (dams/ impoundment or weirs) are built to provide water to these sectors, disrupting river connectivity and altering flow regimes (Marcinkowski and Grygoruk, 2017; Havn et al., 2020). In most cases, these barriers disrupt or hinder the movement of aquatic fauna that migrate to complete their biological processes (Havn et al., 2020). Instream barriers can include estuarine habitats with periodic barriers constructed to regulate the opening and closing of the estuary's mouth, which can restrict the migration of diadromous species (Righton et al., 2021; Hanzen et al., 2022). Migratory species require access to various habitats within an aquatic system on a seasonal or daily basis to complete essential life cycle biological processes (Havn et al., 2020; Righton et al., 2021; Burnett et al., 2024). Potamodromous migrants are fish that migrate within freshwater systems only at different times of the year to carry out processes such as spawning (Gitonga et al., 2022). Potamodromous migrants like the KwaZulu-Natal yellowfish (*Labeobarbus natalensis*) are examples of species for which river connectivity plays a significant role (Benitez et al., 2018; Burnett et al., 2018, 2021). Thus, instream barriers may potentially disrupt these movements, negatively impacting river connectivity and ecosystem resilience (Havn et al., 2020; Righton et al., 2021; Hanzen et al., 2022).

The effects of these barriers became more evident when diadromous species are considered (Havn et al., 2020; Verhelst et al., 2021). Diadromous species are characterised by a requirement for connectivity between the sea and freshwater, a migratory pathway crucial to their survival (Havn et al., 2020). Species with a diadromous life cycle typically face more challenges, as migrating vast distances between two very different habitats exposes them to a

significantly larger number of threats (Havn et al., 2020; Merg et al., 2020). Diadromous migrators can be categorised into: catadromous, breeding in marine environments and living in freshwater; anadromous, breeding in freshwater and living in marine environments; and amphidromous, breeding and living in freshwater, with their larvae growing in brackish water or marine environments (Havn et al., 2020; Verhelst et al., 2021).

Anguillid eels (*Anguilla* spp.) are diadromous species categorised as catadromous diadromous migrants (Tsukamoto and Aoyama, 1998; Hanzen et al., 2019; Havn et al., 2020; Righton et al., 2021). Anguillid eels can live for 7 to 50 years in freshwater systems, depending on the species (Tsukamoto and Aoyama, 1998). As a result, they move throughout these freshwater systems in search of suitable habitats (Righton et al., 2021; Hanzen et al., 2022). Instream barriers in the freshwater environment pose the greatest threat to anguillid eels (Jacoby et al., 2015; Righton et al., 2021; Hanzen et al., 2022). Therefore, these eels are good indicator species of connectivity between freshwater, estuarine and marine ecosystems (Tsukamoto and Aoyama, 1998; Hanzen et al., 2022). African anguillids are considered to spawn at sea in the Mascarene Trench region of the Indo-Pacific Ocean, with larval stages drifting to the mainland, where they then recruit into freshwater through estuaries along the African coast, including those of Madagascar (Hanzen et al., 2019; Righton et al., 2021). There are four anguillid eel species found in South Africa, namely *Anguilla marmorata*, *A. mossambica*, *A. bengalensis*, and *A. bicolour* (Righton et al., 2021; Hanzen et al., 2022).

Generally, the construction of barriers such as weirs and dams along rivers does not consider the migratory requirements of anguillid eels. Consequently, the decreased connectivity can significantly reduce their distribution range inland (Righton et al., 2021; Hanzen et al., 2022). In many countries, fishways are increasingly required as a feature when constructing new weirs and dams. However, this may not always be the case, where it may not

be a requirement in some countries, or older instream barriers may not be retrofitted with a fishway, negatively impacting river connectivity (Silva et al., 2019; Righton et al., 2021; Hanzen et al., 2022). Glass eels can climb certain fishways and bypass the barrier when adequately constructed (Jacoby et al., 2015; Havn et al., 2020). Downstream migration for mature eels is equally important, and if inhibited, they will be unable to reach the marine ecosystem to breed (Jacoby et al., 2015; Havn et al., 2020).

Evaluating whether connectivity persists within freshwater ecosystems is crucial for protecting numerous species, particularly diadromous fish species (Havn et al., 2020). Here, we assessed the impact of four instream barriers (weirs) along the uMkhomazi River catchment in KwaZulu-Natal Province, South Africa, on fish species' presence and migration/ movement, especially anguillid eels, along the river. We predicted that the instream barriers would hinder migration. Furthermore, we predicted that differences in species' ability to bypass the instream barrier would result in uneven species distributions within communities. The outcomes of this study provided us with valuable information that could be used to improve and maintain connectivity within freshwater ecosystems, and in turn, protect migratory aquatic species.

2.3 Methods

2.3.1 Study area

Our study was conducted in the uMkhomazi River catchment in KwaZulu-Natal Province, South Africa. The uMkhomazi River is one of the few relatively free-flowing rivers in South Africa, as only a small percentage of its natural runoff is used for industrial or agricultural purposes (Nel et al., 2018) (Fig. 2.1). Despite this, there are four major instream barriers along its main stem. Two of the four barriers are in close proximity to the uMkhomazi estuary, while the other two barriers were located higher up in the catchment (Fig. 2.1). One instream barrier,

the Good Enough Weir, is presently being upgraded and fitted with a fishway and rock ramp with river connectivity restored during the construction process at the time of the study and thus excluded as a fragmented section of river for the present study. None of the other barriers had fishways constructed within them.

The instream barriers demarcated the fragmented river sections where we evaluated fish communities present (Fig. 2.1). Furthermore, we selected an additional five sample locations higher up in the catchment (Table 2.1, Fig. 2.1), which aided us in determining the cumulative effect that the selected downstream barriers had on the movement of the migratory species in the uMkhomazi River.

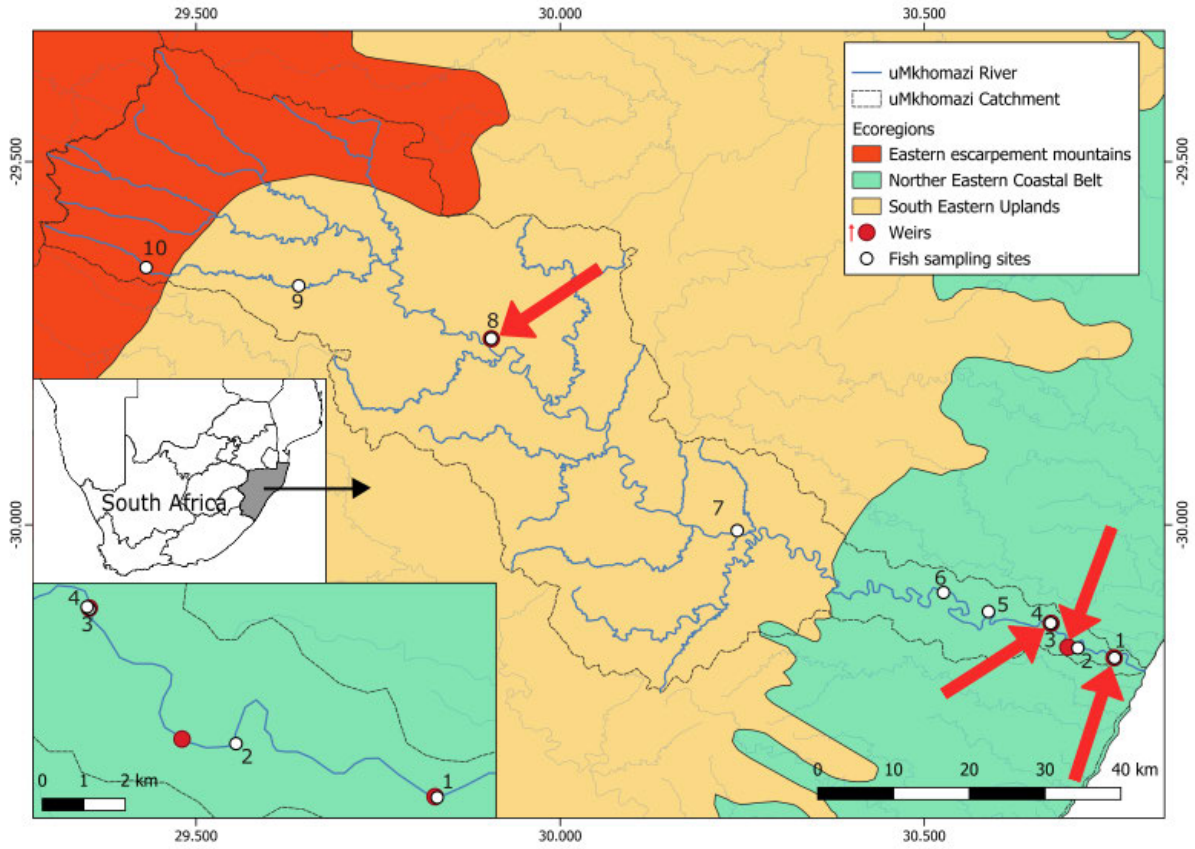


Figure 2.1: A map highlighting the uMkhomazi River, KwaZulu-Natal, South Africa, its tributaries, our sample sites and the selected barriers.

Table 2.1: Geographical locations of the sample sites in the uMkhomazi River catchment, KwaZulu-Natal, in 2024.

Site	Latitude	Longitude	Altitude (m)	Distance from the sea (km)
1	-30.1833	30.76136	4	4.55
2	-30.1697	30.71094	13	9.63
3	-30.1359	30.67422	39	14.4
4	-30.1354	30.67364	39	14.45
5	-30.1195	30.58819	82	22.62
6	-30.0933	30.52646	141	29.23
7	-30.008	30.24323	356	58.14
8	-29.7436	29.9054	911	100.39
9	-29.6709	29.64099	1358	126.71
10	-29.6458	29.43133	1569	146.08

2.3.2 Sampling techniques

We conducted sampling above and below each instream barrier in the lower reaches of the uMkhomazi River (Table 2.1). Sampling was conducted from March 27, 2024, to April 4, 2024 (high flow), and from June 13, 2024, to June 19, 2024 (low flow), to account for seasonal and flow variations. At each sample site, we selected 10 biotopes for sampling, each biotope representing an individual effort. We used an electro-shocker (SAMUS 725M, Electro-fisher, SAMUS Special Electronics, Poland) to electroshock fish within each biotope and then collected them with a sweep net. Collected fish for each biotope were immediately placed into

a bucket (20 L) of river water for processing. We recorded each fish species present and their abundance. We then took the standard morphometric measurements (body mass, total length, fork length and standard length) of each individual and recorded these before releasing them at their capture site. Thereafter, we recorded the habitat and water quality in each biotope. Habitat data were collected at five random locations within the biotope, including depth, flow (velocity), cover features, and substrate type. The cover feature types which we assessed were rock crevices (RC), aquatic vegetation (AV), wood debris (WD), roots (RO), undercut banks (UB), rippled water surface (RS), depth (DEP) and overhanging vegetation (OV). The substrate types which we categorised were mud (MUD), gravel (GRA), cobbles (COB), boulders (BOU), and bedrock (BED). We determined the water parameters using a LAQUA **(**Horiba, Ltd. Head Office / Factory 2, Miyanohigashi-cho, Kisshoin, Minami-Ku, Kyoto, 601-8510, Japan) water quality tester. The measured water parameters included water temperature, pH, total dissolved solids (TDS), electrical conductivity (EC), dissolved oxygen concentration (ml/L), and salinity (%).

2.3.3 Data analyses

Firstly, we divided the river section variable into three parts, separating our 10 sites into three categories: lower, middle and upper reaches of the uMkhomazi River (Table 2.2). Secondly, we separated the river with a fragment variable, where the river was divided into five fragments separated by instream barriers present on the river (Fig 2.1; Table 2.2). Each fragment was the culmination of sites between the barriers which have fragmented the river (Table 2.2). For our diversity analyses, we first compared diversity across all river fragments in the catchment and subsequently compared the diversity of river fragments found only in the lower catchment. We

did the latter because if the connectivity was significantly restricted in the lower section, it would drastically reduce the number of diadromous migratory species found further upriver.

Table 2.2: River reaches and the river fragments and sample sites that fall within each respective river reach

River Reaches	River Fragment	Sample Site
Lower	A	1
	B	2
	C	3
Middle	D	4
		5
		6
		7
Upper		8
	E	9
		10

We used the method of Hilborn and Walters (1992) to calculate our catch per unit effort (CPUE), where our total catch per effort was divided by the time (5 min) that the effort was sampled at each site. We calculated CPUE for each site across both seasons by dividing the total number of fish collected during an effort by the time (in minutes) required to complete it.

We conducted our data analyses in RStudio (2023.04.2.3) (Posit Team, 2023). We analysed data using descriptive statistics to compare abundances between sites, and used Shannon diversity indices (Nolan and Callahan, 2006) to compare species diversity between sites and river fragments.

To understand the significance of the results from the species diversity tests, we used the analysis of variance (ANOVA), general linear models (GLM) and multivariate analyses of variance (MANOVA) to determine the relationship between the different fish species and the cover features, substrate, water quality, sites and seasons (Dixon, 2003; Wang et al., 2012). We

conducted 10 models, two for each of the following categories: cover features, substrate, water quality, eco-hydraulics (the relationship between water velocity and depth), and additional environmental variables (season, river fragment, river reaches, and sample site). For the first model in each category, CPUE of all species per effort was the dependent variable. In the second model for each category, the CPUE of each species per effort was used as the dependent variable.

After calculating the Shannon diversity indices, we initially examined the diversity across all 10 sites, including all fragments (Fig. 2.2a), and then examined the diversity in the lower catchment area, to determine the impact that the barriers in that section had on the movement of the different species (Fig. 2.2b).

We used correlation matrix plots to obtain Pearson values and analysed the relationship between our variables. Variables with a Pearson correlation coefficient above 0.6 were considered multicollinear and were removed. We used the following R-packages: tidyverse (Wickham et al., 2019), mvabund (Wang et al., 2012), vegan (Dixon, 2003), MASSExtra (Venables, 2023), reshape2 (Wickham, 2007), caret (Kuhn, 2008), ggplot2 (Wickham, 2010), ggpubr (Kassambara, 2023), GGally (Schloerke et al., 2024), effects (Fox, 2003), MVN (Korkmaz, 2014), dplyr (Wickham, 2023), and car (Fox, 2012).

2.4 Results

We caught fish at most of the 10 sites, except site 4 (Fig. 2.1, Tables 2.3 and 2.4). A total of 13 fish species were caught, of which two were eel species, *Anguilla marmorata* and *A. mossambica* (Tables 2.3 and 2.4). Eels were caught at sites 1, 3, 6 and 7 (Tables 2.3 and 2.4). Site 1 falls within fragment A, site 3 falls within fragment C, while sites 6 and 7 fall within fragment D (Fig. 2.1).

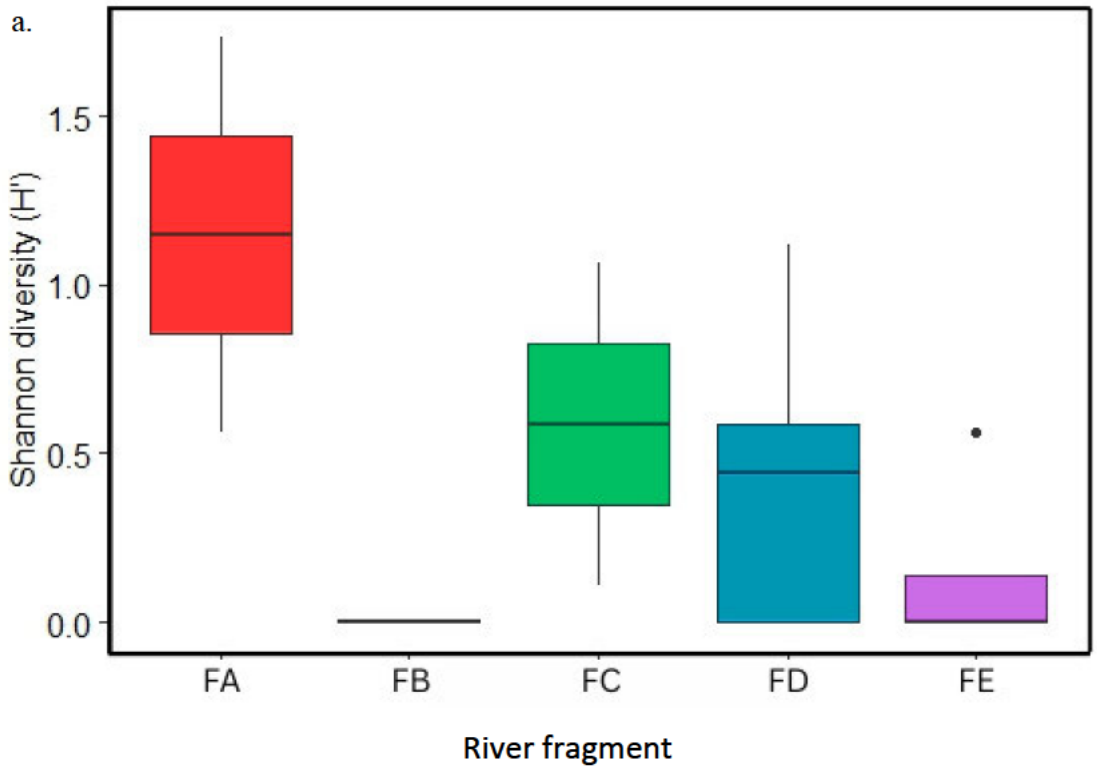
Table 2.3: The catch per unit effort (CPUE) and abundance of each fish species caught at each site in summer in the uMkhomazi River catchment, KwaZulu-Natal, in 2024.

Summer	Site 1		Site 2		Site 3		Site 4		Site 5		Site 6		Site 7		Site 8		Site 9		Site 10	
Fish species	**CPUE**	**Abundance**	**CPUE**	**Abundance**	**CPUE**	**Abundance**	**CPUE**	**Abundance**	**CPUE**	**Abundance**	**CPUE**	**Abundance**	**CPUE**	**Abundance**	**CPUE**	**Abundance**	**CPUE**	**Abundance**	**CPUE**	**Abundance**
Awaous aeneofuscus	0.4	2									0.2	1								
Labeobarbus natalensis	0.4	2	4.0	21	8.8	44			3.0	15	28.8	144	7.0	35	0.2	1				
Anguilla marmorata	0.2	1			0.2	1					1	5	0.6	3						
Anguilla mossambica	0.2	1									0.2	1								
Lutjanus argentimaculatus	0.2	1																		
Neoscorpis lithophilus	0.4	2																		
Ambassis natalensis	0.2	1																		
Oreochromis mossambicus									0.8	4	0.4	2								
Amphilus natalensis											0.2	1	0.4	2			0.6	3		
Clarias gariepinus											0.4	2								
Oncorhynchus mykiss																			0.4	2
Leiognathus equula																				
Enteromius viviparus																				

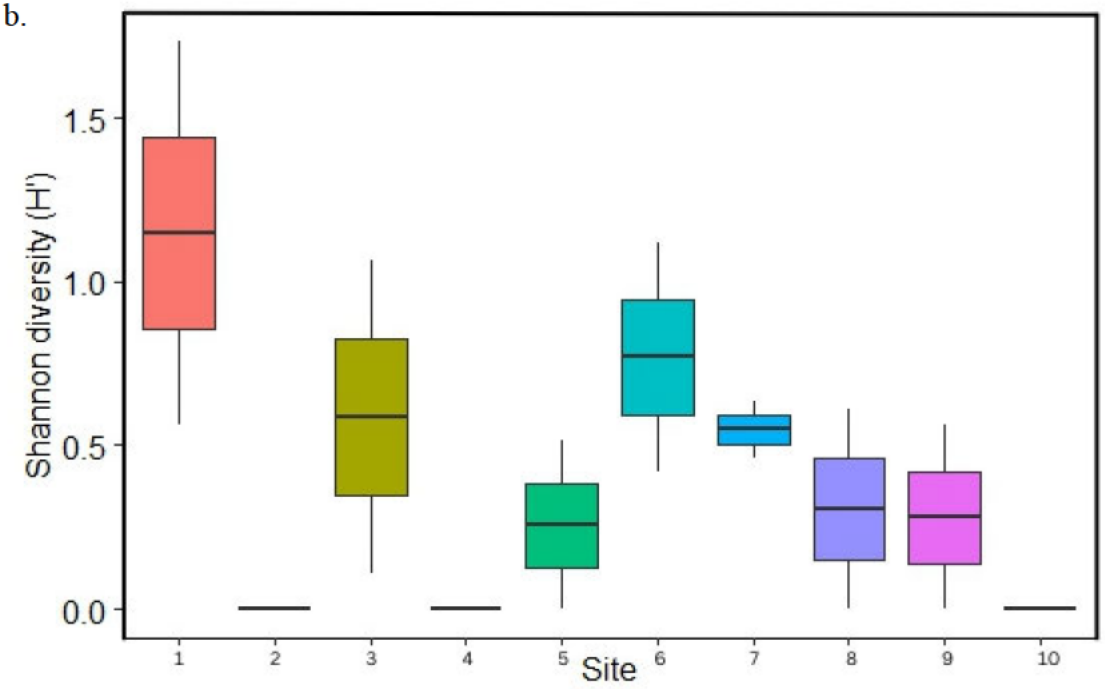
Table 2.4: The catch per unit effort (CPUE) and abundance of each fish species caught at each site in the winter season in the uMkhomazi River catchment, KwaZulu-Natal, in 2024.

Winter	Site 1		Site 2		Site 3		Site 4		Site 5		Site 6		Site 7		Site 8		Site 9		Site 10	
Fish Species	**CPUE**	**Abundance**	**CPUE**	**Abundance**	**CPUE**	**Abundance**	**CPUE**	**Abundance**	**CPUE**	**Abundance**	**CPUE**	**Abundance**	**CPUE**	**Abundance**	**CPUE**	**Abundance**	**CPUE**	**Abundance**	**CPUE**	**Abundance**
Awaous aeneofuscus	0.6	3																		
Labeobarbus natalensis			0.4	2	4.4	22			1.6	8	3.6	18	0.8	4	1.4	12				
Anguilla marmorata					0.2	1					0.2	1								
Anguilla mossambica					0.2	1														
Lutjanus argentimaculatus																				
Neoscorpis lithophilus																				
Ambassis natalensis																				
Oreochromis mossambicus					0.6	3														
Amphilus natalensis											0.6	3	0.4	2	2	10	0.8	4		
Clarias gariepinus																				
Oncorhynchus mykiss																				
Leiognathus equula	0.2	1																		
Enteromius viviparus					2.2	11					2.6	13			0.6	3				

The species diversity decreased further away from the mouth and at higher altitudes (Fig. 2.2a). Furthermore, at sites where a boxplot was not present or only a line was shown, either no species were caught or very few (Fig. 2.2a). Furthermore, at some sites there was either no fish present (Site 4) or very few fish present. The Shannon diversity index, assessed across the lower river fragments only (Fig. 2.2c), showed that diversity decreased as one moved further inland; however, this difference was not found to be significant (Kruskal-Wallis chi-squared, df = 4, p = 0.1388).



b.



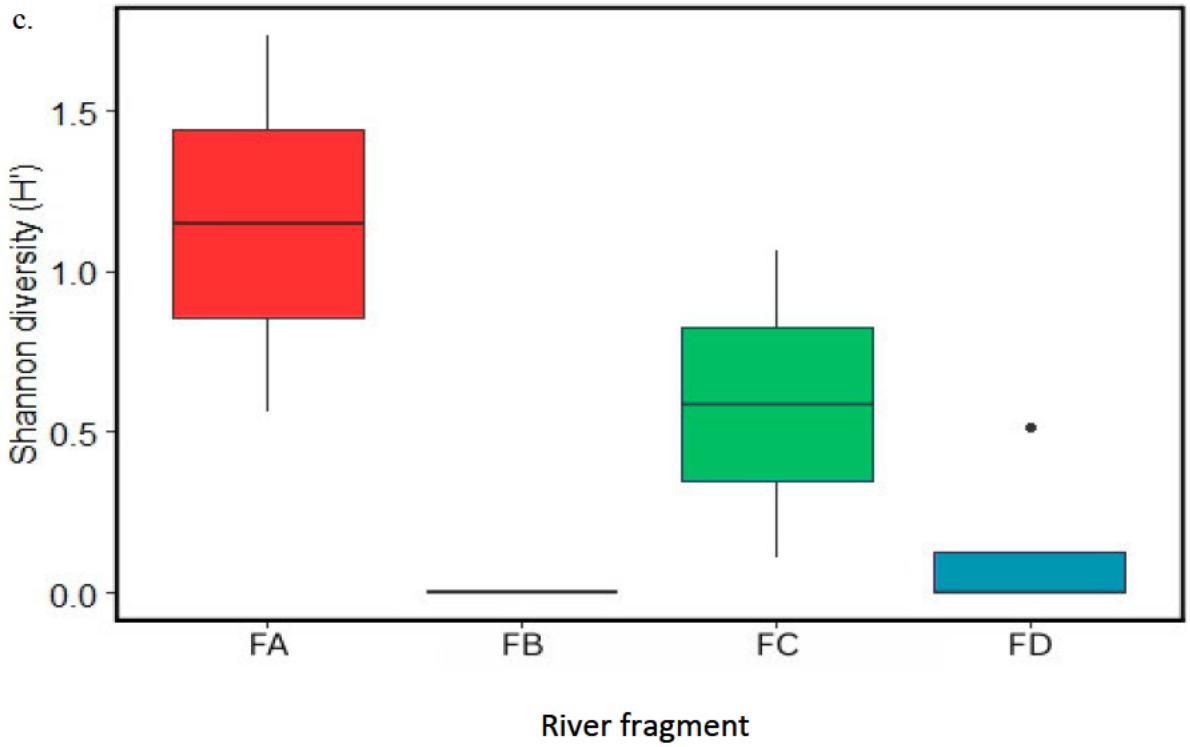


Figure 2.2: Shannon diversity indices where a.) shows the diversity between all five river fragments (FA-FE), b.) shows the diversity across all 10 sites (Sites 1-10), and c) shows the diversity between the river fragments in the lower reaches of the catchment and therefore omits fragment FE.

We were able to assess the diversity between the five river fragments created by the selected weirs (Fig. 2.2a). River fragment B only contained one species, *L. natalensis*; thus, the diversity was extremely low (Fig. 2.2a). Importantly, river fragment B contained only one sample site, namely site 2. Furthermore, for the river fragments upstream of river fragment B, diversity decreased with each consecutive river fragmentation section (Fig. 2.2a).

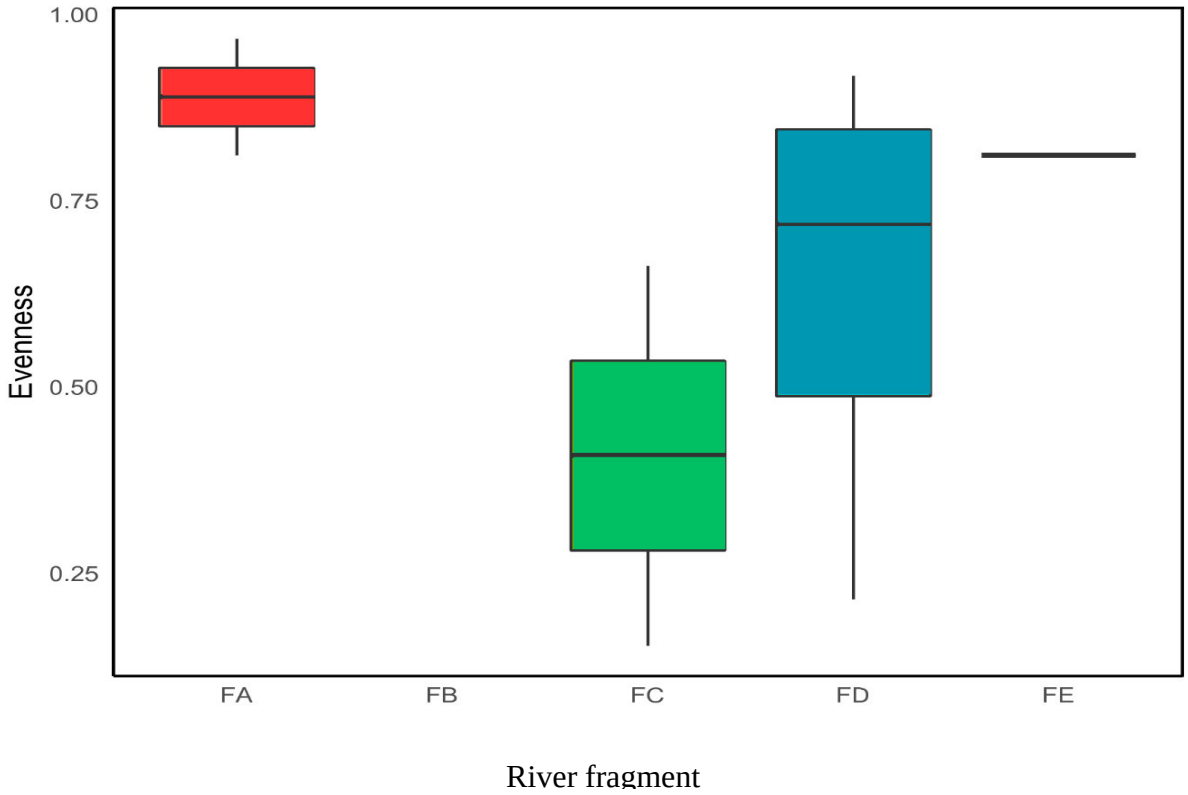


Figure 2.3: A boxplot depicting the evenness of fish species distribution across the three river sections in the uMkhomazi catchment, KwaZulu-Natal, in 2024.

We assessed how evenly fish species were distributed within the communities found in the three river sections (Fig. 2.3). On average, the fish species present within the first river fragment (A) of the river were more evenly spread, as opposed to the other river fragments (Fig. 2.3). Importantly, the degree of evenness was not very high within either river fragment apart from the first (A) (Fig. 2.3).

The CPUE for each fish species at each site had significant relationships between all variables: site (MANOVA, df = 190, p = 0.001), season (MANOVA, df = 189, p = 0.003), river section (MANOVA, df = 187, p =0.001) and river fragment (MANOVA, df = 188, p = 0.001).

We found for sites, there were significant relationships at sites 1 (MANOVA, df = 199, p = 0.001), 3 (MANOVA, df = 197, p = 0.033), 4 (MANOVA, df = 196, p = 0.001), 6

(MANOVA, df = 194, p = 0.009), 9 (MANOVA, df = 191, p = 0.001) and 10 (MANOVA, df = 190, p = 0.001). For the seasons, both summer (MANOVA, df = 199, p = 0.001) and winter (MANOVA, df = 198, p = 0.001) were significant. For the river reaches, we found significant relationships for all three river reaches: lower (MANOVA, df = 199, p = 0.001), middle (MANOVA, df = 198, p = 0.003), and upper (MANOVA, df = 197, p = 0.027). Finally, when we considered the river fragments, significance was found for the first and last river fragments, fragment A (MANOVA, df = 199, p = 0.001) and fragment E (MANOVA, df = 195, p = 0.026).

Comparisons of the CPUE with the habitat variables to determine which habitat variables had significant relationships with the CPUE using GLMs are shown in Table 2.5. None of the substrate types or eco-hydraulic categories had significant relationships with the CPUE of each biotope. However, one of the cover features and two of the water quality variables had significant relationships with CPUE. The only cover feature which had a significant relationship with CPUE was aquatic vegetation (GLM, df = 192, p = 0.0199; Table 2.5). The two water quality variables which had significant relationships with CPUE were TDS (GLM, df = 192, p = 0.0223), and salinity (GLM, df = 192, p = 0.0003).

We assessed the relationships between the cover features present and all fish species and found a significant effect for aquatic vegetation (MANOVA, df = 182, p = $1.998e^{-6}$) and rock crevices (MANOVA, df = 182, p = 0.004745) and most of the fish species (Fig. 2.5). There were exceptions, *Awaous aeneofuscus* did not have a significant relationship with rock cervices. *Anguilla mossambica* had a significant relationship with a rippled surface. *Anguilla marmorata* did not have a significant relationship with rock crevices. *Enteromius viviparus* showed a significant relationship only with rock crevices. *Lutjanus argentimaculatus,* had no significant relationships present with any of the cover features. *Ambassis natalensis* showed a significant relationship only with depth. *Oreochromis mossambica* had no relationship with

rock crevices. *Amphilus natalensis* had significant relationships with aquatic vegetation, rippled surfaces, and rock crevices. *Clarias gariepinus* did not have a significant relationship with rock crevices, and *Oncorhynchus mykiss* and *Leiognathus equula* did not have any significant relationships with any of the cover feature variables (Supplementary Information Fig. S4.1). Regarding the aquatic vegetation cover feature, *A. aeneofuscus* and *A. natalensis* showed negative correlations: their abundance decreased as aquatic vegetation cover increased. In contrast, *A. marmorata, C. gariepinus*, and *O. mossambica* exhibited positive correlations, indicating that as aquatic vegetation increased, so did the abundance of these three species. Regarding the rock crevices cover feature variables, *A. natalensis* showed a negative correlation, while *E. viviparus* had a positive correlation with this cover feature variable.

We found no significant relationships between the CPUE of all fish species per biotope and the different substrate types (MANOVA, df = 184, p (bedrock) = 0.8088, p (boulders) = 1710, p (cobbles) = 0.8932, p (gravel) = 0.9968, p (sand) = 0.9999). However, when plotting the data to examine the effects of the substrate on the different fish species, some species showed correlations with specific substrate types. *A. marmorata* had a positive correlation with cobbles, while *Ambassis natalensis* and *O. mossambica* had positive correlations with gravel. Additionally, *A. natalensis* had negative correlations with cobble substrate type.

Table 2.5: The outcomes of the generalised linear models (GLMS) comparing the catch per unit effort (CPUE) per site and habitat variables along the uMkhomazi River catchment, KwaZulu-Natal, in 2024.

Model	df	R^2	F-statistic	p-value
CPUE / cover features	192	0.03978	1.136	0.342
CPUE / Substrate	194	0.01752	0.692	0.6301
CPUE / Water Quality	192	0.1436	4.6	$8.911e^{-5}$
CPUE / Eco-hydraulic	195	0.007418	0.3643	0.8338

In terms of the water quality variables, the relationship between the CPUE of all fish species and the different water quality variables showed significance for most species with three of the water quality variables, namely pH (MANOVA, df = 184, p = 0.039213), electrical conductivity (MANOVA, df = 184, p = 0.007898), and salinity (MANOVA, df = 184, p = $5.853e^{-6}$). There were exceptions, such as *A. aeneofuscus* also having a significant relationship with the dissolved oxygen percentage, *A. mossambica* not having a significant relationship with any of the water quality variables, *A. marmorata*, not having a significant relationship with pH, but rather with electrical conductivity, salinity and dissolved oxygen percentage, *L. argentimaculatus*, not having a significant relationship with any of the water quality variables, *Ambassis natalensis,* only having a significant relationship with dissolved oxygen percentage, *O. mossambica* only having a significant relationship with water temperature, *A. natalensis*

having significant relationships with all of the water quality variables tested, *C. gariepinus* only having a significant relationship with salinity, *O. mykiss* only having a significant relationship with pH, *L. equula* not having a significant relationship with salinity, but rather with pH, electrical conductivity and dissolved oxygen percentage, and *E. viviparus* not having a significant relationship with electrical conductivity (Supplementary Information Fig. S4.3). For pH, *A. aeneofuscus,* and *O. mykiss* had negative correlations, while *A. natalensis*, *E. viviparus* and *L. equula* had positive correlations. For the electrical conductivity water quality variable, *A. marmorata* and *A. natalensis* both had negative correlations, while *A. aeneofuscus* and *L. equula* had positive correlations. For the final water quality variable, salinity, with which the CPUE of species had a significant relationship, *A. natalensis* and *E. viviparus* both had negative correlations, while *A. aeneofuscus*, *A. marmorata* and *C. gariepinus* had positive correlations.

Finally, when we examined the relationship between the CPUE of each species per sample and the different eco-hydraulic categories, we found no significant correlations between any of the species and the eco-hydraulic categories (MANOVA, df = 4; p = 0.9784).

2.5 Discussion

Comparisons of the abundances of the different fish species caught in both sampling periods (high and low flow) of the present study in the uMkhomazi River catchment showed variations among the species. The KwaZulu-Natal yellowfish, *L. natalensis*, was the most abundant fish caught across the system. Only three sites had no *L. natalensis* individuals. The last two sites may be too high in the catchment, with water being too cold to sustain a population (Burnett et al., 2021; Evans et al., 2022). For site 4, habitat availability and connectivity were factors associated with the absence of fish being caught there. Site 4 was situated above the third weir,

where the habitat types primarily consisted of a sandy substrate, and there were little to no cover features present.

When we compared the locations at which eel species were found in the uMkhomazi River catchment, it suggests that the eels' movement was less restricted compared with many of the other fish species in the river. During these eels' earlier life stages, they can scale certain barriers and, for a short period, move out of water entirely (Jacoby et al., 2015; Williamson et al., 2023). However, as expected, we did not catch eels in the upper reaches (at the last three sample locations, beyond site 7) (Hanzen et al., 2022). The weir upriver of fragment D is tall, and during the low rainfall winter sampling season, there was no water directly below the weir. This was attributed to low rainfall not allowing the water backed up by the weir to flow over, greatly restricting the connectivity of the river at that point (pers. obs.), as found in previous instream barrier studies of weirs (Havn et al., 2020; Righton et al., 2021). When considering anguillid spp., the glass eel stages possess the ability to climb, but this characteristic is lost as the eel grows. Consequently, barriers in the lower reaches may delay migration and, in turn, hinder deeper inland migration (Jacoby et al., 2015; Havn et al., 2020). Furthermore, at site 9, only *A. natalensis* was caught, and at site 10, *O. mykiss* was the only fish species caught, further supporting the significant adverse effects produced by this particular weir. Importantly, other factors also shape the communities, such as the presence of invasive fish species like *O. mykiss*, which often outcompete native fish species, and could explain the absence thereof at site 10 (Shelton et al., 2015; Weyl et al., 2017; Burnett et al., 2024). High altitudinal rivers in KwaZulu-Natal are expected to have lower fish biodiversity (Evans et al., 2022) and may be dominated by trout (*Salmo trutta* and *O. mykiss*) to support the trout angling fishery (Burnett et al., 2023).

Our comparisons of the CPUE of each fish species with the sites, seasons, river reaches, and river fragments all displayed significant relationships. In particular, the significance of certain river fragments was found, namely fragments A and E. River fragment A is the first river fragment found between the ocean and the first barrier, while river fragment E is the last river fragment, found between the final selected barrier and the rest of the upper reaches, representing the two extremes of the river fragments. The significance of the river fragments lies in the fact that the CPUE of each species decreased as fish penetrated further inland because of the presence of the instream barriers. Regarding the river reaches, a similar relationship was also present. Importantly, the middle and upper river reaches experienced compounding effects of the instream barriers in the lower reaches of the river. The significance found for the seasons was related to the rainfall, where in the winter season, the reduced rainfall may further restrict connectivity, like we observed during the winter sampling season at the weir upriver of fragment D. Our comparisons of the Shannon diversity indices for the river fragments further showed a significant difference in the level of diversity between the two river fragments, A and E. Importantly, the diversity index conducted across all 10 sites showed an expected trend where the diversity decreased along the river further inland as in other studies (Lyons and Schnider, 1990; Evans et al., 2022), however, this was not significant for the present study. While the extent of the longitudinal movement of some species remains largely unknown, the instream barriers in the present study indicate that these limiting ranges can have significant impacts on fish populations in the uMkhomazi River. Support for this statement can be seen in the *L. natalensis* distribution, where no *L. natalensis* individuals were caught in the present study at site 4, indicating a poor connectivity between fragmented populations in the uMkhomazi River system.

Furthermore, when we assessed the evenness of fish species distribution between the different river fragments, our data showed that, on average, species were more evenly spread in the communities found in the first river fragment, closest to the river mouth. The mean evenness of the river fragments following inland was less than that of the first fragment, which was close to one. This showed that the abundance of different species caught within each river fragment, apart from the first, was not evenly distributed, indicating that dominant species may be present, as found in some other studies (Das et al., 2013; Zare-Shahraki et al., 2022). The unevenness at some of these locations may also be because some of the fish are estuary associated, where some species like *A. aeneofuscus* would temporarily leave the freshwater system for the estuarine system (Whitfield, 2015).

Labeobarbus natalensis had the highest abundance and was the dominant species within the fish communities of each river fragment except the last (fragment E). However, in the final river fragment (E), we only caught two fish species, *A. natalensis* and *O. mykiss*, with low abundances, which skewed the evenness score of this fragment. Additionally, the reduction in the evenness score may be related to the fragmentation of the uMkhomazi River, which inhibits the movement of certain fish species, as evidenced by the lack of fish detected at site 4, as found in other studies (Das et al., 2013; Cocan et al., 2020). Further examples of this can be seen in *C. gariepinus*, *A. natalensis*, and *O. mossambicus*. While eels have been able to bypass most of the weirs within this study, the same cannot be said for other species. The unevenness of the species abundances within the communities between the river fragments suggests that some species did not bypass the barriers in the same way as the eels.

Our results showed that the connectivity of the river was hindered to a large extent after the first barrier in the lower section, with a decrease in species diversity and evenness in the fragmented communities along the river inland, as found in other studies with barriers affecting

river connectivity and fish presence (Righton et al., 2021; Hanzen et al., 2022). Several dams and weirs in the uMkhomazi River are proposed for the middle and upper reaches (DWS, 2011). These would further restrict the system's connectivity and reduce species' movements and localised species diversity, as found in other river studies on connectivity and its effects on fish species presence (Valenzuela-Aguayo et al., 2019; Righton et al., 2021). Previous studies have shown that dams, such as the Spring Grove Dam, have negative effects on native potamodromous fish species, including *L. natalensis*, hindering the connectivity necessary for their seasonal migration, and in turn, providing a more suitable habitat for non-native species (Burnett et al., 2024). Furthermore, while it appears that the eels have been able to bypass the first three of the four selected weirs in the present study, the proposed dam would have significant drawbacks on their migration unless effective fishways that include eels' migratory requirements are installed to accommodate migrating elver eels (Havn et al., 2020; Righton et al., 2021). The uMkhomazi River is also subjected to abstraction processes by companies like SAPPI Saiccor. Abstraction processes often divert parts of the river to meet industry water needs, significantly reducing water flow and, in turn, reducing connectivity by creating isolated pools (Leibowitz et al., 2018). This may significantly reduce fish distributions as consistent connectivity is lost (Seliger and Zeiringer, 2018).

The effect of the different habitat variables, namely cover features, substrate, water quality and eco-hydraulics, on each fish species showed that various species have different habitat requirements to carry out various processes critical to their life cycles, shown in many studies (Havn et al., 2020; Negro et al., 2021; Verhelst et al., 2021; Stoffers et al., 2022). However, none of the fish species caught during this study exhibited significant relationships with any substrate variables or eco-hydraulic categories; rather, some weak correlations existed between certain species and specific substrate types. This may be attributed to fairly uniform

substrate types across KwaZulu-Natal Rivers (Rivers-Moore and Goodman, 2010). It is important to note that, for some results, particularly those related to water quality, when the number of individuals caught for a given species was low, such as *C. gariepinus*, the data were skewed. A positive relationship between *C. gariepinus and* salinity is uncommon.

When we consider marine and estuarine associated species, they must conform to physico-chemical tolerances (Ter Morshuizen et al., 1996a, b). Salinity is one such tolerance that inhibits the movement of many of these species from saline environments like the ocean and estuaries to freshwater environments, which explains why their distribution does not extend further inland. (Ter Morshuizen et al., 1996a, b). The present study and previous research found that the area where the river and estuary meet is the most species-rich (Ter Morshuizen et al., 1996a). This is related to the amount of nutrients suspended in the water at this point, which is highest compared with other areas (Ter Morshuizen et al., 1996a). Heading further into the freshwater system, this species richness decreases as salinity does (Ter Morshuizen et al., 1996a, b).

In conclusion, assessing the effect of anthropogenic barriers on the movement of these eels and other migrating species, such as *L. natalensis*, aided in determining the connectivity within the uMkhomazi system. We suggest that if the present weirs have suitable and effective fishways installed, it will generate a greater degree of connectivity, as this has facilitated migratory fish movement in other studies (Righton et al., 2021; Hanzen et al., 2022). It is important to note that fishways differ in their designs, depending on which migratory fish would use them, and therefore, emphasis should be placed on the fishway design being suitable for the fish residing in the river in which the barrier is found (Righton et al., 2021; Hanzen et al., 2022). In terms of the proposed dams and weirs for the river system, effective fishways being constructed within them should be a minimum requirement as part of the structure so

that the connectivity within the system may persist (Righton et al., 2021; Hanzen et al., 2022), or an appropriate offset set to restore river connectivity and protect other free flowing rivers (Foldvik et al., 2022). Importantly, the presence of non-native fish species was a limiting factor in the present study, where such species may play a role in outcompeting native species, and in that way reducing the numbers of native fish species recorded (Shelton et al., 2015; Weyl et al., 2017; Burnett et al., 2024). Furthermore, within each fragment of this system, it would be beneficial to promote a heterogeneous mixture of habitat variables to support and conserve all fish species residing within the river (Negro et al., 2021; Stoffers et al., 2022). In addition to maintaining river connectivity using fishways, changes in river flow when the proposed dams are constructed would further change river flows and disrupt habitat, thus ensuring that fish have suitable habitat within each fragment as they migrate throughout the system would aid their migrations (Negro et al., 2021; Stoffers et al., 2022). Future studies on the connectivity of this river system may benefit from examining whether there is gene flow between the fragmented *L. natalensis* populations within different river fragments, as this may provide more valuable information on the state of connectivity at the particular barriers (Leeuwen et al., 2018). Where gene flow has been limited by habitat fragmentation, inbreeding will increase, with adverse effects on the population's plasticity (Pavlova et al., 2017; Leeuwen et al., 2018). Thus, by conducting studies on gene flow between fragmented populations, insights into the degree of connectivity present can be gained, and appropriate action can be taken to restore connectivity and, in turn, gene flow (Pavlova et al., 2017; Leeuwen et al., 2018). If we aim to conserve and protect large-scale migratory species, such as the African freshwater eels, found in river systems such as the uMkhomazi River, then the preservation of connectivity throughout the system from source to mouth should be a priority in all efforts (conservation and water

management) as highlighted in other fish presence and river connectivity studies (Hanzen et al., 2019; Havn et al., 2020; Righton et al., 2021; Hanzen et al., 2022).

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CHAPTER 3

Evaluating African freshwater eel recruitment into selected estuaries along the coast of the KwaZulu-Natal Province, South Africa

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Running header: Cues for eel recruitment

3.1 Abstract

According to the IUCN, of the 19 anguillid eel species, one is categorised as critically endangered, three as endangered, two as vulnerable, four as near threatened, two as least concern, and the remaining seven as data deficient. Those categorised as critically endangered or endangered have declined, primarily because of over-harvesting and exploitation of the species. As long-distance catadromous migratory species, African freshwater eels (*Anguilla* spp.) are important and unique ecological indicators of aquatic connectivity with increasing concern surrounding their conservation. Significant knowledge gaps exist concerning the anguillid eels. In the present study, we aimed to identify potential drivers of anguillid eel recruitment in three selected estuaries along the east coast of KwaZulu-Natal Province, South Africa. We predicted that several variables may influence recruitment, including degree of connectivity, season, moon phase, and water quality. Monthly sampling was conducted from October 2024 to May 2025 in the uThukela, uMkhomazi, and uMtamvuna estuaries by placing eight glass eel nets in each estuary for three consecutive nights per month. Our findings suggest that consistent connectivity between the marine and estuarine environments, the rainy season, high tides, moon phases with lower light intensity, and increases in certain water quality variables, namely dissolved oxygen, oxygen percentage, and electrical conductivity (when related to nutrient concentration), positively influence anguillid glass eel recruitment. The outcomes of this study provided valuable information which improved our understanding of the recruitment of four globally important eels. We suggest that conservation efforts aimed at maintaining the natural degree of connectivity between marine and estuarine systems would allow the continued recruitment of these eels into the systems in question. Furthermore, management practices tailored to preserve naturally occurring water quality would further aid in protecting these ecologically and economically important African freshwater eel species.

Keywords: Glass eel; Anguilla; moon phase; tide; connectivity; migration

3.2 Introduction

As long-distance migratory species with a widespread distribution across the east-flowing rivers of South Africa, East African tropical eels (*Anguilla* spp.) are important and unique ecological indicators with increasing concern around their conservation status (Tsukamoto and Aoyama, 1998; Hanzen et al., 2022). Anguillid eels have a catadromous life cycle (Hanzen et al., 2019; Cresci, 2020). Freshwater eel adults lay their eggs at sea, whereby the eggs hatch and take the form of leptocephalus larvae, which move from the open ocean towards coastal areas (Tsukamoto and Aoyama, 1998; Cresci, 2020). These larvae then morph into glass eels and enter estuaries, where they morph into elvers as they move inland, residing in freshwater bodies (Hanzen et al., 2019; Cresci, 2020; Righton et al., 2021). An eel residing in freshwater is considered to be in its yellow eel phase and, depending on the species, can spend between 7 and 50 years in freshwater bodies (McEwan and Hecht, 1984; Tsukamoto and Aoyama, 1998; Hanzen et al., 2019; Righton et al., 2021). A yellow eel then morphs into its final phase as a "silver eel", and swims back downstream, exits the estuaries, and proceeds to its spawning grounds in the marine ecosystem (Hanzen et al., 2019; Righton et al., 2021). There is no return route for anguillids, and they die after spawning (Williamson et al., 2023).

East African anguillid eels play a crucial ecological role in freshwater systems; for instance, in the rivers of the Eastern Cape Province, South Africa, they are the only native top fish predator (Parker et al., 2011). While the understanding of eels in the Northern Hemisphere has grown, the ecological understanding of eels in the Southern Hemisphere remains limited (Lecomte-Finiger, 2003; Jacoby et al., 2015; Hanzen et al., 2022; Hsu et al., 2024). The European eel *Anguilla anguilla* and the American eel *A. rostrata* are considered Critically

Endangered and Endangered, respectively, by the International Union for the Conservation of Nature (IUCN) (IUCN, 2025). The decline in these species is anthropogenically driven, including habitat fragmentation, exploitation, and pollution, which are partly responsible (Jacoby et al., 2015; Hsu et al., 2024). It is likely that anguillid eels in the Southern Hemisphere also face numerous threats, but the level of understanding of these is poor. Ten species of anguillids occur in the Southern Hemisphere, including four species in Africa, including South Africa (Wasserman et al., 2012; Jacoby et al., 2015; O'Brien et al., 2025): the longfin eel, *Anguilla mossambica*, the shortfin eel, *A. bicolor*, the African mottled eel, *A. bengalensis* and the giant mottled eel, *A. marmorata* (Wasserman et al., 2012; O'Brien et al., 2025).

Recent studies show that the range distribution of African freshwater eels in KwaZulu-Natal has contracted significantly (Hanzen et al., 2020). Little is known about the African eel species, including their habitat use, distribution or behaviour (Hanzen et al., 2019; O'Brien et al., 2025). While young eels, in the glass and elver eel stage of their life cycle, have the capacity to pass barriers, these obstacles impact their distribution in rivers (Jacoby et al., 2015; Havn et al., 2020). Estuarine ecosystems play a significant role for diadromous species, such as the anguillid eels (Potter et al., 2013; Hanzen et al., 2022). While these ecosystems are of great importance, numerous anthropogenic pressures impact these ecosystems and the organisms that utilise them (Hanzen et al., 2020, 2022). The loss, fragmentation, and degradation of estuarine ecosystems because of anthropogenic influences have led to large-scale changes in the ecological functioning of these ecosystems (Hanzen et al., 2019; 2022).

Furthermore, connectivity between marine and estuarine ecosystems is often restricted by anthropogenic processes (Righton et al., 2021; Hanzen et al., 2022). The same occurs further up the estuarine and freshwater systems where structures such as dams/impoundments are constructed (Righton et al., 2021; Hanzen et al., 2022). Thus, the open/closed status of an

estuary may hinder diadromous species from entering or exiting the estuary, with the estuary being closed, hindering this movement (Righton et al., 2021; Stein et al., 2021; Hanzen et al., 2022).

An additional anthropogenic pressure experienced by the African freshwater eels (*Anguilla* spp.) is related to international fish market interest (Robinet et al., 2008). Madagascar and South African fisheries have shown a growing interest in these eels for consumption and traditional practices (Robinet et al., 2008; Nkomo, 2023). As such, the need for a better understanding of these eels and the environments in which they reside becomes increasingly important for effective conservation and protection of these eels.

Glass eel recruitment is an important life-cycle stage for anguillid eels, allowing them to reach the freshwater system where they continue to mature (Hanzen et al., 2019; Cresci, 2020; Righton et al., 2021). Improving our understanding of these species will not only aid in enhancing conservation methods for the species but also contribute to improved water resource management, as they are important indicators of aquatic habitat connectivity (Tsukamoto and Aoyama, 1998; Hanzen et al., 2022). In turn, the improved understanding of glass eel recruitment could be used to determine whether intervention is needed in an estuarine system's degree of connectivity with the marine system (Tsukamoto and Aoyama, 1998; Hanzen et al., 2021).

Here, we assessed which factors influenced the recruitment of glass eels into selected estuaries along the KwaZulu-Natal Province coast of South Africa. We predicted numerous factors would influence recruitment. We predicted that moon phases, season and water quality would be key factors in eel recruitment in the selected estuaries. Eels are good indicators of ecosystem connectivity; hence, determining which factors influence the recruitment and presence of eels in the selected estuaries may provide valuable insight into how to better

conserve the health of these ecosystems in the future, in terms of their fish community structures, which are in part reliant on the connectivity of upstream river systems, but to the estuaries too (Tsukamoto and Aoyama, 1998; Hanzen et al., 2021).

3.3 Methods

3.3.1 Study area

We conducted our study in three estuaries along the coast of the KwaZulu-Natal Province of South Africa, namely the uThukela, uMkhomazi, and uMtamvuna estuaries. The uThukela Estuary lies 98 km north of the city of Durban, and the uMkhomazi situated 52 km south of Durban, while the third estuary is located on the border of the KwaZulu-Natal and Eastern Cape provinces, 152 km south of Durban (Fig. 3.1). These estuaries were selected as they are found along the same coastline and experience similar climatic conditions but differ in size and geographically in their latitudinal position along the coastline.

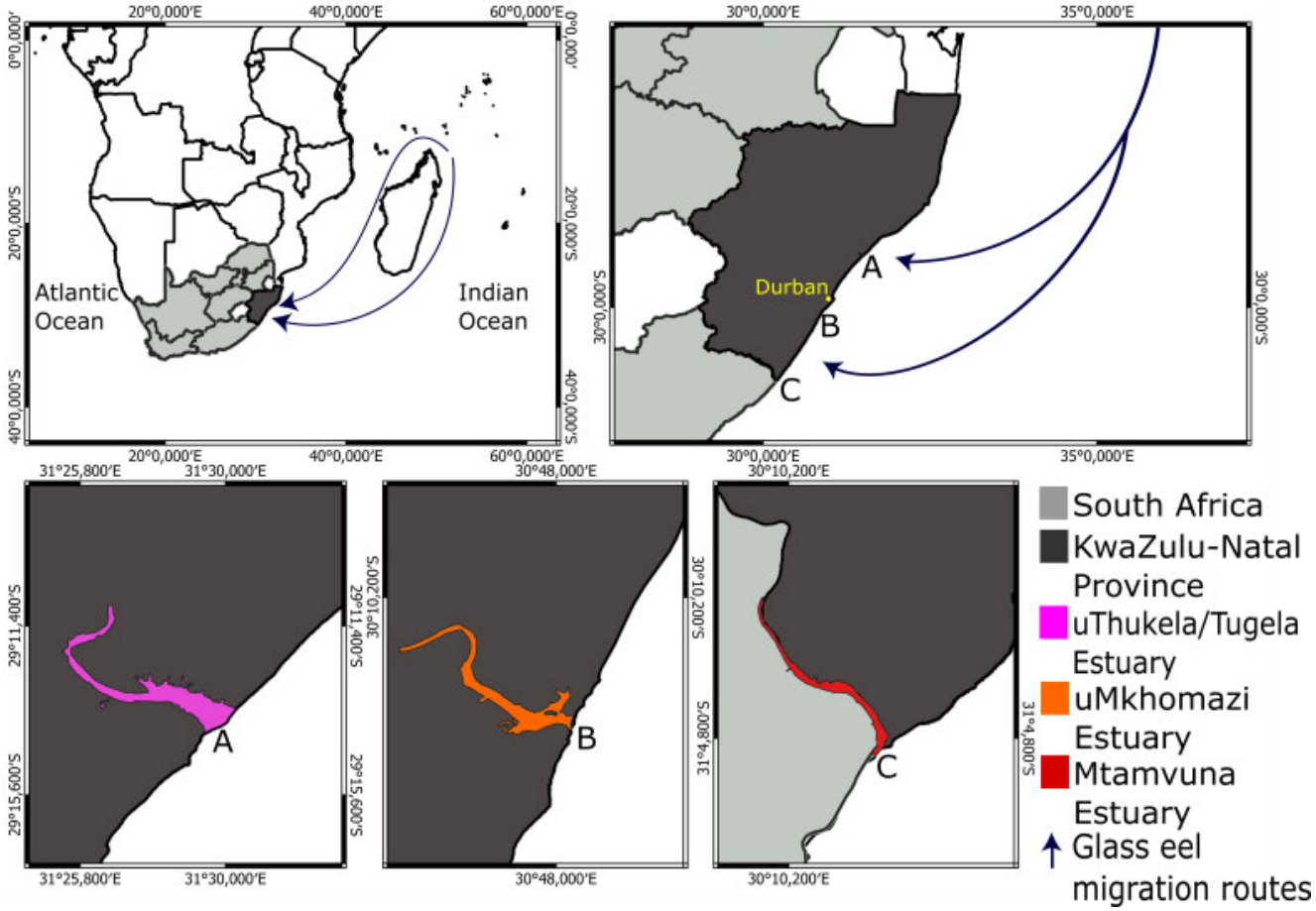


Figure 3.1: The three selected estuaries, A.) uThukela Estuary, B.) uMkhomazi Estuary, and C.) uMtamvuna Estuary in KwaZulu-Natal Province, South Africa, and the depiction of the migration routes used by the glass eels to travel from the east coast of Madagascar to the east coast of South Africa.

3.3.2 Sampling techniques

Each estuary was visited for 3 days each month, from October 2024 to May 2025. We placed eight glass eel nets (T and L Netmaking, Mooroolbar, 1078 Australia) along the banks of the lower portions of each estuary, with the opening of the glass eel net facing the mouth of the estuary. Each net remained in the water overnight, after which it was checked, and the species caught were sampled. The glass eels caught were measured and separated by size, allowing us

to capture their relative abundances. Where anguillid eels at different life-cycle stages were recorded, they were measured, and their respective life-cycle stage was noted. For the present study, we focused on glass eels and elvers. Water quality measurements were also taken, including the pH, water temperature (Temp), electrical conductivity (EC), total dissolved solids (TDS), salinity (SAL), dissolved oxygen (DO), and oxygen percentage (OP), using a water quality meter made by LAQUA (Horiba, Ltd. Head Office / Factory 2, Miyanohigashi-cho, Kisshoin, Minami-Ku, Kyoto, 601-8510, Japan). Additionally, we sampled the surrounding habitat around each glass eel net. We recorded the habitat data at five different spots along the placement of the glass eel net. The habitat data recorded included the water depth at that point, the water velocity (the two variables used to calculate the eco-hydraulic category at that point), the substrate, and the cover feature present (Dixon, 2003; Wang et al., 2012). The substrate types were mud, gravel, cobbles, boulders, and bedrock. The cover features which we examined were rock crevices, aquatic vegetation, wood debris, roots, depth, and overhanging vegetation. We also recorded the moon phases for each sampling day: new moon, full moon, first quarter, and third quarter. Lastly, the tides for each day were also recorded (high and low). Furthermore, catch per unit effort (CPUE) was used as the dependent variable and was calculated as follows:

$$CPUE = \frac{\sum(x1 + x2 + x3 + \cdots x\infty)}{t_h}$$

Where $X_{1\text{-}\infty}$ is the sum of all glass eel individuals in a net, and t_h is the time (h) that the net was in the water prior to being checked (adapted from: Ellender et al. 2012; Nolwazi et al., 2024; McNeill et al., 2025).

3.3.3 Data analyses

We analysed the data in RStudio (version 4.3.2) (Posit team, 2024) using descriptive statistics, along with generalised linear models (GLM) and multivariate analyses of variance (MANOVA) to determine the trends and significant relationships between the glass eels present and the environmental factors. For each of the three sites, we conducted MANOVA's where *Anguilla* spp. has been caught, to determine if any relationships are present between the eel species (dependent variable), and the substrate, cover features, water quality, moon phase, month/season, and the eco-hydraulic categories (independent variables). This allowed us to determine whether either of the selected variables may be drivers of eel recruitment into the selected estuaries. We used the following R-packages: ggplot2 (Wickham, 2010), dplyr (Wickham, 2023), vegan (Dixon, 2003), reshape2 (Wickham, 2007), MASSExtra (Venables, 2023), caret (Kuhn, 2008), and MVN (Korkmaz, 2014).

3.4 Results

Anguilla spp. were only caught in the uThukela Estuary and the uMkhomazi Estuary (Table 3.1). Importantly, glass eels were only caught in the uThukela Estuary (Table 3.1, Fig. 3.2). The glass eel CPUE for the uThukela Estuary was greater during the summer season, with an overall CPUE of 27.92 and an abundance of 335, as opposed to autumn, where the overall CPUE was 2.25 and the abundance was 27 (Table 3.1).

The abundance of glass eels caught in the uThukela Estuary, and the seasons in which sampling was conducted showed a significant relationship present (MANOVA, df = 2, p = 0.0194, Fig. 3.2). There was a significant relationship between the glass eels caught in the uThukela Estuary and the different moon phases (MANOVA, df = 376, p = 0.002105, Fig. 3.3). We found that glass eel recruitment was highest during the new moon and third quarter

moon phases. A comparison of the moon phases between the uThukela Estuary and the uMkhomazi Estuary showed that it was primarily in May when the moon phases at the two sites were different, where in May the uThukela experienced the new moon phase while the uMhkomazi experienced the first quarter moon phase. The first-quarter moon phase is also the time when the fewest glass eels were recorded recruiting into the uThukela Estuary (Fig. 3.3).

There were no significant relationships between the glass eels caught at the uThukela Estuary and the cover features recorded, i.e. overhanging vegetation (MANOVA, df = 185, p = 0.0796), aquatic vegetation (MANOVA, df = 185, p = 0.6012), roots (MANOVA, df = 185, p = 0.5106) and wood debris (MANOVA, df = 185, p = 0.2976). Similarly, there were no significant relationships present between the glass eels and the recorded substrate types in the uThukela Estuary (bedrock (MANOVA, df = 187, p = 0.9801) or sand (MANOVA, df = 187, p = 0.8499)). We found no significant relationship between the glass eels caught in the uThukela Estuary and whether the mouth of the estuary was opened or partially closed (MANOVA, df = 188, p = 0.2711, Fig. 3.4), nor was there a significant relationship present between the glass eels caught in this estuary and the eco-hydraulic categories (MANOVA, df = 376, p = 1).

Table 3.1: Anguillid eel species caught in the selected estuaries, uThukela Estuary (TUK), uMkhomazi Estuary (MKO) and uMtamvuna Estuary (UMT) throughout the eight-month sampling period, separated by their life cycle stages and each season, represented by A) their catch per unit effort (CPUE) and B) their abundance.

Species and common name	**Life cycle stage**	**Season**																	
		Spring						**Summer**						**Autumn**					
		Site																	
		TUK		**MKO**		**UMT**		**TUK**		**MKO**		**UMT**		**TUK**		**MKO**		**UMT**	
		A	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**	**A**	**B**
Anguilla spp. (glass eel)	Glass eel							27.9	335					2.3	27				
Anguilla marmorata (Giant mottled eel)	Yellow eel							0.7	8	0.1	1								
Anguilla mossambica (African long-fin eel)	Yellow eel							0.2	2										

Table 3.2: The open/closed state of the three selected estuaries (uThukela, uMkhomazi and uMtamvuna) over the course of the eight-month sampling period during the time of sampling.

Month	Estuary		
	uThukela	**uMkhomazi**	**uMtamvuna**
October 2024	Closed	Closed	Closed
November 2024	Closed	Closed	Closed
December 2024	Open	Open	Open
January 2025	Open	Closed	Closed
February 2025	Open	Open	Closed
March 2025	Open	Open	Closed
April 2025	Open	Open	Open
May 2025	Open	Closed	Open

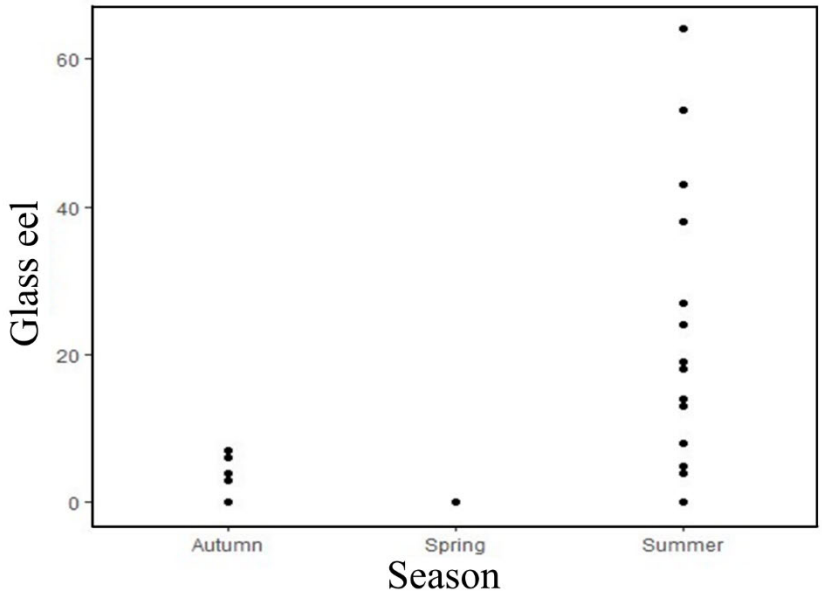


Figure 3.2: Relative abundance of glass eels caught in the uThukela Estuary and their responses to the seasons during which sampling was conducted.

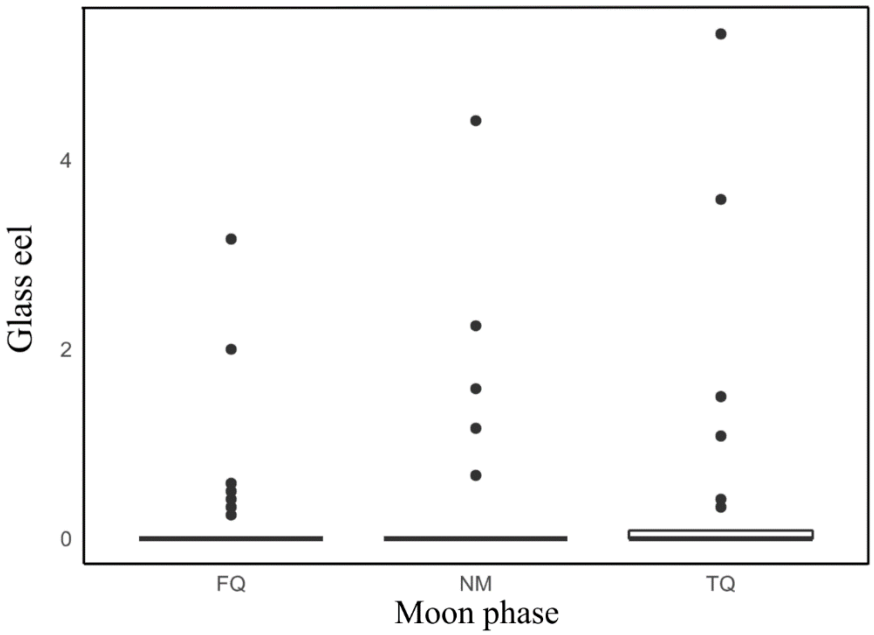


Figure 3.3: The relationship between the relative abundances of glass eels caught in the uThukela Estuary, and the different moon phases encountered during the eight-month sampling period, first quarter (FQ), new moon (NM) and third quarter (TQ), following MANOVA analyses.

When we considered the interaction between the glass eels caught in the uThukela Estuary and the water quality recorded across the eight-month sampling period, significant relationships were found between glass eels and EC (GLM, df =1, p = 0.00150), DO (GLM, df = 1, p = 0.007052) and the oxygen percentage (GLM, df = 1, p = 0.00384). When comparing the average DO between the uThukela Estuary (Average (DO) = 9.05 mg/L) and the uMkhomazi Estuary, the uMkhomazi Estuary had a higher average DO (Average (DO) = 9.43 mg/L). Alternatively, when we compared the average EC between these two estuaries, we found that the EC in the uThukela Estuary (Average (EC) = 485.5 µS/cm) was higher than in the uMkhomazi Estuary (Average (EC) = 87.82 µS/cm). Finally, when we analysed the relationship between the glass eels recorded at the uThukela Estuary and tidal influence, we found a significant relationship (GLM, df = 188, p = 0.01194; Fig. 3.4).

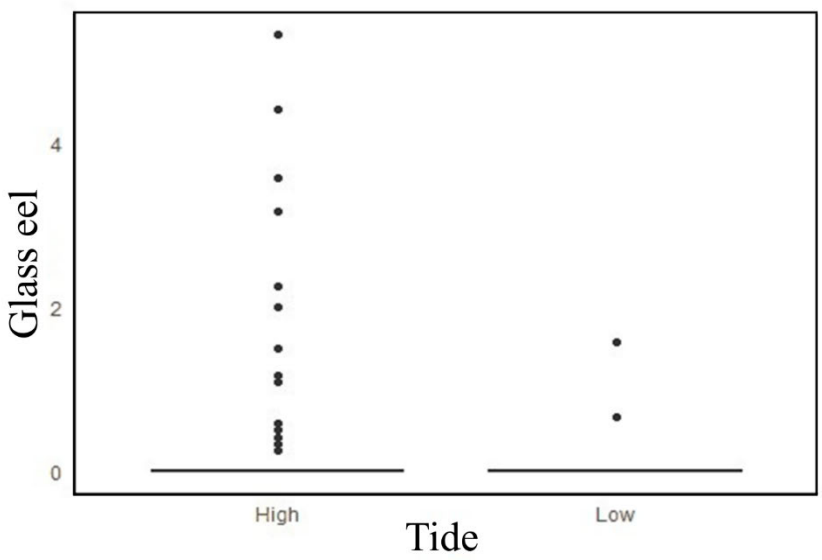


Figure 3.4: The relationship between glass eels caught in the uThukela Estuary and the tidal influence, which was found to be significant.

3.5 Discussion

Throughout the study, *Anguilla* spp. were caught in the uThukela and uMkhomazi estuaries, but not in the uMtamvuna Estuary. However, glass eel recruitment was only recorded in the uThukela Estuary. Importantly, both glass eels and elvers were recorded recruiting into the uThukela Estuary. In relation to the significant relationship found between the glass eels caught at the uThukela Estuary and the months during which sampling was conducted, our results indicated that glass eel recruitment occurred from January to March. This was the austral summer to austral autumn time period. Additionally, summer is the rainy/wet season for the KwaZulu-Natal Province, during which the highest annual rainfall is recorded (Ndlovu et al., 2021). Thereafter, there is generally a steady decline in the mean monthly rainfall until the onset of the dry season in June (Ndlovu et al., 2021). Importantly, freshwater flow from the river which feeds an estuary is critical in sustaining connectivity between the freshwater and estuarine systems (Jellyman and Lambert, 2003). Furthermore, it is also an important factor in maintaining connectivity between the marine and estuarine environments (Jellyman and Lambert, 2003). Thus, the absence of significant freshwater flow may hinder glass eel recruitment (Jellyman and Lambert, 2003). Freshwater flow into an estuary, and the subsequent discharge thereof into the ocean, has been found to be key in glass eel recruitment as the plumes produced by the freshwater discharge into the ocean are used by the glass eels to orientate themselves towards the estuary (Arribas et al., 2012). Our findings were consistent with previous studies on glass eel recruitment worldwide, which indicate that glass eels are generally recruited during seasons with high rainfall (Helme et al., 2018; Hanzen et al., 2019; Hewavitharane et al., 2020; McNeill et al., 2025).

Glass eel recruitment was highest during the new moon and third quarter moon phases in our study. Some studies suggest that the significance of the new moon phase, when the moon

is barely visible or not visible to them, is used to orient themselves (Cresci et al., 2019; 2020). This is related to the changes in the moon's electrical flux and its gravitational forces (Cresci et al., 2019; 2020). Additionally, other studies suggest that the significance of the moon phase is related to the moon's light intensity and its influence on both predation on glass eels and their photophobic behaviour (Helme et al., 2018; Fukuda et al., 2023). Previous studies suggest that light intensity and predation are directly proportional, which also corresponds with our findings in that the majority of glass eels caught at the uThukela Estuary throughout the eight-month sampling period were during the new moon and third quarter moon phases, during which light intensity from the moon is at its lowest (Helme et al., 2018). Furthermore, the photophobic characteristic exhibited by glass eels, which prompts them to move during darker periods with reduced light intensity, is also supported by our findings and other studies (Fukuda et al., 2023).

Regarding the tidal influence on glass eel recruitment, we found that most glass eels in the uThukela Estuary recruited during high tide. The same was observed in previous studies, which also found that glass eel recruitment was significantly affected by tidal influence, with abundance greatest during high tide (Fukunda et al., 2023; Guo et al., 2023). Tidal influence and the moon phases are closely related factors, with tide intensity influenced by the moon phase (Fukunda et al., 2023; Guo et al., 2023). Importantly, the new moon phase, which we found to be significantly positively correlated with our CPUE of glass eels, falls within the same time period as spring tides. Spring tides are characterised by producing the strongest high tides (Fukunda et al., 2023; Guo et al., 2023).

Regarding the effects of water quality on glass eel recruitment in the uThukela Estuary, our findings revealed significant relationships between glass eel recruitment and oxygen percentage, dissolved oxygen, and electrical conductivity. Dissolved oxygen and oxygen percentage are two related variables, and previous studies have suggested that dissolved oxygen

and the abundance of glass eels are directly proportional, provided that oxygen levels are not excessively high (Blakeslee et al. 2018; Podda et al. 2020), a finding consistent with ours. Regarding the electrical conductivity and its significant relationship with glass eels recorded in the uThukela Estuary, previous studies have found similar relationships: the CPUE of glass eels and the water's electrical conductivity are proportional (McKinnon and Gooley, 1998; Arribas et al., 2012). The low EC values recorded at the uMkhomazi Estuary may have played a role in the exclusion of glass eels in this estuary during the course of the study (McKinnon and Gooley, 1998; Arribas et al., 2012). It is important to note that because of the tidal influence, water quality variables can fluctuate frequently, in addition to seasonal (rainy/dry) variation (Cereja et al., 2022). Furthermore, this variation in water quality may be an additional indicator of glass eel recruitment, in conjunction with the other drivers identified in the present study.

According to our analyses, whether the mouth of the uThukela Estuary was open or closed was not significant. However, this was skewed because, from January through May, the uThukela Estuary remained open, and glass eels were only recorded as being recruited into the uThukela Estuary between January and March (mid-summer to the beginning of autumn). As for the uMkhomazi system, only one *Anguilla* spp. was caught throughout the study, an *A. marmorata* individual in the yellow eel life cycle stage. The presence indicates that glass eels have been recruited into the system in previous years, in accordance with their life-cycle requirements (Righton et al., 2021; Hanzen et al., 2022). The occurrence of the yellow eel in an estuary is uncommon and may indicate that the individual was unable to penetrate further inland into the freshwater system (Arai and Chino, 2018).

During May (at the end of autumn), eels were no longer recorded as being recruited into the uThukela Estuary. Furthermore, when glass eels began to be recorded in the uThukela

Estuary in January, the uMkhomazi Estuary was closed because of large amounts of sand/sediment, which may have inhibited the glass eel's ability to enter the estuary (Fernandes and Adams, 2016; Ellero, 2018).

When we considered the uMtamvuna Estuary, the estuary was only open for three of the total eight months of the sampling period. When we compared the months during which recruitment was recorded at the uThukela Estuary (January – March), the uMtamvuna Estuary was closed. While numerous fish species were recorded in the uMtamvuna Estuary, no *Anguilla* spp. were recorded (in any of the life cycle stages) during the study. *Anguilla* spp. require consistent connectivity between marine and estuarine systems to recruit into estuaries (Righton et al., 2021; Hanzen et al., 2022). Thus, the frequent closure of the uMtamvuna Estuary, hindering connectivity, may explain the absence of glass eels in the estuary (Righton et al., 2021; Hanzen et al., 2022).

None of the habitat variables measured (cover features, substrate types or ecohydraulic categories) influenced glass eel recruitment into the uThukela Estuary. This was expected, as previous studies have found that at this life cycle stage, their goal is to move towards the freshwater system and to respond to physico-chemical cues (O'Leary et al., 2022).

In conclusion, the present study has highlighted numerous cues/factors which influence glass eel recruitment into estuaries along the South African east coast, namely moon phase, season (rainy season), tides (high), dissolved oxygen, electrical conductivity and estuarine-marine connectivity. We found that glass eel recruitment on the east coast of South Africa generally occurs between January and March, particularly during high spring tides. When the mouth of the estuary is closed or favourable conditions are not met, recruitment may be hindered. The present study has enhanced our understanding of the recruitment of African freshwater eels (*Anguilla* spp.) into South African rivers; however, further research is needed

to comprehend the recruitment dynamics of each catchment. Additional work is needed to understand the impact of increased abstraction pressures on the uMkhomazi and uThukela rivers and their potential influence on glass eel recruitment. Regarding the uMtamvuna Estuary, previous research suggests that reduced river flow into the estuary results in the formation of a sediment barrier, hindering connectivity between the marine and estuarine systems (Andrew and Cooper, 1993). African freshwater eels are not presently protected species in South Africa; listing them as such under national law would further aid in their protection (Government of South Africa, 2004). The findings of the present study, in conjunction with previous research that has highlighted the importance of freshwater discharge into an estuary as an additional key driver of glass eel recruitment, can be utilised to inform the development of better management practices (Arribas et al., 2012). We suggested that conservation efforts aimed at maintaining the natural degree of connectivity between marine, estuarine and freshwater systems would allow the continued recruitment of these eels into the systems in question, particularly during periods of January to March with high rainfall and moon phases with lower levels of light intensity (Righton et al., 2021; Hanzen et al., 2022). Furthermore, management practices tailored towards preserving naturally occurring water quality and estuarine ecosystem health would further aid in protecting and preserving these ecologically and economically important eel species (Tsukamoto and Aoyama, 1998; Lecomte-Finiger, 2003; Parker et al., 2011; Jacoby et al., 2015; Lin et al., 2015).

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CHAPTER 4

Assessing drivers of estuarine fish community structures on the KwaZulu-Natal coast of South Africa

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Running header: Factors shaping estuarine fish community structures

4.1 Abstract

Estuaries are unique ecosystems that connect marine and freshwater systems, rich in nutrients derived from oceanic tides and terrestrial runoff. This connectivity facilitates diverse fish community structures in estuaries, as some species from marine and freshwater environments migrate into them to support various processes. In this study, we assessed the factors shaping fish community structure in three selected estuaries (uThukela, uMkhomazi, and uMtamvuna) along the southeast coast of KwaZulu-Natal Province, South Africa, and whether a degree of connectivity exists between the different aquatic systems. Our study was conducted from October 2024 to May 2025, during which we placed eight glass eel nets in each estuary for three days each month and recorded the fish species caught. We also measured various abiotic parameters when sampling. Fifteen fish species were recorded in the uThukela Estuary, 12 in the uMkhomazi Estuary, and nine in the uMtamvuna Estuary. We found that the degree of connectivity in the uThukela Estuary was greater than that of the uMkhomazi and uMtamvuna estuaries because of the presence of the greatest number of migratory species. When estuary mouths were open, the same migratory species were caught across the studied estuaries, and abundances of migratory fish were greatest in the uThukela Estuary. Furthermore, we found that the fish communities residing within the three selected estuaries were shaped by numerous abiotic variables, including connectivity, water temperature, salinity, and dissolved oxygen. A combination of these factors and a suitable habitat is required to maintain the fish community structures in the selected estuaries. Factors that may be shaping estuarine fish community structures along the southeast coast of South Africa are complex, but increased temperature and increased closure time of estuaries have a negative effect on fish communities, which have implications for how we conserve these fish communities as the climate changes.

Keywords: Anguilla; connectivity; habitat; nutrients; salinity; season

4.2 Introduction

Estuaries are unique ecosystems that link marine and freshwater systems (Dias et al., 2016; Izegaegbe et al., 2020). The connectivity provided by estuaries plays a crucial role for numerous organisms, particularly for diadromous species (Havn et al., 2020; Whitfield et al., 2023). Diadromous species require both fresh and marine water at either the juvenile or mature stage to complete their life cycles (Havn et al., 2020; Verhelst et al., 2021). Anguillid eels as an example, are spawned at sea then as leptocephalus larvae they migrate towards estuaries, where they morph into glass eels and move into freshwater systems, where they will grow into the yellow eels and then mature as silver eels to return to their spawning grounds and complete their life cycles (Robinet et al., 2008; Hanzen et al., 2019; Righton et al., 2021).

There are certain fish species whose life cycle occurs strictly within the estuaries, while other migratory fish species enter the estuary either from the freshwater or marine ecosystems to which the estuary is attached (Potter et al., 2015; Whitfield et al., 2017). These migratory species form part of the estuarine fish community structures, all of which require connectivity to the estuary (Potter et al., 2015; Righton et al., 2021; Hanzen et al., 2022). Because certain fish species are present when connectivity is not hindered between the estuary and the freshwater system, and between the marine and estuarine systems, we can infer, from the presence or absence of species, whether connectivity is hindered (Potter et al., 2015; Whitfield et al., 2017). Migratory species, such as the four anguillid eel species found in South Africa (catadromous migrators), are good indicator species from which connectivity inferences could be made (Hanzen et al., 2019; Righton et al., 2021). The four species of Anguillid eels found in South Africa are as follows: the longfin eel, *Anguilla mossambica*, the shortfin eel, *A. bicolor*, the African mottled eel, *A. bengalensis* and the giant mottled eel, *A. marmorata*

(Hanzen et al. 2019; 2022). Importantly, other migratory species with amphidromous, anadromous, and oceanodromous migratory pathways could also be used to infer connectivity.

Consequently, the connectivity maintained by estuaries is critical to the survival of numerous aquatic species (Dias et al., 2016; Havn et al., 2020). Furthermore, another important factor related to estuary connectivity is that these pathways enable the transfer of biomass between marine and freshwater ecosystems (Acou et al., 2000; Izegaegbe et al., 2020). Additionally, estuaries are rich in nutrients, as the nutrients found in these estuaries are derived from downstream nutrient transport from the freshwater system, nutrient deposition via the oceans' incoming tides, and runoff from the surrounding terrestrial environments, making them one of the most productive aquatic ecosystems (Dias et al., 2016; Izegaegbe et al., 2020). This abundance of nutrients enables estuaries to support a diverse array of species, resulting in rich fish communities (Dias et al., 2016; Izegaegbe et al., 2020). Despite this, various anthropogenic pressures negatively impact these estuaries, including runoff from agricultural sources, which deposits chemicals into the estuaries and has adverse effects on the fish communities within them (Izegaegbe et al., 2020; Xiao et al., 2024).

South African estuaries have been previously categorised, either as predominantly open, large fluvially dominated, river mouths, estuarine bays, estuarine lakes, estuarine lagoons, arid predominantly closed, small temporarily closed, large temporarily closed or small fluvially dominated (Whitfield 1992; Adams and van Niekerk, 2020; Adams et al., 2022). While naturally occurring temporarily open/closed estuaries are common, various estuaries are periodically opened and closed during the year to facilitate anthropogenic processes, which may have significant adverse effects on the fish community structures present within the estuaries, particularly if the estuary should be permanently open (Whitfield et al., 2017; Righton et al., 2021; Hanzen et al., 2022). These adverse effects may arise from poor

management, pollution, and the hindrance of connectivity between the ocean, estuary, and freshwater systems (Whitfield et al., 2017; Righton et al., 2021; Hanzen et al., 2022).

In this study, we assessed the factors shaping fish community structures in three selected estuaries along the east coast of South Africa in KwaZulu-Natal Province, with a focus on diadromous migrators to determine the degree of connectivity between freshwater and marine waters through estuaries. Furthermore, we predicted that connectivity would influence fish community structure, particularly species richness. This study provides information that aids conservation efforts for the fish community structures found within these estuaries.

4.3 Methods

4.3.1 Study area

We conducted our study in three estuaries along the KwaZulu-Natal Province, South Africa, coast that are considered to be in a subtropical climate (Fig. 4.1). The estuaries we surveyed were the uThukela, the uMkhomazi, and the uMtamvuna estuaries (Fig. 4.1). These estuaries are located latitudinally from north to south along the coast of KwaZulu-Natal, respectively. These estuaries were selected because they are located along the same coastline and experience roughly similar climatic conditions; however, they vary geographically in their latitudinal positions along the coastline (Vetrimurugan et al., 2019; Table 4.1).

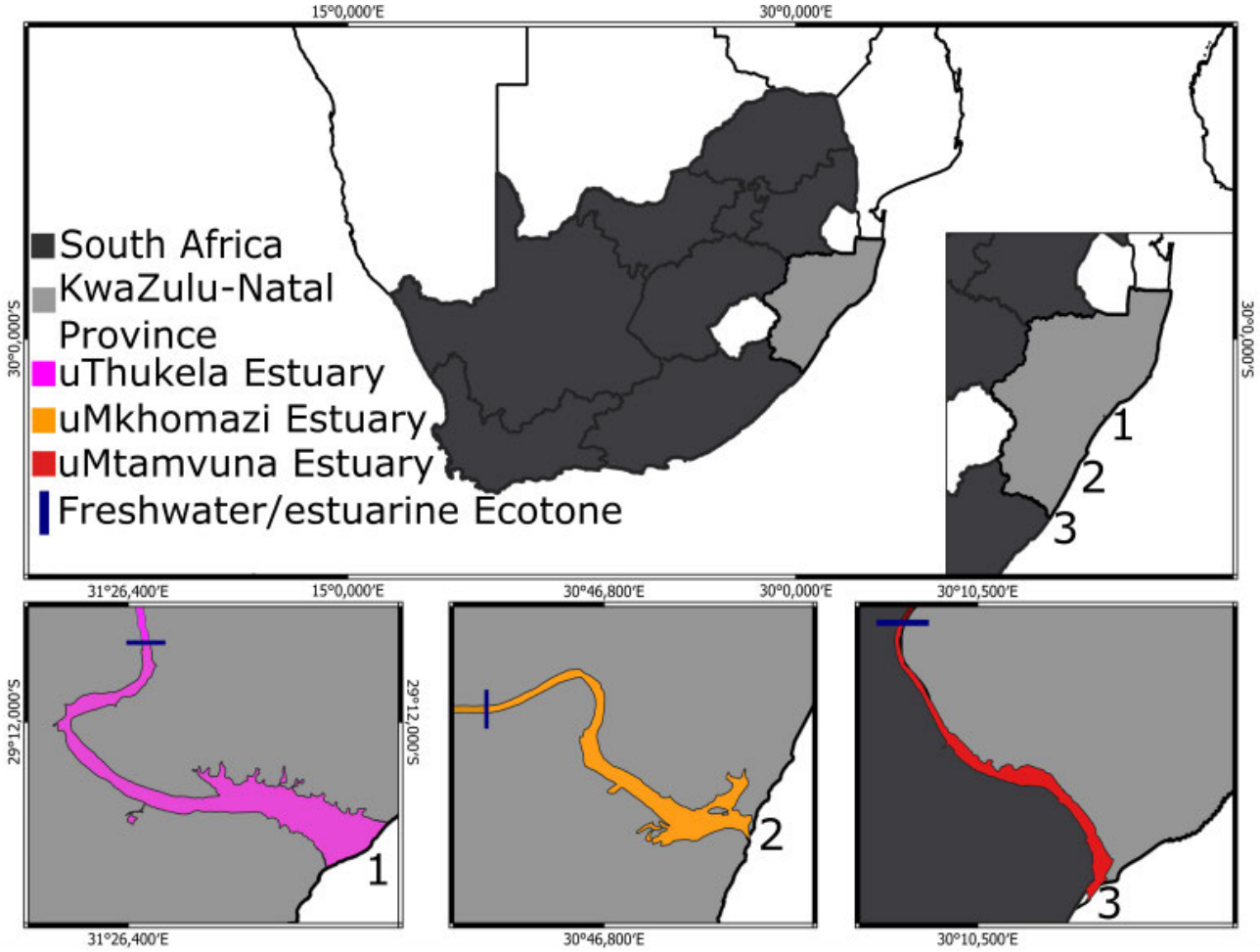


Figure 4.1: The study area on the KwaZulu-Natal coast, South Africa, including the three estuaries sampled, and highlighting the freshwater/estuary ecotones.

Table 4.1: Geographical location of the estuaries sampled in the present study and their area of water surface and length of the associated river (SAEON, 2012; van Niekerk et al., 2020).

Estuary	Ecological status	Latitude (E)	Longitude (S)	Area of water surface (ha)	Length of associated river (km)	Open/ Closed status
uThukela	C - moderately modified	-29.224081	31.499359	106	405	Large fluvially dominated
uMkhomazi	C - moderately modified	-30.200926	30.803306	49.5430	298	Large fluvially dominated
uMtamvuna	B – largely natural with few modifications	-31.085000	30.194000	51.5960	162	Large temporarily closed

4.3.2 Sampling techniques

We visited each sample site for three days per month, from October 2024 to May 2025. Our study used the bycatch from a glass eel study (Chapter 3) where eight glass eel nets (T and L Netmaking, Mooroolbar, 1078 Australia) were placed along the banks of each estuary, with the opening of the glass eel net facing the estuary mouth. While glass eel nets may not be the most suitable technique for assessing fish community assemblages, we caught fish across various size categories, indicating that it would be an appropriate proxy for this purpose. Each net remained in the water for 12-h periods, after which we emptied the nets and sampled the fish species caught. We separated the fish caught in each net by size and species to determine the abundance and species richness. We measured each fish caught before releasing it at the site of capture. Body mass data were not recorded, limited by our scale, which only provides readings ≥ 20 g, and all recorded individuals, apart from the *Anguilla* spp. in the yellow eel life cycle stage, the body mass was less than 20 g. The migratory fish species caught were used to infer connectivity.

In addition, we also undertook water quality measurements at each site when sampling for fish, including the pH, water temperature, electrical conductivity, total dissolved solids, salinity, dissolved oxygen, and oxygen percentage, using a LAQUA (Horiba, Ltd. Head Office / Factory 2, Miyanohigashi-cho, Kisshoin, Minami-Ku, Kyoto, 601-8510, Japan) water quality meter. Furthermore, we undertook habitat sampling around each glass eel net by recording the habitat data at five different spots along the placement of the glass eel net. The habitat data recorded included the depth of the water (cm) and the velocity/flow (for eco-hydraulic purposes), the substrate, and the cover features present. The substrate types were mud, gravel, cobbles, boulders, and bedrock. We recorded the cover features, including rock crevices, in-stream vegetation, wood debris, roots, and overhanging vegetation.

4.3.3 Data analyses

We employed descriptive statistics, diversity indices (Shannon diversity), and multivariate analyses of variance (MANOVA) to investigate the relationships present in our data using RStudio (version 4.3.2) (Posit Team, 2024). We used the Shannon diversity, richness and evenness indices (Nolan and Callahan, 2006) to assess the overall structure of the fish communities in each estuary during open and closed periods, while MANOVAs were conducted to determine which environmental variables may have significant relationships with the fish species caught and may be shaping the community structures within the selected estuaries. Additionally, relative abundance plots were generated to visualise differences in community composition across all three selected estuaries, and canonical correlation analysis (CCA) was conducted to identify which environmental variables were shaping the communities of the selected estuaries as a whole. The RStudio packages used were vegan (Dixon, 2003), reshape2 (Wickham, 2007), MASSExtra (Venables, 2023), ggplot2 (Wickham, 2010), dplyr (Wickham, 2023) and caret (Kuhn, 2008). Additionally, dependent variables with Pearson correlation coefficients greater than 0.6 were considered to have a high level of collinearity and were subsequently removed from the data analysis. Furthermore, we used the catch per unit effort (CPUE) as a measurement of the abundance of particular species caught in a net per unit time using the following formula:

$$CPUE = \frac{\sum(x1 + x2 + x3 + \cdots x\infty)}{t_h}$$

Where $X_{1\text{-}\infty}$ represented the fish caught of the same species, and t_h represented the amount of time that the glass eel net was in the water in hours (adapted from: Ellender et al., 2012;

Nolwazi et al., 2024; McNeill et al., 2025). The same formula was used to calculate a CPUE value for each net, where $X_{1-\infty}$ represented the abundance of the different species (adapted from: Ellender et al., 2012; Nolwazi et al., 2024; McNeill et al., 2025).

4.4 Results

During the sampling period, we observed that the uThukela Estuary was closed on all sampling days for the first two months (October 2024 and November 2024) of the sampling period and then remained open on all subsequent sampling days for the last six months (December 2024 - May 2025). The uMkhomazi Estuary was closed on all sampling days during the months of October 2024, November 2024, January 2025 and May 2025, and was open on all sampling days during December 2024, February 2025, March 2025 and April 2025; therefore, it was only recorded open during four of the eight sampling periods. The uMtamvuna Estuary was closed on the sampling days from October 2024 to November 2024, as well as on the sampling days in January 2025 to March 2025; thus, it was recorded as open for only three of the eight sampling periods.

Throughout the study, encompassing all seasons and sites, a total of 20 fish species were recorded (Tables 4.2 and 4.3). Of the 20 fish species recorded across all sites, 15 were recorded at the uThukela Estuary, 12 were at the uMkhomazi Estuary, and nine were at the uMtamvuna Estuary (Tables 4.2 and 4.3). For the uThukela Estuary, *Ambassis natalensis* was the dominant species caught when the mouth was closed (Table 4.3). When the estuary was open, the dominant species were *A. natalensis*, glass eels (*Anguilla* spp.) and *T. jarbua* (Table 4.2). When the mouth of the uMkhomazi Estuary was closed, *A. natalensis* was the dominant species, and when the mouth was open, *A. natalensis* and *T. jarbua* were the dominant species (Tables 4.2 and 4.3). When the mouth of the uMtamvuna Estuary was closed, there were two

dominant species: *A. natalensis* and *T. jarbua* (Table 4.3). When the mouth was open, *A. natalensis*, *T. jarbua* and *R. holubi* were the main dominant species (Table 4.2). When we compared the average length of each species in each estuary, when that estuary was open and closed, the dominant species across all three estuaries, *A. natalensis* and *T. jarbua*, were all smaller when the estuary was open, and caught in greater abundances, compared with when the estuary was closed, with the exception of abundances being smaller when the uMtamvuna Estuary was open (Table 4.2).

Table 4.2: The CPUE, abundance and average length (mm) of each species caught at each estuary when the estuary was open.

		Estuary								
Estuary Mouth Open		**uThukela**			**uMkhomazi**			**uMtamvuna**		
Fish species and common name	**Migratory pathway**	**CPUE**	**Abundance**	**Average length**	**CPUE**	**Abundance**	**Average length**	**CPUE**	**Abundance**	**Average length**
Ambassis natalensis (Slender glassy)	Marine estuarine-opportunist	72.8	874	41	44.5	534	37	37.3	447	36
Terapon jarbua (Crescent grunter)	Marine estuarine-opportunist	15.4	185	44	11.6	139	37	13.8	165	42
Monodactylus argenteus (Silver moony)	Estuarine and marine				4.4	53	62	6.8	82	56
Rhabdosargus holubi (Cape stumpnose)	Marine estuarine-dependent	2.9	35	47				10.3	123	50
Glass eel (*Anguilla* spp.)	Catadromous	30.2	362	39						
Amblyrhynchotes honckenii (Evileye blaasop)	Marine estuarine-opportunist	2.9	35	64	0.8	9	67			
Mugil cephalus (Common mullet)	Marine estuarine-opportunist	4.6	57	56	6.6	79	56			
Glossogobius callidus (Goby)	Freshwater estuarine-opportunist	0.1	1	41	0.4	5	52	1.0	12	67
Microphis brachyurus (Pipe fish)	Amphidromous	0.1	1	45	0.8	9	120			
Enteromius trimaculata (Three spot barb)	Potamodromous	2.3	27	44						
Taenioides jacksonii (Bearded eelgoby)	Estuarine and marine	0.9	11	134						
Leiognathus equula (Common ponyfish)	Estuarine migrant	0.1	1	60	0.3	3	77	0.8	9	57
Anguilla marmorata	Catadromous	0.7	8	208	0.1	1	500			

(Giant mottled eel)							
Anguilla mossambicus (African longfin eel)	Catadromous	0.2	2	269			
Clarias gariepinus (African sharptooth catfish)	Potamodromous	0.1	1	143			
Strongylura leiurus (Banded needlefish)	Estuarine and marine						
Caranx sexfasciatus (Bigeye trevally)	Marine estuarine-opportunist						
Oreochromis mossambicus (Mozambique tilapia)	Freshwater estuarine-opportunist						
Labeobarbus natalensis (KwaZulu-Natal yellowfish)	potamodromous						
*Ophisurus serpens (*Sand snake eel*)*	Marine estuarine-dependent				0.1	1	430

Table 4.3: The CPUE, abundance and average length (mm) of each species caught at each estuary when the estuary was closed

		Estuary								
Estuary Mouth Closed		**uThukela**			**uMkhomazi**			**uMtamvuna**		
Fish species and common name	**Migratory pathway**	**CPUE**	**Abundance**	**Average length**	**CPUE**	**Abundance**	**Average length**	**CPUE**	**Abundance**	**Average length**
Ambassis natalensis (Slender glassy)	Marine estuarine-opportunist	50.1	601	56	29.3	351	42	23.6	283	41
Terapon jarbua (Crescent grunter)	Marine estuarine-opportunist	2.7	32	85	6.6	79	42	15.9	191	43
Monodactylus argenteus (Silver moony)	Estuarine and marine				0.2	2	53	4.9	59	59
Rhabdosargus holubi (Cape stumpnose)	Marine estuarine-dependent				0.3	3	43	6.3	75	65
Glass eel (*Anguilla* spp.)	Catadromous									
Amblyrhynchotes honckenii (Evileye blaasop)	Marine estuarine-opportunist	0.1	1	55	0.8	10	48			
Mugil cephalus (Common mullet)	Marine estuarine-opportunist	4.3	51	62	3.3	40	75	0.1	1	225
Glossogobius callidus (Goby)	Freshwater estuarine-opportunist				0.2	2	63	3.7	44	76
Microphis brachyurus (Pipe fish)	Amphidromous	0.2	2	72	0.2	2	110			
Enteromius trimaculata (Three spot barb)	Potamodromous	0.2	2	68						
Taenioides jacksonii (Bearded eelgoby)	Estuarine and marine									
Leiognathus equula (Common ponyfish)	Estuarine migrant							0.4	5	79

Anguilla marmorata (Giant mottled eel)	Catadromous									
Anguilla mossambicus (African longfin eel)	Catadromous									
Clarias gariepinus (African sharptooth catfish)	Potamodromous	0.1	1	285						
Strongylura leiurus (Banded needlefish)	Estuarine and marine				0.1	1	390			
Caranx sexfasciatus (Bigeye trevally)	Marine estuarine-opportunist							1.1	13	64
Oreochromis mossambicus (Mozambique tilapia)	Freshwater estuarine-opportunist							0.8	9	35
Labeobarbus natalensis (KwaZulu-Natal yellowfish)	Potamodromous	3.5	42	53						
Ophisurus serpens (Sand snake eel)	Marine estuarine-dependent									

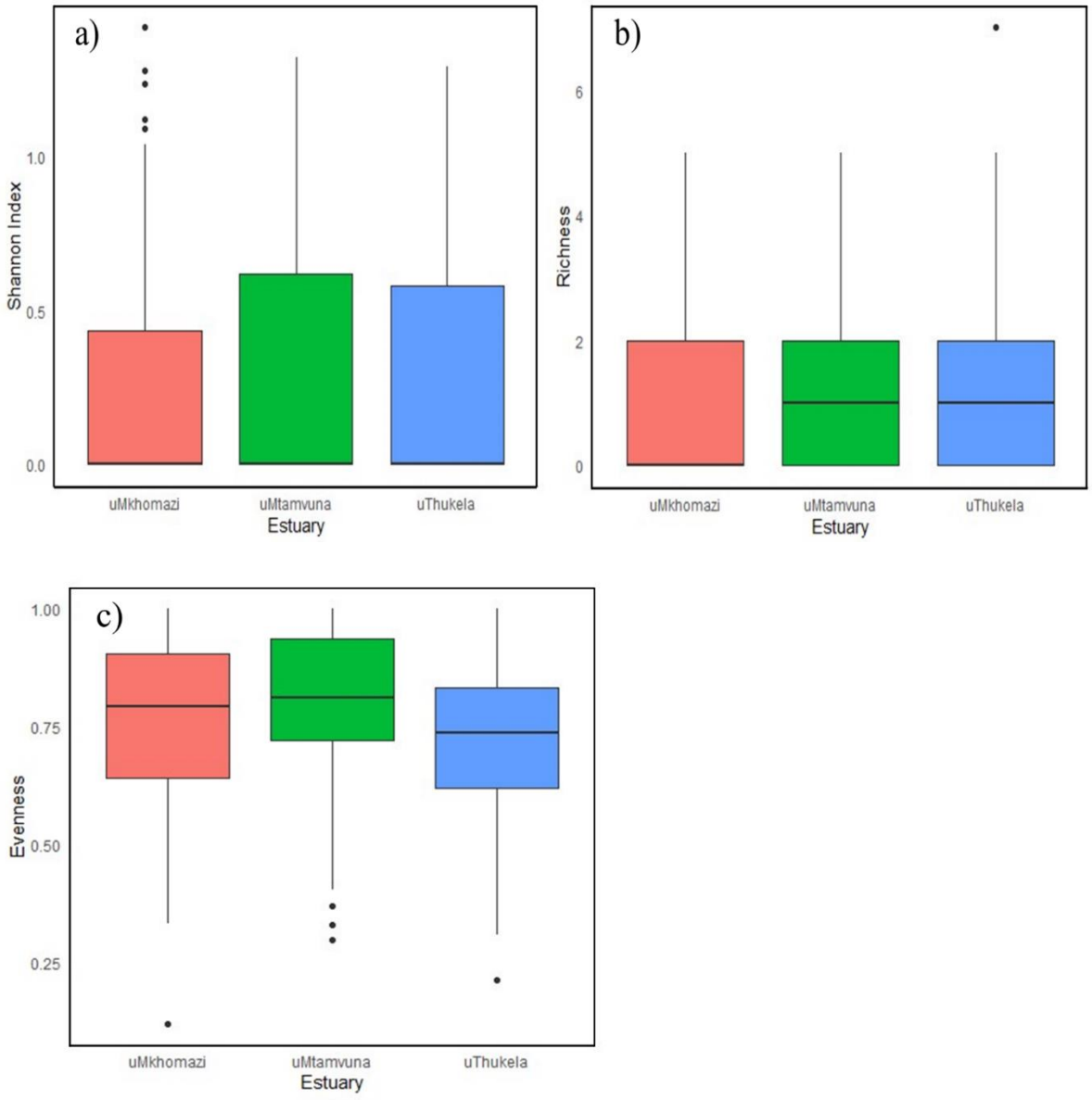


Figure 4.2: Shannon diversity (a), richness (b) and evenness (c) indices across the uThukela, uMkhomazi and uMtamvuna estuaries.

The Shannon diversity between the uThukela and uMtamvuna was higher than that of the uMkhomazi Estuary. The uMkhomazi Estuary exhibited greater variability (Fig. 4.2a). The partially lower Shannon index score for the uThukela resulted from its lower evenness (Fig. 4.2a and 4.2b). The richness per sample was relatively similar between the estuaries (Fig. 4.2b).

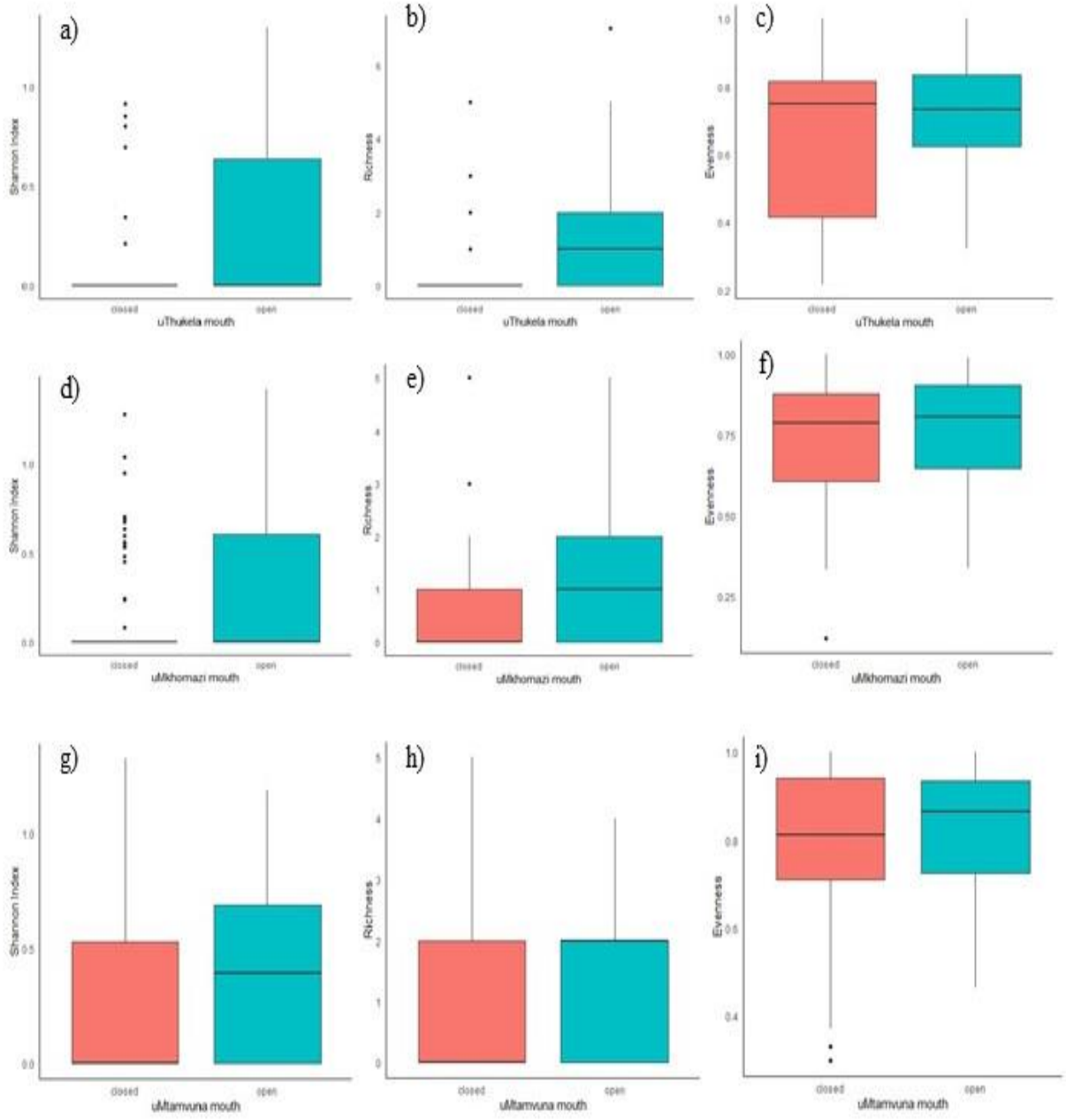


Figure 4.3: Diversity indices, namely Shannon Index, species richness and species evenness for the uThukela Estuary (a-c), uMkhomazi Estuary (d-f) and uMtamvuna Estuary (g-i), during open and closed estuary mouth periods.

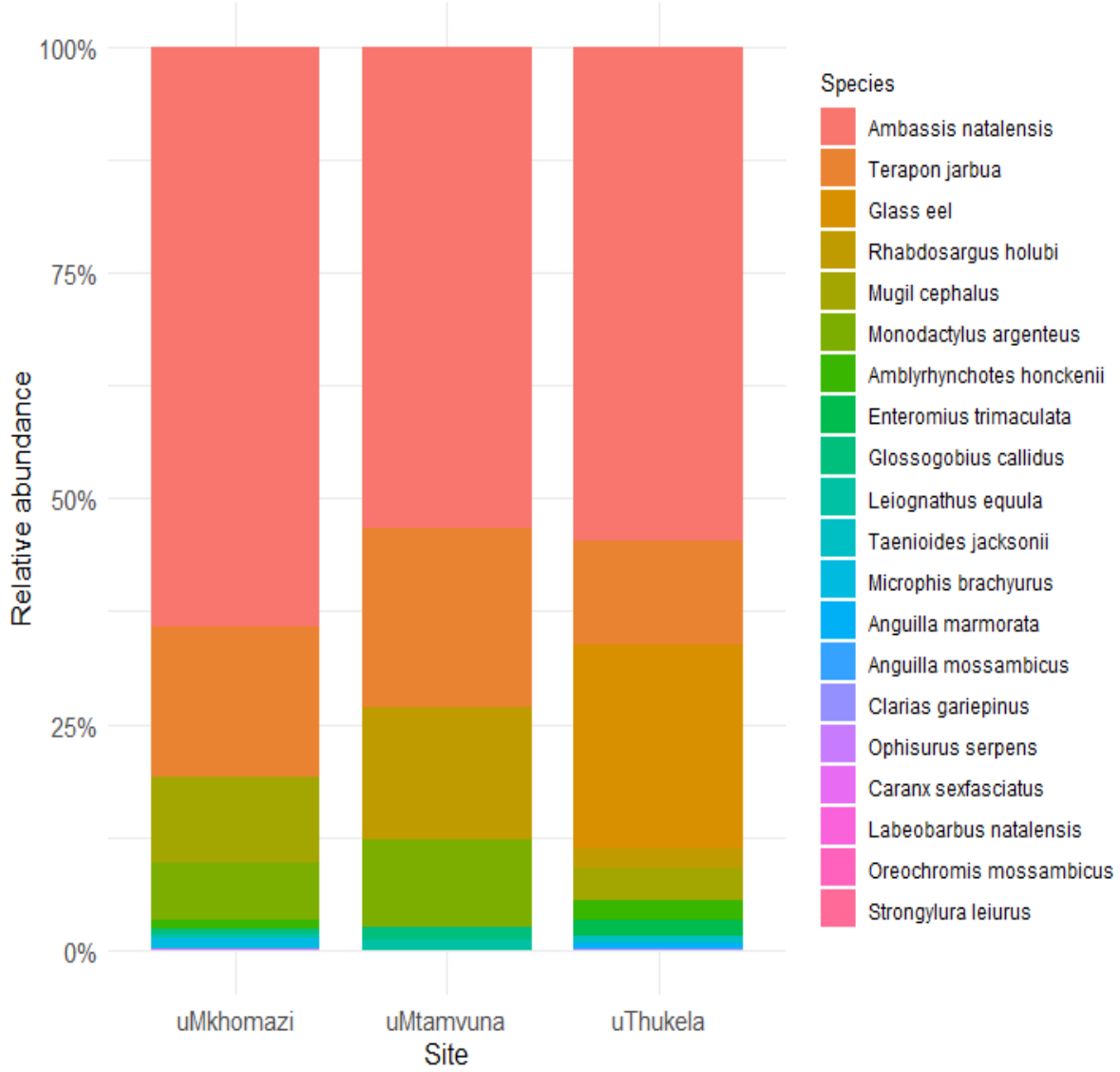


Figure 4.4: Relative abundance plot for each respective fish community in the selected estuaries when the mouth of the estuary was open, where species for each site have been ordered by dominance.

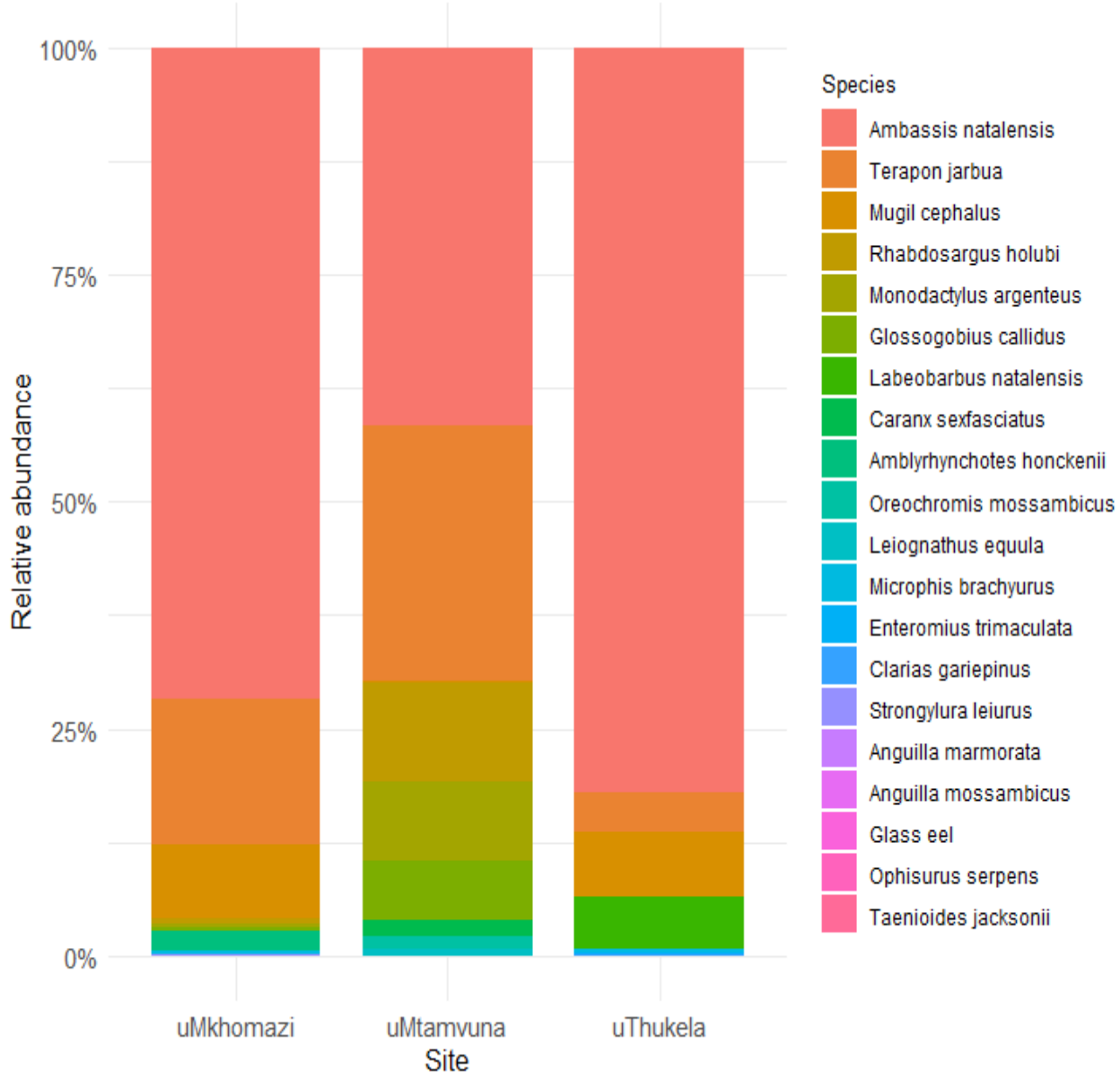


Figure 4.5: Relative abundance plot for each respective fish community in the selected estuaries when the mouth of the estuary was closed, where species for each site have been ordered by dominance.

When we considered the Shannon diversity indices for the uThukela Estuary, we found that the overall diversity and richness were higher when the estuary mouth was open (Figs 4.3a and 4.3b). The uThukela Estuary's evenness was similar during both the open and closed periods (Fig. 4.3c). For the uMkhomazi Estuary, the Shannon diversity indices and the species richness were far higher when the estuary mouth was open (Figs 4.3d and 4.3e). Furthermore, the evenness of the fish community structure of the uMkhomazi Estuary was similarly high during both the open and closed periods (Fig. 4.3f). For the uMtamvuna Estuary, we found that the Shannon diversity indices were higher during the open periods (Fig. 4.3g). However, the open and closed periods for both species richness and evenness in the uMtmavuna Estuary were similar (Figs. 4.3h and 4.3i).

For the habitat variables across all three estuaries, we found that the cover feature variables with significant relationships to the specific species were overhanging vegetation (MANOVA, df = 552, p = 0.0001956) and aquatic vegetation (MANOVA, df = 552, p = $6.759e^{-8}$). The only substrate type across all three estuaries which we found to have a significant relationship with species caught in the selected estuaries was sand (MANOVA, df = 554, p = 0.004482). When we considered the water quality variables, we found that water temperature (MANOVA, df = 550, p = 0.000168), pH (MANOVA, df = 550, p = 0.0117390), electrical conductivity (MANOVA, df = 550, p = $3.126e^{-6}$), salinity (MANOVA, df = 550, p = $4.693e^{-10}$), dissolved oxygen (MANOVA, df = 550, p = $2.518e^{-8}$) and oxygen percentage (MANOVA, df = 550, p = 0.0089626) all had significant relationships with the species caught across the three estuaries.

For the uThukela Estuary, we found that among the cover features recorded in the estuary, only overhanging vegetation had a significant relationship with the different species recorded in the estuary (MANOVA, df = 173, p = $3.208e^{-10}$) (Supplementary Information S4.1).

In terms of the substrate types recorded, we found that none of them had significant relationships with the different species recorded in the estuary (MANOVA (bedrock), df = 175, p = 1.000) and (MANOVA (sand), df = 175, p = 0.09974). When we considered the water quality, we found that the water temperature, electrical conductivity and oxygen percentage had significant relationships with the different species recorded in the uThukela Estuary (MANOVA (Temperature), df = 170, p = 0.02835), (MANOVA (EC), df = 170, p = 0.01761) and (MANOVA (O_2 %), df = 170, p = 0.01226) (Supplementary Information S4.2). When we conducted the CCA model for the uThukela Estuary, we found that the following variables shaped the community as a whole, overhanging vegetation (CCA, df = 1, p = 0.001), aquatic vegetation (CCA, df =1, p = 0.037), dissolved oxygen (CCA, df = 1, p =0.004) and oxygen percentage (CCA, df = 1, 0.006).

For the uMkhomazi Estuary, we found that none of the recorded cover feature variables in the estuary had any significant relationships with the different species recorded in said estuary (MANOVA (OV), df = 176, p = 0.1675), (MANOVA (AV), df = 176, p = 0.3053), (MANOVA (RO), df = 176, p = 0.8330), (MANOVA (WD), df = 176, p = 0.6610) and (MANOVA (RC), df = 176, p = 0.7875). Again, when we considered the substrate types recorded at the uMkhomazi Estuary, none of them showed significant relationships with the different fish species recorded there (MANOVA (sand), df = 180, p = 0.8719). In terms of the water quality, the only variable which had a significant relationship with the different species recorded in the uMkhomazi Estuary was water temperature (MANOVA, df = 174, p = 0.04699) (Supplementary Information S4.3). When we conducted the CCA model for the uMkhomazi Estuary, we found that the following variables shaped the community as a whole, overhanging vegetation (CCA, df = 1, p =0.039), pH (CCA, df = 1, p = 0.02) and TDS (CCA, df = 1, p = 0.015). Finally, when we considered the eco-hydraulic effect on the species recorded in the

uMkhomazi Estuary, we found that none of the recorded eco-hydraulic categories had a significant relationship with any of the recorded species (MANOVA (EcoAv), df = 180, p = 0.3037).

Lastly, when we considered the habitat variable effects on the various fish species recorded in the uMtamvuna Estuary, we found that for the cover features, overhanging vegetation (MANOVA, df = 179, p = 0.04009) and wood debris (MANOVA, df = 179, p = $2.194e^{-8}$) had significant relationships with the specific fish species recorded in the estuary (Supplementary Information S4.4). When we analysed the substrate types recorded and their potential effects on the different fish species recorded in the uMtamvuna Estuary, we found that neither sand (MANOVA, df = 181, p = 0.4803) nor mud (MANOVA, df = 181, p = 1.000) had significant relationships. With regards to the analyses, we performed on the water quality variables, we found that water temperature (MANOVA, df = 176, p = 0.0013618), pH (MANOVA, df = 176, p = 0.0430579), salinity (MANOVA, df = 176, p = 0.0203207) and dissolved oxygen (MANOVA, df = 176, p = 0.0004568) had significant relationships with the different fish species recorded at the uMtamvuna Estuary (Supplementary Information S4.5). When we conducted the CCA model for the uMtamvuna Estuary, we found that the following variables shaped the community as a whole: wood debris (CCA, df = 1, p = 0.006) and salinity (CCA, df = 1, p = 0.015).

4.5 Discussion

Of the three selected estuaries, we found that the uThukela Estuary was the most species-rich, followed by the uMkhomazi Estuary, and then the uMtamvuna Estuary. Previous studies have found that the more persistent the connection between the estuary and the ocean is, the greater the species richness of that estuary would be (Vasconselos et al., 2015; Adams et al., 2021;

Whitfield et al., 2023). Our findings supported this, with the uThukela Estuary having 15 species recorded (continuously open for six out of eight months), the uMkhomazi Estuary having 12 species recorded (open for four out of eight months, inconsistently), and the uMtamvuna Estuary having nine recorded species (open for 3 out of 8 months, inconsistently). Furthermore, in terms of connectivity, the uThukela Estuary was the only estuary in which glass eels were recorded during the course of the study, which is an indication of a fair degree of connectivity between the ocean and the estuarine system in question (Righton et al., 2021; Hanzen et al., 2022). In comparison, we recorded *A. marmorata* in the yellow eel life cycle stage in the uMkhomazi, which is an indication that glass eels have recruited previously into this estuary, an indication that the degree of connectivity has decreased, as we expected to record glass eels in the uMkhomazi (Righton et al., 2021; Hanzen et al., 2022).

The closed status of these estuaries, which should be open more frequently, is concerning and reflects the low species richness in the present study (SAEON, 2012; Fernandes and Adams, 2016; van Niekerk et al., 2020). Presently, a paper mill, Sappi-Saiccor, utilises the uMkhomazi River, abstracting water to facilitate their industrial processes. These abstractions can have significant adverse impacts on connectivity, particularly actions such as the sand berm the company builds during low-flow periods in the winter months (Young et al., 1997; Whitfield, 2005). There have been proposed future abstractions from both the uThukela and uMkhomazi Rivers, which will have adverse effects on the fish communities of the estuaries, by altering flow regimes, alterations in water quality, particularly salinity, all of which have a compounding effect on the fish communities residing within the estuaries in question (Young et al., 1997; Whitfield, 2005). The effects of these proposed abstractions will introduce additional factors related to the exclusion of migratory and estuarine-dependent fish species, further reducing the species richness of these estuaries (Young et al., 1997; Whitfield, 2005).

All three estuaries sampled in the present study, particularly the uThukela and uMkhomazi estuaries, should be open far more frequently than was recorded, as shown in other studies (Stretch and Parkinson, 2006; SAEON, 2012; van Niekerk et al., 2020). In light of the proposed increases in abstraction from both the uThukela and uMkhomazi estuaries in the near future, management practices geared towards maintaining connectivity in these systems become increasingly important, as the increases in abstraction may lead to longer closure times of these estuaries, moving further away from the connectivity which should be present (SAEON, 2012; van Niekerk et al., 2020). Additionally, increased abstraction from these estuaries may lead to salt intrusion, which in turn may lead to the exclusion of estuarine fish with lower saline tolerances, allowing more saline-tolerant species to dominate and thus shift the balance in the present uThukela and uMkhomazi estuarine communities (Zhang et al., 2012; van Niekerk et al., 2022). Freshwater abstraction reduces the volume of freshwater entering the estuary (Young et al., 1997; Whitfield, 2005). The plumes produced by freshwater leaving an estuary has been found in previous studies to be a chemical cue for recruitment utilised by anguillid eels to orientate themselves towards the mouth of the estuary, where a significant reduction therein would further impact recruitment of these catadromous fish negatively (Arribas et al., 2012). The resource quality objectives outlined by the South African government for these rivers include maintaining flow regimes, ensuring water quality, promoting the presence and persistence of species, and enhancing the aquatic habitat to support all native species (Department of Water and Sanitation, 2022). If these resource quality objectives are carried out appropriately and effectively, the fish communities of these estuaries could be restored to their natural state.

In relation to the fish species and their migratory pathways, there were more marine estuarine-dependent species present when the estuary was open (Tables 4.2 and 4.3). However,

the dominant species across all three estuaries, whether open or closed, were marine estuarine-opportunistic species (Table 4.2 and 4.3). Among catadromous species, none were recorded when the mouth of the estuary was closed, further highlighting the importance of connectivity to their migratory pathways (Hanzen et al., 2019; Righton et al., 2021). This was more evidence supporting the importance of connectivity, as the species that dominated these estuaries, which had been frequently closed, were those that did not depend on the estuary but could thrive there (Loneragan et al., 1989; Potter et al., 2001). The reduction in connectivity between marine, estuarine and freshwater systems negatively impacts not only the fish assemblages present within these estuaries, but the fish species who depend on these estuaries for various processes critical to their life cycles, like seeking sheltered habitat, foraging and utilising it either as a breeding ground or a pathway to reach their breeding grounds (Potter et al., 2015; Righton et al., 2021; Hanzen et al., 2022; Elliot and Whitfield, 2025).

For all the selected estuaries, we found that fish species richness was higher when the estuary mouth was open (Nicolas et al., 2010; Vasconcelos et al., 2015). The evenness was relatively similar across both the open and closed periods; however, there were some dominant species present, more so when the estuary was closed. Two species were generally dominant in these estuaries, namely *A. natalensis* and *T. jarbua*, indicating unusual closure periods as found in other studies (Harrison and Whitfield, 1995; Levin et al., 2022). Previous studies have found that when an estuary is closed, dominant species emerge in the fish community, as migratory species from the ocean are cut off and unable to contribute to the estuary's community (Harrison and Whitfield, 1995; Levin et al., 2022). Our findings of increased species richness across all sites when the estuary mouth is open supported this trend. Dominant species may also arise because of factors related to abstraction practices taking place on the uThukela and uMkhomazi estuaries, where decreased freshwater inflow may restrict less saline

tolerant species from entering the estuary because of salt intrusion, or by reducing the connectivity between the estuarine and freshwater environments (Zhang et al., 2012; van Niekerk et al., 2022; Adams et al., 2023).

Our study showed that, when comparing the average length of individual species across estuaries, both when open and when closed, the fish average standard length was generally greater when the estuary was closed. However, species abundances were generally higher when the estuaries were open. These findings are supported by previous studies that have found that when connectivity between the estuary and the ocean is present, large numbers of fish migrate into estuaries to spawn, feed, or seek refuge (Sheaves et al., 2015; Becker et al., 2016). Catadromous fish species use estuaries either as a spawning ground for their larvae or as a migratory pathway for their juvenile life cycle stages to pass through, while juvenile oceanodromous species may use estuaries to seek refuge, which explains why when the estuary mouth is open, the abundance of smaller individuals is greater than when the estuary mouth is closed (Wallace et al., 1984; Potter et al., 2015; Sheaves et al., 2015; Becker et al., 2016; Whitfield et al., 2017; Hanzen et al., 2019; Righton et al., 2021).

When we considered the effects of environmental variables, such as cover features, substrate types, and water quality, on shaping community structures within the selected estuaries. We found that each estuary and its respective fish communities were shaped by a combination of factors that may differ between estuaries (Asha et al., 2015; Molina et al., 2020). For the uThukela Estuary, the environmental variables found to be significant were overhanging vegetation, water temperature, electrical conductivity and oxygen percentage, similar to findings from other studies (Asha et al., 2015; Molina et al., 2020). In the uMkhomazi Estuary, the only environmental variable that significantly influenced the fish community was water temperature, a factor that previous studies have found important in shaping estuarine fish

communities (Asha et al., 2015; Molina et al., 2020). Water temperature is particularly important in estuarine communities, as it serves as a cue for migration in and out of the estuary for some species (Gillanders et al., 2011). Furthermore, water temperature influences other processes and factors in fish, such as metabolism and salinity tolerance, and may dictate which predator or prey species are present (Likongwe et al., 1996; Bœuf and Payan, 2001; Gillanders et al., 2011). Regarding the uMtamvuna Estuary, we found that overhanging vegetation, wood debris, water temperature, pH, salinity, and dissolved oxygen all played significant roles in shaping the fish community (Asha et al., 2015; Molina et al., 2020). Within each estuary, the variables found to be significant influenced the different fish species in these communities in different ways, suggesting that the communities are reliant on a heterogeneous mixture of these variables to remain stable, as in other studies (e.g., Amorim et al., 2017; Asha et al., 2015; Duque et al., 2020; Molina et al., 2020). Importantly, water temperature was a significant factor in shaping community structure across all three estuaries. Thus, in a changing climate, where water temperatures are expected to fluctuate, the impact on estuarine fish communities is also expected to be significant (Whitfield, 2021).

Each estuary exhibited a degree of connectivity when open, hosting migratory species, such as the amphidromous *A. natalensis, T. jarbua, G. callidus,* and *L. equula*, for which connectivity is crucial. However, because of the presence of migratory species in greater abundance and over longer time periods, and others like *M. cephalus*, the connectivity of the uThukela and uMkhomazi was greater than that of the uMtamvuna. While we had recorded a *O. serpens* and an *A. marmorata* individual in the yellow eel life cycle stage, and *M. cephalus* individuals in the uMkhomazi, the uThukela exhibited greater abundances and diversity of migratory individuals like *Anguilla* spp. in their glass eel life cycle stage, and the estuarine -

marine *T. jacksonii*, suggesting that the degree of connectivity in the uThukela Estuary was the strongest across the three selected estuaries.

It was evident through our study that the fish communities residing in the three selected estuaries are shaped by numerous abiotic variables such as connectivity, water temperature, salinity and dissolved oxygen, to name a few (Asha et al., 2015; Hanzen et al., 2022; Molina et al., 2020; Righton et al., 2021). These factors affect the different species within the respective communities differently, and for these communities to persist, a stable heterogeneous mixture of these abiotic factors is needed (Amorim et al., 2017; Asha et al., 2015; Duque et al., 2020; Molina et al., 2020). Presently, certain resource quality objectives like habitat integrity are not being met, as the present study has highlighted functions like connectivity, which have decreased, resulting in estuaries having longer closure times (SAEON, 2012; DWS, 2014; van Niekerk et al., 2020; DWS, 2022; Government of South Africa, 2023). Management practices need to be optimised and adapted to meet the resource-quality objectives for these systems, thereby helping conserve these fish communities as the climate changes.

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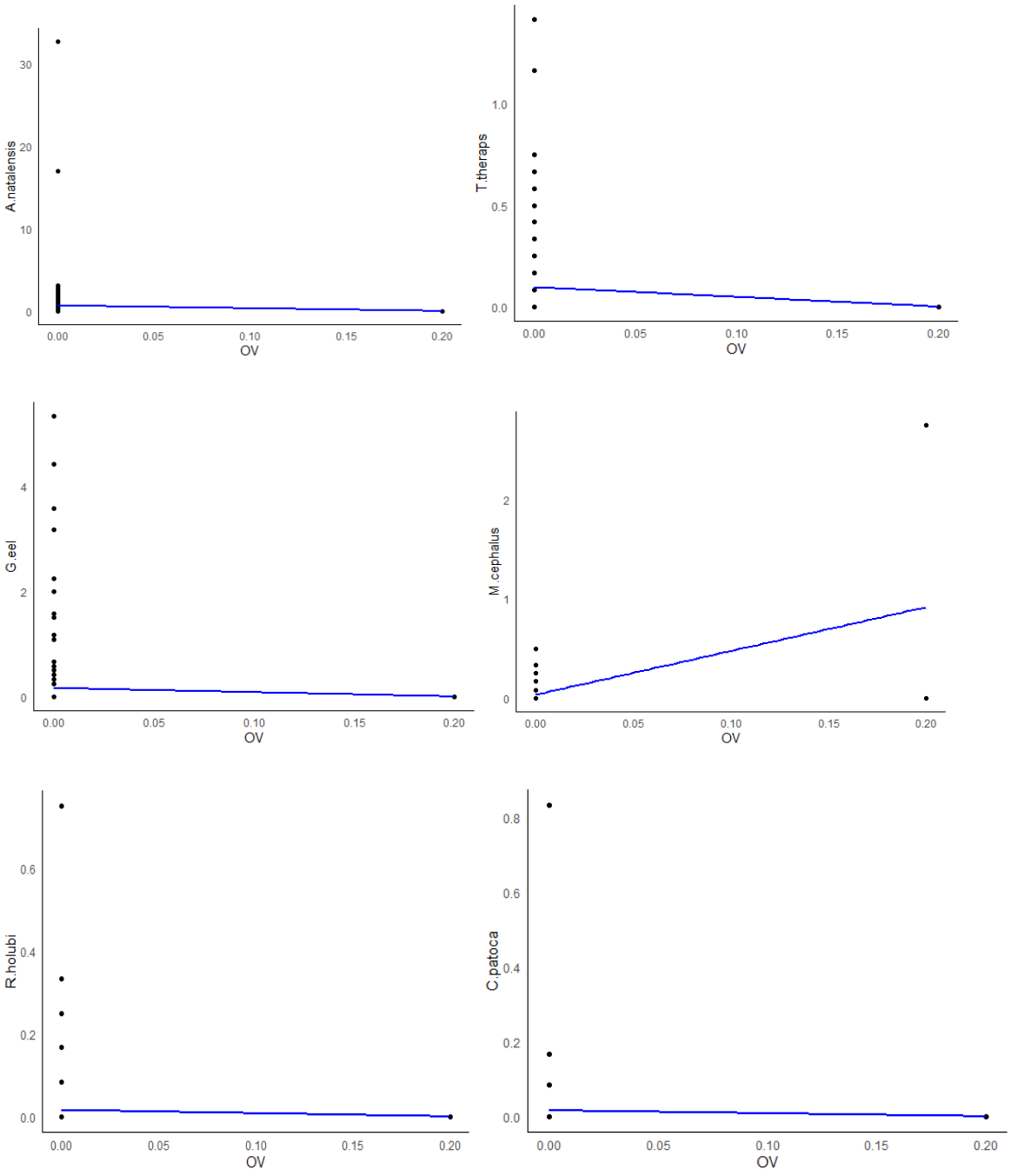
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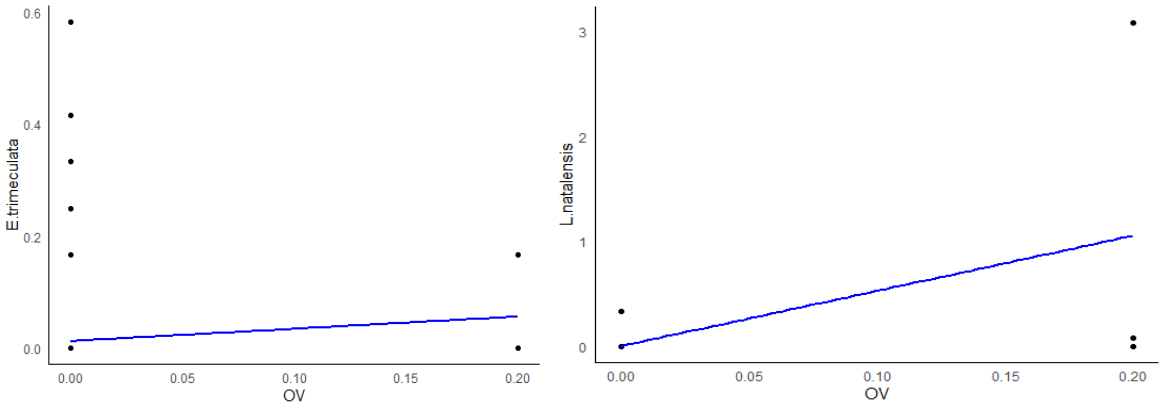
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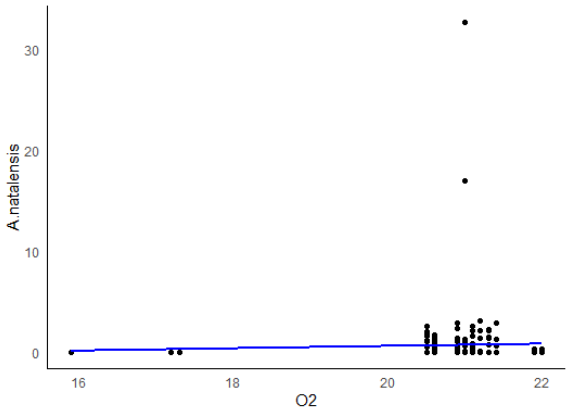
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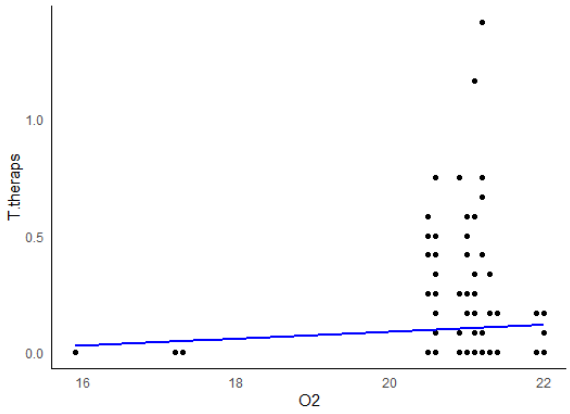
4.8 Supplementary information

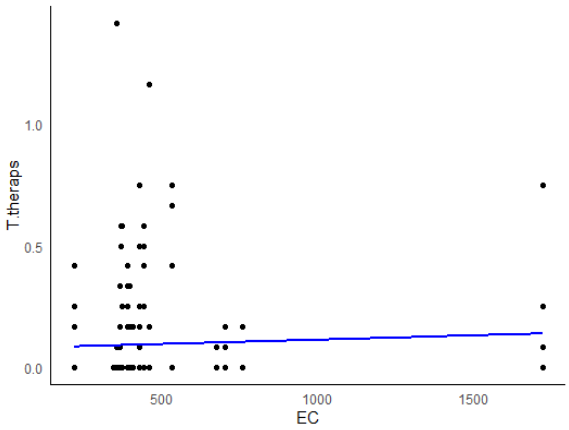


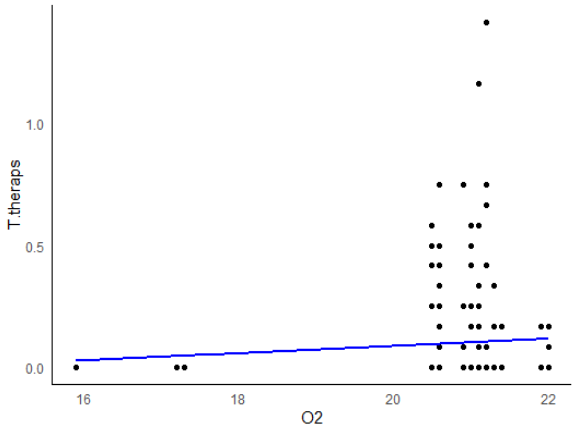


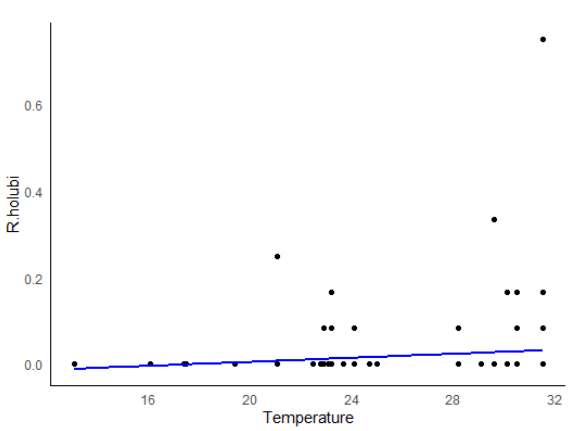
Supplementary information Figure S4.1 (a-h): Significant correlations between certain fish species recorded in the uThukela Estuary and the cover feature found to be significant (OV).

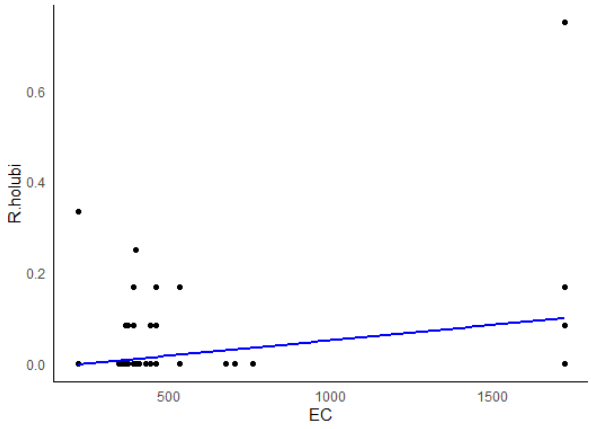

A.natalensis
30
20
10
0
16
18
20
22
O2

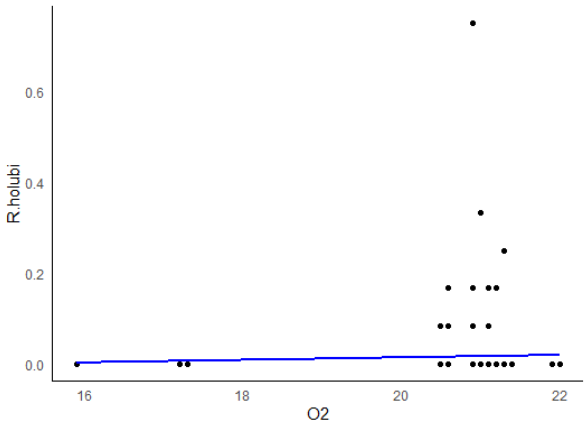

T.theraps
1.0
0.5
0.0
16
18
20
22
O2

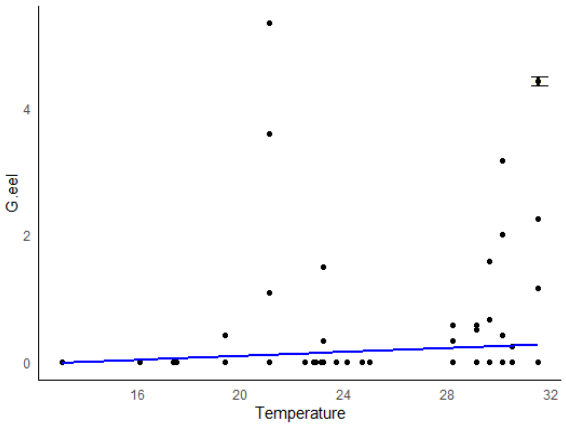

T.theraps
1.0
0.5
0.0
500
1000
1500
EC

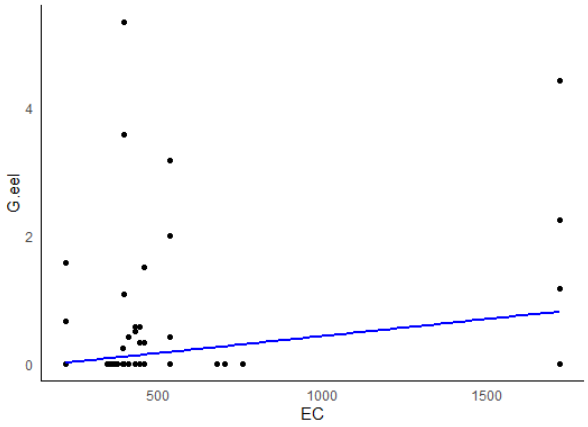

T.theraps
1.0
0.5
0.0
16
18
20
22
O2

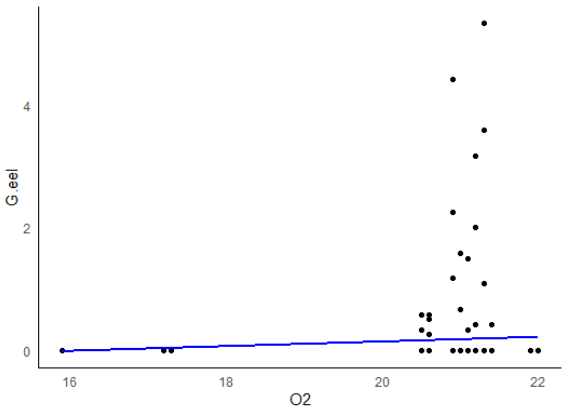

R.holubi
0.6
0.4
0.2
0.0
16
20
24
28
32
Temperature

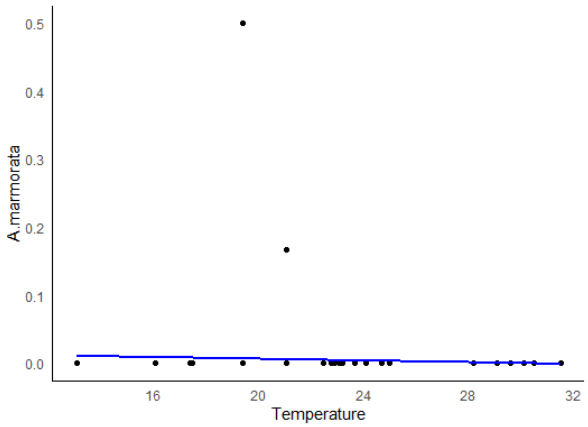

R.holubi
0.6
0.4
0.2
0.0
500
1000
1500
EC

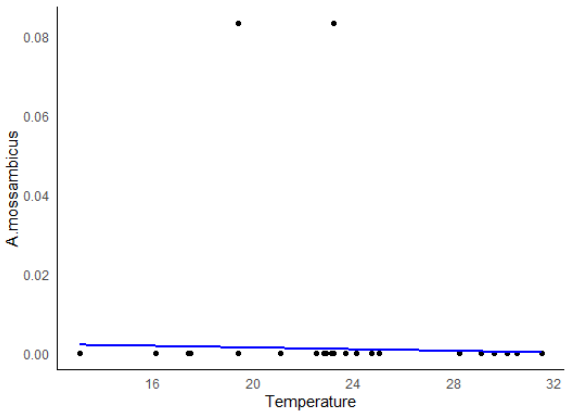

R.holubi
0.0
0.2
0.4
0.6
16
18
20
22
O2

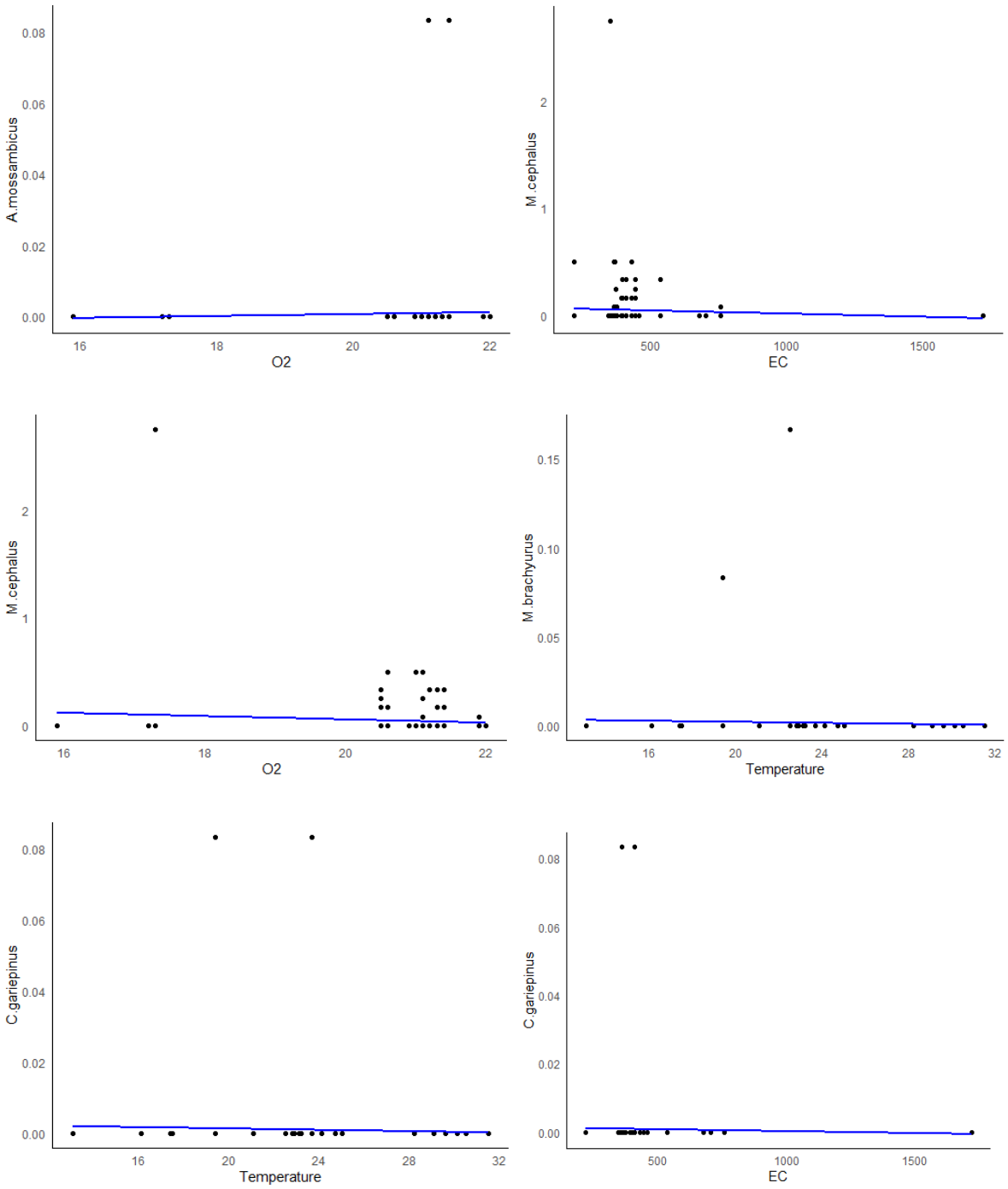

G.eel
0
2
4
16
20
24
28
32
Temperature

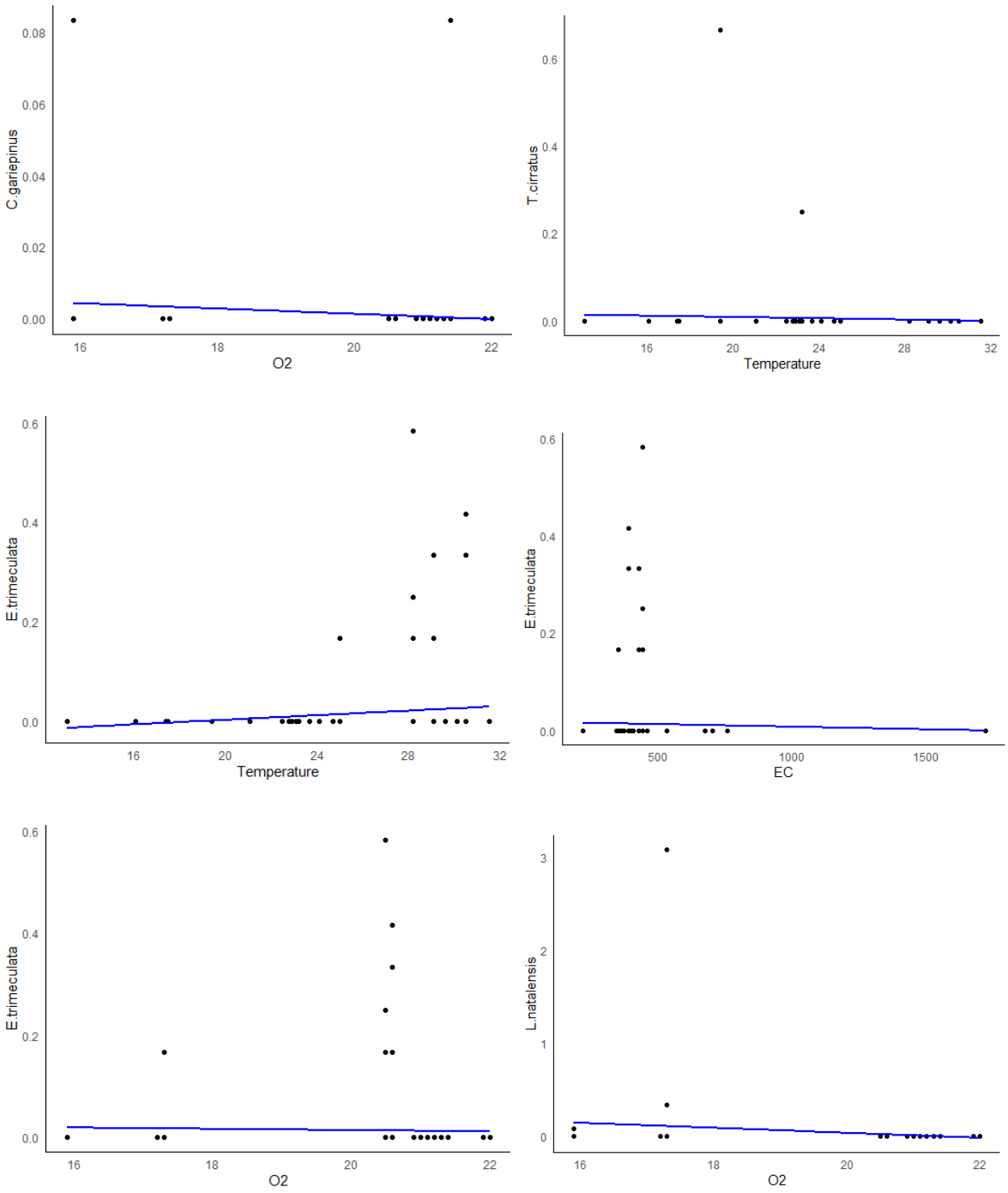

G.eel
0
2
4
500
1000
1500
EC


G.eel
0
2
4
16
18
20
22
O2

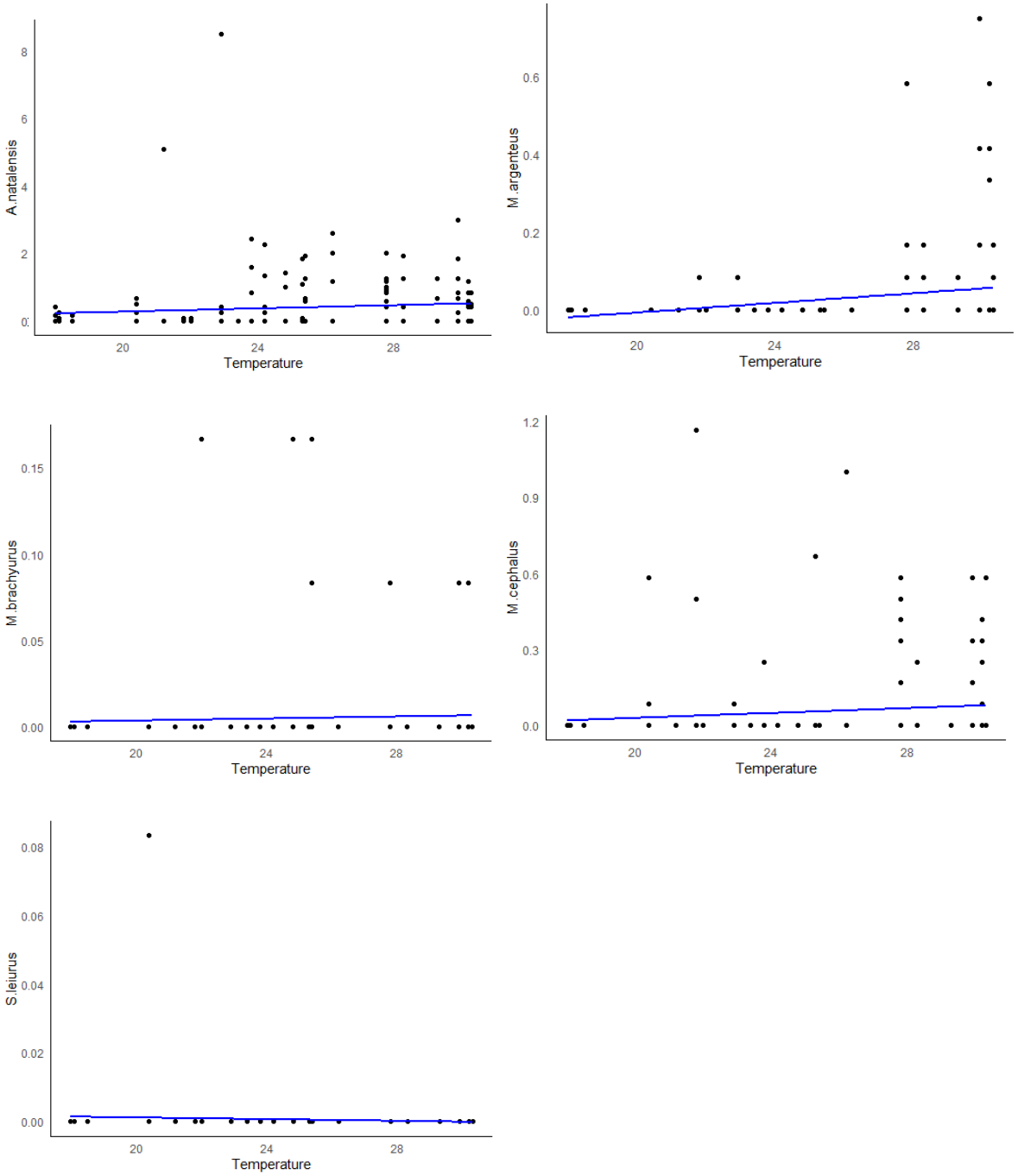

A.marmorata
0.0
0.1
0.2
0.3
0.4
0.5
16
20
24
28
32
Temperature


A.mossambicus
0.00
0.02
0.04
0.06
0.08
16
20
24
28
32
Temperature

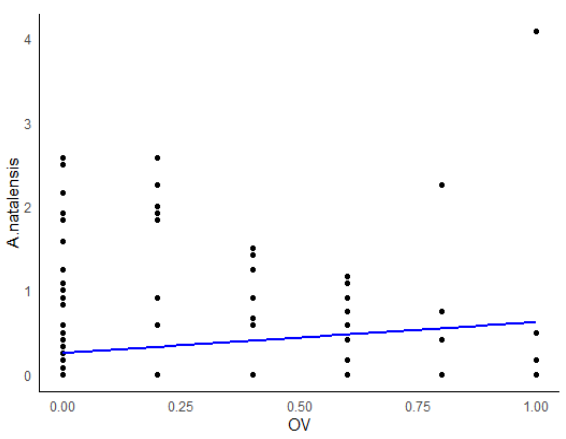

A.mossambicus
0.08
0.06
0.04
0.02
0.00
16
18
20
22
O2
M.cephalus
2
1
0
500
1000
1500
EC
M.cephalus
2
1
0
16
18
20
22
O2
M.brachyurus
0.15
0.10
0.05
0.00
16
20
24
28
32
Temperature
C.gariepinus
0.08
0.06
0.04
0.02
0.00
16
20
24
28
32
Temperature
C.gariepinus
0.08
0.06
0.04
0.02
0.00
500
1000
1500
EC

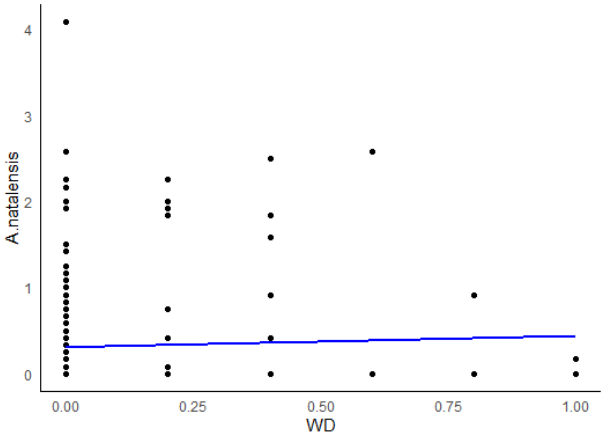


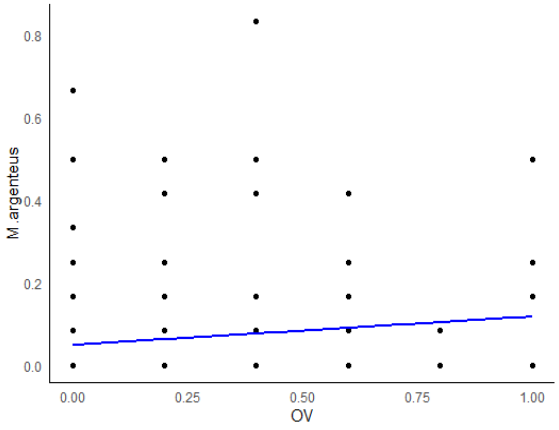
Supplementary information Figure S4.2 (a-x): Significant correlations between certain fish species recorded in the uThukela Estuary and the water quality variables found to be significant (Temperature, EC and O_2 %).

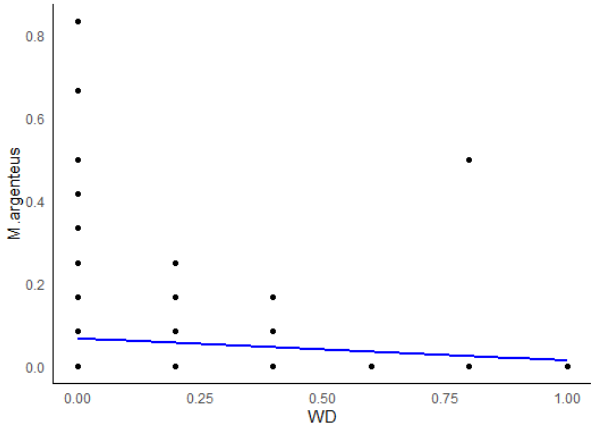


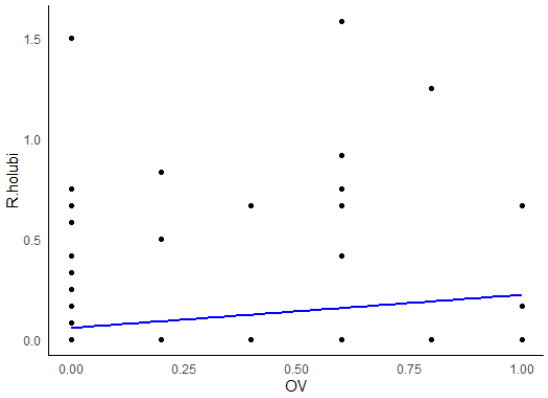
Supplementary information Figure S4.3 (a-e): Significant correlations between certain fish species recorded in the uMkhomazi Estuary and the water quality variable found to be significant (Temperature).

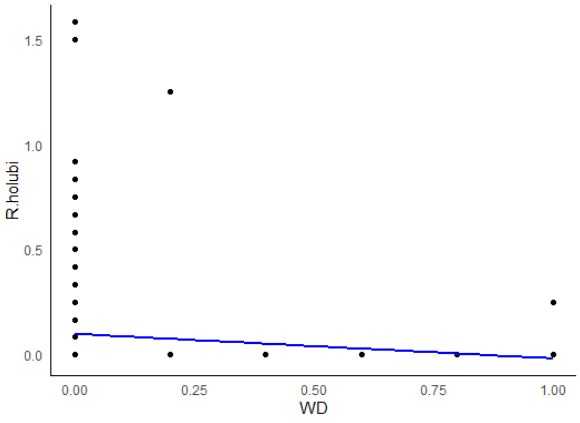

A.natalensis
OV
0
1
2
3
4
0.00
0.25
0.50
0.75
1.00

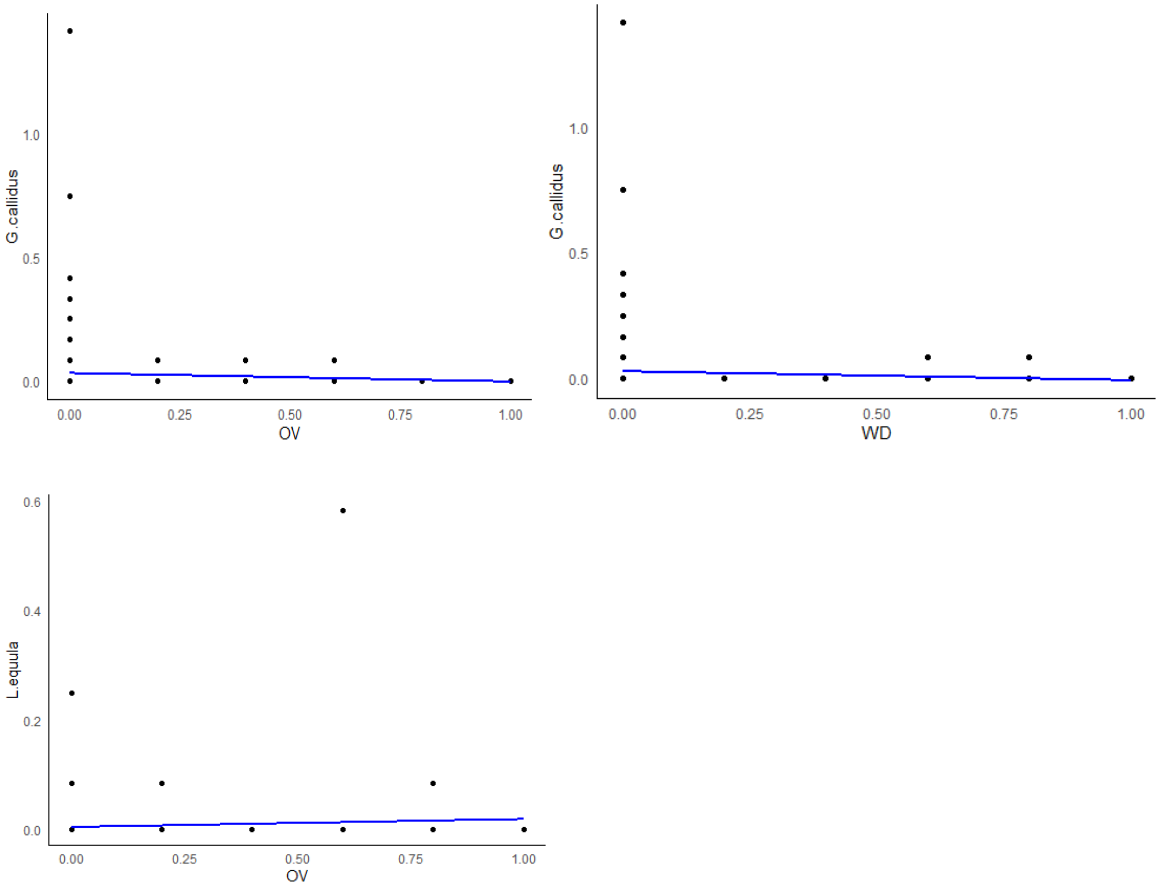

A.natalensis
WD
0
1
2
3
4
0.00
0.25
0.50
0.75
1.00


M.argenteus
OV
0.0
0.2
0.4
0.6
0.8
0.00
0.25
0.50
0.75
1.00

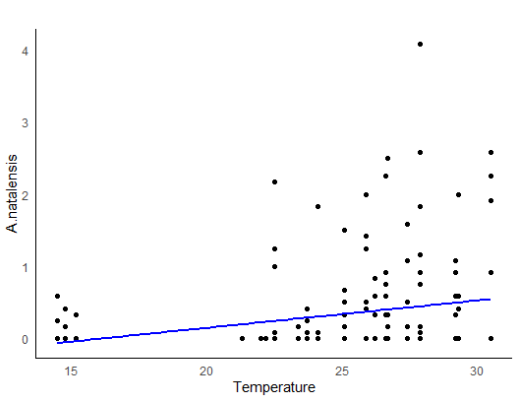

M.argenteus
WD
0.0
0.2
0.4
0.6
0.8
0.00
0.25
0.50
0.75
1.00

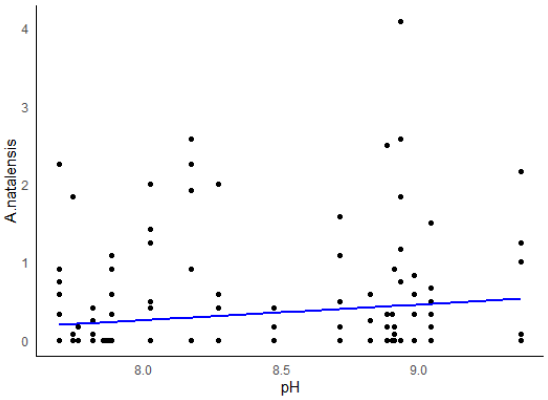

R.holubi
OV
0.0
0.5
1.0
1.5
0.00
0.25
0.50
0.75
1.00

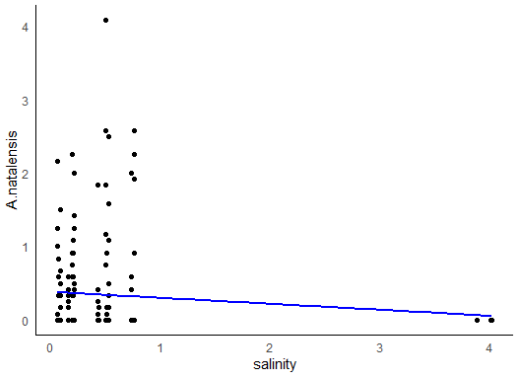

R.holubi
WD
0.0
0.5
1.0
1.5
0.00
0.25
0.50
0.75
1.00

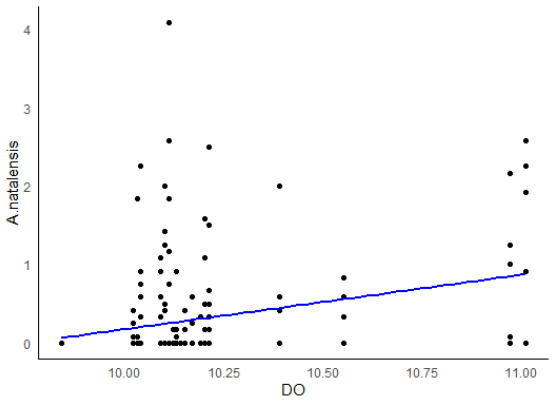


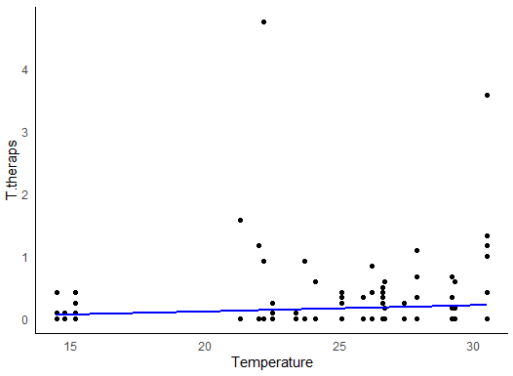
Supplementary Figure S4.4 (a-i): Significant correlations between certain fish species recorded in the uMtamvuna Estuary and the cover feature variables found to be significant (OV, WD).

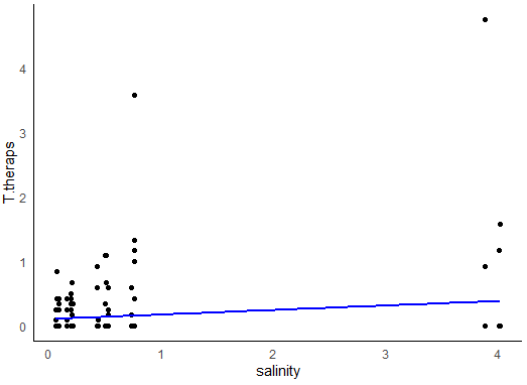

A.natalensis
Temperature

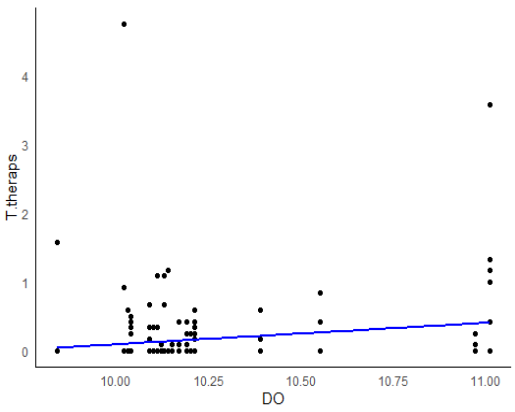

A.natalensis
pH

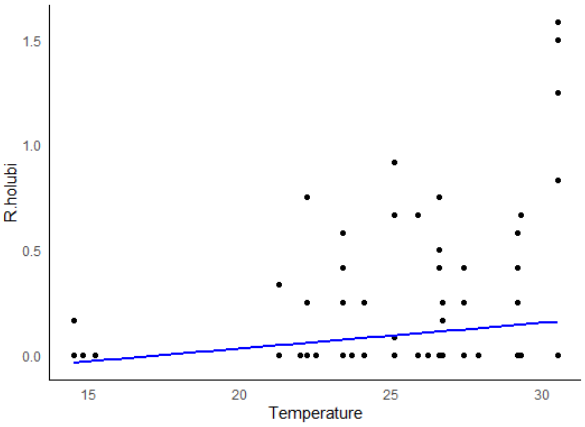

A.natalensis
salinity

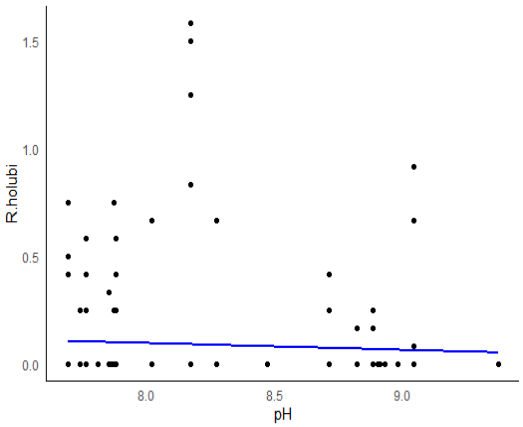

A.natalensis
DO

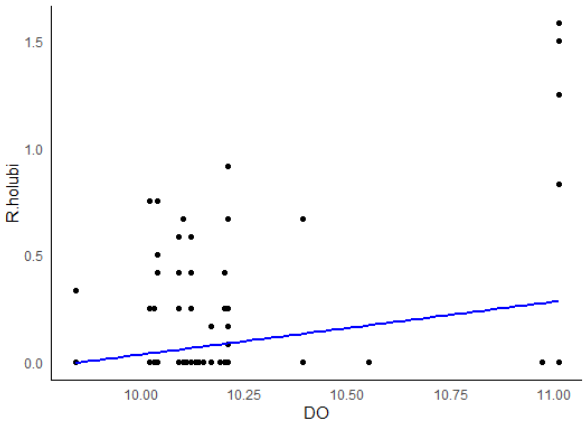

T.theraps
Temperature

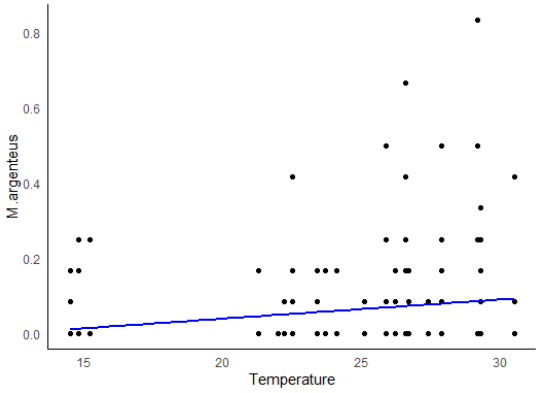

T.theraps
salinity

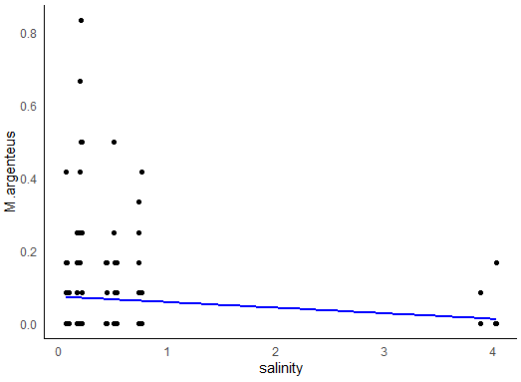

T.theraps
DO

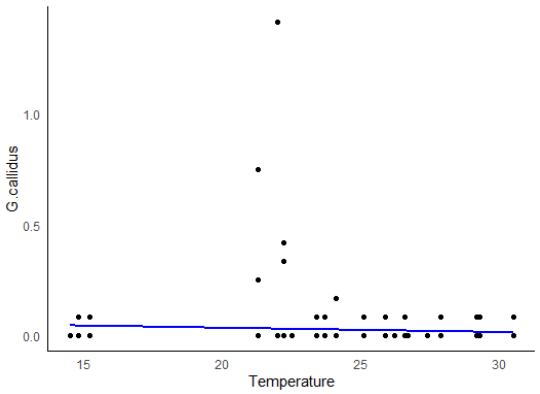

R.holubi
Temperature

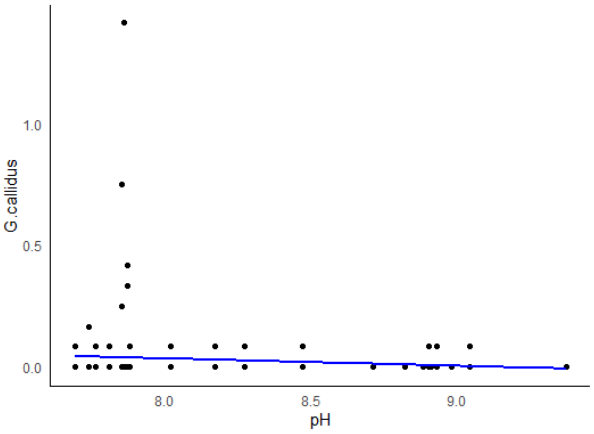

R.holubi
1.5
1.0
0.5
0.0
8.0
8.5
9.0
pH

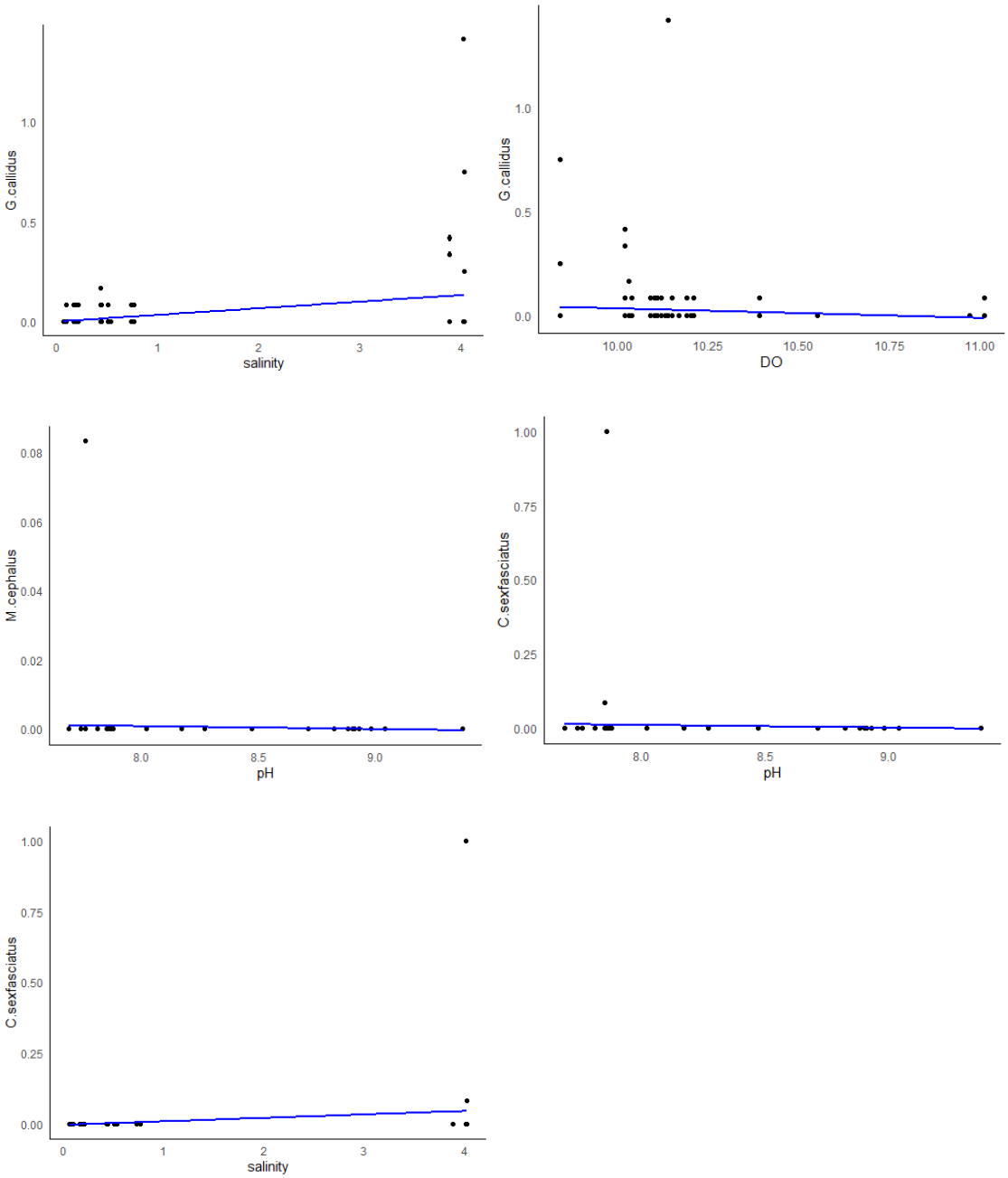

R.holubi
1.5
1.0
0.5
0.0
10.00
10.25
10.50
10.75
11.00
DO


M.argenteus
0.8
0.6
0.4
0.2
0.0
15
20
25
30
Temperature


M.argenteus
0.8
0.6
0.4
0.2
0.0
0
1
2
3
4
salinity


G.callidus
1.0
0.5
0.0
15
20
25
30
Temperature


G.callidus
1.0
0.5
0.0
8.0
8.5
9.0
pH



Supplementary Figure S4.5: Significant correlations between certain fish species recorded in the uMtamvuna Estuary and the water quality variables found to be significant (Temperature, pH, salinity and DO).

CHAPTER 5

General discussion, conclusions, and recommendations

5.1 Background

It is evident that connectivity between aquatic environments is crucial for the fauna inhabiting these ecosystems, as well as for the functioning and resilience of freshwater, estuarine, and marine ecosystems (Hanzen et al., 2019; Havn et al., 2020). While the importance thereof is well known, several anthropogenic activities lead to a reduction in the degree of connectivity present between and within these ecosystems (Marcinkowski and Grygoruk, 2017; Havn et al., 2020; Mishra, 2023). The hindrance of connectivity brings about numerous challenges, particularly in terms of conservation efforts for migratory aquatic fauna (Havn et al., 2020; Righton et al., 2021; Hanzen et al., 2022). While solutions to connectivity issues exist, mismanagement often prevents appropriate action from being taken. These issues highlighted the need to demonstrate how connectivity issues are affecting aquatic fauna in South African rivers. For migratory species like the African freshwater eels (*Anguilla* spp.), and species residing in estuaries, to which connectivity between freshwater, estuarine and marine ecosystems is of great importance, it became evident that being able to determine which factors shaped these community structures and which influenced processes such as recruitment would aid in being able to not only better protect and conserve these fauna, but also to be used as a means to advocate for intervention where connectivity has been impaired (Tsukamoto and Aoyama, 1998; Hanzen et al., 2021).

5.2 Connectivity of the uMkhomazi River

The impact of four selected instream barriers (weirs) on migratory fish species, with a particular focus on the four African freshwater eel species, was assessed in the uMkhomazi River (Chapter 2). While *Anguilla* spp. were recorded in most of the selected river fragments, apart from the last, the findings showed that connectivity was still significantly hindered. Instream barriers fragmented the available habitat, leading to uneven species distributions between each successive river fragment and potentially restricting the longitudinal movement of fish. Species richness displayed a significant decline as the sampling distance from the river mouth increased.

It is recommended that prospective barriers should have appropriate fishways constructed within them to reduce the effects of the fragmented habitat and maintain a certain degree of connectivity within the system (Righton et al., 2021; Hanzen et al., 2022; Chapter 2). For existing barriers, they should be retrofitted with appropriate fishways to restore connectivity (Burnett et al., 2023; Chapter 2). It is also advisable that within each respective river fragment, conservation efforts aimed at providing fish with suitable habitat are conducted to promote and conserve all fish species present (Negro et al., 2021; Stoffers et al., 2022; Chapter 2). Lastly, future studies may benefit from examining whether gene flow exists between *Labeobarbus natalensis* populations across the respective river fragments. It is also advisable that where redundant barriers are present, they are actively managed through removals or upgrades to meet the required aquatic faunal connectivity.

5.3 Cues of eel recruitment into South African estuaries

The recruitment of African freshwater eels into estuaries is a process crucial to their life cycle, where, in most cases, if they are unable to do so, they die (Arai and Chino, 2018). The

recruitment of these African freshwater eels into estuaries is ecologically important too, because following their migration into the estuaries, they migrate to freshwater systems where they will mature, and in many of the rivers in the Eastern Cape Province of South Africa, they are the only native top fish predator (Parker et al., 2011).

The recruitment cues for African freshwater eels (*Anguilla* spp.) were studied in the uThukela, uMkhomazi, and uMtamvuna estuaries (Chapter 3). Consistent connectivity between the estuarine and marine environments, the rainy season, high tides, moon phases with low levels of light intensity, and increases in dissolved oxygen, oxygen percentage and electrical conductivity (when electrical conductivity is related to increased nutrient deposition) were variables which had significant positive correlations with the catch per unit effort of *Anguilla* spp. (in the glass eel stage) (Chapter 3). Furthermore, previous studies have found that freshwater flow rates influence glass eel recruitment through connectivity maintenance, and that the freshwater plumes released into the ocean via the estuary are used by glass eels to orient themselves towards the mouth of the estuary (Arribas et al., 2012). Importantly, the estuaries sampled in the present study should be opened more frequently than recorded, indicating that intervention is required to maintain the naturally occurring connectivity of these estuaries (SAEON, 2012; Fernandes and Adams, 2016; van Niekerk et al., 2020).

While African anguillids are apex fish predators in many South African river systems, they are not categorised as protected species in South Africa (Hanzen et al., 2022). This highlights the need to list these species under the National Environmental Management: Biodiversity Act (NEMBA) Act 10, 2004, as this will provide national-level protection for the species (Government of South Africa, 2004). It is further recommended that conservation efforts tailored towards maintaining the natural degree of connectivity between the marine and estuarine systems would allow the continued recruitment of these four globally important eel

species (Righton et al., 2021; Hanzen et al., 2022; Chapter 3). Additionally, efforts to restore the naturally occurring estuarine water quality would increase the ecosystem health, and in turn allow the persistence of *Anguilla* spp. in estuarine systems.

5.3 Estuarine communities and the factors shaping them

The fish community structures within the uThukela, uMkhomazi, and uMtamvuna estuaries of KwaZulu-Natal, along with the factors shaping them, were assessed (Chapter 4). This study highlighted the complexity of the fish communities residing within these estuaries (Chapter 4). The uThukela Estuary had greater connectivity than the uMkhomazi and uMtamvuna Estuaries, as the presence and diversity of migratory species were greatest (Chapter 4). When the same migratory species were recorded in the other estuaries, their abundances were generally larger in the uThukela Estuary (Chapter 4). Furthermore, it showed that the degree of connectivity, water temperature, salinity and dissolved oxygen were key factors shaping the fish community structures within all three estuaries (Asha et al., 2015; Hanzen et al., 2022; Molina et al., 2020; Righton et al., 2021; Chapter 4).

It is therefore recommended that monitoring programs aimed at maintaining the naturally occurring water quality, as well as ensuring the presence of suitable habitat for the fish species within an estuary and optimising management practices to meet the resource quality objectives for these systems, would be key in protecting and conserving these diverse fish community structures (Amorim et al., 2017; Asha et al., 2015; Duque et al., 2020; Molina et al., 2020; Chapter 4). Additionally, by maintaining the natural degree of connectivity within these ecosystems, we would ensure that migratory pathways of fish species residing within these estuaries remain open, allowing them to complete their life cycles.

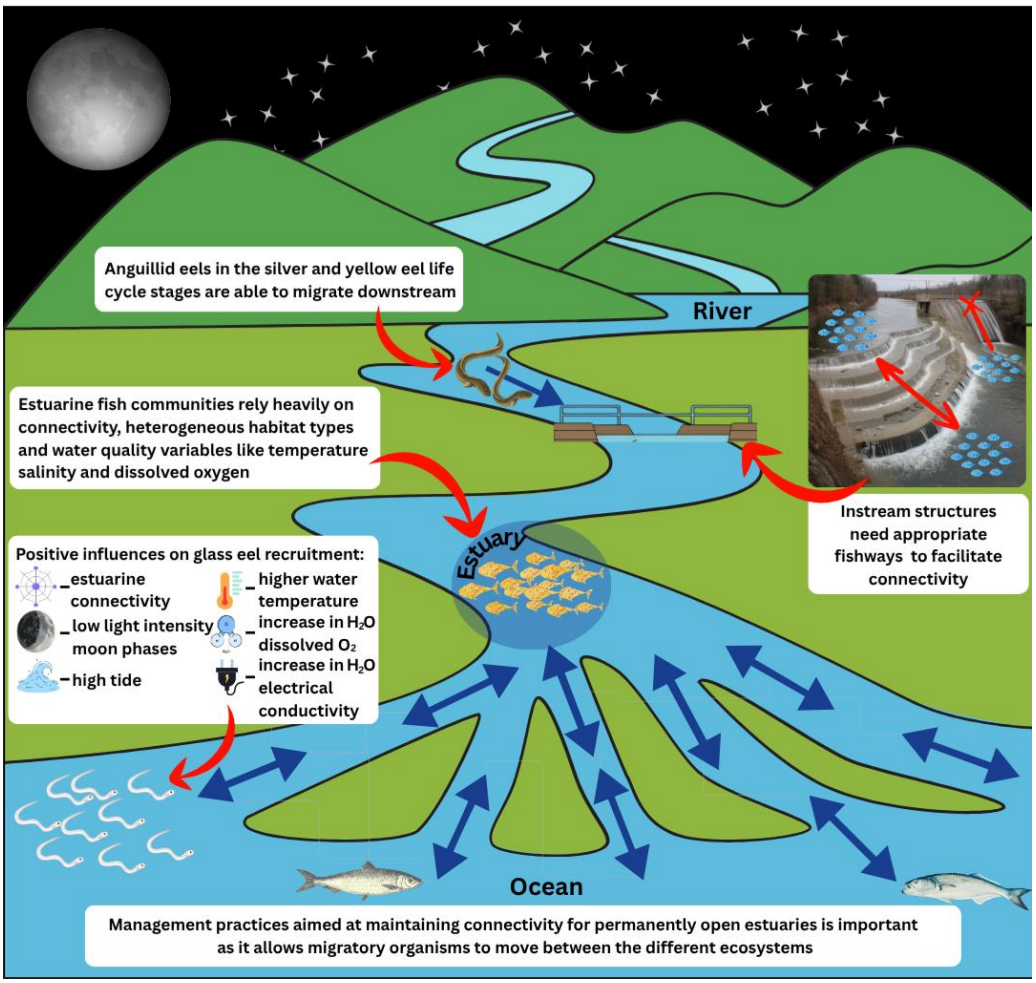


Figure 5.1: A summary diagram highlighting requirements for river connectivity and eel recruitment.

5.4 Conclusions

This study highlighted the importance of connectivity for four globally important freshwater eel species, as well as fish species forming part of the estuarine fish communities (Fig. 5.1). While available research on African freshwater eels is limited, this study highlights numerous challenges faced by them within the uMkhomazi River system, as well as the uThukela, uMkhomazi, and uMtamvuna Estuaries. The African freshwater eels would benefit from being listed as protected species in South Africa, as they are listed on the IUCN Red List of

Threatened Species (IUCN, 2025). In doing so, the African freshwater eels, which play a crucial role in maintaining the ecological integrity of many of South Africa's rivers, would be protected under national laws (Government of South Africa, 2004). It is evident that intervention in the form of conservation efforts aimed at restoring connectivity is required to protect and preserve migratory fish species, including economically and ecologically important species such as the anguillids.

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