Decadal changes in land-use, water quality and fish assemblages in a KwaZulu-Natal urban and non-urban estuary.

by

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PREFACE

The research contained in this dissertation was completed while based at the Council for Scientific and Industrial Research and the Oceanographic Research Institute through the Discipline of Biological Sciences, School of Life Sciences at the College of Agriculture, Engineering and Science, University of KwaZulu-Natal, Westville, South Africa.

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The contents of this work have not been submitted in any form to another university and, except where the work of others is acknowledged in the text, the results reported are due to investigations by the candidate.

As the candidate’s Supervisor and Co-supervisor I agree to the submission of this thesis.

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DECLARATION 1: PLAGIARISM

I, Nikita Van Schoor, declare that:

(i) the research reported in this thesis, except where otherwise indicated or acknowledged, is my original work;

(ii) this thesis has not been submitted in full or in part for any degree or examination to any other university;

(iii) 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;

b) where their exact words have been used, their writing has been placed inside quotation marks, and referenced;

(v) where I have used material for which publications followed, I have indicated in detail my role in the work;

(vi) this thesis is primarily a collection of material, prepared by myself, published as journal articles or presented as a poster and oral presentations at conferences. In some cases, additional material has been included;

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ABSTRACT

Globally, estuaries are recognised as highly dynamic environments which support diverse and productive flora and fauna, and provide numerous goods and services for human wellbeing. These systems are under threat from growing coastal populations that demand the transformation of natural land to accommodate urbanisation, agriculture, harbour, and infrastructure developments. Direct and indirect land-use/land-cover (LULC) changes adversely affect estuarine water quality, directly impacting estuarine biota such as fishes. While the short links between these components are known, few studies have attempted to integrate these links, particularly within the South African context. Therefore, this study aimed to integrate different levels of assessment (LULC and estuarine water quality) to describe changes in estuarine fish ecology over space and time. The study compared two permanently open estuaries in KwaZulu-Natal with distinct land-cover types, namely the uMgeni and uMlalazi estuaries. The uMgeni Estuary is surrounded by urban features and is situated in a highly developed catchment, whereas the uMlalazi is near-natural, with some surrounding agricultural areas.

Historical land-cover imagery from the estuary to the 20 m topographical contour (inclusive of the Estuary Functional Zone), the estuary catchment land-cover, water quality and ichthyofauna data were collected. Land-cover types were grouped into eight categories and 42 feature classes based on modifications to the South African National Land Cover system, the United States Geological Survey and the Coastal Change Analysis Program. Multivariate statistical analysis identified two distinct groupings of land-cover types, Period 1 (before 1989) and Period 2 (during and after 1989). This period factor was then further used throughout the study to determine associated (temporal) responses in water quality and fish assemblages. Strong negative correlations were observed between dissolved oxygen and artificial land-cover types in the uMgeni Estuary. The results suggested that the uMgeni Estuary receives nutrient inputs from various urban activities, which reduce oxygen levels within the water column. Alterations to the hierarchical ichthyofauna structure in the uMgeni occurred on a year to year basis, relative to these anthropogenic impacts. In contrast, good water quality likely associated with fewer developments within the Estuarine Functional Zone has allowed the hierarchical fish structure in the uMlalazi Estuary to remain the same over time, although minor species level differences have occurred.

The current state of each estuary was then investigated by measuring water quality parameters and sampling fish communities along the respective estuary gradients as determined by salinity penetration. Ichthyofauna and water quality data (salinity, turbidity, pH, dissolved oxygen) were collected within the lower, middle, upper and riverine reaches of each estuary. Each fish species sampled was assigned a functional guild depending on their use of the estuary and their feeding methods. The highly urbanised uMgeni Estuary was found to have an exceptionally degraded water quality in the upper reaches (average dissolved oxygen 3.78 mg l^{-1}). It supported a relatively low number of fish species (30) at a total catch per unit effort of 1488.7. In comparison, the less urbanised uMlalazi Estuary displayed much healthier water quality (average dissolved oxygen 6.94 mg l^{-1}), double the number of fish species (60) and higher total fish abundance (catch per unit effort of 2283.67). Salinity was primarily responsible for the longitudinal gradients in fish assemblage, reflecting the role of tidal influence in permanently open estuaries. Differences in fish communities between estuaries, however, were strongly influenced by oxygen levels within the water column. The uMgeni was primarily a detritus-based system that mostly supports small estuarine species (Ambassidae), detritivores (Mugilidae), and freshwater opportunists (Cichlidae). The uMlalazi Estuary is also a detritus based system, however, the diversity and fish assemblage suggests a more complex food web system across various feeding guilds, including piscivores, and is utilised extensively by marine and estuarine species.

The results of this study highlighted the usefulness of incorporating guild and taxonomic distinctness tests in ecological studies. Additionally, they suggest that for the systems studied here, impacts of urban and land-use adjacent to estuaries are more detrimental to estuarine function than forestry or sugarcane cultivation. The results lend support to estuarine management and coastal development goals that aim to limit development in and around estuaries.

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CHAPTER 1: GENERAL INTRODUCTION

1.1 Context of study

This study focuses on various influences on estuaries affecting ecology and estuarine health. Three major components were assessed: land-use/land-cover (LULC), water quality, and fish assemblages. Land-use/land-cover change is a significant pressure on estuarine systems driven by population growth, tourism, industries and politics (Goble and van der Elst, 2013; Adams et al., 2020). Water quality is fundamental in driving estuarine dynamics (Rodrigues et al., 2020) and directly affects estuarine biota. Fish assemblages are specifically useful as indicators of water quality degradation and overall ecosystem impacts (Wang et al., 1997; Selleslagh and Amara, 2008; Valesini et al., 2017; Flipo et al., 2020). Differences and long term trends in the components mentioned above were assessed in two permanently open South African, subtropical estuaries, which occur in two different settings. The uMgeni Estuary is situated within a highly developed catchment; urban setting with a poor ecological state and the uMlalazi Estuary is partially protected, with a rural catchment and a near-natural, good ecological state. Comparisons were made between each estuary's land-cover, water quality, and fish assemblage over time to determine factors that affect overall estuarine health. Each aspect is reviewed below, providing a background to the overall study aims and objectives.

1.2 Defining estuaries

Estuaries are places where rivers meet the sea. These highly dynamic environments have been studied for various reasons, such as providing baseline biological (Wallace et al., 1984; Elliott and Dewailly, 1995), physico-chemical (Harrison, 2004) and morphological (Cooper, 2001; Roy et al., 2001) information. Relationships between biotic and abiotic components (Nicolas et al., 2010b; Pichler et al., 2017; Franco and dos Santos, 2018) and food web dynamics (Nelson et al., 2015) are also commonly studied. Research has increasingly focused on anthropogenic impacts on estuaries (Le Pape et al., 2007; Niu et al., 2020; Waltham et al., 2020), climate change effects (Scanes et al., 2020; Cai et al., 2021) and fisheries management (Xiujuan et al., 2010).

Various definitions of an estuary exist based on geomorphological, biological, hydrological and chemical characteristics (Perillo, 1995; Roy et al., 2001; McLusky and Elliott, 2007). An early definition stated that an estuary was "a semi-enclosed body of water which has a free connection with the open sea and within which seawater is measurably diluted with freshwater derived from land drainage" (Pritchard, 1967). However, this definition did not consider systems that may close during the dry season nor the role of tides and excluded many estuarine types (Perillo, 1995).

Day (1980) modified this definition, stating that an estuary is "a partially enclosed coastal body of water which is either permanently or periodically open to the sea and within which there is a measurable variation of salinity due to the mixture of seawater with freshwater derived from land drainage." Although this definition suited many southern African and Australian estuaries that experience periodic closure, tidal action which is a fundamental component controlling mixing processes, salinity gradients, and sediment deposition, was still excluded (Perillo, 1995). Likewise, the definition does not consider estuaries such as St Lucia in northern KwaZulu-Natal, which are hypersaline due to little freshwater inflow or high evaporation rates (Whitfield, 2019). As such, Potter et al. (2010) proposed a definition that considers an estuary's periodic closure to the sea and possible hypersalinity associated with high evaporative loss and reduced freshwater flow: "An estuary is a partially enclosed coastal body of water that is either permanently or periodically open to the sea and which receives at least periodic discharge from a river(s), and thus, while its salinity is typically less than that of natural sea water and varies temporally and along its length, it can become hypersaline in regions when evaporative water loss is high and freshwater and tidal inputs are negligible."

In the South African context, the most recently applied definition of an estuary is that of Van Niekerk et al. (2019), which similarly allows for the inclusion of temporarily closed systems, but is also specific enough to account for the upstream extent of systems by tidal penetration (when open) and back-flooding (when closed). Thus, in South Africa, an estuary is "a partially enclosed permanent water body, either continuously or periodically open to the sea on decadal time scales, extending as far as the upper limit of tidal action, salinity penetration or back-flooding under closed mouth conditions" (Van Niekerk et al., 2019). The definition acknowledges that during periods of high rainfall, estuaries can become entirely fresh. In contrast, reduced freshwater inflow can result in the formation of a sandbar at the estuary mouth, leaving the system either entirely fresh or hypersaline (Van Niekerk and Turpie, 2012). Sources of freshwater inflow may also arise via groundwater, allowing the inclusion of coastal lagoons (Whitfield, 2005). Therefore, the South African definition recognises the highly complex abiotic factors, often ignored in earlier definitions, which dominate the estuarine environment.

1.3 The importance of estuaries

Estuaries are recognised as one of the most valuable ecosystem types (Van Niekerk et al., 2019) and are geomorphologically (Cooper, 2001), ecologically (Whitfield and Cowley, 2010), economically (Barbier et al., 2011) and culturally (Harrison et al., 2000) important. Compared with adjacent marine systems, estuaries are often less turbulent, have higher water temperatures, provide more shelter, and have fewer predators (Blaber and Blaber, 1980; Wallace et al., 1984; Whitfield, 2019). These conditions provide suitable nursery habitat for juveniles of many species (Wallace et al., 1984; Vorsatz et al., 2021) and support resident and migratory species (Elliott et al., 2007). Additionally, estuarine systems are highly productive environments fuelled by the input of nutrients from fluvial runoff and tidal inflow (Correll, 1978; Kennish, 2002). These nutrients are stored in the water column and sediments, undergoing various geochemical and biochemical processes. The transfer of these nutrients to micro-organisms serves as the base of the estuarine food web; inevitably supporting a variety of species (Roy et al., 2001).

In addition to benefiting flora and fauna, estuaries provide ecosystem goods and services that directly and indirectly affect human welfare (Wilson et al., 2005). Regulatory services such as biochemical cycling, primary productivity, climate regulation, and organic matter mineralisation directly affect ecological processes, indirectly affecting human welfare (de Groot et al., 2002). Critical estuarine habitats such as mangroves, salt marshes, and seagrasses sequester large amounts of carbon and contribute to local and global temperature regulation, subsequently combating the magnitude of climate change (Duarte et al., 2013; McPhearson et al., 2016; Rovai et al., 2021). In contrast, the provision of food, raw materials, medicinal resources, and the use of estuaries for recreational and spiritual purposes benefit human welfare more directly (de Groot et al., 2002; Wilson et al., 2005). Importantly, coastal populations may gain the greatest estuarine benefits through protection from storm surges, erosion control, the filtration of polluted waters, and the replenishment of offshore fish stocks (Whitfield and Cowley, 2010; Barbier et al., 2011).

1.4 Characteristics of South African estuaries

The South African coastline is intersected by 290 true estuaries and numerous micro-outlets (Van Niekerk et al., 2019). Most estuaries are microtidal (with a spring tidal range between 1.8 m and 2 m), are wave energy dominated, occupy drowned river valleys, and have sandbars in the tidal inlets (Whitfield, 1992; Cooper, 2001). Various factors influence the nature of individual estuaries, including catchment size, hinterland steepness, climate, fluvial discharge, marine sediment availability, and salinity (Harrison et al., 2000; Whitfield, 2019). The number of estuaries generally increases from the west to the east coast. They are grouped into four biogeographical regions: the cool temperate, warm temperate, subtropical, and tropical regions that reflect the country's climatic differences, influencing the abiotic and biotic characteristics of its estuaries (Van Niekerk et al., 2020).

In South African coastal marine waters, dissolved oxygen concentrations generally decline from the west to the east coast and are closely associated with water temperatures (Harrison, 2004). The cold Benguela Current flows along the west coast, supplying rich oxygenated waters to inshore systems (Isaac, 1937). In contrast, the warm Agulhas Current influences the east coast and is characterised by lower oxygen levels. Regardless of the negative correlation between dissolved oxygen and temperature, few South African estuaries exhibit oxygen levels below 1 mg l^{-1} unless oxygen-demanding substances are added to the water from industrial and domestic pollution (Wetz et al., 2016; Whitfield, 2019). South Africa's biogeographical regions dictate rainfall patterns that greatly influence river inflow (Van Niekerk and Turpie, 2012). Most estuaries in South Africa are regarded as semi turbid (10-50 NTU) or turbid (>50 NTU), with very few estuaries classified as clear (<10 NTU) (Cyrus, 1988). In addition to transporting inorganic nutrients, organic material, and silt, river inflow is particularly important in influencing estuary mouth states and maintaining vertical and longitudinal salinity gradients (Flindt et al., 1999; Adams et al., 2016; Costa et al., 2017; Mbandzi et al., 2018). Most estuaries experience a full range of salinities (0-34) and may be subdivided into salinity zones where specific organisms occur (Kennish, 2002; Whitfield, 2019).

These factors, namely salinity, tidal prism, mouth characteristics, and mixing processes, provided the basis for the early classification of South African estuaries. Five major categories were identified: estuarine bays, estuarine lakes, river mouths, temporarily open/closed estuaries, and permanently open estuaries (Whitfield, 1992). While useful, this classification has recently been revised to add greater detail and resolution, especially to the diversity of temporarily open/closed estuaries and river mouths that characterise the South African coast, and to include two additional estuarine types, estuarine lagoons and arid predominantly closed estuaries (Van Niekerk et al., 2019).

Estuarine bays are tidally driven, with permanent connections to the sea, deep mouth regions (>3 m) and experience the regular replacement of estuarine waters (Whitfield, 1992; Van Niekerk et al., 2020). These systems may occur naturally or form from harbour developments (Begg, 1984). Estuarine lakes in southern Africa result from the infilling of drowned river valleys with a narrow channel link to the sea, which may be permanent, seasonal or seldom (Hill, 1975). River mouths, referred to as fluvially dominated estuaries under the new classification, are subcategorised based on size, region, substrate type and water clarity with river input driving physical processes (Day, 1981; Van Niekerk et al., 2020). Temporarily open/closed estuaries are cut off from the sea by the formation of a sand bar at the mouth for varying lengths of time. Mouth closure may occur from low river flow, drought conditions or longshore sand movements (Whitfield, 1992).

Permanently open estuaries are systems that maintain a permanent connection with the sea for more than 90% of the year (Van Niekerk et al., 2020). The estuary’s open state may be driven by perennial river flow or a large tidal prism, influencing salinity ranges. This estuary type is the focus of the current study and is discussed in greater detail below (Section 1.4.1). The arid predominantly closed estuaries, are found only on the west coast and remain closed on an annual to decadal time scale (Van Niekerk et al., 2020). Evaporation, winds and water seepage through the berm are responsible for mixing processes. Unlike other estuarine systems, estuarine lagoons receive freshwater inputs via groundwater seepage with tidal amplitude and salinities that remain similar to the marine environment (Van Niekerk et al., 2020).

1.4.1 Attributes of permanently open South African estuaries

Forty-four permanently open estuarine systems occur in South Africa, with the majority in the warm temperate (25) and subtropical (16) regions (Van Niekerk et al., 2019). Permanently open estuaries occur at the outlets of perennial rivers with catchments greater than 500 km^2. They are directly connected to the sea for most of the year and exhibit vertical salinity stratification and distinct longitudinal salinity gradients (Whitfield, 1992). Most of the stratification and mixing processes are dominated by tidal currents, although riverine inflow facilitates mixing during flooding events (Badenhorst et al., 1989). A system’s open state depends on freshwater inflow or strong tidal prisms, which vary from estuary to estuary (Van Niekerk et al., 2020).

On the east coast of South Africa, an estuary’s open state is particularly dependent on river inflow, influenced by high rainfall (Cooper, 2001). These estuaries do not have the tidal prism to maintain an open inlet and often have short estuarine extents due to hinterland steepness, limiting tidal penetration (Cooper, 2001). Most major dams are situated on large rivers which feed permanently open estuaries. These catchments are often larger than those which feed smaller temporarily open/closed estuaries (Whitfield, 2019), increasing the potential for more diverse and widespread anthropogenic impacts on the estuaries downstream. Habitats associated with permanently open South African estuaries include salt marshes in temperate regions and mangroves in subtropical regions. Macrophyte species such as *Zostera capensis* are often encountered (Whitfield, 1992; Van Niekerk et al., 2020).

Salinities can range from 5 to 35 and systems may even enter hypersaline conditions during droughts (Whitfield, 1992). Water temperatures are dependent on the marine and riverine environment, with heterogeneous conditions arising during the wet season where river input may result in a thermocline in the water column (Whitfield, 1992). Dissolved oxygen levels are usually above 5.0 mg l^{-1}, although strong salinity stratifications in deeper waters can result in oxygen depletion (Blaber, 1974; Harrison, 2004). Fish communities in permanently open estuaries tend to be distinct from temporarily open/closed estuaries, river mouths, estuarine bays and lakes. In particular, east coast estuaries are dominated by turbid water species tolerant of turbidity changes associated with heavy floods experienced in this region (Harrison and Whitfield, 2006a). A possible explanation is that these species evolved in turbid oceanic areas of the north-eastern Indian Ocean, which are also characteristically turbid (Blaber, 1981). Species richness and diversity are generally higher in permanently open estuaries than other estuary types. This can be attributed to a more significant contribution of marine species, larger estuarine area and habitat diversity (Harrison et al., 2000; Vorwerk et al., 2003; Saintilan, 2004).

1.5 Anthropogenic effects on estuaries

Estuarine dynamics depend highly on water quality and quantity, and mixing processes, which in turn are influenced by natural drivers such as tides, winds, and river inflow (Harrison et al., 2000; Whitfield, 2019; Rodrigues et al., 2020). However, estuaries' natural variability and resilience are threatened by anthropogenic activities, placing pressure on the functioning of these systems (Van Niekerk et al., 2019). The most significant estuarine pressures include pollution, land-use development, exploitation of living resources, flow modification, mouth state manipulation and invasive species (Van Niekerk et al., 2019; Whitfield et al., 2021). Many of these pressures result from increasing populations in coastal areas, with 600 million people globally occupying low elevation coastal areas (Kennish, 2002; McGranahan et al., 2007). Development in coastal areas is attractive for residence, leisure, recreation, ports, and industry (Goble and van der Elst, 2013). An estuary's transitional position renders it susceptible to these influences from both the terrestrial and marine environments on instantaneous or long term scales (Harrison et al., 2000; Cooper, 2001).

The loss of natural habitat through land-cover change is a growing problem affecting more than 90% of South African estuaries (Van Niekerk et al., 2019). Habitat loss may result in local extinctions, changes in community composition, structure, life-history stages, and increase the occurrence of alien species (Warry et al., 2018; Prosser et al., 2019; Van Niekerk et al., 2019). In many instances, land-cover change reduces natural habitat and may bring about secondary impacts in estuaries. For example, freshwater manipulation through the construction of dams and abstraction for industry, agriculture, mining and urban development reduces the natural water flow to the estuary, resulting in changes in salinity distributions, sedimentation processes, mouth dynamics, and nutrient supply (Lamberth et al., 2008; Adams et al., 2016). Additionally, sources of estuarine pollution arise from municipal and industrial wastewater discharge (Lawrie et al., 2010; Duque et al., 2020), agricultural runoff (Dala-Corte et al., 2016), solid waste (including plastic) input (Naidoo et al., 2015), urban runoff (Kibena et al., 2014) and maritime transportation. These inputs introduce pathogens, faecal coliforms, organic and inorganic matter, and excessive nutrients into receiving waters (Hacioglu and Dulger, 2009; Adeniji et al., 2017; Lemley et al., 2017; Adams et al., 2020). Consequently, algal production increases, turbidity is altered, and hypoxia events become more frequent, with cascading ecological effects (Prosser et al., 2019; Dudley et al., 2020).

Degraded estuaries are more susceptible to the spread of invasive plants, fish and invertebrate species (Whitfield et al., 2021). Excessive nutrient inputs promote invasive macrophytes, which often cause changes in carbon and nutrient dynamics (Chamier et al., 2012; Adams et al., 2020), whereas alien fish and invertebrate species can outcompete native species

(Appleton et al., 2009; Jia et al., 2020). The increased urban population has also resulted in the overexploitation of estuarine fish stocks which subsequently affects population size, trophic structures, distribution, sex ratios and may lead to recruitment failure (Whitfield and Cowley, 2010; Van Niekerk et al., 2020). These pressures often act synergistically, resulting in cumulative ecosystem effects (Whitfield and Elliott, 2002; Forbes and Demetriades, 2009; Chin, 2018; Adams et al., 2020).

Therefore, the manner in which society utilises an estuary and its catchment alters its natural physical drivers (Dudley et al., 2020; Rodrigues et al., 2020). Catchments and estuarine areas which are largely natural and less populated will generally have good water quality and healthy species compositions (Flipo et al., 2020). In contrast, degraded water quality and poor fish species composition are linked to catchment development and nutrient inputs (Heggie and Savage, 2009; Bierschenk et al., 2012; Valesini et al., 2017; Flipo et al., 2020).

1.5.1 Estuarine health and permanently open South African estuaries

Estuarine health has been defined as a systems ability to maintain structure, functioning and resilience against stress (Van Niekerk et al., 2013). Earlier assessments of the health status of South African estuaries involved limited indices of geomorphology, ichthyofauna, aesthetics and water quality (Harrison et al., 2000). A recent improvement to this assessment has incorporated four biotic and five abiotic elements which make up the Estuarine Health Index. Estuarine condition is rated in terms of similarity to the natural state (out of 100) and given an associated category (state) as being natural (A) to severely modified (F), with each category representing a decrease in ecosystem functioning (Van Niekerk et al., 2019). According to the latest National Biodiversity Assessment reports, only 5% of South African estuarine area remains in a natural state, with 14% of subtropical permanently open estuaries severely modified. The key pressures currently affecting permanently open estuaries most severely (high to very high pressure) include fishing (94%), habitat degradation (38%), invasive fish species (32%), pollution (19%), flow modification (13%), mouth manipulation (6%) and invasive plant species (6%). Agricultural areas (21%) and built-up areas (12%) are the greatest contributors to habitat degradation, particularly in the estuarine functional zone (Van Niekerk et al., 2019). Impacted systems will likely continue to degrade, particularly in developed/developing areas, reducing overall estuarine functional resilience.

1.6 Estuarine fishes

Fishes utilise various freshwater, estuarine, and marine environments (Hoeinghaus et al., 2007; Araújo et al., 2018). In an estuarine context, fishes can be grouped as marine (species that spawn at sea but use an estuary to some degree) or estuarine (species that spawn within an estuary). Estuarine species are generally less diverse than their marine counterparts, with all dominant taxa in southern Africa belonging to the class Actinopterygii (Whitfield, 2019). In South Africa, marine species dominate, entering the estuaries during juvenile stages and emigrating back to the marine environment in their sub-adult and adult stages (Wallace and van der Elst, 1975). The variable conditions of estuarine systems, such as salinity fluctuations and flooding events, have limited the speciation potential of fishes (Whitfield, 2019). However, once the factors influencing estuarine fish communities are identified, their abundance and distribution patterns are fairly predictable (Maes et al., 2004; Pfirrmann et al., 2021).

1.6.1 Factors affecting estuarine fishes

Generally, fish assemblage differences between bioregions are driven by geographic changes in the species pool and environmental conditions (Hoeinghaus et al., 2007; Araújo et al., 2018). Estuary to estuary fish assemblage differences are much more variable and may be a result of physico-chemical factors (Harrison and Whitfield, 2006a; Whitfield, 2021), estuary type (Whitfield, 1992), habitat availability (Blaber et al., 1989), seasonality (Barletta et al., 2005), catchment size (Marais, 1988), water quality (Warry et al., 2018) and estuarine productivity (Correll, 1978). In addition to environmental factors, anthropogenic impacts can directly influence food resources, abundance, distributions, growth and fish behaviour or indirectly influence environmental variables that drive fish community structures (Whitfield, 1998; Whitfield and Elliott, 2002).

1.6.2 Fish classification

Although measures of taxonomic diversity such as species richness and abundance help identify differences in biological community compositions, they often fall short in identifying environmental stresses (Tweedley et al., 2017). Incorporating functional attributes in determining estuarine health may be more robust than traditional community metrics when attempting to differentiate between anthropogenic pressures and natural estuarine stressors (Elliott and Quintino, 2007). Classifying species based on functional similarities is useful for studying trophic interactions, species redundancy, coexistence rules, and environmental perturbations (Dumay et al., 2004). This functional grouping into "guilds" made its debut in estuarine studies several decades ago (McHugh, 1967; King and Perkins, 1975; Wallace and van der Elst, 1975; Haedrich, 1983) and included specific southern African estuarine fish groups which have been used extensively in South African studies (Wallace et al., 1984; Whitfield, 1994; Harrison and Whitfield, 2006b; James et al., 2018). Groups of fish species categorised on the basis of how they use an estuary are referred to as estuarine use functional groups (EUFG) (Elliott et al., 2007). Four main groups constitute the EUFG: marine, estuarine, diadromous, and freshwater (Table 1.1).

Table 1.1 Guild categorisation and associated definitions adapted from Elliott et al. (2007) and Potter et al. (2015).

Category	Guild	Definition
	Estuarine Use Functional Group	
Marine	Marine stragglers (MS)	Species that spawn at sea and enter estuaries in low numbers
	Marine estuarine opportunist (MEO)	Utilise estuaries regularly, mainly as juveniles, but also make use of coastal waters
	Marine estuarine dependents (MED)	Juveniles are dependent on the estuarine system and do not utilise coastal waters
Estuarine	Solely estuarine (SE)	Only found in estuaries
	Estuarine and marine (E&M)	Populations found in estuarine and marine environments
	Estuarine and freshwater (E&F)	Populations found in estuarine and freshwater environments
	Estuarine migrants (EM)	Species spawn in estuaries and migrate out to sea as larvae
Freshwater	Freshwater stragglers (FS)	Species that spawn in freshwater but can be found in low numbers in estuaries
	Freshwater estuarine opportunist (FEO)	Often found in estuaries in moderate numbers, occurring beyond oligohaline zones
Diadromous	Anadromous	Species that grow at sea before migrating into the rivers to spawn
	Semi-anadromous	Species that grow at sea, migrating to the upper estuary to spawn
	Catadromous	Species that inhabit freshwater and migrate out to sea to spawn
	Semi-catadromous	Species that inhabit freshwater, migrating to only the downstream estuarine areas to spawn
	Amphidromous	Species that spawn in freshwater. The larvae are flushed out to sea where they can feed. Migration occurs back into freshwater where most growth and spawning occur
	Feeding Mode Functional Group	
	Zooplanktivore (ZP)	Species feed predominantly on zooplankton. e.g., planktonic crustaceans/ fish larvae
	Detritivore (DV)	Species feeding predominantly on detritus or microphytobenthos
	Herbivore (HV)	Species that graze on macroalgae/phytoplankton/

Category	Guild	Definition
		macrophytes
	Omnivore (OV)	Species that feed on filamentous algae, macrophytes, infauna, and epifauna
	Piscivore (PV)	Species that feed on other fish
	Zoobenthivore (ZB)	Species that feed on invertebrates living in, on, or above the substratum
	Opportunist (OP)	Species that feed on a diverse range of food

Each category contains at least two guilds based on characteristics such as spawning location, feeding, refuge, and movements (Potter et al., 2015). The EUFG of marine estuarine dependents, solely estuarine, estuarine migrants, estuarine and marine, estuarine and freshwater, and diadromous guilds are regarded as obligate species and are more likely to suffer if changes occur in estuarine environments (Whitfield, 2019). The remaining groups (marine estuarine opportunists, and freshwater estuarine opportunists) constitute facultative users of estuaries and, if need be, can use the surrounding freshwater or marine environments (Whitfield, 2019). These groups may vary on geographic, cohort-specific, annual, or ontogenetic scales (Able, 2005).

The feeding mode functional groups (FMFG) are defined as fish species that share similar food resources (Elliott et al., 2007). Feeding guilds become useful when looking at the effects of anthropogenic modifications to food webs, predator-prey relationships, and estuary carrying capacities (Elliott et al., 2007). The most common primary sources of food for estuarine fish are phytoplankton, macrophytes, and detritus (Harrison and Whitfield, 2012). These primary food sources act as food for secondary trophic groups such as benthos and zooplankton, which are further utilised by middle and tertiary consumers (Whitfield and Elliott, 2002). Elliott et al. (2007) proposed seven broad categories in the FMFG: detritivores, herbivores, omnivores, zooplanktivores, zoobenthivores, piscivores, and opportunists (Table 1.1).

1.7 Integrating aspects of land-use/land-cover, water quality and fish assemblages in South African estuaries

An estuary’s position between land and ocean requires an integrated approach to assess ecosystem conditions and successfully implement effective management strategies. This involves considerations of land-use and land-cover types, water quality, water allocations, and biotic components (Van Niekerk et al., 2019). A recent estimate places South Africa’s population over 60 million people (Statistics South Africa., 2021), many of whom reside along the coast, accelerating the transformation of natural vegetation. These LULC changes directly or indirectly affect estuarine water quality. The further loss of natural land-cover types can therefore be highly detrimental considering that close to 60% of subtropical South African estuaries have moderately, heavily, or severely affected water quality (Adams et al., 2020). Water quality degradation directly impacts the estuarine biological components, further affecting overall estuarine resilience. Although some studies have addressed LULC (Masefield, 2014), water quality and fish assemblages (McLean, 2008) independently, few South African studies have assessed these in detail and attempted to correlate these factors.

Additionally, the use of fish species as biological indicators has proven to be highly effective in identifying anthropogenic impacts, particularly when a combination of community metrics and functional attributes are utilised (Sheaves, 2016; de Azevedo et al., 2017; Warry et al., 2018; Jiang et al., 2020). However, this can prove challenging when up-to-date scientific information on individual estuarine systems is lacking, which is the case for South African estuaries where fish species checklists are available for less than 10% of systems (Whitfield, 2019). Historical data are often also unavailable, making the assessment of trends in estuarine conditions over time very difficult. Where data do exist, abundance data is often unavailable, rendering indices such as the South African derived Estuarine Fish Community Index (Harrison and Whitfield, 2004) inadequate. The consequences of fragmented historical data lead to “shifting baseline syndrome” (SBS). Shifting baseline syndrome is the acceptance of the environmental state by present generations because of knowledge or memory gaps of past environmental conditions. The current generation is unaffected by further degradation leading to policy makers setting inappropriate management targets (Soga and Gaston, 2018). In order to prevent SBS, continuous recent data on the environment must be collected and trends in available historical data analysed (Gatti et al., 2015; Flipo et al., 2020).

1.8 Project Aims and Objectives:

Estuaries are therefore vitally important for providing coastal protection, recreation and leisure, carbon sequestration, aesthetic appeal and acting as nursery grounds for various fish species. These estuarine services are valued at ZAR 972 million per annum (Turpie et al., 2017), contributing substantially to the national economy. Increasing coastal populations will accelerate the transformation of natural vegetation surrounding these estuaries resulting in habitat loss and adverse water quality effects. The economic, social, and ecological importance of estuaries warrants the urgent implementation of effective management initiatives to prevent future loss of estuarine services. This current study combines several concepts above and individual analyses of the human effects on estuarine fishes in a holistic assessment outlined in the following aims and objectives.

The research conducted here addressed the need for updated information on selected permanently open estuaries, the uMgeni and uMlalazi, in KwaZulu-Natal, South Africa and sought to identify long term ecological trends in these systems. The estuaries were chosen to represent very different land-cover settings. The uMgeni Estuary is severely modified with significant alterations in flow regimes (mean annual runoff), pollution and habitat loss (Van Niekerk et al., 2019). In contrast, the uMlalazi Estuary is still largely natural, situated in a protected area with low pollution pressure and medium habitat loss (Van Niekerk et al., 2019). The project aimed to describe the fish assemblages (species and functional diversity) in these two permanently open estuaries 1) spatially (inter-and intra-spatial distributions) and 2) temporarily (historical trends), and to determine land-cover and physico-chemical factors which may be influencing them. The following objectives were implemented to achieve these aims:

- To collect all available land-cover, physico-chemical, and fish data on the uMgeni and uMlalazi estuaries and compile a usable database.
- To supplement this with current data gained by fieldwork measuring water quality parameters and sampling fish communities in the study systems.
- To determine if land-cover and physico-chemical variables have changed over time.
- To describe the spatial and temporal fish assemblage trends within and between estuaries.
- To identify longitudinal gradients in physico-chemistry and fish assemblages within each estuary.
- To investigate the use of functional guilds and taxonomic indices as measures of fish community differences in space and time.
- To identify relationships between land-use/land-cover, physico-chemical variables and diversity indices.

1.9 Thesis outline

This thesis comprises six chapters namely: a general introduction (Chapter 1), general materials and methods (Chapter 2), three investigative chapters (Chapter 3, 4, 5), and a general discussion and conclusion (Chapter 6). Chapter 1 begins by defining estuaries, their importance and environmental and anthropogenic factors affecting them. The way fishes utilise estuaries is discussed along with the factors affecting fishes, and how they can be used in ecological studies. The chapter ends by integrating human-induced pressures, water quality, and biological components and the significance of assessing all three factors. Chapter 2 details the general methodologies applied in conducting the study, applicable across all chapters. These include field sampling approaches and statistical analyses for land-cover, water quality and biological data. A regional and estuary specific site description is also provided for each estuary. Chapter 3 delves into the historical trends in land-use/ land-cover (LULC) and physico-chemical variables in the two study systems. Land-cover is analysed at the catchment level and at the estuary functional zone level. Possible relationships between land-cover types and physico-chemical variables are investigated. Chapter 4 assesses the present spatial distribution of fishes in each estuary. Physico-chemical variables responsible for each estuary's identified fish community structures are investigated. Guilds (estuarine use functional guilds and feeding guilds) are also explored as a tool to investigate community differences as an alternative to the traditional community metrics. Chapter 5 investigates trends in fish assemblages of both estuaries over time, along with physico-chemical variables or land-cover types most plausibly responsible for these trends. Taxonomic distinctness indices are also investigated as an effective approach in differentiating natural and anthropogenic pressures. Chapter 6 presents a general discussion of the previous chapters' work in the context of urban versus non-urban estuaries and reaches conclusions on the study approach, with recommendations for estuarine management and future research.

CHAPTER 2: GENERAL MATERIALS AND METHODS

2.1 Study systems

The KwaZulu-Natal (KZN) coastline extends from the Mozambique border in the north to the uMthavuna Estuary bordering the Eastern Cape in the south (Figure 2.1). Few estuaries occur in northern KZN in the 80 km wide sandy coastal plain. In contrast, the steep hinterland of the Drakensburg in southern KZN drains several catchments, resulting in the formation of many estuarine systems (Cooper et al., 1998). The east coast climate is subtropical, humid and has an average annual summer rainfall ranging from 650 mm - 1000 mm (Ndlovu et al., 2021). The warm coastal waters of the Indian Ocean influence this climate and dictate the estuarine water temperatures (Harrison, 2004). Regular seasonal flooding forms an essential role in the sediment dynamics of these estuaries through fluvial input and export of accumulated material (Cooper, 2001). Two biogeographical regions occur along the KZN coast. The tropical region from Kosi to uMgobezeleni and the subtropical region from St Lucia to Mbhashe in the Eastern Cape (Van Niekerk et al., 2020). Sixteen permanently open estuaries occur in this subtropical bioregion, with the uMgeni and uMlalazi being two such estuaries (Van Niekerk et al., 2019).

2.1.1 uMgeni Estuary

The uMgeni catchment originates in the KZN Midlands, from where the river flows eastward to the coast (Figure 2.1). The catchment area is approximately 4432 km^2, with a river length of 230 km and an annual runoff of 267.68 x 10^6 m^3 (DWA, 2011). The catchment is a vital water resource for the cities of Pietermaritzburg and Durban, and the surrounding areas (Bartosova et al., 2017). As a result, five dams have been built within the catchment, namely Henley, Midmar, Albert, Nagle, and Inanda. Their combined holding capacity is 753 x 10^6 m^3, more than the annual catchment runoff (DWA, 2011).

The estuary (29˚48’ S; 30˚02’ E) begins about 4 km from the mouth (Figure 2.1a). The systems mouth state and mixing processes are maintained via river inflow (Van Niekerk et al., 2019). Five bridges have been constructed over the uMgeni Estuary: the Ellis Brown viaduct (M4), the Athlone Bridge (M12), the Connaught Bridge (M19), a railway bridge 150 m from Connaught Bridge, and the N2 Freeway bridge (Begg, 1984). Road infrastructure is a key feature contributing to land-use pressure in South African estuaries (Van Niekerk et al., 2019). The construction of bridges across estuarine systems may lead to various ecological impacts such as channel stabilisation, sedimentation, erosion under the bridge and changes in flow velocity (Cuvilliez et al., 2009; Guo et al., 2020). A groyne formed by concrete dolosse has been added to the lower south bank of the system for mouth stabilisation (DWA, 2011). While the estuary is classified as permanently open, it has experienced periodic mouth closures during droughts and low river flows. In these events, the city council breaches the sandbar to prevent back flooding of surrounding public and private properties (DWA, 2011).

The uMgeni Estuary has undergone extensive development and is surrounded by heavily industrialised and urbanised areas (Figure 2.2). According to the estuarine health index, the system's ecological state was determined to be severely modified (Category E), with flow modifications, pollution, habitat loss, fishing and alien invasives having the highest impact (Van Niekerk et al., 2019). Land-use activities immediately surrounding the estuary include a large industrial area in the Springfield Flats region, a golf course on the south bank of the lower reaches, a model yacht pond, and a recreational park (Begg, 1978). The Beachwood Mangrove Reserve is located on the northern bank near the estuary mouth. The estuary is used for recreational and sporting events such as the Duzi canoe marathon (Begg, 1984). Sand mining operations occur in the upper reaches, and illegal gill netting is an increasing concern (Demetriades, 2007; Van Niekerk et al., 2019). The uMgeni system has been subject to various pollutants and solid waste from industrial areas (Begg, 1984), informal settlements (Namugize et al., 2018) and urban stormwater runoff (Ngubane et al., 2019). Treated sewage is discharged into the system from wastewater treatment works in the catchment and outfalls in the immediate estuarine area (Simpson et al., 1972).

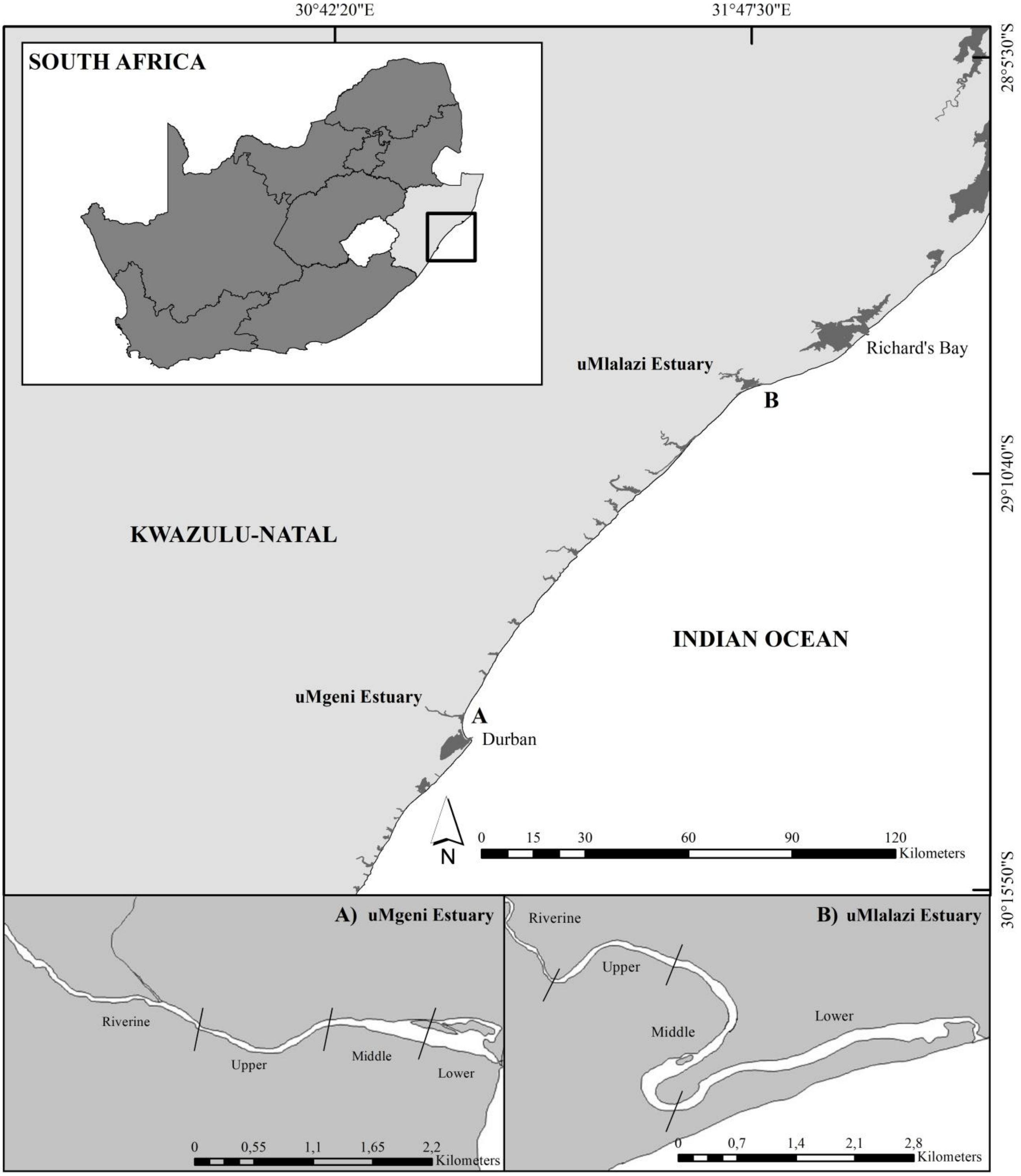


Figure 2.1 Location of study estuaries and associated estuary reaches.

Figure 2.2 Pressures observed on the uMgeni Estuary during field sampling: a) habitat loss and bank stabilisation from golf course b) estuary mouth manipulation c) invasive alien vegetation d) sand mining e) and f) urban runoff g) nearby industries and h) illegal solid waste dumping.

2.1.2 uMlalazi Estuary

The uMlalazi catchment originates above the Ngoye Hills, near Eshowe (Figure 2.1) and covers approximately 454 km^2, with a river length of 54 km and an annual runoff of 124.57 x 10^6 m^3 (Begg, 1978; DWS, 2015). Three small towns are situated in the catchment; Eshowe, Mtunzini, and Gingindlovu (Statistics South Africa., 2011). The Inhlazi Dam is located in the upper catchment, and the Eshowe Dam in the lower catchment (Rasifudi, 2019). The area is primarily rural and governed by 14 tribal authorities (Statistics South Africa., 2011).

The uMlalazi Estuary (28˚56’ S; 31˚48’ E) begins approximately 11 km inland from the mouth, near the confluence of the Ntuze River tributary (Figure 2.1b). It is a tide-dominated estuary (Van Niekerk et al., 2019). Three bridges have been constructed over the uMlalazi: a railway bridge about 7 km from the mouth, the old National Road bridge (R102), and the N2 Road bridge. A road crossing is also present 14 km upstream, which may act as a migration barrier for biological species (DWS, 2015).

The uMlalazi Estuary, up until the railway bridge, forms part of the 1028 ha uMlalazi Nature Reserve and is presently in a largely natural state with good ecological health (Traynor, 2008). According to the Estuarine health index, the estuarine ecological state has remained near-natural with few modifications (Category B) (Van Niekerk et al., 2019). The lack of protection of the upper estuary has resulted in land transformation to accommodate agricultural practices such as sugarcane farming and subsistence farming (Rasifudi, 2019) alongside the estuary (Figure 2.3). Additional land-use activities surrounding the estuary include the Mtunzini Wastewater Treatment Works and aquaculture finfish farming. The estuary is used as a recreational area for boating and fishing, with an estimated take of 23.4 tons of fish per year (Van Niekerk et al., 2019). Illegal gill netting contributes substantially to this fishing pressure (DWS, 2015).

Figure 2.3 Condition and pressures observed on the uMlalazi Estuary during field sampling: a) coastal forest b) mangroves c) middle reach vegetation and mangroves d) agricultural (sugarcane farming) e) estuary manipulation in the riverine reach and f) disturbed lower reach (bank stabilisation for car park and recreational amenity).

2.2 Data sources and general sampling procedures

2.2.1 Land-cover classification

Land-cover imagery, earlier as orthophotos and more recently aerial photography, of the uMgeni Estuary to at least the 20 m contour were available for 1937, 1959, 1960, 1971, 1989, 2002, 2013, 2016, and 2018. Likewise, land-cover imagery of the uMlalazi Estuary and surrounds to the 20 m contour were available for 1937, 1957, 1960, 1975, 1989, 2009, 2013, and 2018. Land-cover imagery obtained from the National Geo-Spatial Information repository was heads-up digitised in ArcGIS (Version 11). Polygons were assigned to land-cover classes modified from a combination of the South African National Land Cover (SANLC), United States Geological Survey (USGS) and Coastal Change Analysis Program (C-CAP) standards. Modifications to land-cover classes were made based on local estuarine systems and associated habitats. Details of the land-cover analysis and modifications to the classification system can be found in Chapter 3.

2.2.2 Historical water quality and fish community data

Data on the study systems water quality and ichthyofauna were sourced from published literature, grey literature (including technical reports), national estuarine surveys, and unpublished sources. Ichthyofauna and physico-chemical data for the uMgeni Estuary were available for 1979-1981, 1985, 1986, 1987, 1989, 1998, 2007, 2008, 2010, 2013, 2017, and 2019 (Table 2.1). Additional physico-chemical data were available for 1960, 1972, 1992, and 2014 (Table 2.2). Ichthyofauna and physico-chemical data for the uMlalazi Estuary were available for 1966, 1980, 1986, 1989, 2010, 2011, 2013, and 2019 (Table 2.1). Additional physico-chemical data were available for 1969 and 2014 (Table 2.2). Specific sampling procedures for the 2019 sampling trips are discussed in Chapter 4. All historical data, together with data generated by field sampling conducted for the purposes of this study in 2019, were used to analyse historical trends (Chapter 5).

Table 2.1 Historical sources of fish community data and associated information for the uMgeni and uMlalazi estuaries.

Estuary	Year	Reference	Sampling frequency	Fish sampling gear
uMgeni	1979-1981	Begg, 1984	Monthly trips	Beam trawl
	1985-1987	CSIR_NEC 1985	July 1985 -January 1987	Unknown
	1985-1986	Ramm et al., 1986	winter and autumn	Gill, seine, trawl
	1987-1988	CSIR_NEC 1987	Unknown	Unknown
	1989-1990	Ramm et al., 1989	July 1989- February 1990	Beam trawl, otter trawl, gill nets
	1998	Harrison, 1998	summer	Seine and gill nets
	2007	Mclean,2008	autumn, summer, winter	Seine and gill nets
	2007-2008	Forbes and Demetriades, 2009	summer and winter	Seine and gill nets
	2010-2011	Weerts, 2010	summer and winter	Seine and gill nets
	2013	Weerts, 2013	spring	Seine net
	2017	Weerts, 2017	spring	Seine net
	2019	This study, 2019	winter, spring, summer	Seine net
uMlalazi	1966	Hill, 1966	Unknown	Unknown
	1980-1982	CRUZ, 1980(RDM)	Monthly trips	Seine and gill nets
	1986	Ramm et al., 1986	summer	Gill, seine, trawl, trap
	1989-1990	CRUZ, 1989(RDM)	Monthly trips	Seine and gill nets
	1998-1999	Harrison, 1998	summer	Seine and gill nets
	2010	Weerts, 2010b	autumn	Seine net
	2011	Weerts, 2011b	autumn	Seine net
	2013	DWS, 2015	autumn	Seine and gill nets
	2019	This study, 2019	winter, spring, summer	Seine net

Table 2.2 Historical sources of environmental data for the uMgeni and uMlalazi estuaries.

Estuary	Year	Reference	Sampling frequency	Reach
uMgeni	1972	Simpson et al., 1972	autumn, winter	Lower, middle, upper, riverine
	1979-1981	Begg, 1984	Monthly trips	Lower, middle, upper
	1985-1986	Ramm et al., 1986	winter, summer	Lower
	1989-1990	Ramm et al., 1989	winter, summer	Lower, middle, upper
	1992	Cooper et al., 1993	spring, summer	Lower, middle, upper
	2008-2009	Olaniran et al., 2014	summer, autumn, winter, spring	Lower, riverine
	2007	Mclean,2008	autumn, winter, summer	Lower, middle, upper
	2007-2008	Forbes and Demetriades, 2008	winter, summer	Lower, middle, upper
	2010	Weerts, 2010	winter, summer	Lower, middle, upper, riverine
	2011	Weerts, 2011	autumn	Lower, middle, upper, riverine
	2013	Weerts, 2013	winter	Lower, middle, upper, riverine
	2019-2020	This study, 2019	winter, spring, summer	Lower, middle, upper, riverine
uMlalazi	1966	Archibald et al., 1969	summer and winter	Riverine
	1986	Ramm et al., 1986	summer	Lower, middle
	2010	Weerts, 2010	summer	Lower, middle, upper, riverine
	2011	Weerts, 2011	summer	Lower, middle, upper, riverine
	2013	RDM (2015)	autumn	Lower, middle, upper, riverine
	2015-2016	Tagliarolo and Scharler, 2018	spring, winter, autumn	Lower, middle
	2019-2020	This study, 2019	winter, spring, summer	Lower, middle, upper, riverine

2.2.3 Field sampling

2.2.3.1 Physico-chemical parameters

Each estuary was divided into four zones, i.e., the lower, middle, upper, and riverine reach (Figure 2.1a, b). Zonation of the estuaries was based on average salinities and followed the

Venice System salinity criteria with added modifications (Whitfield et al., 2012; Whitfield, 2015). The euhaline and polyhaline salinity zones were combined to represent the lower reaches. Likewise, the limnetic and oligohaline zones were combined to represent the riverine reach (Table 2.3). Historical and present physico-chemical data were grouped into one of the four reaches as described above. Historical fish data were only available at an estuary spatial level of detail and could not be allocated to reaches.

2.2.3.2 Ichthyofauna

Sampling gear utilised in the surveys from which historical data were sourced varied between collectors and years, although seine and gill nets were frequently used (Table 2.1). All sampling equipment imposes selection criteria, and the choice of sampling gear is dependent on depth of water, and the size of the species sampled. Gill nets are usually used in deeper, open waters but are destructive and lead to fish mortality (Whitfield, 2019). Seine nets are used in shallow waters, with the net spanning the water column from the surface to the substrate (Klemm et al., 1993). Seine netting allows fish to be captured, identified, counted and returned alive to the water. Begg (1978) sampled KwaZulu-Natal estuaries using a beam trawl. This sampling gear is selective for smaller-sized fishes (juveniles and small-bodied species) and slow moving species, particularly bottom-dwelling fishes. Fieldwork for the purposes of this study (2019) was conducted using a seine net, chosen primarily for its general applicability in the study systems and because it allowed fish to be returned alive to the water after field identification.

Table 2.3 Salinity ranges associated with estuary reach classification adapted from Whitfield et al. (2012).

Salinity zone	Salinity range	Estuary reach
Euhaline + Polyhaline	> 25	Lower
Polyhaline	18-24.9	Middle
Mesohaline	5-17.9	Upper
Limnetic + Oligohaline	<5	Riverine

2.3 Statistical analysis

Plymouth Routines In Multivariate Ecological Research (PRIMER Version 6.1.13) has been primarily designed for analysis of ecological community data, and as such, has been the choice of multivariate analyses for many studies (Harrison and Whitfield, 2008; Kamrani et al., 2016; Amezcua et al., 2019; Jiang et al., 2020). Its overall non-parametric approach is highly appropriate for most ecological data, which are often over-dispersed, contains many zeros, and almost always have more variables than samples (Anderson et al., 2008). This multivariate software was therefore chosen as the primary analysis software for the ichthyofauna and physico-chemical data. Within PRIMER, various univariate and multivariate analyses were performed on estuary, reach, and period factors (periods introduced in Chapter 3). The general statistics used throughout the thesis are discussed below, with more specific analyses described in the relevant chapters.

2.3.1 Univariate analysis

Univariate indices condense full sets of multiple species assemblage data into single coefficients reflecting characteristics of community structure which can be analysed by comparing the means and 95% confidence intervals of each site/group (Clarke and Warwick, 2001a). The indices computed using the DIVERSE routine in PRIMER included total species (S), abundance (N), Shannon-Weiner diversity index (H'), and Simpsons index (λ). The Shannon-Weiner diversity index (Equation 2.1) estimates the assemblage diversity using a combination of species richness and evenness (Magurran and McGill, 2011).

$$\mathrm{H}' = -\Sigma\, P_i \log(P_i) \qquad (2.1)$$

Where the natural logarithm is used, and P is the proportion of the total count from the *i*th species.

The Simpsons index in its natural form is the probability that two individuals from a sample belong to the same species (Equation 2.2). It can be regarded as a dominance index in which higher numbers correspond to abundances in an assemblage dominated by a few species only (Clarke and Warwick, 2001a).

$$\lambda = \Sigma\, p_i^2 \qquad (2.2)$$

Significant differences between univariate measures of sample groups were assessed in SigmaPlot (Version 12.5) using an Analysis of Variance (ANOVA) or T-tests. The parametric ANOVA and T-test assumptions, i.e. normal distribution, equal variance, and independent samples, were tested using the Shapiro-Wilk and Equal Variance tests. If the assumptions failed, a Kruskal-Wallis one way ANOVA on Ranks and a Mann-Whitney U Rank Sum test were performed, respectively.

2.3.2 Multivariate analysis

For the analysis of environmental data, Draftsman plots were used to identify data with a skewed distribution and requiring transformation. These were individually transformed by square root, fourth root, or logarithmic transformation to represent normal distribution of the data best. Environmental variables were then normalised to obtain equal scaling of the variables simultaneously used in a resemblance matrix (Clarke and Gorley, 2006), in this case, based on Euclidean distance. Subsequent ordinations of environmental data were analysed using principal coordinate analysis (PCO). The purpose of the PCO is to capture as much of the variability in the resemblance matrix as possible by representing the samples in a high dimensional variable space (Anderson et al., 2008). A PCO that explains 70% or more of the variability is considered a reasonable representation of the data structure (Anderson et al., 2008). In general, the first two axes will explain most of the variance between the samples (Anderson et al., 2008).

Biological data were either fourth root or presence/absence transformed, and a similarity matrix constructed to assess sample or variable similarity in a pairwise manner (Clarke and Warwick, 2001a). The Bray-Curtis similarity coefficient was used for the biological data analyses except for presence/absence data, in which case the Sorensen resemblance matrix was constructed. Sorensen is frequently used for simple species lists as it is calculated on the presence/absence data of the Bray-Curtis matrix, making them related matrices (Clarke and Gorley, 2006). Biological distance similarities were assessed using Nonmetric multidimensional scaling (nMDS) (Clarke and Warwick, 2001a). Points close together on the ordination plot represent samples similar in community composition (Clarke and Gorley, 2006). Ordination plots with stress values < 0.1 were considered reliable, whereas values > 0.25 depicted a poor representation of the data, in which case alternative transformations of the data were assessed (Clarke, 1993; Clarke and Gorley, 2006).

To consider interaction effects of data, permutational multivariate analysis of variance (PERMANOVA) was used to assess differences between groupings as it provides complementary information by analysing more complex datasets with greater variables using permutations instead of ranks (Anderson et al., 2008). The output is dependent on a p-value and a test statistic (Pseudo-F statistic) (Anderson et al., 2008).

The general method of permutation utilised in all PERMANOVA's was the permutation of residuals under a reduced model. However, if sample sizes were small ($n < 4$ replicates) or only one factor was tested, unrestricted permutation of raw data was implemented (Anderson et al., 2008). A type 3 Sum of Squares was run for all PERMANOVA tests as this approach is the most sensible for unbalanced designs (Anderson et al., 2008). In cases where fewer than 100 unique permutations were identified, a Monte Carlo p statistic was run. This method uses an asymptotic permutation of the denominator or numerator and relies on sample approximations (Anderson et al., 2008). In particular, this approach was used for the analysis of historical data where replication was low. A pairwise test was then run on factors that were shown to be statistically significant by PERMANOVA.

To satisfy the assumption of homogeneity of multivariate dispersions, a PERMDISP procedure was run prior to PERMANOVA. This test compares the distances from observations to group centroids using the ANOVA F statistic (Anderson et al., 2008). The null hypothesis which is tested is no differences in the dispersion among *a priori* groups. The recommended setting for ecological data was used, that is, distances to centroids using permutations. If significant group differences were identified in PERMANOVA, a Similarity percentages (SIMPER) routine was run to determine which species or functional groups contributed to the separation of groups. The similarity percentage routine is not a hypothesis testing method but rather a justification of groupings (Clarke and Warwick, 2001a). Species identified by SIMPER as important in causing dissimilarities amongst sample sets can then be superimposed onto an nMDS for visualisation.

2.3.3 Relationships between environmental and biological parameters

Relationships between variables were tested using correlation, regression, and permutational tests. Pearson correlation analyses were performed in SigmaPlot (Version 12.5). If data were not normally distributed after transformation, a Spearman's correlation was performed. The resultant correlation coefficient (r, ranging between -1 and +1) measures the strength of the relationship between the two variables. Regression analyses were run on variables that were significantly correlated to one another. The predictor variable was hypothesised to affect the response variable (Quinn and Keough, 2002).

To investigate specific environmental variables most likely influential as determinants of the fish community in the study estuaries (Chapter 4), the BEST routine in PRIMER was used.

However, BEST does not consider how much biological data variation is explained by the environmental data (Clarke and Warwick, 2001a). For this reason, distance-based linear models (DISTLM) were also employed. This method models the relationships between a biological data set and one or more predictor variables using permutations (Anderson et al., 2008). The approach by which DISTLM works is through Distance-based redundancy analysis (dbRDA), i.e., multivariate multiple regression models that investigate correlations between predictor variables and biological data (Anderson et al., 2008). It identifies the predictor variables which explain the greatest variation in the biological data. The distance-based linear model tests the null hypothesis that no relationship exists between the biotic and abiotic matrix. The model created for this study used the stepwise selection procedure and Akaike’s Information selection criterion (AIC). The stepwise selection procedure adds one variable at a time to the model while simultaneously removing a variable (Anderson et al., 2008). The AIC was chosen as it will not improve with increases in the predictor variables. This selection criterion has been used by various researchers (Pichler et al., 2017; Franco and dos Santos, 2018; McCarthy et al., 2018). In cases where the sample size was small or for univariate analyses, the AICc selection criterion was used. This selection criterion is a modification of the AIC selection and has been shown to perform best with smaller sample sizes (Anderson et al., 2008).

CHAPTER 3: LONG TERM TRENDS IN LAND-USE/ LAND-COVER AND WATER QUALITY IN THE UMGENI AND UMLALAZI ESTUARIES

3.1 Introduction

Often erroneously used interchangeably, land-use and land-cover are two different characteristics of the landscape. Land-use is defined as activities occurring in a particular area with socio-economic implications, and land-cover refers to the physical characteristics observed on the earth's surface, both natural and artificial (Rawat and Kumar, 2015). Land-use affects land-cover, and land-cover affects land-use. Land-use/land-cover (LULC) information is used for many different applications. These include biodiversity assessments (Adams et al., 2016), land-use planning to reduce water pollution (Chang et al., 2021), predicting future urbanisation impacts and management (Croft-White et al., 2017), riparian zone protection (Dala-Corte et al., 2016), assessing effects of water quality (Dudley et al., 2020) and hydrological changes (Gergel et al., 2002), and methods to maximise ecosystem service values (Hoque et al., 2020). Social and economic conditions, political policies, and climate-induced factors influence LULC (Goble and van der Elst, 2013; Adams et al., 2020) and are collectively influenced and compounded by growing populations (Biggs and Scholes, 2002). A growing population demands more housing, infrastructure, food and water resources, contributing to land-cover changes (Hua, 2017). Coastal areas, in particular, are affected as they are often more densely populated than inland areas. As transition areas between land and sea, estuarine systems are often subject to the transformation of estuarine floodplains (Cooper, 2001). Estuarine areas are physically transformed to accommodate transport infrastructure, riparian infrastructure, in-stream infrastructure, urban development, agricultural practices, harvesting of raw materials, mining, harbour developments and marina infrastructure (Van Niekerk et al., 2019).

These LULC changes can have detrimental effects on estuarine systems through various pathways. Direct effects may occur through habitat loss (Mwandya et al., 2009; Jewit et al., 2015; Prosser et al., 2019), indirect effects via the transport of pollution downstream (Dala-Corte et al., 2016; Warry et al., 2018), induced effects from industries (Pérez-Fernández et al., 2020), or cumulative effects through impacts on water quality and quantity (Le Pape et al., 2007; Lamberth et al., 2008) whereby multiple spatial scales may be impacted (Valiela and Bowen, 2002; Bierschenk et al., 2012; Kibena et al., 2014). At the larger catchment scale, the transformation of natural areas to urban areas increases impervious surfaces resulting in increased runoff, soil erosion and bank destabilisation (Wang et al., 1996; Gergel et al., 2002; McCarthy et al., 2018). Catchment land-use activities such as wastewater treatment works (WWTW) introduce excessive nutrient loads, pollutants and pathogens into receiving waters, which are transported downstream into estuaries and coastal waters (Valiela and Bowen, 2002; Hacioglu and Dulger, 2009; Hua, 2017; Dudley et al., 2020). Natural vegetation's filtration and absorption services are reduced, resulting in increased runoff, soil erosion, siltation, and flooding (Masefield et al., 2014; Van Niekerk et al., 2020). On a smaller scale, vegetated areas adjacent to an estuary, estuarine mudflats and mangroves are significant for regulating estuarine productivity (Roy et al., 2001; Peer et al., 2018). Removing estuarine habitats such as seagrasses and mangroves can adversely affect the estuarine food web structure and limit habitat availability for endangered species (Akin et al., 2003; Franco and dos Santos, 2018).

The effects of LULC changes in the estuarine area are often more significant than similar changes in the catchment (Masefield et al., 2014; Van Niekerk et al., 2019). Urban development in the estuarine area results in direct input of discharges into an already ecologically sensitive system, reducing its overall integrity (Masefield et al., 2014). However, an estuary's resilience is also dependent on the state and correct management of its catchment (Van Niekerk and Turpie, 2012). Highly developed catchments will generally contain estuaries with poor water quality, whereas more natural catchments exhibit good water quality (Heggie and Savage, 2009; Bierschenk et al., 2012; Valesini et al., 2017; Flipo et al., 2020). Catchment development and associated nutrient inputs may enter rivers upstream, accumulating downstream if further land-use activities are present or in the absence of natural buffering vegetation. The resultant inputs to the estuarine system can exceed the natural contributions of organic matter (Valiela and Bowen, 2002), reducing the resilience to cope with increased water residence time (Adams et al., 2020). Cascading ecological effects are likely to follow as physico-chemical variables directly affect estuarine biota. Changes often associated with reduced water quality include decreased species richness, abundance and diversity (Wang et al., 1997; Selleslagh and Amara, 2008; Valesini et al., 2017; Calle et al., 2018; Duque et al., 2020; Flipo et al., 2020). Community composition and functional attribute changes may follow if the conditions persist and are often best identified over longer temporal scales (de Santiago et al., 2020; Flipo et al., 2020).

Mapping of land-cover is critical for environmental assessments, land-use planning, and global change research (Fairbanks et al., 2000). Land-use/land-cover mapping also introduces the concept of delineating buffer areas around ecosystems that require protection (Masefield et al., 2014). In South Africa, estuaries are delineated by the estuarine functional zone (EFZ). The EFZ is defined as the estuarine water body area, supporting physical and biological processes and habitats required for estuarine functioning (Van Niekerk et al., 2019). A boundary, typically taken at 5 m above mean sea level (amsl), and including surrounding wetlands, salt marshes, swamp forests, intertidal mud and sand flats, beaches and foreshores currently delineates the EFZ in South Africa (Van Niekerk and Turpie, 2012; Van Niekerk et al., 2019). An expansion of the EFZ may be necessary for specific estuaries to protect estuarine biodiversity successfully. This was evident in a study on multiple KwaZulu-Natal estuaries, which showed a relationship between land-cover in the 20 m contour and estuarine macrobenthic communities (Sheppard and MacKay, 2018).

More than 90% of South African estuaries currently experience some form of pressure from development due to increasing coastal populations and demand for resources and space (Van Niekerk et al., 2013). Many studies have investigated estuarine physico-chemical characteristics (Harrison, 2004; Harrison and Whitfield, 2006a; Whitfield and Baliwe, 2013; Ortega-Cisneros and Scharler, 2014) and LULC changes independently (Goble and van der Elst, 2013; Masefield et al., 2014; Jewit et al., 2015). Few South African studies have attempted to correlate LULC change with water quality responses. The consequences of an underestimated EFZ or a poorly managed catchment could result in the loss of estuarine function in future years. This chapter investigates the relationship between LULC and estuarine water quality, as outlined in the following aims.

3.2 Aims, Objectives and Hypotheses

This chapter aims to identify and describe links between LULC changes and water quality, primarily physico-chemical variables, comparing a highly urbanised estuary (uMgeni) with a rural, non-urban estuary (uMlalazi).

Objectives

- To identify land-cover changes in the respective estuarine catchments and below the 20 m estuary contour.

- To identify trends in water quality (defined by selected physico-chemical variables) in each system over time.
- To compare LULC and water quality between the uMgeni and uMlalazi estuaries.
- To determine if land-cover changes are correlated with physico-chemical variable changes.

Null Hypotheses

- There have been no changes in land-cover around each estuary over time.
- Within an estuary, physico-chemical variables did not change over time.
- Land-use/land-cover is comparable around the uMgeni and uMlalazi estuaries.
- Changes in land-cover are not directly correlated with changes in estuarine physico-chemical variables.

3.3 Materials and methods

General descriptions of the study estuaries, sampling approaches, historical data collections and statistical procedures can be found in Chapter 2.

3.3.1 Land-cover classification and mapping

Land-cover data were obtained from the South African National Land Cover (SANLC) archived GIS database for 1990, 2013, and 2018. This was used to identify land-cover changes at the catchment scale of each estuary over decadal timescales. Aerial photographs were obtained online from the National Geo-Spatial Information repository to capture the land-cover classes, specifically to the 20 m estuary contour. Specific years for which photographs were available are given in Chapter 2. These were heads-up digitised by a single individual at the Oceanographic Research Institute (ORI) to avoid variability associated with the subjective nature of digitising images. Within the 20 m contour, digitised polygons were assigned to a specific land-cover class based on the SANLC, the United States Geological Survey (USGS) and Coastal Change Analysis Program (C-CAP) to align with globally accepted standards (Fairbanks et al., 2000). These land-cover classes were modified based on expert knowledge of local estuarine systems and associated habitats. Classification of polygons occurred at three hierarchical levels (Table 3.1). Level One (L1), the lowest order of detail, classified an area as being natural, disturbed, or transformed. Level Two (L2) included eight higher-order classifications: cultivated, managed vegetation, artificial, waterbodies, bare, wetland, vegetation, and waterways. Level Three (L3), the most detailed descriptor of land-cover types, included 29 classes that fall within the higher-order classifications. Light detection and Radar (LiDAR) data, sourced from eThekwini Municipality GIS website via the Economic Development, Tourism and Environmental Affairs (EDTEA) and ORI, were used to determine each estuary's 20 m contour boundary. All imagery within this boundary was digitised and assigned a land-cover type as described above. The land-cover classification was then represented in a spatial colour-coded GIS map using ArcMap version 10.5.1. The metadata for each year (see Chapter 2 for land-cover availability) were checked for inconsistencies and errors in the classification classes corrected as needed. Each land-cover class was represented as area (m^2) at each level and exported for further analysis. The percentage contribution of each land-cover class to the total area in the 20 m contour was then calculated for each year.

Table 3.1 Description and examples of land-cover categories (Based on SANLC, USGS and C-CAP) in levels 1, 2, and 3 modified by the Oceanographic Research Institute.

L1	L2	L3	DESCRIPTION & EXAMPLES
Natural [a]	Bare	Unconsolidated Sediment	Material such as sand, dunes or gravel which is subject to redistribution
		Consolidated Sediment	Accumulations of earth material such as bedrock, desert pavement, volcanic material
	Waterbodies	Saline Influence	Habitat associated with the water column of an estuary
		Fresh or Saline	Natural lakes, ponds, pans
	Waterways	Fresh	Rivers/Streams
	Vegetation	Herbaceous	Predominantly herbaceous vegetation (grasslands, sparse bushland) (>90% vegetation cover)
		Foredunes	Pioneer dune vegetation (>90% foredune vegetation cover)
		Terrestrial Forests	Dense forests/woodlands where tree canopy height is >5m (>90% woody vegetation cover)
		Coastal Forest	Coastal and dune forest vegetation forming supporting habitat to estuary function.
		Mixed	Mixture of woody and herbaceous cover (>90% vegetation cover)
	Wetland	Reeds & Sedges	Vegetation buffering the water's edge, often associated with freshwater inlets. e.g., *Phragmites australis*
		Mangroves	Forest and shrub vegetation occurring in slow-moving water or tidal areas along the shore of an estuary. e.g., *Avicennia marina, Bruguiera gymnorrhiza*
		Vegetated	Any form of native vegetation covering wetland area
		Non-Vegetated	Natural waterbodies in which free floating macroalgae are found. e.g., *Ulva and Cladophora*
		Bare	Sand or mud banks which provide habitat to microphytobenthos
		Swamp forest	Freshwater forested ecosystems associated with tropical and subtropical regions. e.g., *Barringtonia racemosa, Hibiscus tiliaceous, Ficus trichopoda*
		Salt Marshes	Coastal wetlands flooded and drained by salt water brought in by tidal action. e.g., *Sarcocornia, Salicornia, Triglochin, Limonium and Juncus*
Disturbed [b]	Vegetation	Herbaceous Invasives	Floating/submerged/emergent invasive vegetation within the estuary. e.g., *Eichhornia crassipes, Pistia stratiotes*
		Herbaceous	Predominantly herbaceous vegetation (grasslands)
		Foredunes	Pioneer dune vegetation with distinct human interference

L1	L2	L3	DESCRIPTION & EXAMPLES
		Terrestrial Forests	Dense woody vegetation
		Coastal Forest	Coastal and dune forest vegetation forming supporting habitat to estuary function.
		Mixed	Mixture of woody and herbaceous cover with distinct human interference
	Wetland	Reeds & Sedges	Vegetation buffering the water's edge, often associated with freshwater inlets. e.g., *Phragmites australis*
		Mangroves	Forest and shrub vegetation occurring in slow-moving water or tidal areas along the shore of an estuary. e.g., *Avicennia marina, Bruguiera gymnorrhiza*
		Vegetated	Any form of native vegetation covering wetland area
		Non-Vegetated	Natural waterbodies in which free floating macroalgae are found. e.g., *Ulva and Cladophora*
		Bare	Sand or mud banks which provide habitat to microphytobenthos
		Swamp Forest	Freshwater forested ecosystems associated with tropical and subtropical regions. e.g., *Barringtonia racemosa, Hibiscus tiliaceous, Ficus trichopoda*
		Salt Marshes	Coastal wetlands flooded and drained by salt water brought in by tidal action. e.g., *Sarcocornia, Salicornia, Triglochin, Limonium and Juncus*
Transformed	Bare	Bare	Non-vegetated ground surfaces resulting from mining activity (clearings, sand mining, waste dumps)
	Waterbodies	Water structures	Dams, canals, tidal pools (Only the water area)
	Artificial	Infrastructure	Built structures for transport, electricity and water-related activities (roads, railways, bridges, parking areas, piers, substations, sewage works)
		Formal - residential	Formal settlements of all densities, including garden area and pools (Urban/Metro)
		Formal - mixed	Mixed-use areas comprising residential and non-residential areas
		Informal - residential	Residential buildings and structures in rural areas, including garden areas surrounding the building
		Commercial	High-density buildings associated with commercial, transport and administrative structures
		Industrial	Buildings associated with industrial and manufacturing activities
		Non-Residential	Other built structures that do not fall under the above two artificial categories (Schools, churches, hospitals, agricultural farm buildings, built recreational areas)
	Managed Vegetation	Open spaces	Non-built open vegetated areas (parks, golf course, sports fields and other public amenities)
	Cultivated	Formal Cultivation	Cultivated lands used for permanent crop production and fallow areas (agricultural, forestry)
		Informal Cultivation	Informal patches of cultivated land used for rain-fed crops sold in market gardens or for home use

[a] Land-cover with limited human interference

[b] Land-cover with distinct human interference

3.3.2 Physico-chemical data collection

Physico-chemical data including depth (m), temperature (°C), salinity, dissolved oxygen (mg l^{-1}), turbidity (NTU), and pH were collated from published literature, grey literature (including technical reports), national estuarine surveys, and unpublished sources for the uMgeni and uMlalazi estuaries. The units of measurement from different sources were converted as necessary to ensure a standardised historical dataset. All data points were assigned to a specific estuary reach (lower, middle, upper, riverine) depending on the site's location. Details on the data sources, reach descriptions, and locations can be found in Chapter 2.

3.3.3 Statistical analysis

3.3.3.1 Land-cover data

Land-cover data at the catchment scale were only available at Level Two classification for three years (1990, 2013 and 2018), preventing any statistical analysis at this scale. The percentage contribution of each L2 land-cover class to the overall land-cover in the catchment region was graphically represented. Draftsman plots (using L2 land-cover in the 20 m contour) were run in Plymouth Routines in Marine Ecological Research Software (PRIMER Version 6.1.13) to identify collinear variables ($r > 0.95$), which were removed from further analyses (Clarke and Gorley, 2006). Natural (N)-vegetation and Transformed (T)-managed vegetation were strongly collinear with other variables and removed from the uMgeni analysis, while N-vegetation, T-bare and N-wetland were removed from the uMlalazi analysis. Land-cover data were analysed using the Bray-Curtis similarity matrix because of the characteristics land-cover percentage data shared with biological data. These include a uniform measurement of scale across all variables, positive entries, and zeros in the data (Clarke and Gorley, 2006).

A similarity profile (SIMPROF) and hierarchical cluster analyses (using group averages, 1000 permutations and 999 simulations to calculate the departure statistic) were performed to determine if land-cover formed significantly distinct groupings over time in each estuary. These groups were used to form the “period” factor. The resultant “periods” were used as the basis for analysis of temporal changes in physico-chemical variables (Chapter 3) and fish assemblages (Chapter 5). Land-cover groupings were chosen as the basis for the “period” factor based on literature which suggested that major changes in land-cover correspond with changes in water quality and estuarine biota (Le Pape et al., 2007; Valesini et al., 2017). Clustered groups for each estuary were visualised through a nonmetric multidimensional scaling plot (nMDS). Differences in estuary land-cover over different periods were tested using a one-way PERMANOVA by unrestricted permutations of raw data. Location differences were confirmed by the homogeneity of dispersion of samples (PERMDISP). A similarity percentage (SIMPER) routine was used to identify land-cover classes responsible for estuary differences.

3.3.3.2 Physico-chemical data

The diverse sources and collection methods of physico-chemical data introduced comparability issues. To further analyse the environmental data, missing historical data were dealt with using an expected maximisation algorithm (EM) in PRIMER Version 6.1.13. Assumptions of EM are that samples must follow normality, missing values must be few (not more than 5% of the data), more samples than variables should be present, data points must be missing at random, and samples must be unstructured and not part of *a priori* groups. Variables with > 60% of the samples missing, e.g., pH, were excluded from further analysis but were still retained in the summative physico-chemical table of results (represented as mean ± SD). Only turbidity (NTU) needed to be transformed (square root) to meet the assumption of normality. All other assumptions of EM mentioned above were met for each variable.

Multivariate analyses (PRIMER Version 6.1.13) were performed on salinity, dissolved oxygen (mg l^{-1}) and turbidity (NTU). Averaged data were used for each reach_ year_ estuary combination. Reaches were defined as lower, middle, upper, and riverine (refer to explanation in Chapter 2). All variables were normalised to obtain equal scaling of the variables and account for the different units of measurement. The abiotic data were represented via the Euclidean distance resemblance matrix, which best describes the natural distance between two data points (Clarke and Warwick, 2001a). A similarity profile (SIMPROF) and hierarchical cluster analyses (using group averages, 1000 permutations and 999 simulations to calculate the departure statistic) were performed to identify any temporal physico-chemical groupings and visualised by a principal coordinate plot (PCO). A fixed two-way PERMANOVA (period and reach), type 3 under a reduced model, was run to test the hypothesis that there were no significant differences between periods (as determined by the Land-cover SIMPROF), reach, and reach across periods. Significant differences in the overall physico-chemical variables between the uMgeni and uMlalazi were tested using a one-way PERMANOVA, type 3, under raw data permutations. The dispersion of the samples in each estuary_ period was tested via the homogeneity of dispersion test (PERMDISP, PRIMER v6) to determine if significant differences between locations, obtained from PERMANOVA, are realistic or a result of dispersion among samples. Detailed explanations on PERMANOVA choices can be found in Chapter 2.

3.3.3.3 The relationship between land-cover and physico-chemical variables

Correlation analyses were run in SigmaPlot (Version 12.5) to explore relationships between land-cover classes and physico-chemical variables. Land-cover classes were represented as the independent variable and physico-chemical variables as the dependent variable. The average physico-chemical values for salinity, dissolved oxygen (mg l^{-1}), turbidity (NTU) and temperature (°C) were calculated for each year. These were matched with the percentage of land-cover recorded in the same year. Linear interpolation (Equation 3.1) was employed to correspond each physico-chemical data point with each land-cover data point. The equation for linear interpolation function is:

$$f_{(x)} = f(x_0) + \frac{f(x_1) - f(x_0)}{x_1 - x_0}(x - x_0) \qquad (3.1)$$

Where the independent variable is x, known values of the independent variable are x_0 and x_1, and $f_{(x)}$ is the value of the dependent variable for the given value x.

Interpolation is adequate for time series data that exhibit trends (Noor et al., 2014). If the time between recorded land-cover and physico-chemical data was too great, that data point was removed from the analysis. This was the case for the 1937 land-cover data. A Spearman's rank correlation between physico-chemical variables and land-cover data was performed because assumptions of normality could not be met even after data transformation (this applied to most land-cover classes). Simple linear regression analyses were performed on individual land-cover classes and physico-chemical variables that met the regression analysis assumptions: normal distribution, independence of residuals, and constant variance of residuals.

3.4 Results

3.4.1 Land-cover characteristics

3.4.1.1 The uMgeni Estuary

In the uMgeni catchment, there has been an increase in artificial land-cover from 1990 (7.69%) to 2018 (18.74%) (Figure 3.1). This has replaced the natural catchment vegetation, as evident in the simultaneous decrease of N-vegetation from 1990 (55.32%) to 2018 (43.01%). Cultivation constitutes a large portion of the catchment land-cover (36.40% in 2018), although increases over the years have been minimal. Presently, the uMgeni catchment is dominated by natural vegetation (43.01%), although this includes a large portion of invasive species, followed by cultivated land (36.40%), and artificial land-cover (18.74%).

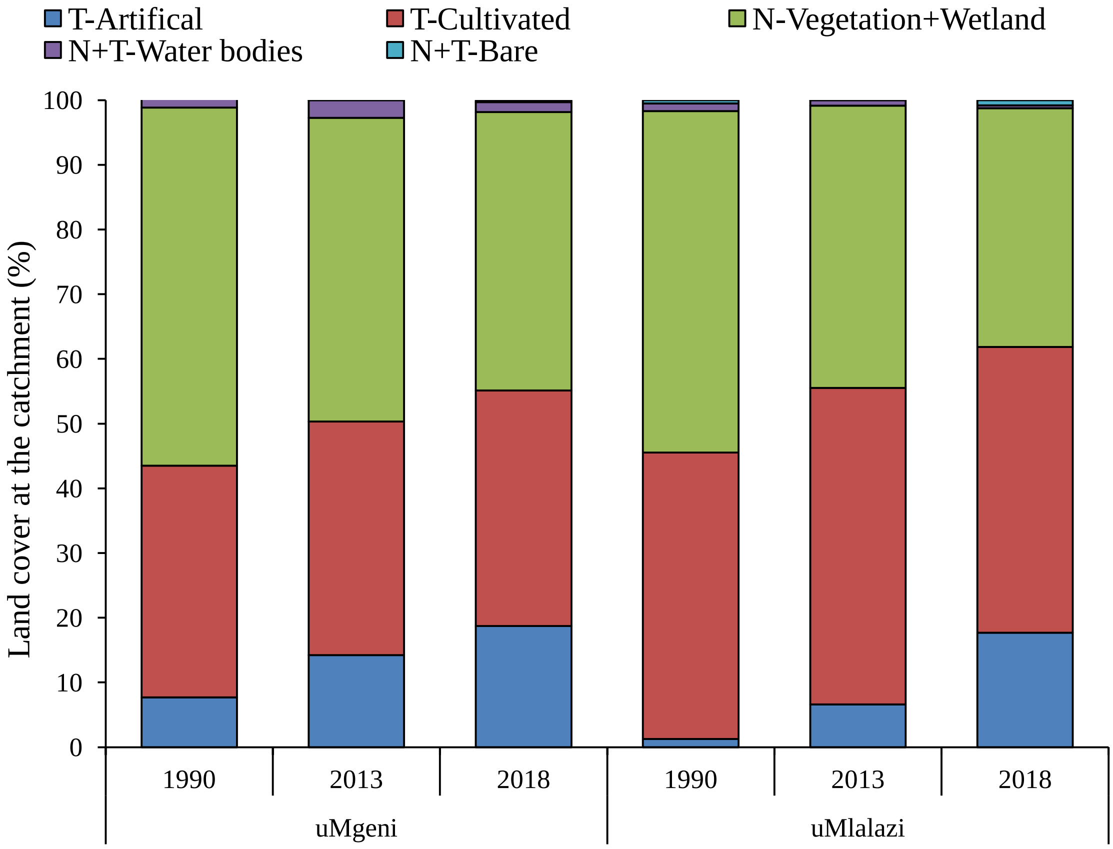


Figure 3.1 Level 2 land-cover types, represented as a percentage of the total area in each catchment for 1990, 2013, and 2018. N = Natural, T = Transformed, N+T = Natural and Transformed land-cover combined. Land-cover classes with minor percentage contributions to the total area (e.g., Bare and Waterbodies) were only available as combined classes at the catchment scale.

A significant portion of the LULC was disturbed at levels such that natural land-cover was not discernible. Therefore, at Level One classification, no distinction was made between these two classes. All subsequent references to natural classes are still disturbed to some degree, but were deemed more natural than transformed. At a finer level of classification, immediately surrounding the estuary to the 20 m contour, land-cover in the uMgeni is 38.34% natural, interspersed with exotic and alien invasive species, and 61.66% transformed. The current dominant L3 land-cover classes in the uMgeni 20 m contour include commercial (18.67%), open spaces (13.79%), infrastructure (12.63%), herbaceous (11.33%), and coastal forest (7.6%) (Figure 3.2). These classes constitute 64.02% of the total land-cover in the 20 m contour.

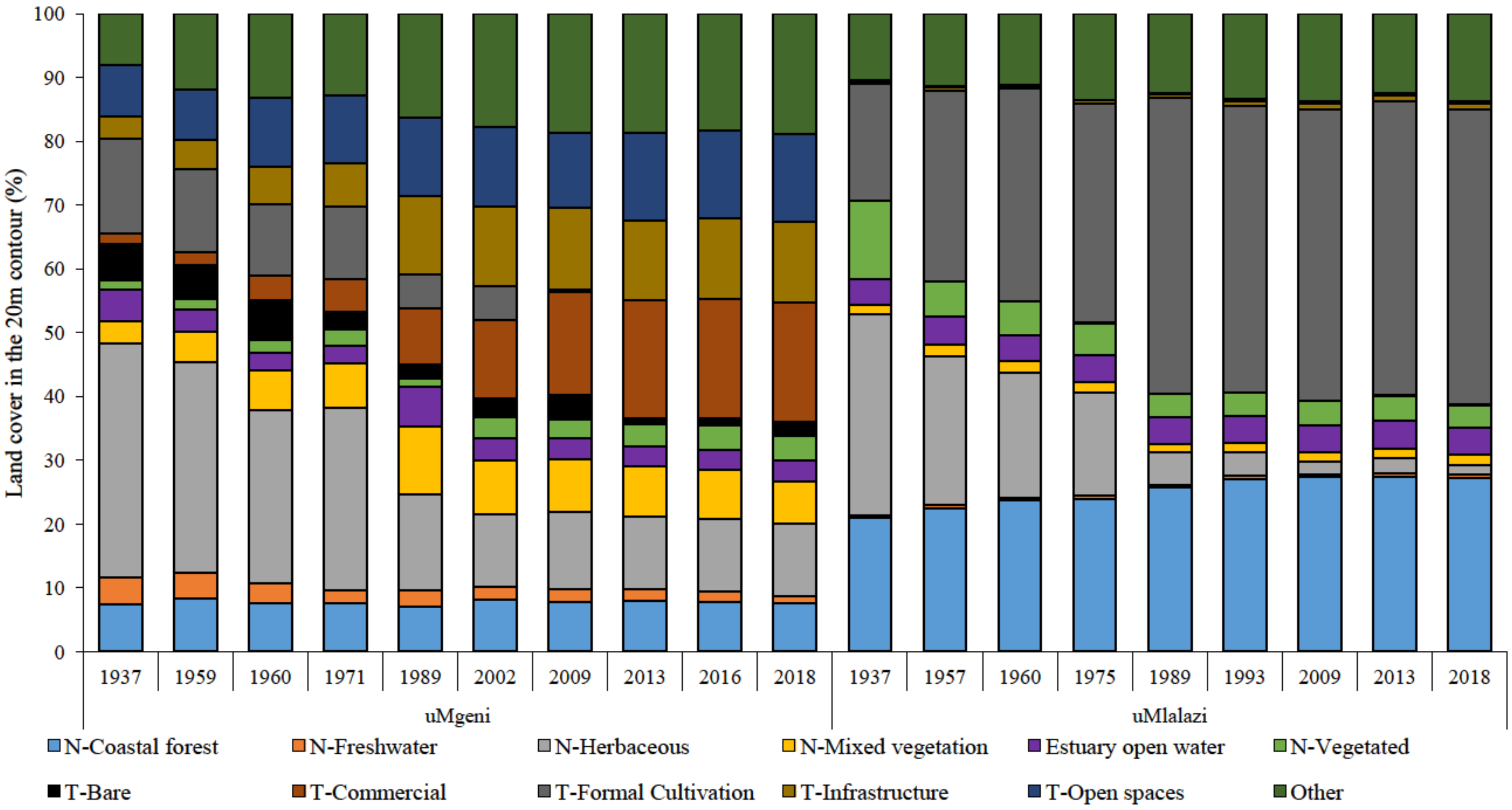


Figure 3.2 Level 3 land-cover types represented as a percentage of the total area in the 20 m contour of the uMgeni and uMlalazi estuaries from 1937-2018. N = Natural, T = Transformed. Only land-cover types contributing more than 3% to the total area were represented. The remaining classes were grouped as "other."

From 1937, the greatest land-cover increases have occurred in artificial (35% increase) and managed vegetation (5% increase) for the uMgeni Estuary (Figure 3.3). Managed vegetation dominates the lower southern bank of the estuary, whereas artificial land-cover has encroached on the lower, middle, upper and riverine reaches (Figure 3.4). The morphological changes to the estuarine water body due to canalisation are evident, as is the loss of a wetland island in the lower reaches. Natural waterways were easily identifiable in 1937 but are now confined to small areas in the riverine reaches of the system (Figure 3.4). A 3.37% increase in wetlands (mangroves and vegetated area) has also occurred since 1937. Wetland area in 2018 penetrated upstream into the riverine reach compared to occurring only in the middle and lower reaches in 1937. Cultivation has decreased by 14.58% (Figure 3.3) and is currently insignificant in the uMgeni 20 m contour (Figure 3.4), being replaced by artificial land-cover.

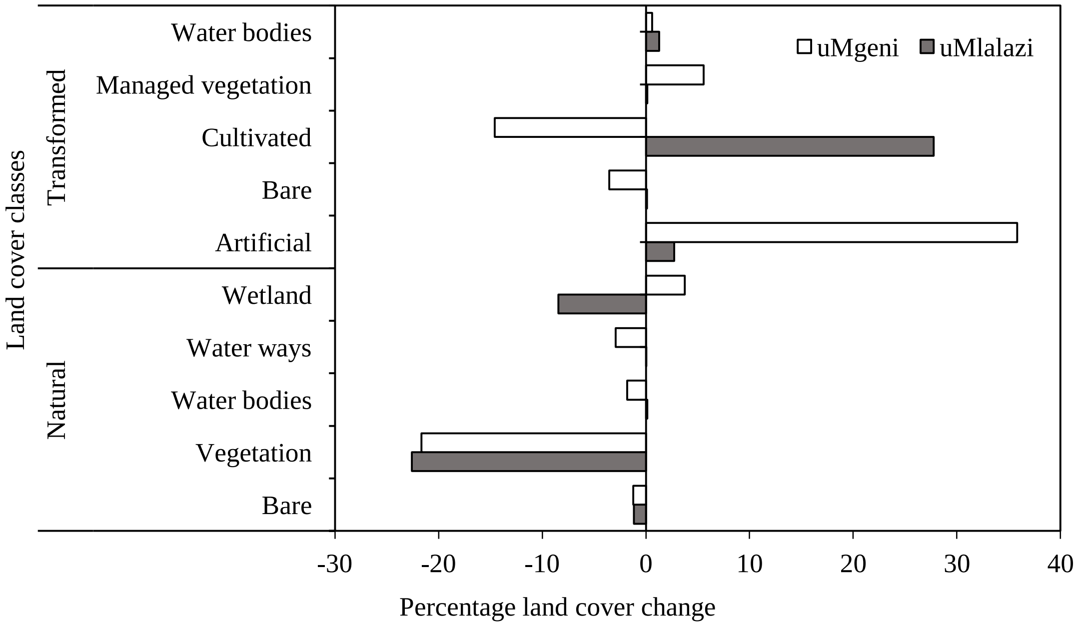


Figure 3.3 Land-cover changes around the uMgeni and uMlalazi estuaries to the 20 m contour from 1937-2018 represented as a percentage change. Level 1 classes = Natural and Transformed. Level 2 classes = Waterbodies, Managed vegetation, Cultivation, Bare, Artificial, Wetland, Vegetation, and Waterways.

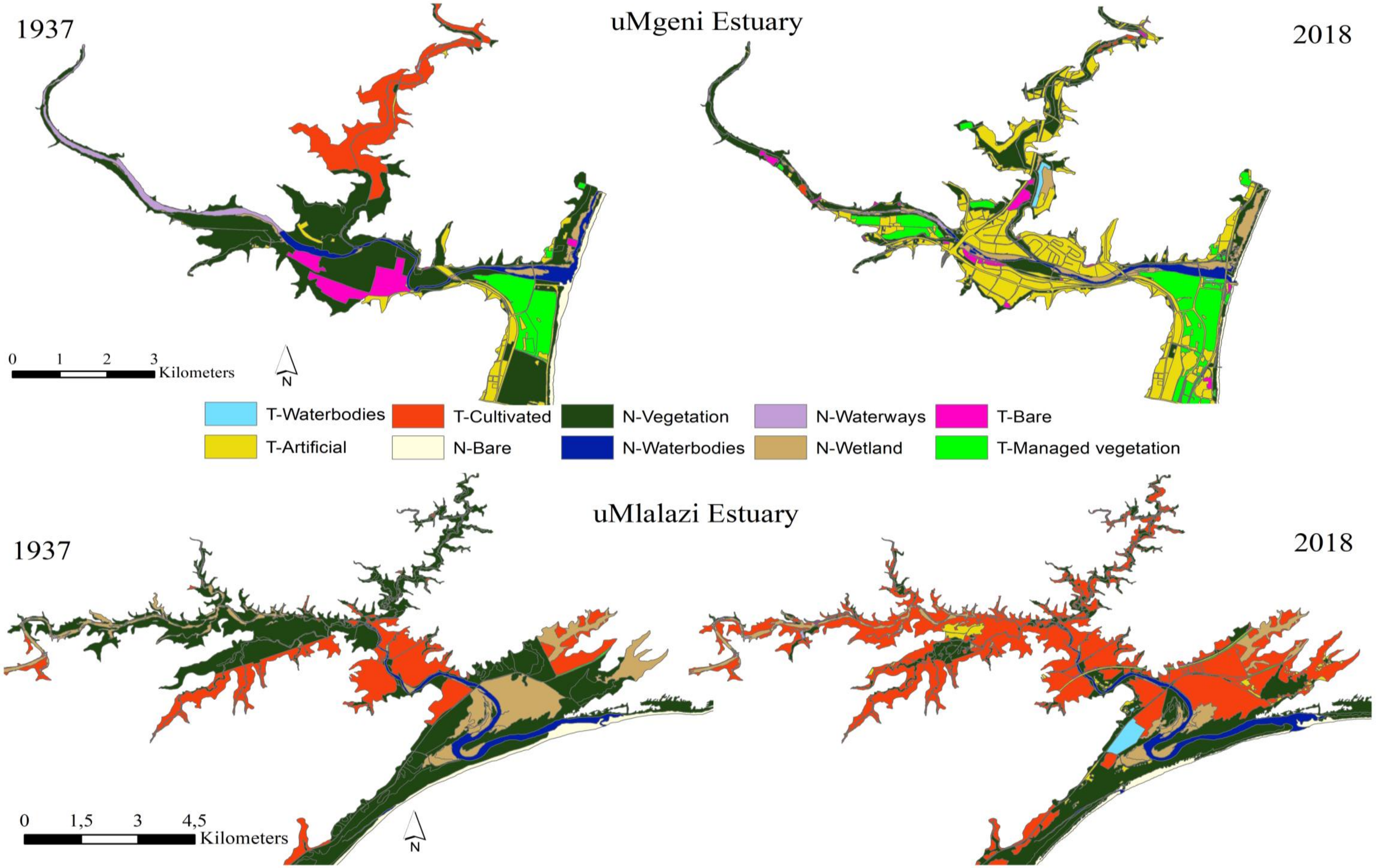


Figure 3.4 Land-cover changes around the uMgeni and uMlalazi estuaries to the 20 m contour from 1937-2018 represented in GIS map. Level 1 classes = Natural and Transformed. Level 2 classes = Waterbodies, Managed vegetation, Cultivation, Bare, Artificial, Wetland, Vegetation, and Waterways.

Hierarchical clustering and SIMPROF identified four groups (red dotted line and brackets in the dendrogram (Figure 3.5)) of land-cover immediately (within the 20 m contour) around the uMgeni Estuary at 88.89% (pi = 1.54, p = 0.018) similarity. The overall Bray-Curtis similarity was high, with all groups more than 77% similar. Samples in groups I, III, and IV shared distinct land-cover patterns, whereas group II samples had greater variability. Overall, two broad clusters of groups were identified. Groups I and II formed one cluster at 87.45% similarity (pi = 1.66, p = 0.005) and included years 1989 - 2018. Groups III and IV formed a separate cluster at 88.89% similarity (pi = 1.54, p = 0.018) and included years 1937 - 1971. For the purpose of the analyses going forward, and specifically, to achieve a more balanced distribution of physico-chemical and ichthyofauna data points over time with which to conduct statistical analyses, these groups were designated as Period 1 (1937 - 1988) and Period 2 (1989 - 2018) at 77.08% similarity (pi = 3.12, p = 0.001). This factor was used to represent changes in land-cover, water quality and fish assemblages in the uMgeni Estuary over time. The nMDS analysis based on the 77.08% similarity groups showed that land-cover classes associated with Period 1 were characterised by mostly natural land-cover (Figure 3.6). Natural land-cover classes included N-freshwater, N-unconsolidated sediment and N-bare (sand and mud banks). Transformed land-cover classes were strongly associated with Period 2. These included T-commercial, T-residential, T-herbaceous invasive, T-industrial, and T-open spaces.

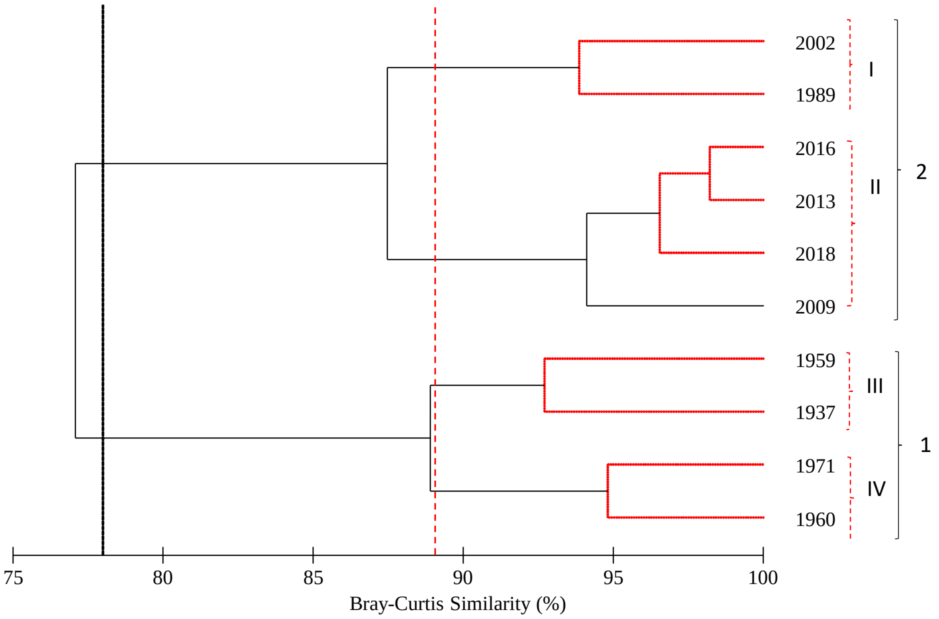


Figure 3.5 Dendrogram of hierarchical clustering of land-cover years of the uMgeni Estuary. Solid red lines represent non-significantly different samples at p < 0.05 according to SIMPROF testing. Solid black line represents the separation of years at 77.07% into Periods 1 and 2. Dotted red line represents the separation of years at 88.87% into clusters I-IV.

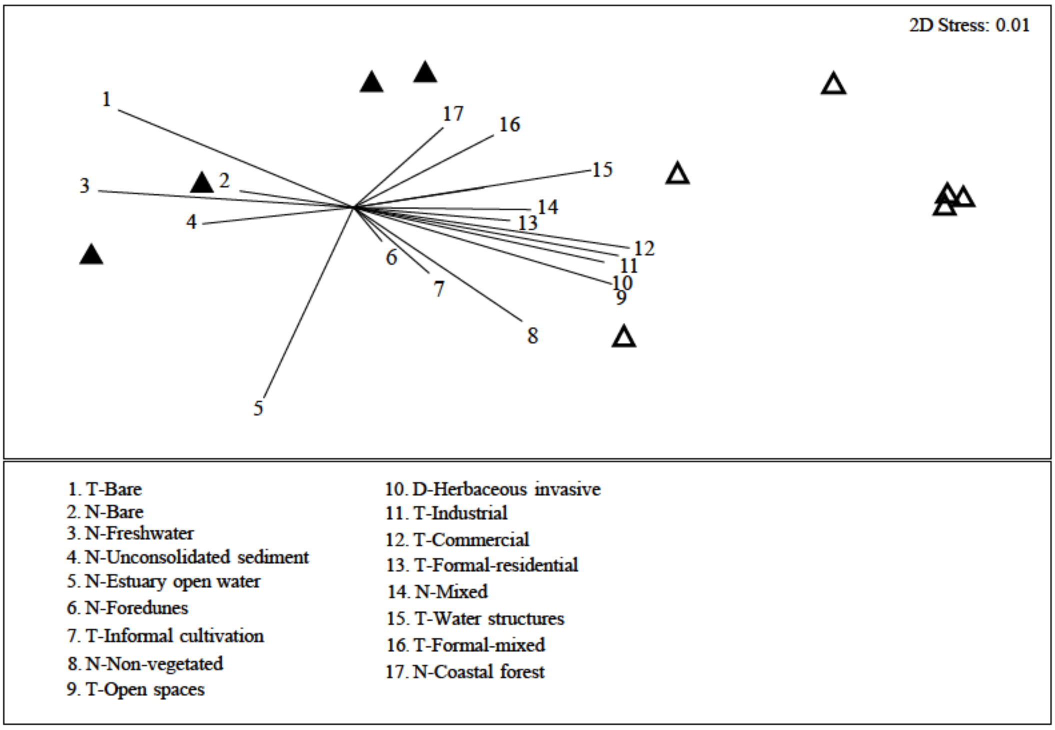


Figure 3.6 nMDS of uMgeni land-cover groups according to periods. Vectors represent land-cover L3 classes most associated with period samples. N = Natural, T = Transformed. Closed triangle = Period 1, Open triangle = Period 2.

3.4.1.2 The uMlalazi Estuary

Artificial land-cover in the uMlalazi catchment increased substantially from 1990 (1.28%) to 2018 (17.70%) (Figure 3.1). The percentage of cultivated land was greatest in 2013 (48.88%) and decreased to 44.15% in 2018. Increases in artificial land-cover have resulted in the decline of natural vegetation from 1990 (52.79%) to 2018 (36.88%). The latest land-cover data revealed that to the 20 m contour of the uMlalazi Estuary, 47.43% of land-cover is natural and 52.56% is transformed. As for the uMgeni Estuary, the proportion of purely natural land-cover classes were indiscernible from disturbed classes in the uMlalazi Estuary. Therefore, subsequent references to natural classes were disturbed to some degree but more natural than transformed. The current dominant land-cover classes in the 20 m contour include formal cultivation (46.17%), coastal forest (27.26%), and estuary open water (4.27%), contributing 77.7% to the total land-cover (Figure 3.2). The uMlalazi Estuary, up to the 20 m contour, has seen a 27% increase in cultivation and a much smaller increase of 2.72% in artificial land-cover (Figure 3.3). Cultivated areas have encroached on the natural riparian vegetation and a large portion of the wetland area in the upper and mid estuary (Figure 3.4). In the 2018 land-cover data, the largest artificial area was observed in the upper limits of the 20 m estuary contour, in contrast to the lower coverage of artificial land-cover in the estuary protected area (Figure 3.4). The establishment of an aquaculture farm on the south bank of the mid-estuary resulted in a 0.13% increase in transformed waterbodies. Despite a decrease in most natural land-cover types, natural foredune vegetation and coastal forest have increased by 1.35% in the uMlalazi Estuary (Figure 3.2), particularly in the lower and mouth regions (Figure 3.4).

Hierarchical clustering and SIMPROF identified two land-cover groups (solid black line and brackets) for the uMlalazi Estuary at 86.01% (pi = 1.44, p = 0.002) similarity (Figure 3.7). Group 1 formed a cluster at 90.83% similarity (pi = 0.43, p = 0.607) and included years 1937 - 1975. Group 2 formed a separate cluster at 92.52 similarity (pi = 0.63, p = 0.116) and included years 1993 - 2018. As with the uMgeni Estuary, samples were separated into Period 1 (1937 - 1988) and Period 2 (1989 - 2018) to achieve a more balanced dataset, which was subsequently used throughout the study for the uMlalazi analyses. The nMDS analysis based on the 86.01% similarity groups showed that land-cover classes associated with Period 1 were mostly natural (Figure 3.8). These included N-terrestrial forest, N-swamp forest, N-salt marsh and N-unconsolidated sediment. Transformed land-cover classes associated with Period 2 include T-residential, T-infrastructure, T-open spaces, and T-formal cultivation.

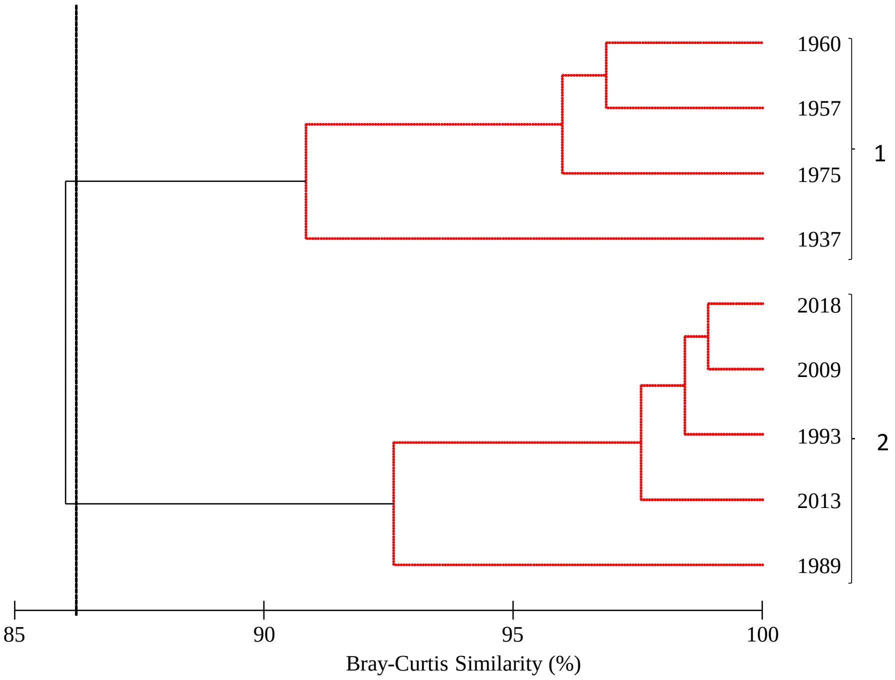


Figure 3.7 Dendrogram of hierarchical clustering of land-cover years for the uMlalazi Estuary. Red lines represent non-significantly different samples at p < 0.05 according to SIMPROF testing. Solid black line represents the separation of years at 86.01% similarity into Periods 1 and 2.

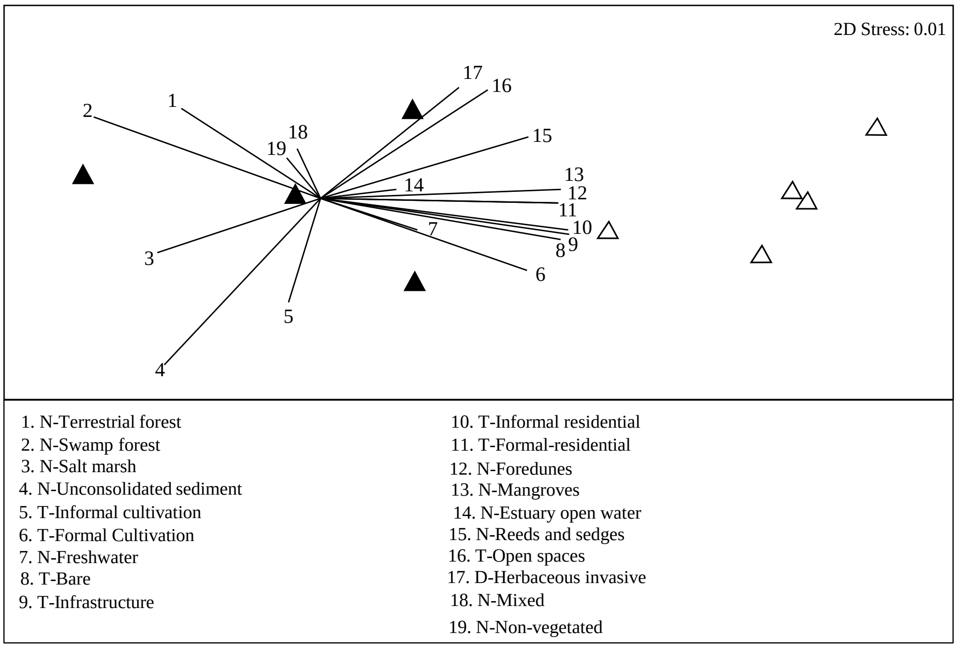


Figure 3.8 nMDS of uMlalazi land-cover samples according to periods. Vectors represent land-cover L3 classes most associated with period samples. N = Natural, T = Transformed. Closed triangle = Period 1, Open triangle = Period 2.

3.4.1.3 Land-cover comparison of the uMgeni and uMlalazi estuaries

Significant differences were observed between the uMgeni and uMlalazi 20 m contour land-cover patterns (PERMANOVA: Pseudo-F = 83.747, df = 1, p(perm) = 0.0001), although the average dissimilarity was not high (35.10%, Table 3.2). A PERMDISP test confirmed location effects, not sample dispersion, as responsible for these differences (F=3.078, df = 1, p(perm) = 0.09). The higher average dissimilarity suggested that artificial land-cover, cultivation, and managed vegetation contributed the most to system differences (69.90%). Overall, SIMPER confirmed that the uMgeni Estuary had higher contributions of artificial and managed vegetation types, whereas cultivated land dominated the uMlalazi Estuary.

Table 3.2 Land-cover (LC) level 2 classes contributing to the average dissimilarity of 35.10% between the uMgeni and uMlalazi estuaries.

	uMgeni	**uMlalazi**				
L2 class	**LC%**	**LC%**	**Av.Diss**	**Diss/SD**	**Contrib%**	**Cum.%**
T-Artificial	5.36	1.20	11.54	2.85	25.85	25.85
T-Cultivated	2.13	6.32	11.54	2.67	25.84	51.69
T-Managed vegetation	3.39	0.45	8.13	7.78	18.21	69.90
T-Bare	1.76	0.16	4.43	2.96	9.92	79.82
N-Wetland	2.06	3.10	2.92	2.03	6.54	86.36
N-Waterways	1.53	0.66	2.42	2.74	5.42	91.78
T-Waterbodies	0.71	0.50	1.62	1.60	3.62	95.41
N-Bare	1.26	1.70	1.27	1.87	2.84	98.24
N-Waterbodies	1.89	2.06	0.78	3.41	1.76	100.00
				Average dissimilarity = 35.10		

3.4.2 Physico-chemical characteristics

3.4.2.1 The uMgeni Estuary

Water quality data for each reach and period are presented in Table 3.3. A general increase in salinity was noted from Period 1 to Period 2, with the greatest salinity increases occurring in the lower reaches. Dissolved oxygen (DO) was variable, with greater ranges occurring in Period 2. Over the entire data range, a general decreasing trend in dissolved oxygen was seen in all but the lower reaches of the uMgeni Estuary. Average dissolved oxygen in the riverine reaches decreased from 8.13 (± 0.34 SD) in Period 1 (1937-1988) to 3.59 (± 2.13 SD) mg l^{-1} in Period 2 (1989-2020). Over the same periods, dissolved oxygen in the upper reaches decreased from 4.89 (± 1.32 SD) to 3.95 (± 1.28 SD) mg l^{-1}, and in the middle estuary from 5.35 (± 1.08 SD) to 4.88 (± 1.55 SD) mg l^{-1}. Temperature increases of ± 1 °C were observed from Period 1 to Period 2 in all reaches. Turbidity was highly variable in Period 1, ranging between 4 - 241 NTU. In Period 2 average turbidity was below 20 NTU, despite two incidents of exceptionally high turbidity in 1989 and 1990 (241 NTU). pH remained stable over the study periods.

Table 3.3 Mean ± Standard deviation of physico-chemical variables according to periods for the uMgeni and uMlalazi estuaries. DO=dissolved oxygen

Estuary	Period	Reach	Salinity	DO	Temp	Turbidity	Depth	pH
uMgeni			**14.68±13.30**	**5.27±1.5**	**23.53±3.7**	**51.29±78.55**	**0.95±0.46**	**7.43±0.43**
	1937-1988	**Lower**	17.65±12.93	5.78±1.13	22.88±3.33	75.00±98.91	0.82±0.41	7.50±0.25
		Middle	15.39±12.11	5.35±1.08	23.21±3.79	69.94±79.98	0.80±0.39	-
		Upper	7.89±10.55	4.89±1.32	23.20±4.13	96.81±97.69	1.40±0.43	7.42±0.29
		Riverine	0.06±0.04	8.13±0.34	-	-	1.08±0.25	7.50±28.00
	1989-2020	**Lower**	26.13±11.70	6.24±1.36	24.01±3.84	7.51±6.60	0.86±0.35	7.77±0.38
		Middle	16.87±12.26	4.88±1.15	24.66±3.71	13.58±6.86	0.94±0.42	7.40±0.36
		Upper	11.82±13.84	3.95±1.28	24.77±3.46	15.39±11.03	1.32±0.47	7.29±0.37
		Riverine	0.39±0.51	3.59±2.13	23.71±4.13	12.17±8.61	1.07±0.52	7.23±0.49
uMlalazi			**21.16±11.10**	**6.20±1.79**	**26.23±3.06**	**15.36±9.26**	**1.26±0.61**	**7.61±0.49**
	1937-1988	**Lower**	27.40±7.45	5.56±2.53	28.17±2.71	9.63±12.51	1.25±0.77	-
		Middle	15.63±9.66	2.85±2.33	27.50±0.71	19.33±18.01	1.25±0.42	-
		Upper	11.01±9.46	-	-	7.50±0.71	2.63±0.43	-
		Riverine	12.46±16.37	5.20±0.85	22.20±3.82	-	1.93±0.83	7.16±0.29
	1989-2020	**Lower**	28.51±7.91	7.53±0.95	24.97±2.58	13.67±5.96	0.99±0.4	7.91±0.41
		Middle	23.75±7.31	6.58±1.21	25.60±3.12	22.5±10.63	0.94±0.35	7.75±0.39
		Upper	16.34±5.79	5.31±1.17	27.84±2.42	18.94±9.02	1.51±0.26	7.39±0.26
		Riverine	9.26±7.69	4.62±1.61	27.91±3.03	12.35±3.65	1.32±0.44	7.05±0.26

Similarity profile testing on the yearly physico-chemical data averaged across reaches identified three significantly different clusters of samples at a distance of 2.24 (pi = 0.08. p =

0.001) (Figure 3.9). Groups I and II showed distinct physico-chemical conditions, whereas group III displayed variability between samples. Multivariate testing confirmed significant differences between clusters I-III (PERMANOVA: df = 2, Pseudo-F = 43.461, p(perm) = 0.0001, Table 3.4) and between reaches (PERMANOVA: df = 6, Pseudo-F = 2.276, p(perm) = 0.03, Table 3.4). However, spatial and temporal differences were not as obvious across the entire estuary but rather occurred at the reach level over time (PERMANOVA: df = 3, Pseudo-F = 2.238, p(perm) = 0.011, Table 3.4). Physico-chemistry in the lower reach was significantly different between cluster groups I and III (PERMANOVA Pairwise comparison: t = 4.880, p(perm) = 0.0001). Physico-chemistry in the middle, upper and riverine reaches differed significantly in all cluster group combinations (Table 3.4).

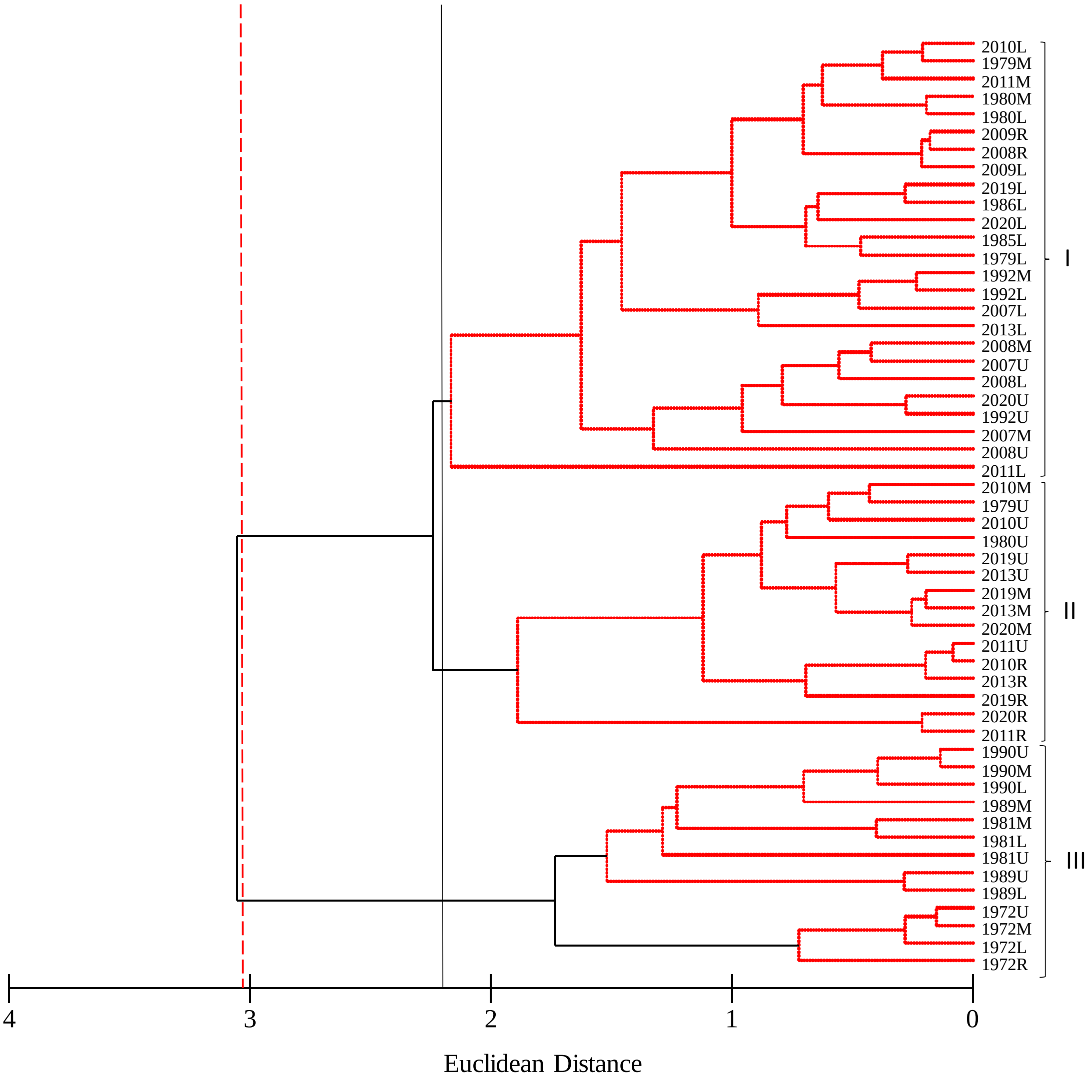


Figure 3.9 Dendrogram of hierarchical clustering of physico-chemical uMgeni data. Red lines represent non-significantly different samples at $p < 0.05$ according to SIMPROF testing. Solid black line represents the separation of years at Euclidean distance 2.24 into cluster groups I-III. Dotted red line represents the separation of samples at a distance of 3.06 into similar land-cover groups.

Principal coordinate analysis revealed that salinity, dissolved oxygen and turbidity were primary drivers of differences in the uMgeni Estuary physico-chemistry across years and over different reaches (Figure 3.10). Axes PCO 1 and 2 explained a cumulative total variation of 89.7% of the resemblance matrix. Turbidity (Spearman's: r = 0.8) and salinity (Spearman's: r = - 0.86) correlated to PCO axis 1. Dissolved oxygen (Spearman's: r = 0.92) was correlated with PCO axis 2 and was higher in the lower reaches of the estuary in the 1980s and 1990s (represented in cluster I) (Figure 3.10). Group I samples, according to SIMPROF and hierarchical clustering, were characterised by higher salinities in the lower and middle reaches across different years. Group II comprised samples from the middle, upper and riverine reaches of the uMgeni and were characterised by the lowest oxygen levels. Group III was characterised by samples from the 1970s, 1980s and 1990s, when the highest turbidity and dissolved oxygen levels occurred in all reaches.

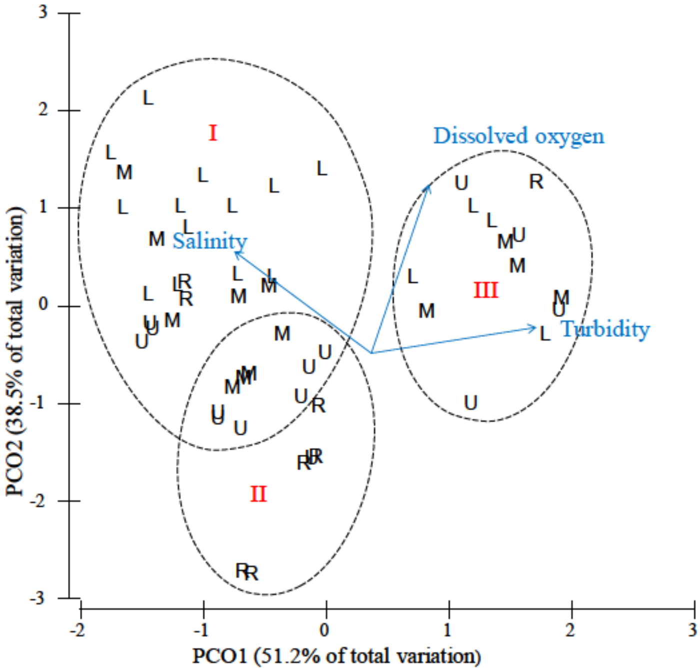


Figure 3.10 Principal coordinate plot of uMgeni physico-chemical samples (represented per year_reach). Clustered groups are shown via dashed ellipses (I-III). Reaches are represented as R = riverine, U = upper, M = middle, and L = lower. Vectors represent physico-chemical variables correlated with samples.

The separation of physico-chemical samples by years, when sliced at a distance of 3.06 (pi = 0.1, p = 0.003) (Figure 3.9), appeared similar to the "period" groups of the land-cover samples. Multivariate permutational testing confirmed that physico-chemical variables were different between the two distinct land-cover periods (PERMANOVA: df = 1, Pseudo-F = 7.284, p(perm) = 0.001, Table 3.4). However, PERMDISP (PERMDISP: F = 1.818, df = 1, p(perm) = 0.249) revealed that land-cover changes, which would be reflected temporally, might not have been the primary cause of the overall physico-chemical changes of the uMgeni Estuary. The cluster dendrogram and PCO revealed the natural spatial variability of the physico-chemical variables. Overall changes in physico-chemical variables were more distinct when looking at specific reaches over time.

Table 3.4 PERMANOVA and pairwise comparison results of physico-chemical differences in the uMgeni Estuary according to land-cover periods and physico-chemical cluster groups. Clusters are derived from SIMPROF and hierarchical clustering according to the yearly physico-chemical averages per reach. Df = degrees of freedom, Pseudo-F = critical values. Asterisks denote significance at p<0.05. MC denotes Monte Carlo test.

Source		PERMANOVA				PERMANOVA	
	Df	Pseudo –F	P(Perm)		Df	Pseudo-F	P(Perm)
Land-cover Period				**Physico-chemical Clusters**			
Period	1	7.284	0.001*	Clusters (I-III)	2	43.461	0.0001*
Reach	3	2.611	0.015*	Reach	6	2.276	0.030*
Period x Reach	3	1.314	0.258	Cluster x Reach	3	2.238	0.011*
Reach Pairwise comparison							
	T	Perms	P(perm)		T	Perms	P(perm)
Lower vs. Middle	1.341	9943	0.161	Lower vs. Middle	0.970	9950	0.378
Lower vs. Upper	2.367	9955	0.005*	Lower vs. Upper	2.179	9939	0.009*
Lower vs. Riverine	1.828	9953	0.028*	Lower vs. Riverine	1.173	9961	0.257
Middle vs. Upper	0.980	9943	0.378	Middle vs. Upper	1.558	9943	0.091
Middle vs. Riverine	1.176	9960	0.272	Middle vs. Riverine	1.632	9955	0.070
Upper vs. Riverine	1.162	9958	0.267	Upper vs. Riverine	1.958	9946	0.025*
Physico-chemical Cluster x Reach Pairwise comparison							
	T	Perms	P(perm)		T	Perms	P(perm)
Lower Reach				Upper Reach			
I vs. III	4.880	2348	0.001*	I vs. III	4.270	35	0.001(MC)*
				I vs. II	3.899	210	0.006*
				II vs. III	3.239	210	0.005*
Middle Reach				Riverine Reach			
I vs. III	4.842	210	0.005*	I vs. III	22.411	3	0.019(MC)*
I vs. II	5.577	35	0.001(MC)*	I vs. II	4.001	6	0.014(MC)*
II vs. III	2.597	210	0.015*	II vs. III	3.371	21	0.008(MC)*

3.4.2.2 The uMlalazi Estuary

Water quality data for each reach and period are presented in Table 3.3. A general increase of salinity in each reach from Period 1 to Period 2 was observed, except for the riverine reach. Dissolved oxygen levels ranged from 1.6 - 9.3 mg l^{-1}, although a general increase in the range of dissolved oxygen (DO) levels was observed over time. In the riverine reach average dissolved oxygen levels decreased from 5.52 (± 0.85 SD) mg l^{-1} in Period 1 to 4.62 (± 1.61 SD) mg l^{-1} in Period 2. Over the same periods, dissolved oxygen varied from 2.85 (± 2.33 SD) mg l^{-1} to 6.58 (±1.21 SD) mg l^{-1} in the middle reaches and 5.56 (± 2.53 SD) mg l^{-1} to 7.53 (± 0.95 SD) mg l^{-1} in the lower reaches. Temperature fluctuated between periods, likely a result of seasonal sampling differences. The greatest turbidity ranges were recorded in 1986 (4 - 40 NTU) and 2010 (6.25 - 40 NTU). pH remained stable over the study periods.

Similarity profile testing on the physico-chemical data of the uMlalazi Estuary revealed that all samples clustered together at a distance of 3.2 (pi = 0.07, p = 0.013, Figure 3.11). There were no significant differences in water quality over the years analysed. Multivariate testing on the factor period according to land-cover SIMPROF groups also produced no significant differences between physico-chemical samples over time (PERMANOVA, Pseudo-F = 1.569, df = 1, p(perm) = 0.202, Table 3.5). Variability between samples in the factor period were also not significantly different (PERMDISP: F = 1.077, df =1, p(perm) = 0.424) confirming no location or dispersion effects. However, these results should be interpreted with caution due to the small sample size in Period 1 (n = 3) (Figure 3.12).

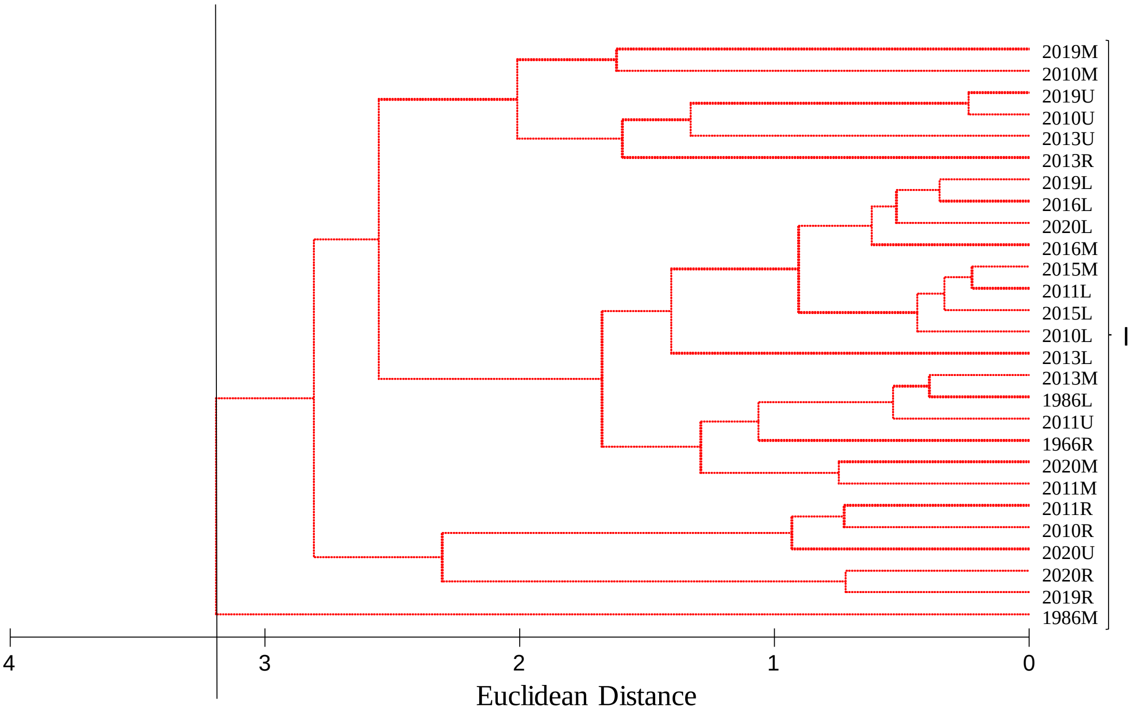


Figure 3.11 Dendrogram of hierarchical clustering of physico-chemical uMlalazi data. Red lines represent non-significantly different samples at $p < 0.05$ according to SIMPROF testing. Solid black line represents the clustering of all physico-chemical samples into group I at a distance of 3.2.

With no changes in water quality in the uMlalazi Estuary over time, it is clear that for this study, land-cover changes have not impacted the overall physico-chemical conditions in the system. Rather, differences in physico-chemistry are dependent on location (reach) in the estuary (PERMANOVA, Pseudo-F = 6.084, df = 3, p(perm) = 0.0001, Figure 3.12). Principal coordinate Axes 1 and 2 explained a cumulative total variation of 80.1% in the resemblance matrix (Figure 3.12). Dissolved oxygen (Spearman's: r = 0.83) and salinity (Spearman's: r = 0.85) were more closely correlated with PCO axis 1. Samples in the lower reaches were associated with higher salinities and dissolved oxygen. Turbidity was correlated to PCO axis 2 (Spearman's rank: r = 0.9) (Figure 3.12), with most upper and middle reach samples showing higher turbidity values.

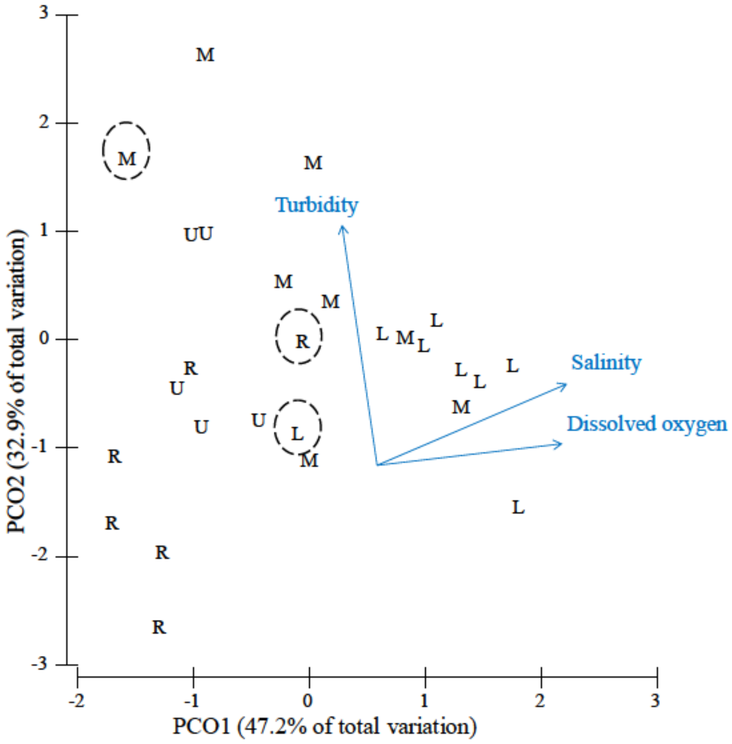


Figure 3.12 Principal coordinate plot of uMlalazi samples (represented per year_reach). Reaches are represented as R = riverine, U = upper, M = middle, and L = lower. Vectors represent physico-chemical variable correlations with samples. Dashed ellipses represent samples from 1966 and 1986 (Period 1).

Table 3.5 PERMANOVA and pairwise comparison results of physico-chemical differences in the uMlalazi Estuary according to land-cover periods and reaches. Df = degrees of freedom, Pseudo-F = critical values. Asterisks denote significance at p<0.05.

Source	**PERMANOVA**		
	Df	Pseudo-F	P(Perm)
Period	1	1.569	0.202
Reach	3	6.084	0.0001*
Pairwise comparison	T	Perms	P(perm)
Reach			
Lower vs. Middle	3.634	2878	0.0004*
Lower vs. Upper	2.238	2903	0.002*
Lower vs. Riverine	1.250	462	0.244
Middle vs. Upper	2.297	5008	0.012*
Middle vs. Riverine	4.087	1286	0.001*
Upper vs. Riverine	1.334	1286	0.168

3.4.2.3 Physico-chemical comparison of the uMgeni and uMlalazi estuaries

Overall physico-chemical conditions in the uMgeni Estuary were significantly different from those in the uMlalazi Estuary (PERMANOVA: Pseudo-F=4.462, df = 3, p (perm) = 0.0006). PERMDISP confirmed that PERMANOVA significant differences between uMgeni and uMlalazi during Period 1 resulted from estuary effects and not dispersion (PERMDISP: t = 2.806, p(perm) = 0.087). uMgeni Period 2 and uMlalazi Period 2 differences were driven by dispersion effects (PERMDISP: t = 2.915, p(perm) = 0.0.011). The average distance of uMgeni samples in Period 2 (2.356) was greater than the uMlalazi Period 2 samples (1.610), depicting the uMgeni samples' variability during this period. Location effects, however, may still be present.

3.4.3 Relating land-cover and physico-chemical variables

Dissolved oxygen was the only physico-chemical variable significantly correlated to land-cover classes in the uMgeni Estuary and was evident in all three land-cover levels. However, it should be noted that turbidity showed a moderate correlation with artificial land-cover (Spearman's: r = - 0.617, p = 0.067), although not significantly so. In Level One (L1) land-cover, dissolved oxygen was strongly positively correlated with natural land-cover (Spearman's: r = 0.63, p = 0.043) and negatively correlated with transformed land-cover (Spearman's: r = - 0.82, p = 0.002). Strong negative relationships were found between artificial land-cover types (L2) and dissolved oxygen in the uMgeni (Polynomial Inverse First Order regression: $r^2 = -0.81$, F = 40.21, df = 1, $p < 0.0001$, Figure 3.13), with increases in artificial cover resulting in reduced oxygen levels. These L3 artificial land-cover types included commercial (Spearman's: r = - 0.81; p = 0.003) and infrastructure (Spearman's: r = - 0.76, p = 0.009). Dissolved oxygen was also negatively correlated with managed vegetation, primarily represented by open spaces (L3) (Linear regression: $r^2 = -0.63$, df = 1, F = 13.86, p = 0.006, Figure 3.13). The correlation between dissolved oxygen and wetland land-cover types was negative (Linear regression: $r^2 = -0.468$, F = 7.045, df = 1, p = 0.029, Figure 3.13). Although salt marshes (L3 class of wetlands) were positively related to dissolved oxygen (Spearman's: r = 0.86; $p < 0.001$), mangroves (Spearman's rank: r = - 0.82, p = 0.002) more strongly influenced the overall negative relationship between wetlands and dissolved oxygen.

Spearman's rank correlation analyses on specific reach dissolved oxygen levels revealed correlations with similar land-cover classes to the analyses above (Table 3.6). Dissolved oxygen in the middle reaches was negatively correlated to artificial land-cover (Spearman's: r

= - 0.70, p = 0.022) and wetland (Spearman's: r = - 0.62, p = 0.048) land-cover. Similar correlations were also observed in the upper reaches. Despite no overall correlation between natural waterbodies and the estuary oxygen levels, a moderate correlation was observed between this land-cover class and dissolved oxygen in the lower reaches (Spearman's rank: r = - 0.64, p = 0.032).

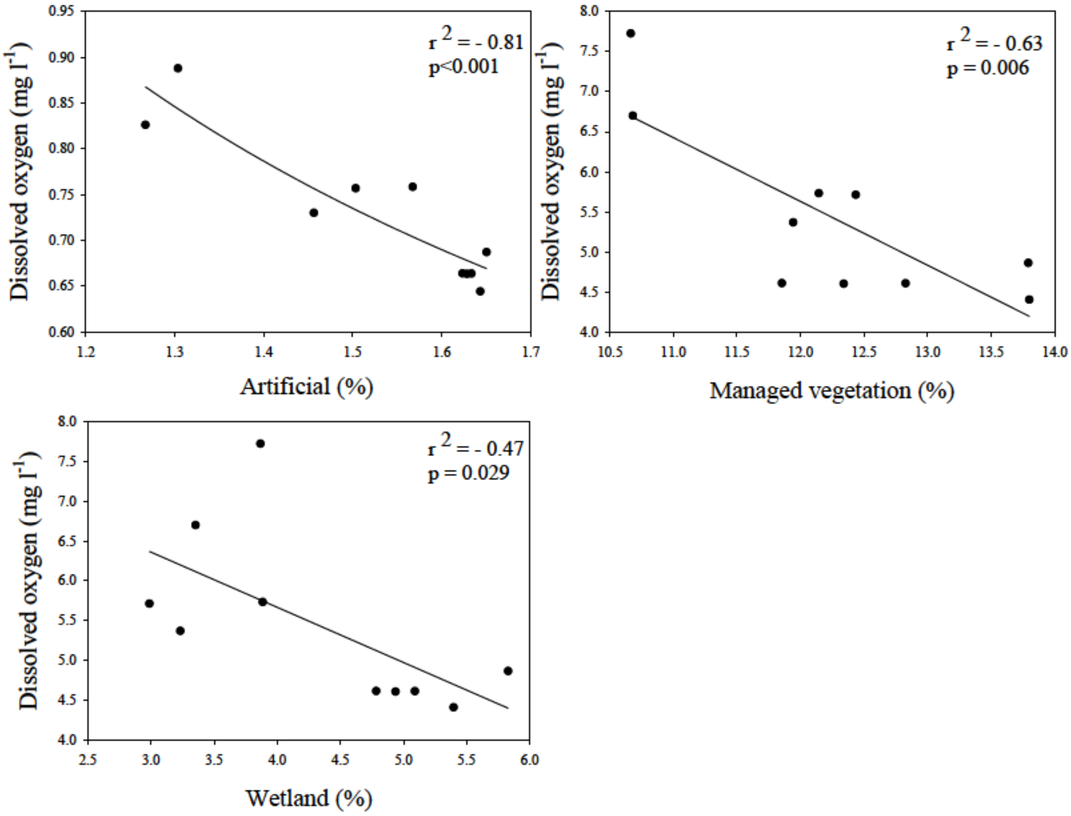


Figure 3.13 Correlations between land-cover classes and physico-chemical variables in the uMgeni Estuary. Only significant correlations were represented.

Table 3.6 Spearman's correlation (r) of land-cover classes and dissolved oxygen in various reaches in the uMgeni Estuary. Bold numbers represent significant correlations at $p < 0.05$.

	Lower	Middle	Upper	Riverine
N-Bare	-0.536	0.43	0.164	0.0714
N-Waterbodies	**-0.636**	0.0667	-0.1	-0.429
N-Wetland	0.336	**-0.624**	**-0.682**	-0.643
T Waterbodies	-0.445	0.103	-0.327	-0.536
T-Artificial	0.164	**-0.697**	**-0.745**	-0.643
T-Managed vegetation	0.291	-0.43	-0.491	-0.714
T-Bare	-0.418	0.164	0.109	0.429

Fewer correlations between water quality variables and land-cover classes were observed in the uMlalazi Estuary. Transformed land-cover was positively correlated with dissolved oxygen (Spearman's: r = 0.89, p < 0.001) but the sample size was less than recommended for this test (< eight samples); therefore, these results should be interpreted with caution. Strong positive relationships were found between artificial land-cover types and dissolved oxygen in the uMlalazi (Linear regression: $r^2 = 0.89$, F = 14.878, df = 1, p = 0.012). Level three artificial types contributing towards relationships with dissolved oxygen included formal residential (Spearman's: r = 0.83, p < 0.0001), informal cultivation (Spearman's: r = -0.93, p < 0.0001) and non-residential (Spearman's rank: r = 0.92, p < 0.0001).

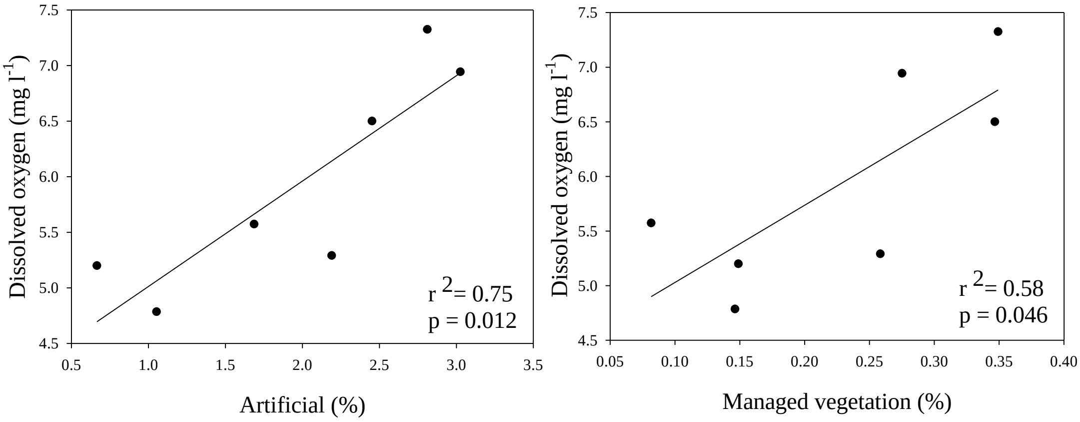


Figure 3.14 The relationship between artificial land-cover, managed vegetation and dissolved oxygen over time in the uMlalazi Estuary.

For reach-specific correlations, good results were found in comparisons between dissolved oxygen in the middle reaches and artificial land-cover (Spearman's: r = 1.00, p = 0.003, Table 3.7). Natural bare land-cover was negatively correlated with dissolved oxygen (Spearman's: r = - 0.94, p = 0.017, Table 3.7).

Table 3.7 Spearman's correlation (r) of land-cover classes and dissolved oxygen in various reaches in the uMlalazi Estuary. Bold numbers represent significant correlations at p <0.05.

	Lower	**Middle**	**Upper**	**Riverine**
N-Vegetation	-0.771	-0.6	0.6	-0.6
N-Waterways	-0.257	0.0286	0.4	0
N-Bare	-0.714	**-0.943**	0.8	-0.5
N-Waterbodies	0.143	0.257	0.4	0.3
N-Wetland	-0.771	-0.829	0.8	-0.5
T Waterbodies	0.841	0.754	-1	0.667
T-Artificial	0.771	**1.00**	-0.8	0.5

3.5 Discussion

3.5.1 Drivers of land-cover change

The uMgeni Estuary is a highly modified system that has undergone extensive morphological changes. Transformation of the uMgeni Estuary was already evident in 1937. Alterations to the estuary began long before this, with use of the system originally by Zulu and later European settlers. Historical records from the 1600s reveal that the system was once joined to Durban Bay with only a sandbar separating it from the Indian Ocean (Begg, 1978). City engineers, however, breached the sandbar to redirect the mouth to its current position due to fears of flooding and malaria (Begg, 1978). The estuary now remains predominantly open, directly to the sea north of Durban Bay, and closes only during extreme low flows (DWA, 2011).

Alterations to the land-cover within the uMgeni 20 m contour, from natural to artificial, were consistent from 1937 - 1971. A significant increase in artificial land-cover occurred between 1972 and 1989. During this period, coverage by infrastructure doubled, followed by commercial land-cover. These increases were primarily the result of large development changes in the estuary's upper reaches in 1980. The Connaught Bridge was broken down and replaced with the M19 (Begg, 1978) and a causeway was built to divert the meandering estuary channel. In the process, 187 ha of the uMgeni floodplain was converted into the Industrial Springfield Flats region, removing large quantities of sediment and vegetation (Begg, 1978). Initially, the removed material was stored in retention ponds; however, this silt charged water spilt into the upper reaches of the uMgeni River in 1981 resulting in the infilling of the estuary (Begg, 1978).

The majority of the lower estuary's southern bank has been transformed by clearing vegetation for open spaces. It consists of the Windsor Park Golf Course, a model yacht pond, a restaurant, and other amenities for public use. Removing riparian vegetation has had detrimental effects on the system, such as habitat loss and bank destabilisation (DWA, 2011). These land-cover changes were a response to the booming economy post World War 2 (Goble and van der Elst, 2013). Agricultural land was replaced with developed areas to accommodate the growing tourism industry and activities associated with imports and exports (Goble and van der Elst, 2013). These trends were evident in the land-cover analysis conducted for this study, which showed an inverse relationship between agricultural and artificial area.

The naturally vegetated area surrounding the uMgeni Estuary has been greatly altered and reduced over the years in response to increasing urbanisation. The construction of a concrete causeway, which interfered with tidal fluctuations, threatened the ecological state of the mangrove community decades ago (Begg, 1984). This causeway was removed in 1975 and in 1976 the Beachwood Mangrove Nature Reserve was proclaimed, allowing the protection of the mangroves and associated species (Begg, 1984). Benefits of these management initiatives have been seen in the increases in mangrove seedlings and saplings (Rajkaran et al., 2009) and overall increase in mangrove area over time.

A vegetated island consisting of mangroves, coastal woodland species, and various alien species was present in the lower uMgeni Estuary before the September 1987 flood (Begg, 1978). The island formed from reduced water flow and increased sedimentation post-canalisation (Begg, 1978; Glennie, 2001; Rajkaran et al., 2009). During the flood of 1987, water levels rose 5 m above the usual high tide levels, and surface water runoff was accelerated because of the steep river gradient (Badenhorst et al., 1989). The flooding event removed the vegetated island, parts of the mangrove swamps, mouth sandbar, and scoured sediments, dramatically changing the system’s morphology (Badenhorst et al., 1989). The event reset the system’s natural sedimentation levels reflective of those in 1917 (Badenhorst et al., 1989). Land-cover data revealed the significant decrease in wetland vegetation in 1989 and increased estuary open water area in response to this flooding event.

In addition to the direct consequences of land-cover change, the uMgeni Estuary has been significantly affected by a reduction in freshwater flow. Historically, the uMgeni Estuary was dominated by two states: 1) Freshwater dominated (little salinity penetration during high tide) and 2) Freshwater pulsed (salinities restricted to the lower and middle reaches) (DWA, 2011). However, the construction of dams along the river system, Inanda being most recent, has reduced the freshwater flow to the system. The estuary’s state has changed from freshwater to marine, with salinities penetrating as far as the Springfield Industrialised area (DWA, 2011). These changes were evident in the decrease in freshwater area from 1937 - 2018.

As with the uMgeni Estuary, the uMlalazi Estuary has undergone significant changes in land-cover within the 20 m contour over time. However, the nature of the land-cover and changes in the two systems differs. Formal cultivation has dominated the uMlalazi Estuary compared with artificial land-cover in the uMgeni. Encroachment of sugar cane along the uMlalazi

Estuary banks is apparent in the upper reaches (Begg, 1984) as are canals leading into the estuary channel for field drainage (DWS, 2015). As a result, an inverse relationship is seen between cultivation and herbaceous vegetation. Formal agricultural practices were identified in the earliest land-cover data, occupying the estuarine area up to the 20 m contour. In 1951, this figure almost doubled and continued to increase until 1989, after which the land-cover percentage remained constant. Population growth and economic conditions for exports were responsible for the initial increases in agricultural area (Biggs and Scholes, 2002). After the 1960s, crop yield increased by introducing higher yield cultivars, pesticides, and inorganic fertilisers (Biggs and Scholes, 2002). In more recent times (from 1989), changes in farming technologies to deliver higher yields may be the reason for the stable, non-increasing area used for agricultural practices in the uMlalazi area. The role of formal protection of estuarine areas can also be recognised here. The formation of the uMlalazi Nature Reserve has successfully prevented the further development of the surrounding area.

The present study revealed a decrease in wetland area in the uMlalazi Estuary from 1937. The majority of this decrease was in vegetated wetland areas and swamp forests. According to Macnae (1963), “the river ran between sandbanks to the sea, and a lagoon was associated with the estuary” before 1913. By 1963, the siltation of the estuary from artificial drainage, destruction of riparian trees, and agricultural activities resulted in the replacement of the estuary basin with a marsh dominated by *Phragmites* and *Juncus kraussii* (Hemens et al., 1971). This marsh area was situated between the middle and upper estuary reaches (Hemens et al., 1971). In 1965, the estuary was dredged, and the soil in the *Phragmites* swamp released, resulting in the loss of supratidal habitat (Hemens et al., 1971).

Slight increases in mangrove area have occurred since 1937, despite the overall decrease in wetland area. Mangroves are recognised for their role in ecosystem functioning. They are an important source of particulate organic carbon (Rajkaran et al., 2009), provide refugia for juvenile fish (Saintilan, 2004), and prevent erosion (de Groot et al., 2002). Before 1937, mangrove communities were not present in the uMlalazi Estuary (Hill, 1966). According to Hill (1966), the establishment of mangroves (*Bruguiera gymnorrhiza* and *Avicennia marina*) became apparent in the early fifties, although the current study identified mangroves as early as 1937. The establishment of the mangrove communities results from both fine silt deposits and an open estuary mouth state (Macnae, 1963; Hill, 1966). The encroachment of sugar cane along the upper estuary banks deposited fine silt in the lower estuary aiding in the spread of the mangrove community (Macnae, 1963). The frequent mouth closures before 1952 prevented any significant establishment of a mangrove community as the lack of a tidal flux drowned the mangroves (Hill, 1966). Therefore, the estuary’s open state has allowed for the recruitment of mangrove seedlings (Peer et al., 2018). The uMlalazi Estuary currently supports three mangrove species: *Bruguiera gymnorrhiza*, *Avicennia marina* and *Rhizophora mucronata*, with the latter identified more recently (Peer et al., 2018).

The significant increase in foredunes and coastal forest over time resulted from primary succession in a protected area. These coastal forests are highly valued for their floristic composition and ecosystem functionality (Zungu et al., 2018). The inclusion of these forests in the uMlalazi Nature Reserve has ensured its protection and ecological health, a circumstance in which not many forests outside protected areas are presented (Zungu et al., 2018).

3.5.2 The relationship between land-use/ land-cover and physico-chemical variables

The study findings confirmed a significant relationship between land-cover types and dissolved oxygen. Artificial land-cover was the most strongly significant variable correlating with dissolved oxygen in the uMgeni and uMlalazi estuaries. Other studies have identified similar correlations between built-up areas and turbidity (Rabalais et al., 2009), dissolved nutrients (Bierschenk et al., 2012), salinity (Niu et al., 2020), and water quality indexes (Croft-White et al., 2017). In most cases, nutrient concentrations such as nitrates and phosphates are used as proxy measures of water quality that might be correlated with land-cover changes. This study, however, made use of physico-chemical variables due to data availability constraints. Specifically, dissolved oxygen concentrations have been frequently correlated with estuarine conditions (Kamrani et al., 2016; Costa et al., 2017; Whitfield, 2019; Duque et al., 2020). Most open estuaries along the east coast of South Africa are well oxygenated, with levels typically exceeding 5 mg l^{-1} (Harrison and Whitfield, 2006a). Dissolved oxygen levels below this could indicate excessive nutrient or organic matter input, which results in the above-normal growth of primary biomass referred to as algal blooms (Costa et al., 2017). Nutrient inputs can be point source or non-point source. Point source nutrient inputs occur as discharges from particular sites, such as sewage works (Paerl et al., 2014). Non-point sources arise from a wide area, for example, agricultural runoff, urban and residential runoff (Kibena et al., 2014).

This study showed that as residential and commercial areas increased, dissolved oxygen decreased. Economic growth and urban housing have vastly expanded since the 1980s (Adams et al., 2020), particularly in the uMgeni catchment. Increasing coastal populations have increased waste generation and waste treatment facilities of which the carrying capacities of many have been reached (Whitney and Vlahos, 2021). Overloaded treatment facilities lead to malfunctioning and effluent spillage into rivers and estuaries (Mema, 2010; Lemley et al., 2019). Informal settlements are often not serviced with adequate waste removal, reticulation or treatment services, resulting in further untreated sewage transported via stormwater runoff into estuaries (Adams et al., 2020). Negative ecosystem effects occur when a system cannot sustain the vast increase in primary production due to these nutrient inputs. Algal blooms increase organic matter and deplete oxygen levels during decomposition (Lemley et al., 2021). Mobile fish species subsequently migrate from the area, whereas sessile invertebrates either adapt (pollution tolerant species) or begin to die (Henriques et al., 2014). Additionally, algal blooms may limit light penetration and form filamentous mats over submerged macrophytes species, resulting in their dieback (Flindt et al., 1999; Staehr et al., 2017).

Apart from anthropogenic causes of algal blooms and oxygen depletion, mangroves are also associated with high carbon loading, nutrient inputs, and high respiration rates, which subsequently affect oxygen levels. Sufficient tidal mixing and water flow prevent the prolonged occurrence of reduced oxygen concentrations (Boto and Bunt, 1981; Mattone and Sheaves, 2017). Therefore, the negative relationship observed between wetlands and dissolved oxygen in the present study is likely a result of increasing mangrove area, although reduced tidal flushing may be a contributor during environmental events (e.g., drought).

Additionally, lowered bottom water oxygen levels can promote the accumulation of toxic compounds such as ammonia gas and hydrogen sulphide (Whitfield, 2019). Anoxic conditions in the sediment have been recorded in the uMgeni Estuary as early as 1984 opposite stormwater drains (Begg, 1984). The current study clearly indicated anoxic water conditions in the estuary’s upper reaches and confirmed Adams et al. (2020) classification of the uMgeni Estuary as eutrophic.

Despite no significant relationships between salinity and land-cover, average salinities in the uMgeni post-1989 (Period 2) were greater than pre-1989 (Period 1), highlighting the influence of a reduction in freshwater flow. The estuary's natural mean annual runoff (MAR) is estimated at 671.3 x 10^6 $m^{3;}$ however, only 262.68 x 10^6 m^3 currently reaches the system (DWA, 2011). A study conducted on ten New Zealand estuaries showed a positive correlation between salinity and catchment development (Bierschenk et al., 2012). Factors contributing to freshwater reduction include dam construction and water abstraction, both of which occur in the uMgeni catchment. A similar trend was depicted in the Pearl Estuary, China, in which increased salinities were identified after dam construction and sand mining activities (Niu et al., 2020).

The principal coordinate analysis confirmed that environmental variables were significantly different in the estuaries' upper and riverine reaches compared with the lower and middle reaches. In particular, dissolved oxygen concentrations in the upper and riverine reaches of the uMgeni Estuary were almost half that of the lower reaches. This suggests that organic matter and nutrient loading are transported downstream from catchment activities or point sources within the upper estuary reach. The dominant land-cover classes in the catchment were different from the 20 m contour EFZ. Despite natural land-cover dominating the wider uMgeni catchment (43.01%), catchment water quality was still degraded. Namugize et al. (2018) identified high nutrient and *Escherichia coli* (*E.coli*) concentrations above the Midmar Dam, the uMgeni catchment's uppermost reaches. Sources of pollutants were livestock, informal settlements, and poor sanitary practices (Namugize et al., 2018). This pattern presents itself progressively down the catchment, with natural vegetation, cultivation, and informal settlements replaced with commercial, residential, and industrialised areas. Reduced buffer zones and catchment derived pollutants, therefore, affect the estuary's water quality.

Sources of pollutants in the estuarine area identified in the 1980s included industrial areas around the Palmiet, Zeekoe (or Piesang) Rivers, the Springfield Industrial Flats area, and various sewage works (Simpson et al., 1972; Begg, 1978). Treated sewage is discharged into the system from the wastewater treatment works (WWTW) in Pietermaritzburg, Cato Ridge, Clermont, New Germany, KwaMashu and Durban. In earlier surveys, excessive concentrations of *E. coli* (1900 / 100 ml) and *Salmonella* were recorded in the uMgeni Estuary (Simpson et al., 1972). Major pollution events have also occurred, including a crude furnace oil spill in 1971, the release of fibres into the system by the South African Board Mills and incidences of severe air pollution (Begg, 1978). Researchers have considered the

Durban North WWTW discharge as a major contributor to sewage input and water quality degradation in the uMgeni Estuary (Simpson et al., 1972).

Recent reports confirm that pollution and poor water quality remain an issue (Harrison et al., 2000; Van Niekerk and Turpie, 2012). *Escherichia coli* readings have been recorded above the South African Water Quality guidelines of 0 - 130 counts / 100 ml (DWAF, 1996a; Forbes and Demetriades, 2009). Nitrate concentrations in the upper estuary recorded between 0.94 - 1.79 mg l^{-1}, far exceeding the recommendations (< 0.5 mg l^{-1}) (DWAF, 1996b). The progressive deterioration of the upper uMgeni Estuary was also evident in this study, suggesting an increase in land-cover derived nutrient inputs. This is supported by the significant negative correlation between artificial land-cover and dissolved oxygen over time.

A moderate but non-significant correlation between turbidity and artificial land-cover was identified in this study (uMgeni). Similar trends have been seen in other highly developed systems (Croft-White et al., 2017). Turbidity is generally influenced by river inflow, winds, tides, rainfall, and substrate type (Harrison, 2004; Zhou et al., 2021); however, human activities may exacerbate these effects. Urbanisation leads to increased surface runoff of nutrients and transportation of eroded sediments downstream (Cyrus, 1988; Croft-White et al., 2017). Turbidity may act as a pollution indicator, with high turbidity values indicating the presence of organic matter which further promotes the growth of microorganisms (Momba et al., 2006). For example, high turbidity levels in the upper uMgeni catchment resulted from dysfunctional sewer and informal settlements (Namugize et al., 2018).

In contrast, some studies have reported that increases in impervious surfaces associated with artificial land-cover reduce the sediment runoff and total suspended solid concentrations, which would otherwise be greater in more agriculturally based catchments (McCarthy et al., 2018). The latter could explain the higher turbidity in the uMlalazi Estuary in Period 2 compared to the uMgeni Estuary. Higher turbidity was also evident during periods in which agriculture was more prevalent in the uMgeni Estuary (Period 1), with turbidity decreasing as agricultural activities were replaced with artificial development.

Dam construction may also act as a sink for sediments and nutrients, resulting in improved downstream water quality (Eccles et al., 2020). This may explain the reduced turbidity in the uMgeni Estuary after the Inanda dam construction in 1989. Principal coordinate analysis revealed turbidity was more closely correlated to the riverine, upper and middle reaches of recorded samples in the 1980s. The canalisation of the estuary in the early 1980s released large amounts of sediment into the system, consequently increasing turbidity. Declines in turbidity after that period may reflect pre-canalisation levels. Although dam construction and increased impervious surfaces may be factors reducing sediment deposition and flow in the uMgeni Estuary, low dissolved oxygen levels suggest that point sources and non-point sources of pollutants still occur in the uMgeni 20 m contour area and its wider lower catchment.

As in the uMgeni Estuary, a relationship was identified between artificial land-cover and dissolved oxygen in the uMlalazi Estuary. Despite this positive relationship, artificial land-cover increases were minimal; therefore, it is unreasonable to conclude that artificial land-cover in this area increases dissolved oxygen. Time lags between the disturbance (artificial development or agriculture) and the effects (changes in dissolved oxygen) may be impeding any adverse effects on the system currently (Croft-White et al., 2017). Other water quality variables relating to LULC, which were not measured, may better explain this trend.

Current land-cover patterns in the wider uMlalazi catchment are similar to those in the 20 m contour, primarily cultivated and vegetated land. Tribal authorities manage most of the land, with subsistence or commercial agriculture being the primary land-use (Pillay et al., 2014). A significant difference arises in the higher percentage of catchment artificial land-cover in comparison to the EFZ. Despite higher artificial area in the wider catchment, water quality in the uMlalazi catchment is not degraded. Past studies have recorded high dissolved oxygen (8.8 mg l^{-1}), low nitrates (0.15 mg l^{-1}), and low phosphates (0.11 mg l^{-1}) in the upper catchment near the Eshowe weir (Archibald et al., 1969). These inorganic nitrogen readings were below 0.5 mg l^{-1}, common in un-impacted aerobic South African waters (DWAF, 1996b). Populations in the uMlalazi area (213 601) are lower than the eThekwini area (3 442 361) and any other sub-catchments within the uMgeni catchment (Statistics South Africa, 2011). Smaller settlements in the uMlalazi catchment have prevented widespread urbanisation and water quality issues associated with LULC.

The uMlalazi Estuary health has remained good despite the sugar cane farming in the upper reaches. The protection of the EFZ up to the railway bridge has preserved some of the system’s resilience to perturbations and nutrient inputs from agricultural activities upstream.

Buffer zones reduce erosion, filter receiving waters, regulate estuarine productivity and provide habitat to estuarine biota (Roy et al., 2001; Masefield et al., 2014; Van Niekerk et al., 2019). Historical records reveal that phosphate and nitrate concentrations in the uMlalazi lay within the normal ranges of other coastal KwaZulu-Natal estuaries (Hemens et al., 1971). More recent studies reveal a slight increase in phosphate and nitrate concentrations due to increased agriculture (DWS, 2015). Concern also arises with the overflow of the Mtunzini WWTW during high runoff periods and the nutrient input from the aquaculture Kob farm established in 2004 (Peer et al., 2018). Other studies have recorded strong positive relationships between total nitrates, phosphates and suspended solids with agricultural area (Heggie and Savage, 2009; Chang et al., 2021). These excessive nutrients are derived from fertilisers used in catchment agricultural practices (Kibena et al., 2014). Phosphates and nitrates promote algal production, which depletes oxygen levels (Valiela and Bowen, 2002). Lower oxygen levels may therefore be indicative of excessive nutrient input from agricultural activities. This study found that average oxygen levels have increased over time, perhaps suggesting a time lag between the nutrient input and the water quality response. Alternatively, higher nutrient levels in the system may be increasing algal productivity and daytime oxygen levels through respiration (Rabalais et al., 2009).

Compared with the uMgeni Estuary, the uMlalazi Estuary’s present day MAR is only 24% lower than its reference condition, and the system has fewer dams and weirs that influence freshwater flow. Therefore, the uMlalazi Estuary receives allochthonous sources of nutrients that the system can adequately utilise, with excess nutrients being flushed out to sea. Longer water residency times in the riverine reaches of the uMgeni Estuary, associated with reduced water flow, allow nutrients to accumulate, increasing the chances of eutrophic conditions (Lemley et al., 2017). From the data reviewed here, there is little to suggest that critical thresholds in water quality have been exceeded in the uMlalazi Estuary. However, increases in dissolved oxygen levels over time suggest increased nutrient inputs which could result in negative estuary impacts if not adequately monitored and controlled.

Climate change is an emerging pressure on estuarine ecosystems. This study provided evidence of an increase in estuarine water temperatures over time in both estuaries. These water temperature increases correlate with a recent study that showed an increase in overall minimum air temperatures over time in KwaZulu-Natal (Ndlovu et al., 2021). James et al. (2013) also revealed water temperature increases in various South African estuaries, affecting the proportion of tropical species entering the systems. Increasing temperatures strengthen the pycnocline, preventing vertical mixing resulting in reduced bottom surface oxygen levels and various other ecological consequences (Ficklin et al., 2013). Generally, this is not an important consideration in shallow estuaries, although further research on this topic is warranted.

3.5.3 Conclusion

This study confirmed that land-cover within the uMgeni Estuary EFZ (within the 20 m contour) differed significantly from that around the uMlalazi Estuary. The uMgeni Estuary was dominated by artificial and managed vegetation, whereas the uMlalazi was dominated by agricultural and coastal forest land-cover types. Formally protected areas (nature reserves) are present in the lower reaches of both estuaries, namely the Beachwood Mangrove Reserve and the uMlalazi Nature Reserve. The latter estuary’s protected area is much greater in size. Both estuaries presented land-cover activities that can result in water quality deterioration through the input of nutrients. However, the relationship of each land-cover type with water quality variables was different. The minimal negative water quality effects in the uMlalazi Estuary highlight the importance of maintaining a buffer zone around an estuary and point to different impacts from different land-cover types. The uMlalazi Nature Reserve has protected estuarine supporting habitat and restricted developments in this zone. The EFZ allows the system to remain resilient against perturbations and continue providing ecosystem services (Correll, 1997; Masefield et al., 2014).

Urbanisation (especially in freshwater deprived systems) impacts estuaries more severely than agricultural activities in more rural, less populated settings. According to Adams et al. (2020), estuaries with dominant nutrient sources from agricultural returns had only moderate water quality deterioration than estuaries with nutrient sources from urban runoff and WWTW discharges. The establishment of WWTW is strongly influenced by increased populations and residential areas associated with urbanisation. Although the presence of natural vegetation in catchments can act as a buffer for pollutant inputs in estuaries, a marked increase in populations and associated artificial development greatly hinders a catchment’s natural buffering capacity (Valiela and Bowen, 2002). Therefore, in the case of the study systems investigated here, agricultural activities have a lower impact on estuarine systems physico-chemistry than activities associated with urban development at the EFZ or catchment scale.

CHAPTER 4: AN ASSESSMENT OF THE CURRENT FISH COMMUNITIES IN THE UMGENI AND UMLALAZI ESTUARIES

4.1 Introduction

Estuaries are highly dynamic, undergoing rapid fluctuations in environmental variables and displaying distinct vertical and longitudinal gradients (Richardson et al., 2006; Medeiros et al., 2018; Connelly et al., 2020). These gradients are often more defined in estuaries with continuous freshwater and marine influences resulting from a permanent connection to the sea (Nicolas et al., 2010b; Taddese and Closs, 2019). The most common longitudinal estuary classifications revolve around salinity (e.g., The Venice system). In particular, a typical estuarine longitudinal gradient involves a riverine reach dominated by river inflow (salinity <5), an upper reach which marks the tidal limit (5-18), an intermediate mixing zone (middle reach), and a lower reach where tidal currents and salinity are the greatest (Kaiser et al., 2011; Whitfield et al., 2012). The ability of fishes to adapt to different salinities will often determine their distribution in an estuary (Barletta et al., 2005; Neves et al., 2011). Most fishes that utilise South African estuaries are eurytopes, tolerant of a wide range of conditions (Whitfield, 2019). Marine taxa constitute the majority of the euhaline species in South Africa (42% of the total 172 species found on the subcontinent), although estuarine spawners such as *Atherina braviceps* and *Gilchristella aestuaria* are also regarded as eurytopic (Whitfield, 2019).

In addition to salinity, many researchers report turbidity as a significant factor influencing fish species distribution, with turbid water providing protection from predatory fishes (Blaber and Blaber, 1980; Cyrus and Blaber, 1987a), and greater food sources (Cyrus and Blaber, 1987a; Taddese and Closs, 2019). Estuarine temperatures generally remain relatively constant longitudinally and over tidal cycles (Kaiser et al., 2011). Instead the influence of temperature is greater on regional fish distributions, which are primarily controlled by ocean currents (Harrison and Whitfield, 2006b). Sudden temperature drops, however, may result in mass fish mortalities as previously recorded in the Kosi Bay and St Lucia systems of KwaZulu-Natal (Cyrus and McLean, 1996). In addition to latitudinal temperature differences, seasonal temperature differences result in increases in fish abundances and diversity during the warmer summer months, corresponding to the recruitment of marine species (Kamrani et al., 2016; Pichler et al., 2017; Kisten et al., 2020). Dissolved oxygen concentrations greatly influence the distribution and movement of fishes in estuaries (Whitfield, 2019) and affect trophic interactions (Breitburg et al., 1997). Naturally high levels of organic material, typical of the middle reaches of estuaries, often reduce oxygen levels due to aerobic bacterial respiration (Kaiser et al., 2011). Generally, oxygen levels at the head and mouth of an estuary should be normal (>5 mg l^{-1}) unless oxygen-demanding substances are added to the water from industrial and domestic pollution (Wetz et al., 2016; Whitfield, 2019). Other variables which may influence fish species distributions include habitat complexity (Blaber et al., 1989; Young et al., 2021), estuary depth (Blaber, 1974; Mont'Alverne et al., 2016), catchment size (Marais, 1988), water quality (Valesini et al., 2017; Warry et al., 2018), and habitat alteration (Baptista et al., 2015).

Abundances of fishes in different functional groups (estuarine usage or feeding modes) may also differ along an estuary longitudinal salinity gradient (Selleslagh and Amara, 2008). In many estuaries, marine stragglers dominate the euhaline lower regions (Nicolas et al., 2010a; Taddese and Closs, 2019), whereas estuarine species are found in greater numbers in the mesohaline middle regions (Jaureguizar et al., 2003; Whitfield et al., 2012). Estuarine systems typically support few freshwater species, and these are often restricted to the riverine and upper reaches where salinities are low (Neves et al., 2011; Whitfield, 2015). Primary and secondary food sources determine predator-prey interactions (Elliott and Dewailly, 1995; Wilson and Sheaves, 2001; Nyitrai et al., 2012), competition avoidance (Whitfield and Blaber, 1978; Mwandya, 2019), and energy flows which also influence the number of species and the distribution of functional feeding groups in an estuary (Kamrani et al., 2016; Ferreira et al., 2019).

Limited studies are available on the ichthyofauna of permanently open estuaries in KwaZulu-Natal. Research on the degraded uMgeni Estuary has mostly been limited to the effects of the Inanda dam (Diab and Scott, 1989; Glennie, 2001; Tinmouth, 2009), sediment contamination (Naidoo et al., 2018), heavy metal presence (Olaniran et al., 2014), mangrove communities (Rajkaran et al., 2009), sediment dynamics (Badenhorst et al., 1989) and water quality (Mbambo et al., 2019; Ngubane et al., 2019). The earliest published study on the uMgeni ichthyofauna dates to 1979, with the most recent study in 2008. No published studies on the ichthyofauna of the uMgeni Estuary have been conducted post-2008. Published studies conducted on the more pristine uMlalazi Estuary have focused on carbon and nutrient fluxes (Tagliarolo and Scharler, 2018), macrobenthic communities (Tagliarolo et al., 2018), mangrove ecosystems (Rajkaran et al., 2009; Peer et al., 2018; Taylor, 2020), single species ecology (Weerts et al., 1997; Davis et al., 2004), estuarine flora (Zungu et al., 2018) and zooplankton communities (Ortega-Cisneros and Scharler, 2014; Tagliarolo et al., 2018). As with the uMgeni Estuary, ichthyofauna data for the uMlalazi Estuary is scarce with the last updated species lists presented in an environmental flow study report (DWS 2015). Detailed estuary-specific assessments of the usage of fishes in the uMgeni and uMlalazi estuaries are essential for efficient management plans. This study will contribute to the ichthyofauna knowledge of South African subtropical estuaries, which currently support 16% of the countries endemic fishes (Whitfield, 2019).

4.2 Aims, Objectives and Hypotheses

This chapter aims to assess and compare the spatial distribution patterns of fish assemblages (both taxonomic and functional) in the uMgeni and uMlalazi estuaries. Additionally, physico-chemical variables responsible for the fish assemblage distributions will be assessed and compared between estuaries.

Objectives

- In each estuary:
    - To describe the current abiotic longitudinal gradients.
    - To describe the current fish community structure along the longitudinal gradient.
    - To evaluate the relationships between physico-chemical variables and fish communities.
- To compare fish assemblages and physico-chemical variables between the uMgeni and uMlalazi estuaries.

Null Hypotheses

- Within an estuary, the longitudinal distribution of species does not differ.
- Within an estuary, the longitudinal distribution of functional guilds does not differ.
- There is no difference between the fish assemblages of the uMgeni and uMlalazi estuaries.
- There is no difference between the functional guilds of the uMgeni and uMlalazi estuaries.

4.3 Materials and methods

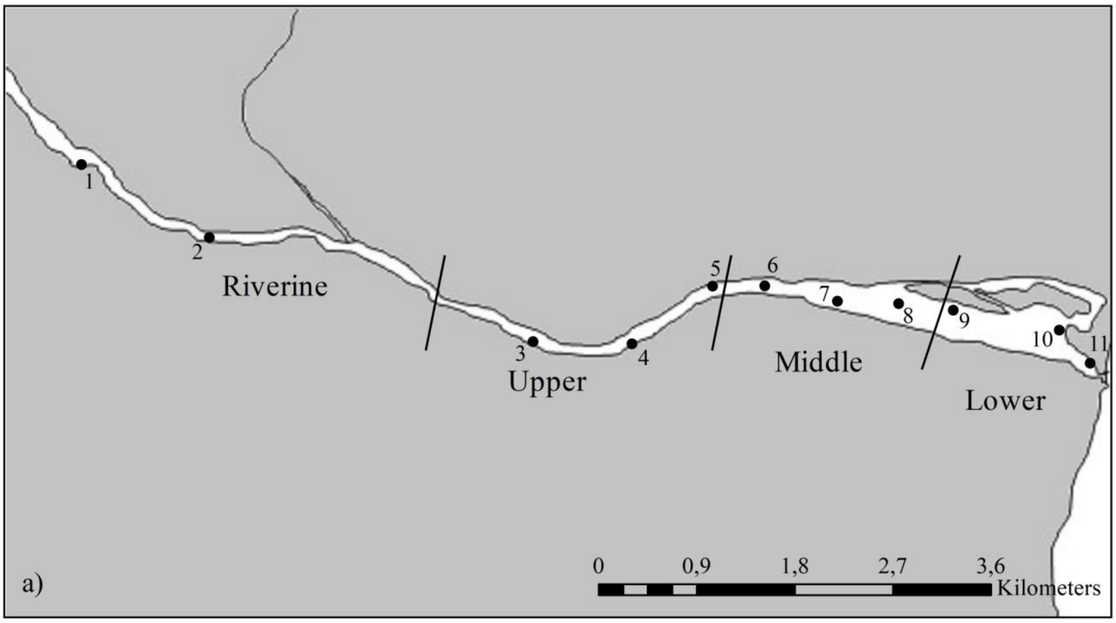
General descriptions of the study estuaries, sampling approaches and statistical procedures can be found in Chapter 2.

4.3.1 Physico-chemical measurements

An EXO 2 multiparameter water quality sonde was used to collect physico-chemical data at each site. The instrument was held near the water's surface and released slowly to the bottom to obtain a vertical profile of the water column and again held just off the substrate. Where the instrument was left at the surface and bottom to stabilise, these readings were averaged. Surface and bottom values were further averaged to reflect a single depth-integrated water quality parameter value for each measured variable. Water quality parameters measured included depth (m), temperature (°C), salinity, dissolved oxygen (mg l^{-1}), pH, turbidity (NTU), and chlorophyll-a (µg l^{-1}). Observations were also recorded on the tidal state (low, high, incoming, outgoing), weather, vegetation, and surrounding land-use activities.

4.3.2 Present ichthyofauna sampling approach

Fish sampling was conducted on the uMgeni and uMlalazi estuaries over three trips, namely: winter (June 2019), spring (September 2019) and summer (January 2020). Sites were chosen at the time of sampling depending on the availability of exposed sandbanks for successful seine netting. Within each system, between 8-14 sites were sampled during daylight hours over two days (Figure 4.1). In most instances, two or three sites were sampled in each reach. Reaches were determined according to salinity ranges in each estuary (Figure 4.1) (refer to Chapter 2 for details). Fish communities sampled from sites were treated as replicates in estuary reaches. Typically, two hauls were pulled at each site to ensure representative catches from each locality. On rare occasions, the nature of the site precluded more than one haul being done.



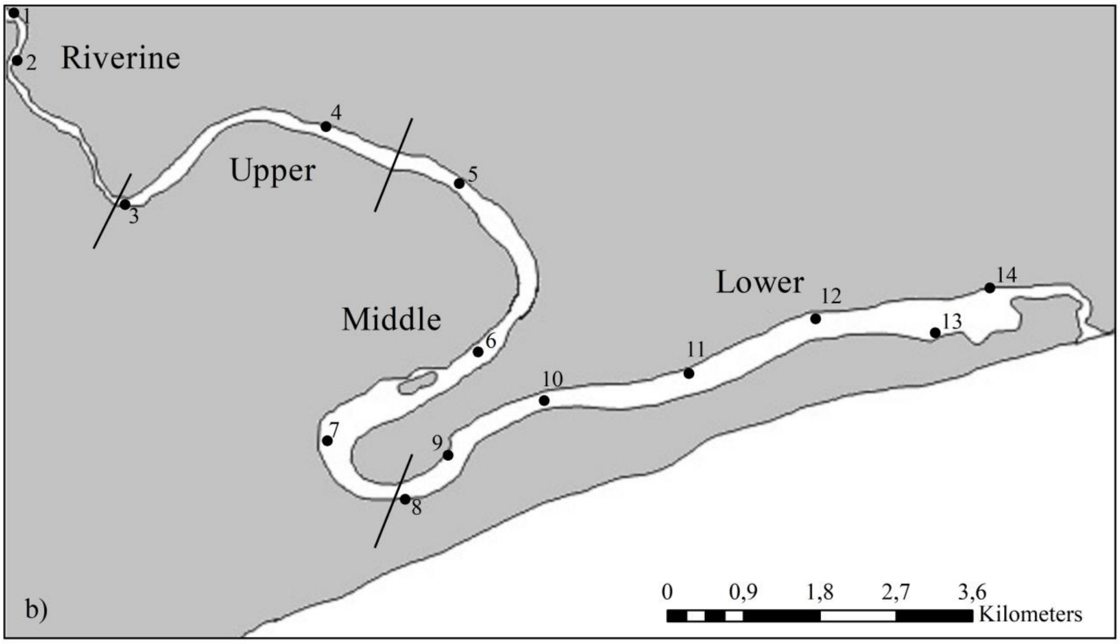


Figure 4.1 Location of reaches and sites sampled during one or more trips in the a) uMgeni and b) uMlalazi estuaries.

A 30 m, 10 mm mesh seine net was used for sampling. Weights along the foot line and floats along the top rope ensured the net sampled the entire water column. In shallower sampling sites, the net was walked out and pulled back towards the shore. In deeper waters, (>1.5 m) the net was deployed off the sampling boat in a semi-circular manner and pulled back onto the nearest available beach. Seine netting does have disadvantages as a fish sampling method. Snagging can be a problem in some areas where debris litters the estuary bed. Small species are often omitted from catches, and fast swimming species can also avoid capture (Baker et al., 2016). Nevertheless, it is a sampling method that can be deployed with some consistency, and catches can be standardised across reaches and systems. All fish caught were removed from the net and held in 25 l buckets filled with water. Fish were identified, measured (Standard length in cm), and released back into the water. Any fish which could not be positively identified were preserved in 5% formalin and taken back to the laboratory for identification.

4.3.3 Laboratory processing

Fishes returned to the laboratory were identified to species level with the aid of a microscope and identification keys in Smith and Heemstra (1986). Fish data (catches) were recorded in a database according to the Linnaeus classification system, from order to species level. Guilds were also recorded. Estuarine use functional groups (EUFG) were determined from a reference list of southern African species provided in Whitfield (2019), which was based on guild classifications by Potter et al. (2015). Feeding guilds (FMFG) were determined from a species reference list provided in Harrison and Whitfield (2012), based on the guild classification by Elliott et al. (2007). If species were not found on these lists, guilds were obtained from biological information on the World Register of Marine species (WORMS).

4.3.4 Statistical analysis

4.3.4.1 Physico-chemical data

Multivariate analyses (PRIMER Version 6.1.13) were performed on salinity, dissolved oxygen (mg l^{-1}), temperature (˚C), turbidity (NTU), pH and Chlorophyll-a (µg l^{-1}). Mean data were used for each reach_ trip_ estuary combination. Reaches constituted *a priori* groups defined as lower, middle, upper, and riverine based on salinity regimes (see above and refer to Chapter 2 for explanation). All variables were normalised to obtain equal scaling of the variables and account for the different units of measurement. The abiotic data were represented via the Euclidean distance resemblance matrix, which best describes the natural distance between two data points (Clarke and Warwick, 2001a). A two-way type 3 Permutational multivariate analysis of variance (PERMANOVA) was conducted with factors ‘estuary’ and ‘reach’ (nested in ‘estuary’) using permutation of residuals under a reduced model. Detailed explanations on PERMANOVA choices can be found in Chapter 2.

4.3.4.2 Fish assemblage data

To standardise fish catches, catch per unit effort (fish per haul) was used as a measure of fish abundance. Catch per unit effort of each species, per site was calculated by dividing the number of individuals caught at each site by the number of hauls per site. Guild species richness (number of species belonging to a particular guild) and the proportion of the community species belonging to a guild was also calculated (Total number of species in a guild/ total species richness X 100).

Univariate indices of community structure such as total species (referred to in this chapter as species richness (S)), abundance (N), Shannon-Weiner diversity index (H'), and Simpson's index (λ) were calculated in PRIMER Version 6.1.13 (refer to Chapter 2 for details). Seven missing values were produced in the diversity test due to some samples recording only one species. Missing data estimation was then run to estimate missing values after all assumptions were verified (refer to Chapter 3 for details). Analysis of Variance (ANOVA) tests were performed using SigmaPlot Version 12.5 to test the hypothesis that community structure (univariate indices) across different reaches in the uMgeni Estuary (or uMlalazi Estuary), or between estuaries, were the same. Tukey's pairwise comparison test was used when required. If the assumption of normality or equal variance failed, a Mann-Whitney U non-parametric test was performed, and differences were tested via Dunn's pairwise test.

For multivariate tests, data were fourth root transformed to downweight the effects of abundant species and better represent the rarer species (Clarke and Warwick, 2001a). Fourth root transformation produced a lower stress value in the nonmetric multidimensional scaling plot (nMDS), depicting a more robust representation of the data cloud. The biotic data was represented via a Bray-Curtis similarity matrix (refer to Chapter 2 for explanations) and *a priori* sample groups (reaches) visualised via ordination plots. Differences in reach fish assemblages were not easily represented in unconstrained ordination (nMDS). Canonical analysis of principal coordinates (CAP) is known to discriminate *a priori* groups more easily. The ordination was deemed appropriate if more than 60% of the variation of the original data matrix was represented (Anderson et al., 2008). A two-way type 3 PERMANOVA with factors estuary and reach (nested in estuary) using permutation of residuals under a reduced model was run. Location differences were confirmed by the homogeneity of dispersion of samples test (PERMDISP). Detailed explanations on PERMANOVA choices can be found in Chapter 2. Taxa contributing the most to group specific assemblages were determined using the Similarity percentages (SIMPER) routine. Environmental variables most likely responsible for assemblage groupings were tested using BEST analysis. Distance-based linear models (DISTLM) using the stepwise selection and Akaike's information criterion (AIC) followed to determine the proportion of variation explained by selected environmental variables (refer to Chapter 2 for details). These relationships were visualised in Distance-based redundancy (dbRDA) plots.

The functional composition of the fish assemblage was analysed through the estuarine use functional groups and the feeding mode functional groups. Taxa that were not identified to species level (Mugilidae spp. and *Caranx* sp.) could not be correctly allocated an estuarine use functional guild and were removed from the analysis. Feeding modes for the above taxa applied for all species and did not have to be excluded from analyses. Each guild's total abundance (CPUE) per site was calculated, and analyses proceeded as per species composition.

4.4 Results

4.4.1 Physico-chemical conditions

Water quality parameters were variable across reaches and estuaries (Table 4.1). In the uMgeni Estuary, the highest salinities occurred in the lower reaches (25.18 ± 10.97 SD) with a general decreasing trend towards the riverine reaches (0.33 ± 0.28 SD) (Figure 4.2a). High standard deviations in the upper and middle reaches depicted the system's tidal induced variability. Average dissolved oxygen concentrations were highest in the lower reaches (6.29 mg l^{-1} ± 1.63 SD), decreasing with increasing distance upstream from the mouth (Figure 4.2b). During most sampling trips, dissolved oxygen was lower than levels typical of South African subtropical estuaries (<5mg l^{-1}). In Trips 2 and 3 waters were hypoxic in the upper and riverine reaches. High dissolved oxygen was recorded in the riverine reaches of Trip 1 (7.41 mg l^{-1} ± 1.91 SD), likely associated with high levels of photosynthesis (primary production, Chlorophyll-a 9.06 µg l^{-1} ± 1.74 SD, Table 4.1). Oxygen consumption would occur during the night from respiration processes resulting in the overall reduction in dissolved oxygen within the water.

Water temperature was constant across reaches but differed significantly between the sampling trips. Higher temperatures were observed during the spring and summer sampling trips (Trips 2 and 3), with winter temperatures (Trip 1) at least 5˚C lower. Turbidity and chlorophyll-a followed similar trends (Figure 4.2d, f). Turbidity was lowest in the lower reaches (6.4 NTU ± 3.02 SD) and highest in the riverine reaches (10.71 NTU ± 1.71 SD). Similarly, chlorophyll-a was lowest in the lower reaches (4.3 µg l^{-1} ± 1.54 SD) and highest in the riverine reaches (8.55 µg l^{-1} ± 2.97 SD). pH was recorded below 8 in all reaches, reflecting the lower salinities in the uMgeni Estuary.

The uMlalazi Estuary exhibited a clear salinity gradient, with the highest salinities occurring in the lower reaches (31.8 ± 2.41 SD) and the lowest salinities occurring in the riverine reaches (Figure 4.2a). Within reaches, salinities varied less than the uMgeni Estuary resulting in lower standard deviations. Dissolved oxygen was markedly higher in the lower reaches (8.08 mg l^{-1} ± 0.59 SD) than the uMgeni Estuary, decreasing toward the riverine reaches (5.58 mg l^{-1} ± 0.67 SD). The lowest levels were recorded during Trip 3 (summer) in the upper reaches. Lowered dissolved oxygen was possibly related to higher temperatures during this sampling trip (Table 4.1). Temperatures in the uMlalazi lower reaches averaged 24.3 °C ± 2.84 SD and increased by 2 °C in the middle and upper reaches (26.58 °C ± 2.64 SD and 26.46 °C ± 3.43 SD, respectively). Slightly lower temperatures in the riverine reaches may be associated with cooling from river inflow. More obvious temperature differences were seen between sampling trips in which winter temperatures were lower than spring and summer (Table 4.1).

Overall turbidity was higher in the uMlalazi Estuary than the uMgeni (Figure 4.2d). Turbidities were greatest in the middle (18.6 NTU ± 4.20 SD) and upper (22.83 NTU ± 15.15 SD) reaches. These reaches are where muds, silts, and clays, delivered by inflowing river waters fall out of suspension and accumulate, increasing turbidity. Higher turbidity was recorded during the beginning of the rainy season when freshwater inflow was most likely highest (Trip 2). Chlorophyll-a followed a similar trend, with the highest levels occurring in the middle (15.17 µg l^{-1} ± 4.61 SD) and upper (10.82 µg $^{-1}$ ± 6.44 SD) reaches. Chlorophyll-a contributes to particles in suspension, directly affecting turbidity. pH followed the salinity gradient, with the highest pH levels occurring in the lower reaches (8.36 ± 0.10 SD).

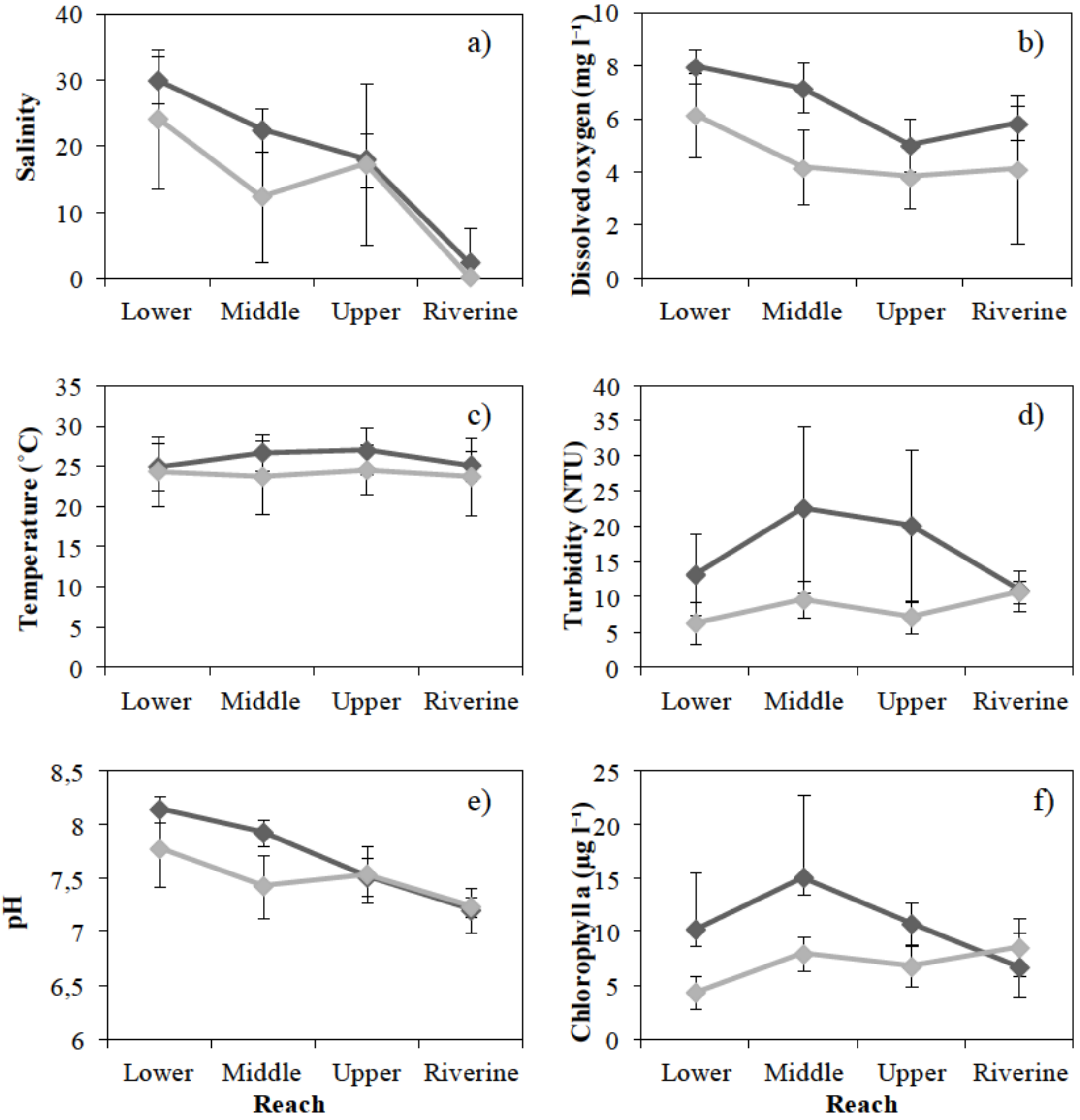


Figure 4.2 The average (±SD) water column a) salinity b) dissolved oxygen c) temperature d) turbidity e) pH and f) chlorophyll-a across reaches in the uMgeni (grey line) and uMlalazi (black line) estuaries.

Table 4.1 Physico-chemical variables recorded during Trips (1,2,3) across reaches in the uMgeni and uMlalazi estuaries expressed as mean (±SD).

Reach	uMgeni						uMlalazi					
	1		2		3		1		2		3	
Salinity												
Lower	19.19	(10.73)	28.66	(7.97)	24.61	(10.3)	31.79	(1.78)	29.83	(2.45)	28.31	(4.60)
Middle	10.27	(7.37)	17.07	(15.43)	11.33	(1.13)	22.28	(0.00)	21.61	(2.62)	23.16	(4.05)
Upper	18.92	(13.20)	9.02	(11.99)	24.56	(4.25)	21.21	(0.00)	14.14	(3.16)	20.48	(2.13)
Riverine	0.25	(0.04)	0.18	(0.01)	0.57	(0.32)	14.28	(0.00)	0.24	(0.02)	0.18	(0.02)
Dissolved oxygen (mg l^{-1})												
Lower	4.71	(1.98)	6.56	(0.65)	6.97	(0.79)	7.95	(0.33)	7.92	(0.98)	8.10	(0.42)
Middle	3.77	(0.94)	4.57	(2.20)	4.41	(0.25)	7.73	(0.00)	7.37	(0.89)	6.87	(1.04)
Upper	4.39	(1.02)	3.01	(1.18)	4.24	(0.81)	6.50	(0.00)	5.21	(0.16)	4.12	(0.70)
Riverine	7.41	(1.91)	3.20	(1.48)	1.76	(0.43)	6.22	(0.00)	5.36	(0.63)	6.05	(0.48)
Temperature (°C)												
Lower	19.35	(0.91)	24.24	(1.72)	28.15	(3.07)	21.29	(0.62)	25.88	(0.43)	27.74	(1.46)
Middle	19.01	(0.78)	24.84	(1.58)	29.50	(0.33)	21.71	(0.00)	27.52	(1.46)	27.72	(0.52)
Upper	19.47	(0.13)	25.76	(1.38)	26.61	(0.64)	21.23	(0.00)	28.05	(0.19)	28.59	(0.32)
Riverine	17.29	(0.46)	24.89	(0.45)	28.87	(0.13)	21.58	(0.00)	26.56	(0.99)	25.27	(0.65)
Turbidity(NTU)												
Lower	6.25	(2.34)	7.73	(3.16)	5.21	(2.83)	10.27	(3.42)	15.83	(6.16)	13.88	(5.94)
Middle	12.22	(0.77)	7.16	(1.58)	8.08	(0.69)	11.69	(0.00)	33.98	(13.90)	18.53	(2.92)
Upper	7.29	(3.17)	8.66	(0.95)	5.49	(1.31)	10.02	(0.00)	31.48	(8.22)	13.64	(2.13)
Riverine	12.72	(0.89)	9.84	(0.55)	9.58	(0.37)	7.11	(0.00)	14.22	(1.40)	9.94	(1.62)
pH												
Lower	7.43	(0.35)	7.99	(0.20)	7.88	(0.25)	8.27	(0.02)	8.00	(0.08)	8.14	(0.03)
Middle	7.25	(0.18)	7.65	(0.39)	7.48	(0.01)	8.05	(0.00)	7.85	(0.04)	7.94	(0.13)
Upper	7.43	(0.30)	7.42	(0.21)	7.73	(0.14)	7.81	(0.00)	7.36	(0.11)	7.52	(0.01)
Riverine	7.24	(0.13)	7.19	(0.05)	7.28	(0.02)	7.45	(0.00)	6.93	(0.04)	7.31	(0.09)
Chlorophyll- a (µg l^{-1})												
Lower	3.74	(0.59)	4.68	(1.04)	4.65	(2.06)	10.43	(5.50)	13.57	(5.12)	7.42	(3.08)
Middle	7.77	(1.24)	7.71	(2.36)	8.47	(0.67)	0.47	(0.00)	20.88	(0.99)	16.10	(4.79)
Upper	6.73	(2.97)	7.72	(0.69)	5.91	(1.19)	11.14	(0.00)	10.92	(3.07)	10.43	(0.50)
Riverine	9.06	(1.74)	5.42	(1.41)	11.15	(0.36)	12.23	(0.00)	3.72	(0.27)	6.91	(2.26)

Clear environmental gradients were observed across the uMgeni and uMlalazi estuaries (PERMANOVA: df = 6, Pseudo-F = 4.938, p(perm) = 0.0001, Figure 4.3, Table 4.2). Variables responsible for the observed reach gradient in both systems included salinity, pH, and dissolved oxygen, which were higher in the lower reaches, decreasing along PCO axis 1 to the riverine reaches. Within the uMgeni Estuary significant differences were observed between the lower and middle reaches (t = 1.906, p(perm) = 0.034, Table 4.2) and the lower and riverine reaches (t = 2.582, p(perm) = 0.002, Table 4.2). Environmental variables grouped more clearly into reaches in the uMlalazi Estuary (Figure 4.3), resulting in significant differences between all reaches except for two pairwise comparisons (Table 4.2). The overall environmental conditions between the uMgeni and uMlalazi estuaries were significantly different (PERMANOVA: df = 1, Pseudo-F = 12.005, p(perm) = 0.0001, Figure 4.3, Table 4.2), separating along PCO axis 2. Chlorophyll-a, turbidity and temperature were typically higher in the uMlalazi than the uMgeni Estuary.

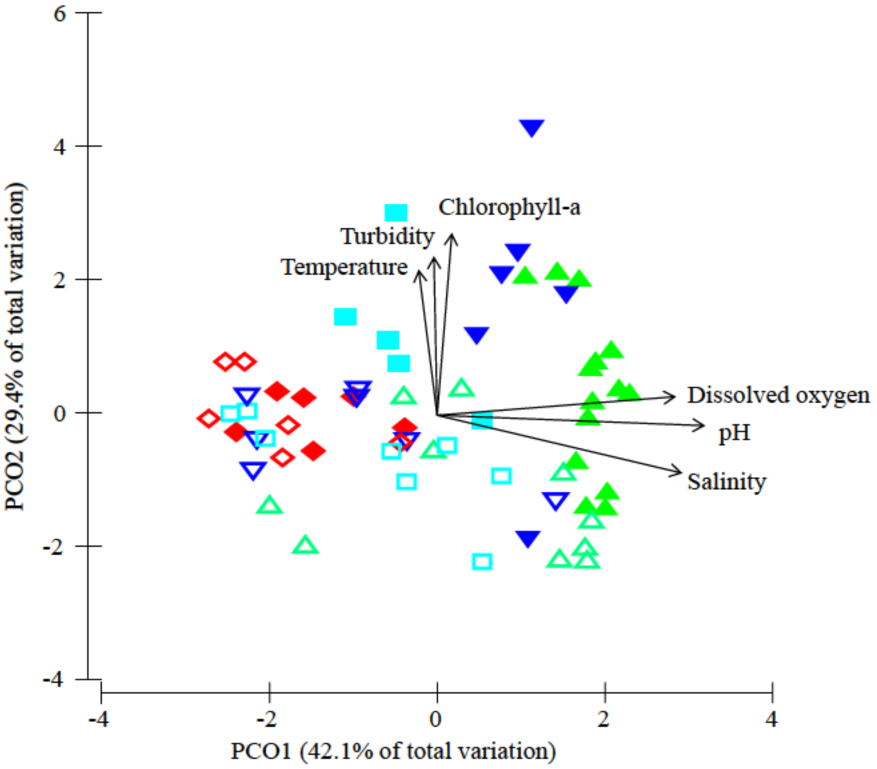


Figure 4.3 Principal coordinate plot (PCO) of environmental variables recorded in reaches of the uMgeni (open symbols) and uMlalazi (closed symbols) estuaries. Spearman rank correlations of environmental variables are representative of the strength of the variables with PCO axes. Reaches = ▲-Lower; ▼-Middle; ■-Upper; ◆-Riverine.

Table 4.2 PERMANOVA results of environmental variables within and between the uMgeni and uMlalazi estuaries. Asterisks denote significance at p<0.05. Df = degrees of freedom, Pseudo-F = critical values.

Source	**PERMANOVA**		
	Df	**Pseudo-F**	**P(Perm)**
Estuary	1	12.005	0.0001*
Reach (Nested in Estuary)	6	4.938	0.0001*
Pairwise Comparison	**T**	**Perms**	**P(perm)**
uMgeni			
Lower vs. Middle	1.906	7818	0.034*
Lower vs. Upper	1.632	8858	0.068
Lower vs. Riverine	2.582	5736	0.002*
Middle vs. Upper	0.773	5041	0.585
Middle vs. Riverine	0.956	1710	0.436
Upper vs. Riverine	1.639	2874	0.060
uMlalazi			
Lower vs. Middle	1.727	8791	0.054
Lower vs. Upper	2.808	6699	0.0005*
Lower vs. Riverine	4.388	8787	0.0001*
Middle vs. Upper	1.203	462	0.221
Middle vs. Riverine	2.783	462	0.004*
Upper vs. Riverine	2.231	462	0.005*

4.4.2 Spatial and temporal abundances

Fish abundance in the uMgeni Estuary was generally low in all reaches and during all trips (Figure 4.4). The highest mean abundance (CPUE) in the uMgeni Estuary (196 fish/haul ± 185.2 SD) and the greatest number of taxa (17 taxa) were recorded in the lower reaches of Trip 3. The high variability resulted from two sites where high abundances of *Ambassis natalensis* and *Ambassis gymnocephalus* were caught. The number of taxa generally followed a decreasing trend from the lower reaches to the riverine reaches, with the lowest taxa recorded in the riverine reach Trip 2 (2 taxa) and Trip 3 (2 taxa). Between trips, the number of taxa present in the lower reaches increased from 10 in Trip 1 to 17 in Trip 3. Similarly, taxa in the upper reaches increased from four to eight species. In the middle reaches the number of taxa was highest in Trip 2. Across the sampling trips, the numbers of taxa in the riverine reach remained consistently low.

Fish abundance in the uMlalazi Estuary was much higher than in the uMgeni (Figure 4.4b). A general decreasing abundance trend was observed from the lower reaches to the riverine reaches. Abundances in the lower reaches were similar across all trips (Trip 1: 103.13 fish/haul ± 65.35, Trip 2: 100.5 fish/haul ± 66.03, Trip 3: 102.9 fish/haul ± 94.14), but were highly variable in other reaches, especially in the middle and upper reaches of the estuary. This was primarily a result of occasional high abundances of *A. natalensis* and *A.*

gymnocephalus. The CPUE recorded in the middle reach of Trip 1 was 131 fish/haul; however, only one site was sampled in this reach during Trip 1, possibly resulting in the overestimation of abundances. The upper reach abundance increased from 61 fish in Trip 1 to 95 fish/haul ± 13.45 SD in Trip 3. Likewise, abundances increased in the riverine reaches from Trip 1 to Trip 3 (3.5 fish/haul and 28.83 fish/haul ± 11.02 SD, respectively). The number of taxa increased across trips in all reaches, except for the lower reach.

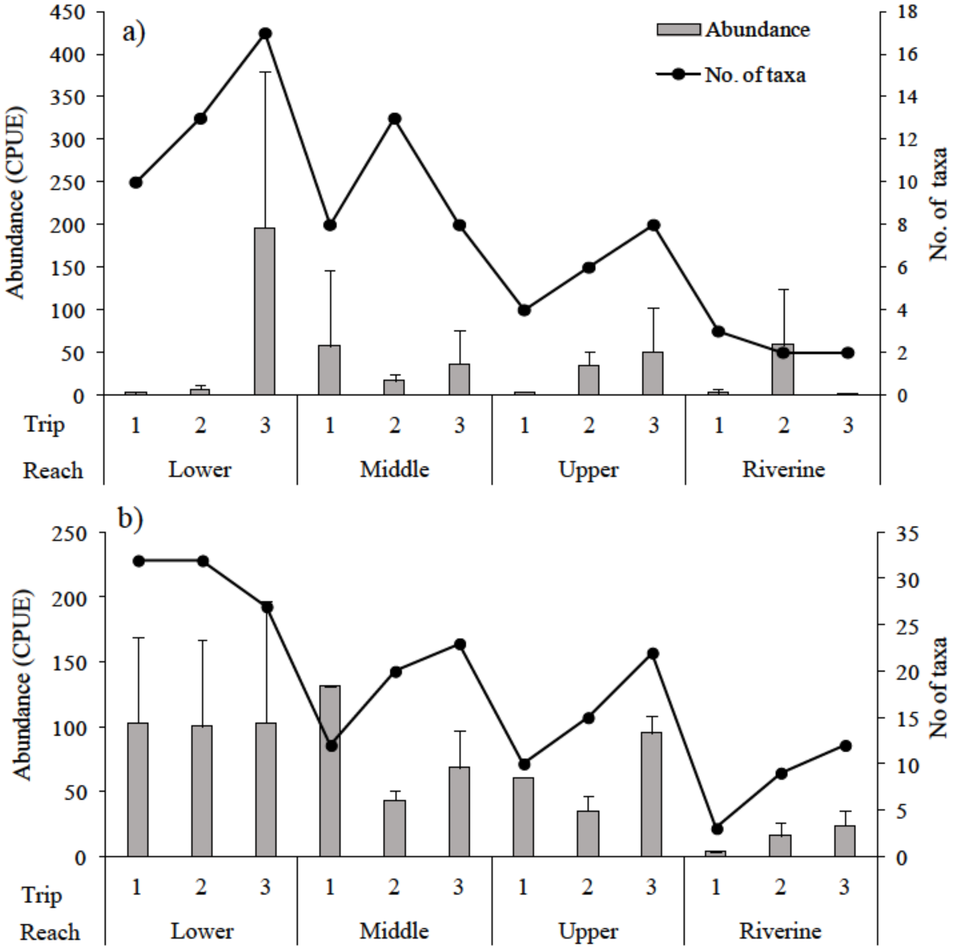


Figure 4.4 Mean fish abundance (CPUE) and the number of taxa in each reach across trips for a) the uMgeni Estuary and b) the uMlalazi Estuary.

4.4.3 Taxonomic composition

Throughout the study period, 3023 individual fish comprising 30 species and 15 families were caught in the uMgeni Estuary. Families with high numbers of representative species were the Gobiidae (7 species), Mugilidae (6 species) and Ambassidae (3 species). The contribution of Gobiidae species to the total abundance of all catches was low (1.37%, Table 4.3). All other families contained only one or two species. Families occurring in the greatest abundances included the Ambassidae (64.39% of total catch), Mugilidae (15.56% of total catch), and Cichlidae (13.26% of total catch) (Figure 4.5a). The most abundant species were *Ambassis gymnocephalus* (fish/haul = 479, 32.19% of the total catch), *Ambassis natalensis* (fish/haul = 419, 28.16% of the total catch), *Chelon dumerili* (fish/haul = 154.67, 10.39% of the total catch) and *Oreochromis mossambicus* (fish/haul = 231.83, 15.58% of the total catch). Fishes from the estuarine and marine guild dominated the abundance (63.90%), followed by marine estuarine dependents (18.37%) and freshwater estuarine opportunists (16.14%) (Figure 4.5b). Guilds with the greatest number of species were marine estuarine dependents (10 species, 33.33% of total species), followed by marine estuarine opportunists (7 species, 23.33%), estuarine and marine (4 species, 13.33%) and freshwater estuarine opportunists (3 species, 10%). All remaining guilds contained less than three species. Several abundantly occurring estuarine and marine species feed on zooplankton resulting in zooplanktivores (63.06%) being the dominant feeding guild (Figure 4.5c). Detritivores were the second most abundant feeding guild (30.44%), followed by a smaller proportion of zoobenthivores (5.25%). In contrast, zoobenthivores contributed the highest number of species (13 species, 40.63%), followed by detritivores (7 species, 23.33%) and zooplanktivores (5 species, 16.67%). The remaining guilds contained fewer than three species.

In the uMlalazi Estuary, 4548 individual fish comprising 60 species and 26 families were caught. The families containing the most species included Mugilidae (8 species), Gobiidae (7 species), Carangidae (5 species) and Sparidae (4 species). Three representative species were recorded in Ambassidae, Engraulidae, Gerreidae, and Clupeidae. While multiple species represented the Gobiidae, Carangidae, Gerreidae, and Clupeidae, they did not dominate the catch abundance (Table 4.3). Ambassidae (48.24% of total catch) followed by Mugilidae (22.08% of total catch) and Leiognathidae (16.64% of total catch) dominated the catch in terms of abundances (Figure 4.5a). The most abundant species were *Ambassis gymnocephalus* (fish/haul = 653.33, 28.61% of total catch), *Ambassis natalensis* (fish/haul = 432.50, 18.94% of total catch), *Leiognathus equulus* (fish/haul = 387.50, 16.75% of total catch), *Chelon dumerili* (fish/haul = 135, 5.91% of total catch) and *Moolgarda cunnesius* (n = 135, 5.91% of total catch). The estuarine and marine guild dominated the catch (49.57%) in terms of abundance, followed by marine estuarine opportunists (26.49%) and marine estuarine dependents (20.99%) (Figure 4.5b). The greatest number of species belonged to the marine estuarine opportunists (28 species, 46.67% of total species), followed by marine estuarine dependents (11 species, 18.33%), marine stragglers (9 species, 15%) and freshwater estuarine opportunists (4 species, 6.67%). In terms of feeding guilds, zooplanktivores were the most abundant group of fishes (50.14%), followed by detritivores (22.78%) and zoobenthivores (22.91%) (Figure 4.5c). The greatest number of species belonged to the zoobenthivores (24 species, 40.00%), piscivores (12 species, 20.00%), detritivores (10 species, 16.67%), and zooplanktivores (10 species, 16.67%).

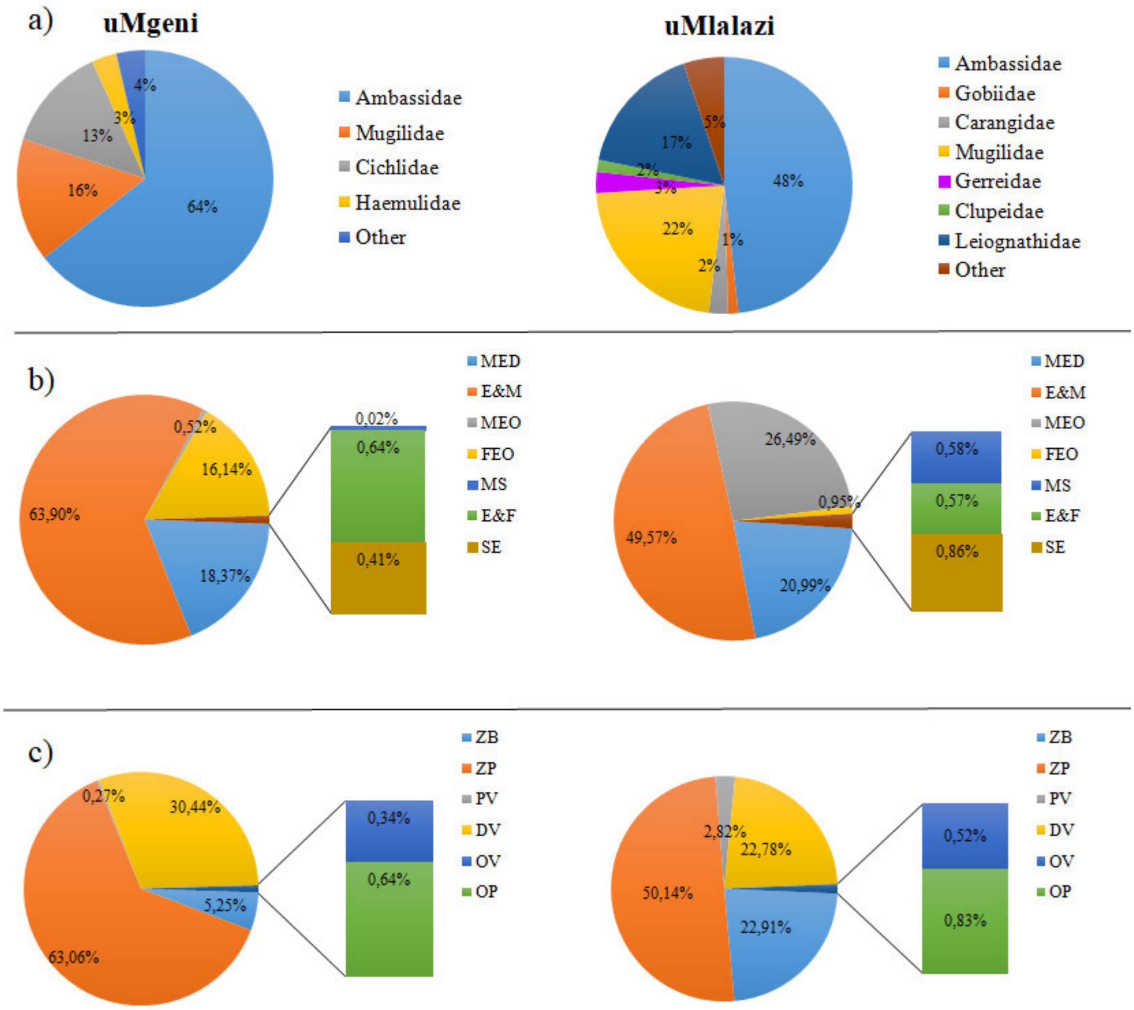


Figure 4.5 Abundance percentage contributions to the overall a) family composition b) estuarine use functional guilds and c) feeding guilds in the uMgeni and uMlalazi estuaries. Functional guilds are represented as MED=Marine estuarine dependants, E&M=Estuarine and Marine, MEO=Marine estuarine opportunist, FEO=Freshwater estuarine opportunist, MS=Marine straggler, E&F=Estuarine and freshwater, SE=Solely estuarine. Feeding modes are represented as ZB=Zoobenthivore, ZP=Zooplanktivore, PV=Piscivore, DV=Detritivore, OV=Omnivore, OP=Opportunist.

Table 4.3 Total abundance (expressed as CPUE, fish/haul) and the percentage contribution of fish species and functional guilds sampled in the uMgeni and uMlalazi estuaries.

				uMgeni		uMlalazi	
	Species	**EUFG**	**FG**	**Abundance (CPUE)**	**% contribution**	**Abundance (CPUE)**	**% contribution**
Ambassidae	*Ambassis ambassis*	E&M	ZP	39.17	2.63	4.00	0.18
	Ambassis gymnocephalus	E&M	ZP	479.00	32.19	653.33	28.61
	Ambassis natalensis	E&M	ZP	419.00	28.16	432.50	18.94
Bothidae	*Bothus pantherinus*	MS	ZB	0.00	0.00	0.50	0.02
Carangidae	*Caranx heberi*	MS	PV	0.00	0.00	1.50	0.07
	Caranx ignobilis	MEO	PV	0.00	0.00	6.50	0.28
	Caranx papuensis	MEO	PV	0.00	0.00	31.50	1.38
	Caranx sexfasciatus	MEO	PV	1.50	0.10	13.00	0.57
	Caranx sp.	MEO	PV	1.00	0.07	0.50	0.02
	Scomberoides lysan	MEO	PV	0.00	0.00	2.50	0.11
Cichlidae	*Oreochromis mossambicus*	FEO	DV	231.83	15.58	5.50	0.24
Clupeidae	*Gilchristella aestuaria*	SE	ZP	1.00	0.07	17.00	0.74
	Herklotsichthys quadrimaculatus	MS	ZP	0.33	0.02	4.67	0.20
	Hilsa kelee	MEO	ZP	0.00	0.00	10.50	0.46
Dasyatidae	*Himantura uarnak*	MEO	ZB	0.00	0.00	0.50	0.02
Drepaneidae	*Drepane longimana*	MS	ZB	0.00	0.00	1.50	0.07
Engraulidae	*Stolephorus holodon*	MEO	ZP	0.00	0.00	1.00	0.04
	Stolephorus indicus	MEO	ZP	0.00	0.00	11.50	0.50
	Thryssa vitrirostris	MEO	ZP	0.00	0.00	0.50	0.02
Gerreidae	*Gerres filamentosus*	MEO	ZB	0.00	0.00	38.83	1.70
	Gerres longirostris	MEO	ZB	0.00	0.00	7.50	0.33
	Gerres methueni	MEO	ZB	0.50	0.03	14.00	0.61
Gobiidae	*Awaous aeneofuscus*	FEO	ZB	3.00	0.20	0.50	0.02
	Favonigobius reichei	E&F	ZB	5.33	0.36	0.00	0.00
	Glossogobius callidus	E&F	ZB	4.00	0.27	10.50	0.46
	Glossogobius giuris	FEO	ZB	2.00	0.13	14.83	0.65
	Oligolepis acutipennis	SE	ZB	1.00	0.07	0.00	0.00
	Oligolepis keiensis	SE	ZB	4.00	0.27	1.50	0.07
	Psammogobius biocellatus	SE	ZB	0.00	0.00	0.50	0.02
	Psammogobius knysnaensis	E&M	ZB	0.50	0.03	0.00	0.00
	Silhouettea sibayi	E&F	ZB	0.00	0.00	2.00	0.09
Haemulidae	*Pomadasys commersonnii*	MED	ZB	45.50	3.06	14.50	0.63
Leiognathidae	*Leiognathus equulus*	MEO	ZB	1.00	0.07	382.50	16.75
Lutjanidae	*Lutjanus fulviflamma*	MEO	ZB	0.00	0.00	1.50	0.07
Monodactylidae	*Monodactylus argenteus*	MEO	ZP	0.00	0.00	10.00	0.44
Mugilidae	*Chelon dumerili*	MED	DV	154.67	10.39	135.00	5.91
	Chelon tricuspidens	MEO	DV	0.00	0.00	1.00	0.04
	Moolgarda cunnesius	MED	DV	17.17	1.15	135.00	5.91
	Moolgarda robusta	MED	DV	1.00	0.07	0.00	0.00
	Moolgarda seheli	MEO	DV	0.00	0.00	20.50	0.90
	Mugil cephalus	MED	DV	1.00	0.07	13.67	0.60
	Mugilidae spp.	MED	DV	19.83	1.33	84.50	3.70
	Planiliza alata	MED	DV	0.00	0.00	59.50	2.61
	Planiliza macrolepis	MED	DV	17.50	1.18	32.00	1.40
	Planiliza melinopterus	MEO	DV	0.00	0.00	1.00	0.04
	Pseudomyxus capensis	MED	DV	10.00	0.67	32.50	1.42
Paralichthyidae	*Pseudorhombus arsius*	MS	ZB	0.00	0.00	1.50	0.07
Platycephalidae	*Platycephalus indicus*	MEO	PV	1.50	0.10	2.00	0.09
	Pomatomus saltatrix	MEO	PV	0.00	0.00	1.00	0.04
Scorpaenidae	*Pterois miles*	MS	PV	0.00	0.00	0.50	0.02
Serranidae	*Epinephelus malabaricus*	MS	ZB	0.00	0.00	0.50	0.02
Sillaginidae	*Sillago sihama*	MEO	ZB	0.00	0.00	9.00	0.39
Soleidae	*Solea turbynei*	MED	ZB	10.33	0.69	8.00	0.35
Sparidae	*Acanthopagrus vagus*	MED	ZB	0.00	0.00	9.50	0.42
	Rhabdosargus holubi	MED	OV	2.83	0.19	2.83	0.12
	Rhabdosargus sarba	MEO	OV	2.17	0.15	5.50	0.24
	Rhabdosargus thorpei	MEO	OV	0.00	0.00	3.50	0.15
Sphyraenidae	*Sphyraena barracuda*	MEO	PV	0.00	0.00	0.50	0.02
	Sphyraena jello	MEO	PV	0.00	0.00	1.00	0.04

				uMgeni		uMlalazi	
	Species	**EUFG**	**FG**	**Abundance (CPUE)**	**% contribution**	**Abundance (CPUE)**	**% contribution**
	Sphyraena qenie	MS	PV	0.00	0.00	1.50	0.07
Terapontidae	*Terapon jarbua*	MED	OP	9.50	0.64	19.00	0.83
Tetraodontidae	*Amblyrhynchotes honckenii*	MEO	ZB	0.50	0.03	2.00	0.09
	Arothron hispidus	MEO	ZB	0.50	0.03	1.00	0.04
	Arothron immaculatus	MEO	PV	0.00	0.00	2.50	0.11
	Chelonodon laticeps	MS	ZB	0.00	0.00	0.50	0.02
	Total abundance (CPUE)			**1488.17**		**2283.67**	
	Total taxa			**30**		**60**	

4.4.4 Univariate analysis

Species richness was highest in the lower reaches (5.5 ± 2.91 SD) of the uMgeni Estuary and followed a decreasing trend to the riverine reaches (1.5 ± 0.83 SD). Significant differences were evident between the lower and riverine reaches (q = 5.097, p = 0.007), and the middle and riverine reaches (q = 4.308, p = 0.025) (Figure 4.6a). The Shannon-Weiner diversity index followed the same trend (Figure 4.6c). Similarly, fish abundance was greatest in the lower reaches (81.3 fish/haul ± 145.5 SD), decreasing towards the riverine reaches (21.75 fish/haul ± 41.51 SD). However, fish abundance within each reach was highly variable, possibly explaining the lack of significance between reaches (Kruskal-Wallis: H = 3.099, p = 0.377) (Figure 4.6b). Simpson's index was lowest in the lower reaches and highest in the riverine reaches (Figure 4.6d). This indicated that only one or a few species dominated the riverine reaches. In comparison, the lower reaches had fish communities characterised by a much more even spread of species and dominance by few species. As a result, significant differences in Simpson's index were observed between the lower and riverine reaches (q = 5.336, p = 0.004), and the middle and riverine reaches (q = 4.473, p = 0.019).

Species richness and abundance were also highest in the lower reaches and decreased towards the riverine reaches in the uMlalazi Estuary. Significant differences in species richness occurred between the riverine reach and the upper (q = 4.257, p = 0.027), middle (q = 5.062, p = 0.007), and lower reaches (q = 6.626, p < 0.001) (Figure 4.6a,). Shannon-Weiner diversity was relatively even in all reaches (Figure 4.6c). Likewise, Simpson's index did not vary much between reaches depicting the evenness in fish species and abundance between reaches (Figure 4.6d). Overall species richness (Mann-Whitney Rank Sum: U statistic =233, p < 0.001), abundance (Mann-Whitney Rank Sum: U statistic =233, p < 0.001) and Shannon-Weiner diversity (t = 6.224, p = <0.0001) were significantly different between the uMgeni and uMlalazi estuaries. Higher species richness and lower Simpson's index (more evenness, less dominance) correspond with the greater Shannon-Weiner diversity index.

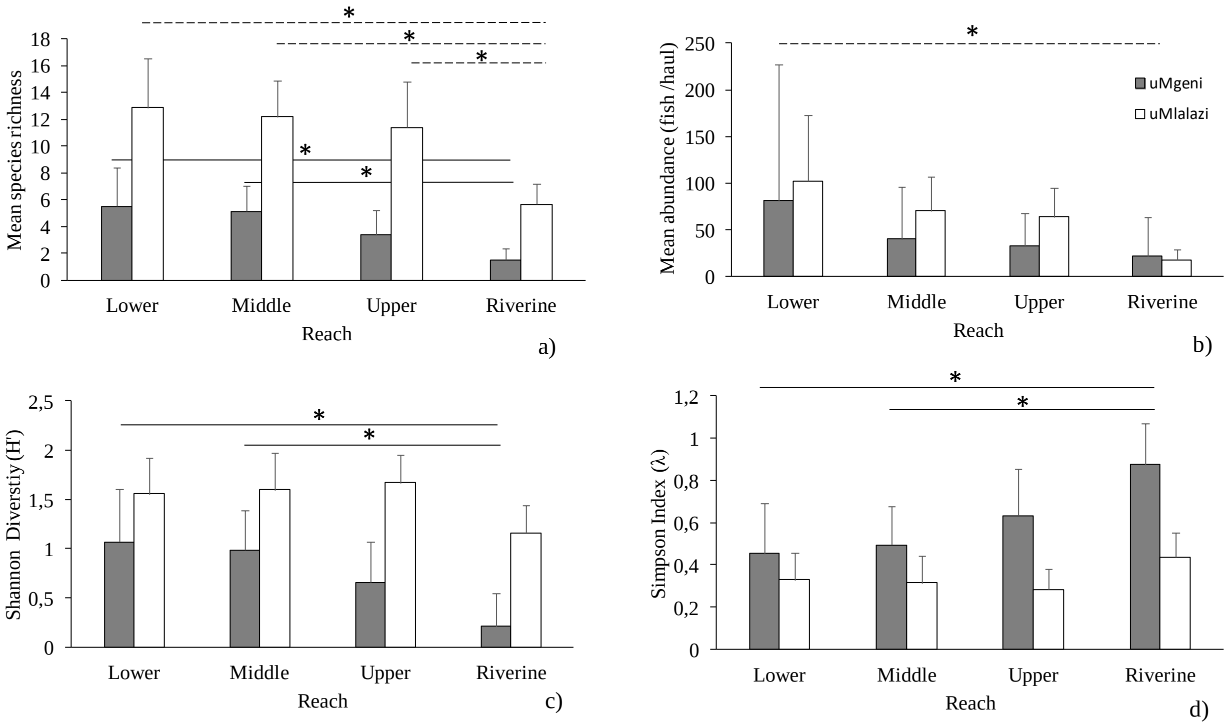


Figure 4.6 Average values (± SD) of a) species richness b) abundance c) Shannon-Weiner diversity (H') and d) Simpson Index (λ) across reaches in the uMgeni and uMlalazi estuaries. Between reach differences (at p<0.05) are represented by asterisk solid lines (uMgeni) and asterisk dotted lines (uMlalazi).

4.4.5 Multivariate community analysis

To visualise patterns in fish communities from reaches identified *a priori*, a principal coordinates (CAP) analysis was run (Figure 4.7). The total variation in the original matrix (64.53%) exceeded the minimum suggested percentage (60%), indicating that the plot provided a good representation of the data (Anderson et al., 2008). The fish community in the uMgeni Estuary appeared to display a response to estuarine reach. Statistical PERMANOVA testing confirmed significant differences between fish communities in different estuarine reaches (Table 4.4) except for those in the lower and middle reaches (t = 1.234, p(perm) = 0.150), and in the upper and riverine reaches (t = 1.152, p(perm) = 0.237).

In all reaches, five or fewer species contributed at least 79% to the overall similarity in fish communities within reaches (Table 4.5). The species contributing the most to community similarities were often found in more than one reach but with different abundances and varying contributions to the overall average reach similarity. Overall average similarities of the fish communities in the lower and upper reaches were low (18.07% and 15.68%, respectively), showing that the similarity amongst communities at different sites in the same reach was low. In the lower reach, *A. natalensis*, Mugilidae spp., and *Solea turbynei* were the greatest contributors to similarities in fish communities (total contribution of 67.84%). *Chelon dumerili* (30.70%) contributed the most to community similarities in the middle reaches, followed by *Ambassis ambassis and A. natalensis*. Three species, *O. mossambicus, A. gymnocephalus* and *A. ambassis* contributed 92.08% to the cumulative similarity in the upper reach (Table 4.5). *Oreochromis mossambicus* accounted for 100% of the similarity in fish communities sampled in the riverine reach.

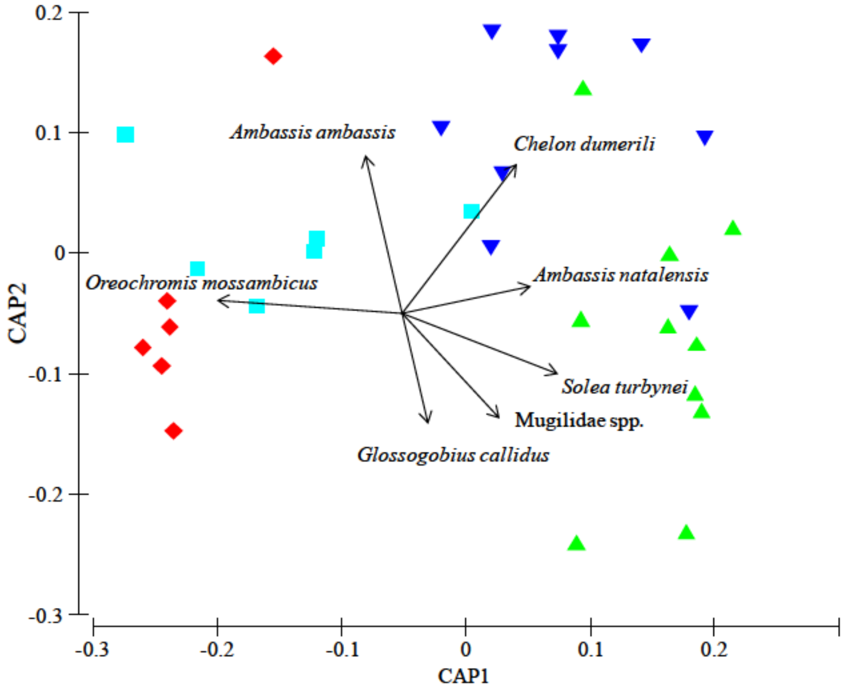


Figure 4.7 Canonical analysis of principal coordinates plot of the fish community distribution in the uMgeni Estuary. Vectors represent species that are correlated to axes (Spearman's rank r > 0.4). Reaches = ▲-Lower; ▼-Middle; ■-Upper; ◆-Riverine.

Table 4.4 PERMANOVA and pairwise results of estuary and reach fish assemblage differences. Asterisks denote significance at p<0.05. Df = degrees of freedom, Pseudo-f = critical values.

Source	**PERMANOVA**						
	Df	**Pseudo-F**	**P(Perm)**				
Estuary	1	9.223	0.0001*				
Reach	6	3.334	0.0001*				
Pairwise Comparison	**T**	**Perms**	**P(perm)**		**T**	**Perms**	**P(perm)**
uMgeni:				**uMlalazi:**			
Lower vs. Middle	1.234	7821	0.150	Lower vs. Middle	1.496	8763	0.002*
Lower vs. Upper	1.808	8895	0.0002*	Lower vs. Upper	1.736	6669	0.0001*
Lower vs. Riverine	2.215	5669	0.0002*	Lower vs. Riverine	2.738	8761	0.0001*
Middle vs. Upper	1.613	5077	0.021*	Middle vs. Upper	1.094	462	0.306
Middle vs. Riverine	2.265	1711	0.002*	Middle vs. Riverine	2.058	462	0.003*
Upper vs. Riverine	1.152	2891	0.237	Upper vs. Riverine	1.504	462	0.014*

Dominant species responsible for within reach similarities were also accountable for the dissimilarities between reaches. Fish communities were the most dissimilar between the lower and riverine reaches (98.77%) and the lower and upper reaches (93%) (Figure 4.7, Table 4.6). Nine species accounted for 60% of the difference between the lower and upper reaches (Table 4.6). These included the species responsible for similarities in the lower and upper reaches (as above) as well as *C. dumerili, Oligolepis keiensis and Pseudomyxus capensis*. The discriminating taxon between the lower and riverine reach communities was *O. mossambicus* (18.09%), followed by six other taxa with higher abundances in the lower reach except for *P. capensis* (Table 4.6).

Table 4.5 Taxa contributing towards the similarity within reaches of the uMgeni and uMlalazi estuaries. Only species contributing more than 4% to the average similarity are represented.

	uMgeni		uMlalazi	
Reach	**Species**	**Contrib%**	**Species**	**Contrib%**
Lower	*Ambassis natalensis*	33.28	*Ambassis natalensis*	22.62
	Mugilidae spp.	20.92	*Leiognathus equulus*	17.21
	Solea turbynei	13.64	*Ambassis gymnocephalus*	16.84
	Chelon dumerili	7.07	*Chelon dumerili*	14.36
	Ambassis gymnocephalus	5.60	*Gerres filamentosus*	6.43
	Average similarity: 18.07		**Average similarity: 41.86**	
Middle	*Chelon dumerili*	30.70	*Leiognathus equulus*	30.41
	Ambassis ambassis	18.43	*Ambassis natalensis*	12.53
	Ambassis natalensis	17.69	*Moolgarda cunnesius*	8.97
	Moolgarda cunnesius	13.12	*Chelon dumerili*	8.67
	Ambassis gymnocephalus	9.69	Mugilidae spp.	6.80
			Ambassis ambassis	5.20
	Average similarity: 30.91		**Average similarity: 40.29**	
Upper	*Oreochromis mossambicus*	64.54	*Leiognathus equulus*	28.21
	Ambassis gymnocephalus	17.58	*Ambassis natalensis*	23.32
	Ambassis ambassis	9.96	*Moolgarda cunnesius*	13.75
			Planiliza macrolepis	11.33
			Glossogobius callidus	4.67
	Average similarity: 15.68		**Average similarity: 40.68**	
Riverine	*Oreochromis mossambicus*	100.00	*Pseudomyxus capensis*	38.45
			Glossogobius giuris	16.76
			Ambassis natalensis	12.68
			Moolgarda cunnesius	10.26
			Acanthopagrus vagus	7.54
			Glossogobius callidus	4.21
			Leiognathus equulus	4.03
	Average similarity: 31.05		**Average similarity: 29.00**	

Table 4.6 Taxa contributing towards the dissimilarity between reaches in the uMgeni Estuary. Only species contributing more than 4% to the average dissimilarity are represented.

Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
	Lower	**Upper**				
Ambassis natalensis	1.33	0.34	11.45	1.16	12.31	12.31
Oreochromis mossambicus	0.00	0.96	10.6	0.93	11.40	23.70
Ambassis gymnocephalus	0.87	0.68	10.16	0.85	10.92	34.62
Mugilidae spp.	0.64	0.17	7.21	0.86	7.75	42.38
Chelon dumerili	0.34	0.00	4.77	0.52	5.13	47.51
Solea turbynei	0.44	0.00	4.46	0.84	4.80	52.30
Oligolepis keiensis	0.00	0.36	4.14	0.54	4.45	56.76
Ambassis ambassis	0.00	0.35	4.01	0.61	4.31	61.07
Pseudomyxus capensis	0.20	0.21	3.90	0.51	4.20	65.26
				Average dissimilarity = 93.00		
	Lower	**Riverine**				
Oreochromis mossambicus	0.00	1.33	17.87	1.15	18.09	18.09
Ambassis natalensis	1.33	0.00	12.51	1.08	12.67	30.76
Mugilidae spp.	0.64	0.00	8.45	0.79	8.56	39.32
Chelon dumerili	0.34	0.00	6.29	0.48	6.36	45.68
Ambassis gymnocephalus	0.87	0.00	5.69	0.60	5.76	51.44
Solea turbynei	0.44	0.00	5.25	0.82	5.31	56.76
Pseudomyxus capensis	0.20	0.24	3.99	0.56	4.04	60.79
				Average dissimilarity = 98.77		
	Middle	**Upper**				
Chelon dumerili	1.12	0.00	11.33	1.32	13.72	13.72
Oreochromis mossambicus	0.61	0.96	9.98	1.13	12.09	25.81
Ambassis gymnocephalus	0.83	0.68	9.46	0.95	11.46	37.27
Ambassis natalensis	1.01	0.34	9.20	1.09	11.14	48.41
Ambassis ambassis	0.90	0.35	7.84	1.17	9.50	57.90
Moolgarda cunnesius	0.68	0.14	6.76	0.96	8.19	66.09
Solea turbynei	0.30	0.00	3.98	0.51	4.82	70.91
Oligolepis keiensis	0.09	0.36	3.89	0.65	4.71	75.62
				Average dissimilarity = 82.57		
	Middle	**Riverine**				
Oreochromis mossambicus	0.61	1.33	14.30	1.25	15.71	15.71
Chelon dumerili	1.12	0.00	13.20	1.33	14.5	30.21
Ambassis natalensis	1.01	0.00	10.02	1.07	11.01	41.22
Ambassis ambassis	0.90	0.20	9.23	1.13	10.14	51.35
Moolgarda cunnesius	0.68	0.00	8.11	0.86	8.91	60.27
Ambassis gymnocephalus	0.83	0.00	8.10	0.79	8.90	69.16
Solea turbynei	0.30	0.00	4.81	0.51	5.28	74.44
				Average dissimilarity = 91.05		

The longitudinal gradient in fish communities was more apparent in the uMlalazi than the uMgeni Estuary (Figure 4.8). Principal coordinates analysis (CAP) represented 77.42% of the original matrix's total variation, illustrating a good representation of the data (Figure 4.8). Statistical testing confirmed significant differences in fish communities from all reaches except for the middle and upper reaches (t = 1.094, p(perm) = 0.306, Table 4.4).

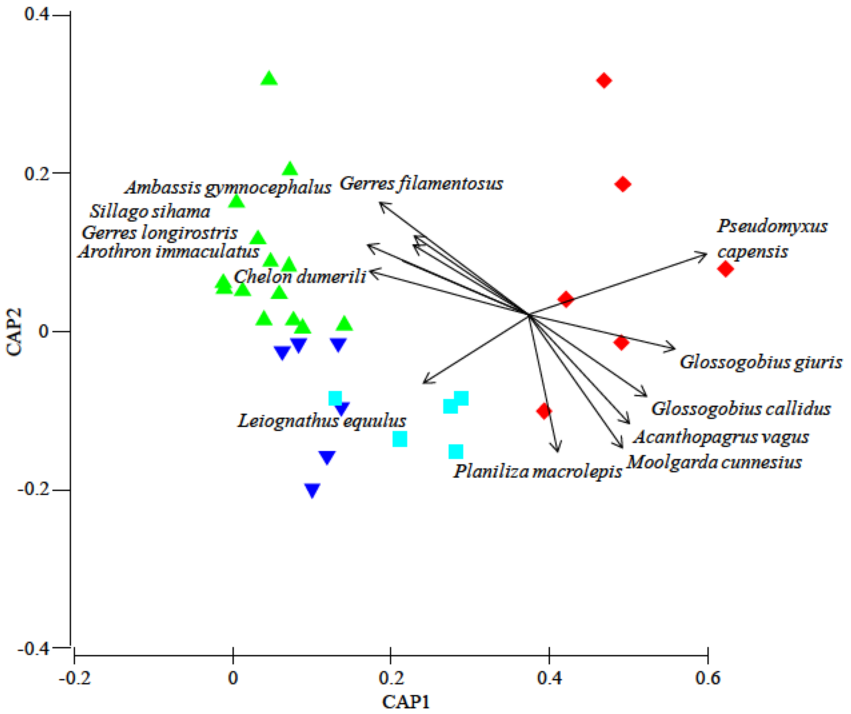


Figure 4.8 Canonical analysis of principal coordinates plot of the fish community distribution in the uMlalazi Estuary. Vectors represent species that are correlated to axes (Spearman's rank r > 0.45). Reaches = ▲-Lower; ▼-Middle; ■-Upper; ◆-Riverine.

As in the uMgeni Estuary, five or fewer species contributed at least 70% to the overall similarity in fish communities within reaches, often occurring in more than one reach in varying abundances. Overall average similarities of the fish communities in the lower, middle, and upper reaches were relatively high (± 40%). Therefore, the fish communities at different sites in the same reach were similar (Table 4.5). The similarity in fish communities in the lower reach was mainly made up of contributions from four species: *A. natalensis* (22.62%), *L. equulus* (17.21%), *A. gymnocephalus* (16.84%) and *C. dumerili* (14.36%), although smaller contributions (<2%) were made *from Sillago sihama, Gerres filamentosus* and *Arothron immaculatus* (Table 4.5, Figure 4.8). *Leiognathus equulus* and *A. natalensis* were also primary contributors to similarity in communities in the middle and upper reaches. The riverine reach was significantly different from other reaches and characterised by contributions largely from *P. capensis* (38.45%) and *Glossogobius giuris* (16.76%).

Species responsible for within reach similarities were also responsible for between reach dissimilarities. As in the uMgeni Estuary, the most significant differences in fish communities were between the lower and riverine reaches (85.12%), with contributions from six species. These included *A. gymnocephalus, C. dumerili, A. natalensis, L. equulus, P. capensis* and *G. filamentosus* (Table 4.7). The individual contributions of species to the dissimilarities between reaches were relatively low (<10%), portraying species diversity within each reach. Differences in fish communities were also relatively high between the middle and riverine reaches (81.82%). Discriminating species included those contributing to similarities within the middle reaches as well as *A. gymnocephalus* and *P. capensis.*

Table 4.7 Taxa contributing towards the dissimilarity between reaches in the uMlalazi Estuary. Only species contributing more than 4% to the average dissimilarity are represented.

Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
	Lower	**Middle**				
Ambassis gymnocephalus	1.86	0.95	4.90	1.38	7.80	7.80
Moolgarda cunnesius	0.40	1.09	3.43	1.22	5.46	13.26
Ambassis natalensis	1.91	1.22	3.02	1.33	4.80	18.06
Chelon dumerili	1.34	1.10	2.91	1.37	4.63	22.69
Gerres filamentosus	0.83	0.00	2.73	1.18	4.35	27.04
Mugilidae spp.	0.63	0.78	2.56	1.25	4.08	31.12
				Average dissimilarity = 62.86		
	Lower	**Upper**				
Ambassis gymnocephalus	1.86	0.40	5.54	1.39	8.37	8.37
Moolgarda cunnesius	0.40	1.35	4.08	1.37	6.17	14.54
Chelon dumerili	1.34	0.37	3.52	1.61	5.31	19.86
Mugilidae spp.	0.63	0.80	3.03	1.02	4.57	24.43
Planiliza macrolepis	0.33	0.98	2.66	1.36	4.02	28.45
Gerres filamentosus	0.83	0.17	2.65	1.14	4.00	32.45
				Average dissimilarity = 66.18		
	Lower	**Riverine**				
Ambassis gymnocephalus	1.86	0.00	8.18	1.52	9.61	9.61
Chelon dumerili	1.34	0.00	5.91	1.88	6.95	16.55
Ambassis natalensis	1.91	0.88	5.82	1.38	6.84	23.39
Leiognathus equulus	1.69	0.46	5.82	1.64	6.83	30.22
Pseudomyxus capensis	0.00	1.15	5.14	1.67	6.04	36.27
Gerres filamentosus	0.83	0.00	3.84	1.16	4.51	40.78
				Average dissimilarity = 85.12		
	Middle	**Riverine**				
Leiognathus equulus	1.98	0.46	7.31	1.82	8.93	8.93
Pseudomyxus capensis	0.00	1.15	5.36	1.74	6.55	15.48
Chelon dumerili	1.10	0.00	5.21	1.26	6.37	21.85
Ambassis natalensis	1.22	0.88	4.85	1.39	5.92	27.77
Moolgarda cunnesius	1.09	0.59	4.40	1.19	5.38	33.15
Ambassis gymnocephalus	0.95	0.00	4.31	0.82	5.27	38.43
Mugilidae spp.	0.78	0.00	3.88	1.18	4.75	43.17
				Average dissimilarity = 81.82		
	Upper	**Riverine**				
Leiognathus equulus	1.78	0.46	6.42	1.73	8.79	8.79
Ambassis natalensis	1.64	0.88	5.21	1.43	7.14	15.93
Moolgarda cunnesius	1.35	0.59	5.13	1.21	7.02	22.95
Pseudomyxus capensis	0.20	1.15	5.08	1.44	6.96	29.91
Planiliza macrolepis	0.98	0.17	4.15	1.52	5.68	35.59
Mugilidae spp.	0.80	0.00	3.64	0.75	4.98	40.56
Glossogobius callidus	0.59	0.46	3.21	1.20	4.39	44.96
Planiliza alata	0.55	0.33	3.19	0.83	4.37	49.32
				Average dissimilarity = 73.02		

Ordination plots indicated that fish communities in the uMlalazi Estuary differed from the uMgeni Estuary (Figure 4.9). uMgeni samples were widely interspersed, although samples did occur predominately within the plot's upper area. Statistical analysis confirmed significant differences between the fish assemblages of the uMgeni and uMlalazi estuaries (PERMANOVA: df = 1, Pseudo-F = 9.223, p(perm) = 0.0001, Table 4.4), however dispersion effects were also identified (Permdisp: F = 24.328, p(perm) = 0.0001). This was expected as evident in the nMDS; however, location effects are also clearly evident.

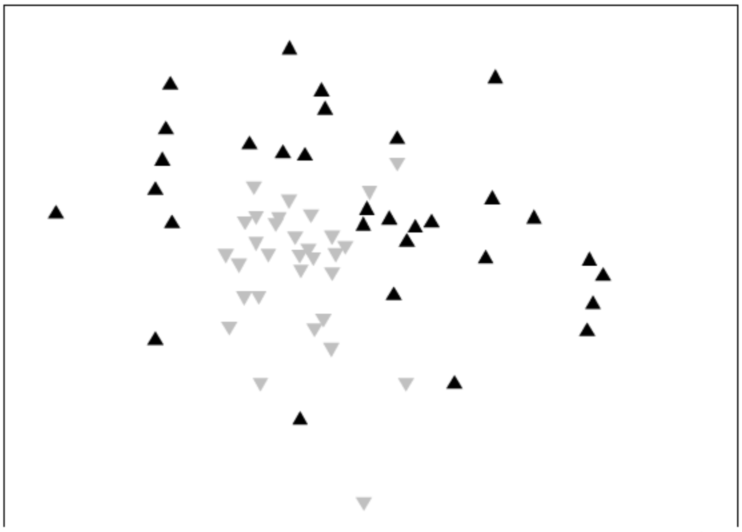


Figure 4.9 nMDS of fish assemblage differences between the uMgeni (▲) and uMlalazi (▼) estuaries.

Similarity analysis identified that the average dissimilarity between the estuaries (85.67%) was greater than the similarities within each estuary (Table 4.8). All species contributing more than 3% to the between estuary dissimilarity had greater abundances in the uMlalazi Estuary except for *O. mossambicus,* which was more abundant in the uMgeni. Species contributing more than 3% individually to the between estuary dissimilarity included *L. equulus* (8.9%), *A. natalensis* (8.41%), *A. gymnocephalus* (7.17%) and *C. dumerili* (5.47%).

Table 4.8 Taxa contributing towards the dissimilarity between the uMgeni and uMlalazi estuaries. Only species contributing more than 3% to the average dissimilarity are represented.

	uMgeni	**uMlalazi**				
Species	**Av.Abund**	**Av.Abund**	**Av.Diss**	**Diss/SD**	**Contrib%**	**Cum.%**
Leiognathus equulus	0.05	1.52	7.62	1.66	8.90	8.90
Ambassis natalensis	0.79	1.54	7.21	1.38	8.41	17.31
Ambassis gymnocephalus	0.65	1.09	6.14	0.96	7.17	24.48
Chelon dumerili	0.44	0.87	4.69	1.05	5.47	29.95
Moolgarda cunnesius	0.28	0.72	4.14	0.90	4.83	34.79
Oreochromis mossambicus	0.62	0.11	3.87	0.65	4.52	39.31
Mugilidae spp.	0.30	0.57	3.34	0.84	3.89	43.20
Pseudomyxus capensis	0.18	0.25	2.69	0.54	3.14	46.34
					Average dissimilarity = 85.67	

4.4.6 Functional guild analysis

Trends in fish communities characterised by EUFG depended on the uMgeni Estuary's salinity gradient (Figure 4.10). Significant differences in abundances of different EUFG were noted amongst all reaches of the uMgeni Estuary except for lower versus middle, middle versus upper, and upper versus riverine reaches (Table 4.9). Marine guilds contributed the most to the similarity in guild structure in the lower reaches (66.92%). Marine estuarine dependents were the most significant contributors to similarities in guild structure in the middle reach (54.69%), with an increased contribution from estuarine guilds (42.56%). Two guilds namely E&M, and FEO, contributed the most to similarity in guild structure (85.19%) in the upper reaches, followed by smaller contributions from MED (9.37%) and SE guilds (5.44%). In the riverine reach, contributions from only the FEO guild indicated the strong influence of freshwater in this reach (Table 4.10).

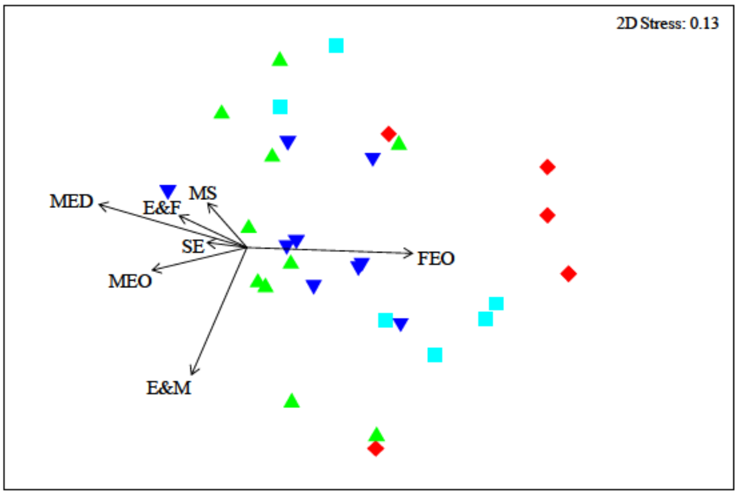


Figure 4.10 nMDS of current fish assemblages in the uMgeni Estuary based on the abundance of Estuarine Use Functional Guilds. Vector overlays represent the EUFG's with longer vectors representing greater correlations to estuary reaches. Reaches = ▲-Lower; ▼-Middle; ■-Upper; ◆-Riverine.

The EUFG groups, which were most dominant in each reach, also contributed to the dissimilarities between reaches. Guild structures were the most different between the lower and riverine reaches (88.48%) and the middle and riverine reaches (84.35%). The discriminating guilds for the lower and riverine reaches were MED (26.89%) and E&M (24.23%) guilds which had greater abundance contributions in the lower reaches, and FEO (24.93%), which had greater abundance contributions in the riverine reaches. The same guilds were the primary contributors to differences in guild structure between the lower and upper reaches with changes to the order of individual guild contributions (Table 4.11). Marine estuarine dependents were the main contributors of guild structure dissimilarities between the middle and riverine reaches (43.38%).

Table 4.9 PERMANOVA and pairwise comparison results of estuary and reach differences according to EUFG and FMFG. Df = degrees of freedom, Pseudo-F= critical values. Asterisks denote significance at p<0.05.

Source	PERMANOVA			Source	PERMANOVA		
	Df	Pseudo-F	P(Perm)		df	Pseudo-F	P(Perm)
EUFG				**FMFG**			
Estuary	1	13.01	0.0001*	Estuary	1	14.519	0.0001*
Reach (nested in Estuary)	6	4.227	0.0001*	Reach (nested in Estuary)	6	1.702	0.026*
Pairwise comparison	T	Perms	P(Perm)	Pairwise comparison	t	Perms	P(Perm)
uMgeni							
Lower vs. Middle	1.237	7768	0.205	Lower vs. Middle	0.792	7843	0.665
Lower vs. Upper	1.914	8919	0.018*	Lower vs. Upper	1.260	8899	0.197
Lower vs. Riverine	2.589	5703	0.0006*	Lower vs. Riverine	1.355	5757	0.135
Middle vs. Upper	1.697	5043	0.055	Middle vs. Upper	0.683	5060	0.711
Middle vs. Riverine	2.650	1708	0.002*	Middle vs. Riverine	1.254	1711	0.190
Upper vs. Riverine	1.227	2884	0.227	Upper vs. Riverine	0.922	2887	0.511
uMlalazi							
Lower vs. Middle	1.700	8791	0.027*	Lower vs. Middle	0.711	8773	0.748
Lower vs. Upper	1.973	6724	0.005*	Lower vs. Upper	1.363	6709	0.121
Lower vs. Riverine	3.715	8794	0.0001*	Lower vs. Riverine	2.633	8783	0.0002*
Middle vs. Upper	0.818	461	0.623	Middle vs. Upper	0.604	462	0.860
Middle vs. Riverine	2.036	462	0.005*	Middle vs. Riverine	1.956	462	0.005*
Upper vs. Riverine	1.764	462	0.018*	Upper vs. Riverine	1.551	462	0.035*

Table 4.10 Estuarine use functional guilds contributing towards the similarity between reaches in the uMgeni and uMlalazi estuaries. Only guilds contributing more than 5% to the average similarity are represented.

	uMgeni		uMlalazi	
Reach	**Species**	**Contrib%**	**Species**	**Contrib%**
Lower	MED	47.91	MEO	50.51
	E&M	27.27	E&M	26.74
	MEO	19.01	MED	20.80
	E&F	5.81		
	Average similarity: 43.62		**Average similarity: 69.98**	
Middle	MED	54.69	MED	36.64
	E&M	36.52	MEO	34.39
	FEO	6.08	E&M	19.11
	Average similarity: 49.16		**Average similarity: 65.86**	
Upper	E&M	50.08	MED	42.22
	FEO	35.11	MEO	34.90
	MED	9.37	E&M	14.44
	SE	5.44	FEO	5.43
	Average similarity: 30.73		**Average similarity: 69.39**	
Riverine	FEO	100.0	MED	58.98
			MEO	17.40
			FEO	14.77
			E&M	6.64
	Average similarity: 46.80		**Average similarity: 55.36**	

Table 4.11 Estuarine use functional guilds contributing towards the dissimilarity between reaches within the uMgeni and uMlalazi estuaries.

	uMgeni							uMlalazi					
Species	Av.Abu	Av.Abu	Av.Diss	Diss/SD	Contrib%	Cum.%	Species	Av.Abu	Av.Abu	Av.Diss	Diss/SD	Contrib%	Cum.%
	Lower	Middle						Lower	Middle				
E&M	2.28	1.96	20.65	1.40	35.86	35.86	MEO	7.29	4.51	11.99	1.41	34.35	34.35
MED	2.17	3.09	18.60	1.10	32.30	68.16	MED	3.73	4.69	8.88	1.31	25.46	59.81
MEO	0.96	0.24	7.33	1.13	12.73	80.89	E&M	3.77	2.82	6.15	1.31	17.62	77.42
E&F	0.53	0.23	4.54	0.98	7.88	88.77	SE	0.26	0.83	2.86	0.95	8.20	85.63
FEO	0.08	0.32	3.53	0.62	6.14	94.91	FEO	0.35	0.68	2.16	1.26	6.20	91.82
SE	0.08	0.24	2.07	0.65	3.60	98.51	MS	0.44	0.60	2.12	1.20	6.07	97.90
MS	0.08	0.00	0.86	0.32	1.49	100.00	E&F	0.06	0.20	0.73	0.51	2.10	100.00
						Average dissimilarity = 57.58							Average dissimilarity = 34.90
	Lower	Upper						Lower	Upper				
E&M	2.28	2.41	24.22	1.43	32.33	32.33	MEO	7.29	5.01	11.67	1.31	32.83	32.83
MED	2.17	0.73	17.75	1.47	23.69	56.02	MED	3.73	5.43	9.69	1.54	27.28	60.11
FEO	0.08	1.26	12.42	1.06	16.58	72.60	E&M	3.77	2.04	7.09	1.41	19.94	80.06
MEO	0.96	0.00	9.71	1.17	12.96	85.56	FEO	0.35	0.83	2.36	1.44	6.64	86.69
SE	0.08	0.48	5.09	0.61	6.79	92.35	E&F	0.06	0.59	2.09	1.10	5.88	92.57
E&F	0.53	0.00	4.66	0.87	6.23	98.58	MS	0.44	0.20	1.78	0.80	5.01	97.58
MS	0.08	0.00	1.07	0.32	1.42	100.00	SE	0.26	0.00	0.86	0.50	2.42	100.00
						Average dissimilarity = 74.92							Average dissimilarity = 35.53
	Lower	Riverine						Lower	Riverine				
MED	2.17	0.24	23.79	1.50	26.89	26.89	MEO	7.29	1.16	27.02	2.38	45.44	45.44
FEO	0.08	1.55	22.05	1.10	24.93	51.82	E&M	3.77	0.88	13.33	1.63	22.42	67.86
E&M	2.28	0.20	21.44	1.08	24.23	76.05	MED	3.73	2.79	8.86	1.31	14.91	82.77
MEO	0.96	0.00	12.70	1.16	14.35	90.40	FEO	0.35	1.12	4.38	1.05	7.37	90.14
E&F	0.53	0.17	6.51	0.90	7.36	97.76	E&F	0.06	0.46	2.09	0.72	3.52	93.65
MS	0.08	0.00	1.48	0.32	1.67	99.44	MS	0.44	0.00	2.03	0.63	3.42	97.07
SE	0.08	0.00	0.50	0.30	0.56	100.00	SE	0.26	0.00	1.13	0.51	1.89	98.96
							FM	0.00	0.14	0.62	0.44	1.04	100.00
						Average dissimilarity = 88.48							Average dissimilarity = 59.46
	Middle	Riverine						Middle	Riverine				
MED	3.09	0.24	36.59	1.80	43.38	43.38	MEO	4.51	1.16	15.30	1.71	30.54	30.54
E&M	1.96	0.20	21.65	1.15	25.67	69.05	MED	4.69	2.79	10.70	1.03	21.37	51.91
FEO	0.32	1.55	16.83	1.26	19.95	89.00	E&M	2.82	0.88	10.35	1.48	20.66	72.57
E&F	0.23	0.17	4.25	0.72	5.04	94.04	SE	0.83	0.00	4.06	0.89	8.10	80.67
MEO	0.24	0.00	2.59	0.62	3.07	97.11	FEO	0.68	1.12	3.79	0.95	7.56	88.23
SE	0.24	0.00	2.44	0.62	2.89	100.00	MS	0.60	0.00	2.80	1.36	5.58	93.81
							E&F	0.20	0.46	2.45	0.79	4.89	98.70
							FM	0.00	0.14	0.65	0.44	1.30	100.00
						Average dissimilarity = 84.35							Average dissimilarity = 49.99
	Upper	Riverine						Upper	Riverine				
E&M	2.41	0.20	28.14	1.37	39.40	39.40	MEO	5.01	1.16	18.06	2.03	39.00	39.00
FEO	1.26	1.55	20.82	1.22	29.15	68.55	MED	5.43	2.79	12.33	1.35	26.62	65.61
MED	0.73	0.24	13.09	0.72	18.33	86.88	E&M	2.04	0.88	7.04	1.39	15.20	80.82
SE	0.48	0.00	7.07	0.61	9.90	96.78	FEO	0.83	1.12	3.66	0.86	7.90	88.72
E&F	0.00	0.17	2.30	0.42	3.22	100.00	E&F	0.59	0.46	3.37	1.21	7.27	95.98
							MS	0.20	0.00	1.19	0.49	2.58	98.56
							FM	0.00	0.14	0.67	0.43	1.44	100.00
						Average dissimilarity = 71.43							Average dissimilarity = 46.24

The nMDS ordination of uMlalazi fish communities by EUFGs revealed that guilds conformed to the typical salinity gradient associated with the estuary reaches (Figure 4.11). Significant differences in the EUFG structure were evident between all reaches except for the middle and the upper reach pairwise comparison (Table 4.9). The average similarity of samples in each reach was relatively high (>55%) (Table 4.10). Estuarine use functional guilds in the lower and riverine reaches were the most dissimilar (59.46%, Table 4.11), shown by the highly significant difference in the PERMANOVA test (PERMANOVA pairwise comparison: t = 3.715, p(perm) = 0.0001, Table 4.9). Marine estuarine opportunists and E&M

groups cumulatively contributed 77.25% to the community similarities in the lower reach (Table 4.10). The primary guilds contributing towards reach community similarities in the middle and upper reaches were the same with the exception of increased contributions of estuarine guilds (FEO) in the upper reaches. In the riverine reaches, the contribution of MEO to similarities (17.40%) decreased while contributions of FEO increased (14.77%).

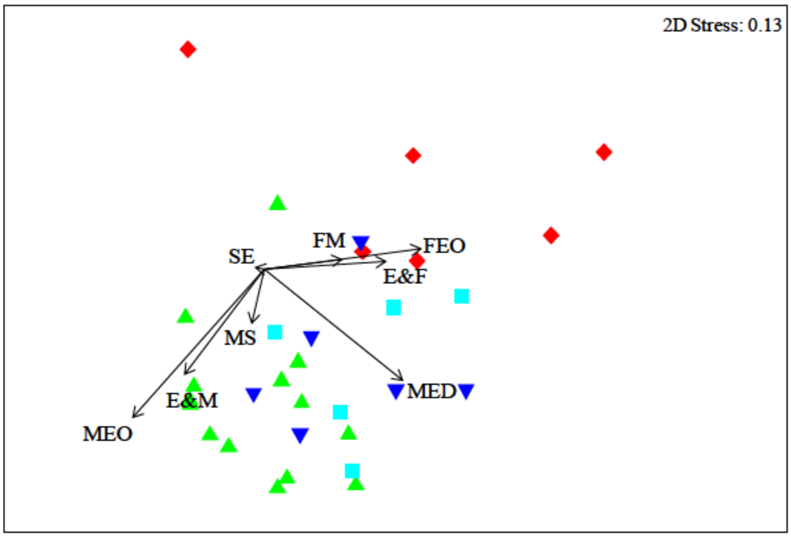


Figure 4.11 nMDS of the current fish assemblage in the uMlalazi Estuary based on the abundance of Estuarine Use Functional Guilds. Vector overlays represent the EUFG's with longer vectors representing greater correlations to estuary reaches. Reaches = ▲-Lower; ▼-Middle; 🟦-Upper; ◆-Riverine.

Unlike species composition or EUFG's, fish communities characterised by FMFG's in the uMgeni Estuary were not significantly different between reaches (Figure 4.12a, Table 4.9). In the uMlalazi Estuary, significant differences in the FMFG structure occurred between the lower and riverine (t = 2.633, p(perm) = 0.0002), the middle and the riverine reaches (t = 1.956, p(perm) = 0.005) and the upper and riverine (t = 1.551, p(perm) = 0.035) reaches (Table 4.9). All guild abundances were higher in the lower, middle and upper reaches contributing to dissimilarities with the riverine reach (Figure 4.12b). The main guilds (ZP, ZB and DV) contributing towards reach dissimilarities between the lower and riverine reaches (cumulative total of 78.58%) were the same for the middle and riverine reach comparison (cumulative total of 83.43%) (Table 4.12). Detritivores were the discriminating guild between the upper and riverine reaches with greater abundance contributions occurring in the upper reaches.

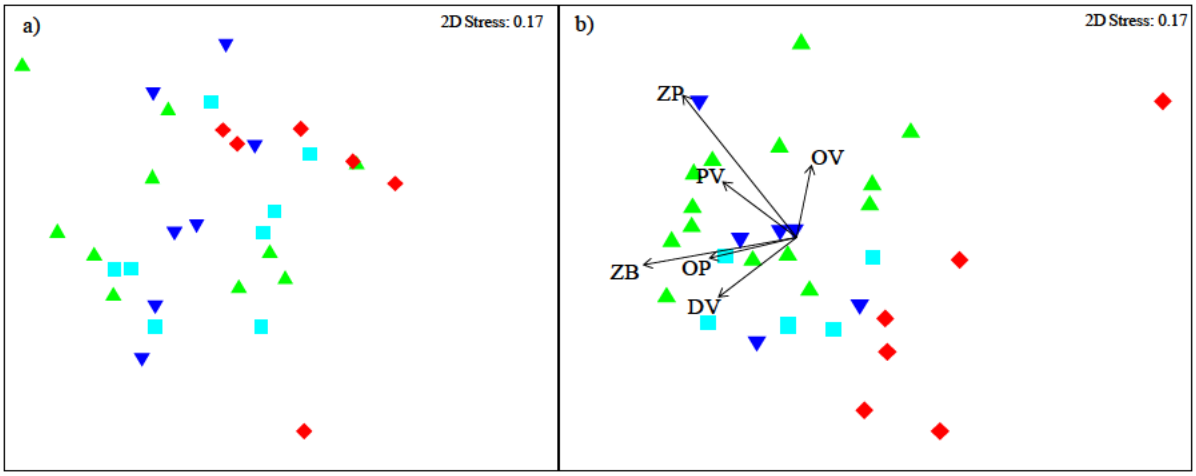


Figure 4.12 nMDS of current fish assemblages based on the abundance of Feeding Guilds in a) the uMgeni Estuary and b) the uMlalazi Estuary. Vector overlay represents the FMFG's, with longer vectors representing greater correlations to estuary reaches. Reaches = ▲-Lower; ▼-Middle; ■-Upper; ◆-Riverine.

Table 4.12 Feeding mode functional guilds contributing towards the dissimilarity between reaches in the uMlalazi Estuary.

Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
	Lower	**Riverine**				
ZP	4.85	1.09	16.71	1.87	32.67	32.67
ZB	5.46	2.54	15.47	1.63	30.24	62.91
DV	3.59	2.62	8.02	1.37	15.68	78.58
PV	1.79	0.31	7.06	1.15	13.8	92.38
OV	0.58	0.00	2.76	0.66	5.4	97.79
OP	0.32	0.00	1.13	0.57	2.21	100.00
				Average dissimilarity = 51.15		
	Middle	**Riverine**				
ZP	4.25	1.09	14.65	1.53	31.86	31.86
ZB	5.04	2.54	12.7	1.23	27.62	59.48
DV	4.01	2.62	11.02	1.63	23.96	83.43
PV	1.53	0.31	6.34	1.30	13.78	97.22
OP	0.14	0.00	0.68	0.44	1.48	98.70
OV	0.14	0.00	0.60	0.44	1.30	100.00
				Average dissimilarity = 45.99		
	Upper	**Riverine**				
DV	5.48	2.62	12.9	1.24	31.04	31.04
ZB	4.71	2.54	11.72	1.23	28.21	59.24
ZP	2.94	1.09	9.28	1.71	22.32	81.56
PV	1.20	0.31	4.82	1.3	11.6	93.16
OP	0.41	0.00	1.85	0.74	4.45	97.61
OV	0.17	0.00	0.99	0.49	2.39	100.00
				Average dissimilarity = 41.57		

Estuarine use functional guild structures and feeding mode functional guild structures significantly differed between the two study systems (Table 4.9). However, dispersion effects were identified for the EUFG (Permdisp: F = 60.397, p(perm) = 0.0001) as well as the FMFG

(Permdisp: F = 27.033, p(perm) = 0.0001). Dispersion effects were most likely due to the variation present in the uMgeni fish assemblage, which was moderately dispersed. Similarity percentages identified that the average dissimilarity of functional groups between the estuaries (67.69%) was greater than the similarities in each estuary (Table 4.13). All guilds, contributing more than 3% to the between estuary dissimilarity, had greater abundances in the uMlalazi Estuary except FEO, which was more abundant in the uMgeni. Three marine guilds (MEO, E&M and MED) contributed a cumulative total of 82.26% to the dissimilarity of EUFG between the uMgeni and uMlalazi estuaries. Zoobenthivores, zooplanktivores and detritivores were the main feeding guilds contributing to the dissimilarity of FMFG structures (82.54%) between the uMgeni and uMlalazi estuaries.

Table 4.13 Guilds contributing towards the dissimilarity in fish assemblages between the uMgeni and uMlalazi estuaries.

	uMgeni	**uMlalazi**				
EUFG	**Av.Abund**	**Av.Abund**	**Av.Diss**	**Diss/SD**	**Contrib%**	**Cum.%**
MEO	0.36	5.20	25.61	1.72	37.87	37.87
E&M	1.63	4.01	16.45	1.41	24.33	62.20
MED	1.84	2.75	13.57	1.44	20.06	82.26
FEO	0.72	0.67	5.53	0.86	8.18	90.44
E&F	0.25	0.25	2.39	0.67	3.53	93.98
SE	0.21	0.28	2.17	0.60	3.21	97.19
MS	0.02	0.35	1.90	0.62	2.81	100.00
				Average dissimilarity = 67.63		
FMFG						
ZB	1.01	4.69	20.29	1.82	33.8	33.80
ZP	1.89	3.70	16.12	1.48	26.87	60.67
DV	1.97	3.79	13.13	1.40	21.87	82.54
PV	0.15	1.36	6.69	1.03	11.14	93.68
OV	0.20	0.32	2.33	0.62	3.88	97.56
OP	0.14	0.24	1.47	0.61	2.44	100.00
				Average dissimilarity = 60.02		

4.4.7 Linking environmental variables to biological community patterns

BEST analysis identified dissolved oxygen, temperature, turbidity and Chlorophyll-a as the most appropriate variables explaining the overall biotic patterns in the uMgeni Estuary (rho = 0.23, p = 0.003), although the assemblage correlations were not particularly strong. Marginal tests in the distance-based redundancy model (DISTLM) showed that the proportion of variation explained by the environmental variables (Table 4.14), independently of one another, was relatively low (<10 % each). Collinear variables cannot be simultaneously imputed into the DISTLM (Anderson et al., 2008); therefore, pH was excluded from the test. Sequential tests identified salinity and temperature as the most important variables explaining the biological assemblages in the uMgeni Estuary. Axes 1 and 2 explained 100% of the fitted model (Figure 4.13) and 14.3% of the total variation in the resemblance matrix. The results suggest that factors other than the measured environmental variables may be responsible for the biological community patterns.

Reach differences of the fish community in the uMgeni were best explained by salinity (dbRDA 2), with higher salinities occurring in the lower and middle reaches, decreasing toward the riverine reach (Table 4.1, Figure 4.13). Temperature was a critical factor separating communities sampled in different trips along axis 1 (dbRDA 1, Figure 4.13). Temperature was higher during Trips 2 and 3 and lowest in Trip 1 (Table 4.1). According to the DISTLM model, dissolved oxygen, Chlorophyll-a, and turbidity did not contribute significantly to the biological community structure.

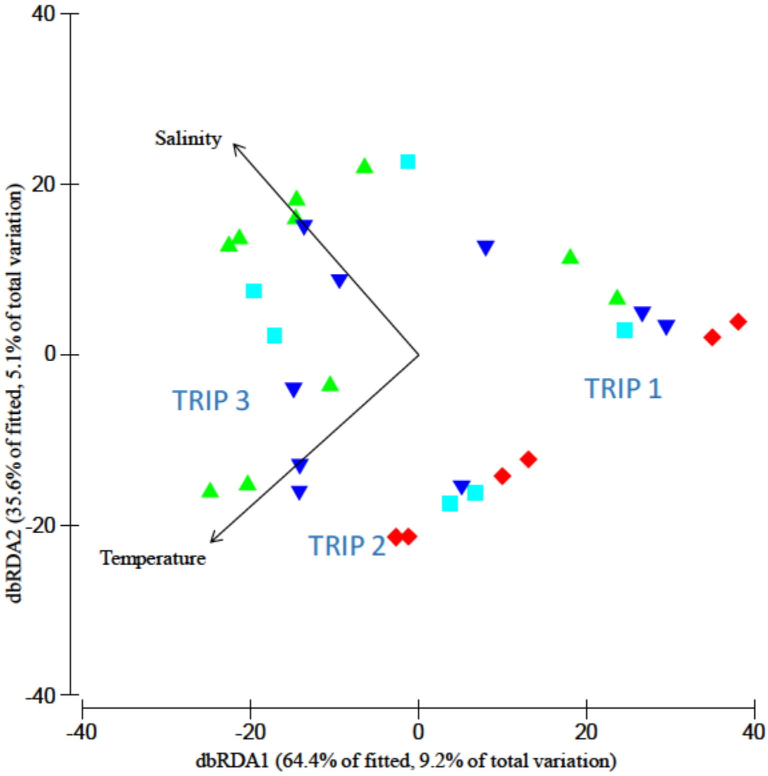


Figure 4.13 dbRDA plot of the fish community structure of the uMgeni Estuary separated by reach. Overlaid vectors are environmental variables chosen from the DISTLM model, contributing significantly to the biotic community's variation. Reaches = ▲-Lower; ▼-Middle; ■-Upper; ◆-Riverine.

Table 4.14 DISTLM results (Marginal and sequential) for the relationship between fish community structure within the uMgeni Estuary and environmental variables. Prop= proportion of variation explained. Asterisks denote significance at p<0.05.

MARGINAL TESTS					
Variable		**Prop.**	**Pseudo-F**	**P**	
Salinity		0.069	2.135	0.025*	
Temperature (°C)		0.073	2.299	0.018*	
Turbidity (NTU)		0.054	1.670	0.087	
DO (mg l^{-1})		0.041	1.259	0.246	
Chlorophyll-a (µg l^{-1})		0.047	1.436	0.167	
SEQUENTIAL TESTS					
Variable	**AIC**	**Prop.**	**Pseudo-F**	**P**	**Cum(%)**
Temperature (°C)	255.65	0.073	2.299	0.019*	
Salinity	255.23	0.070	2.272	0.019*	14.30

BEST analysis identified salinity as the most appropriate variable explaining the overall biotic patterns in the uMlalazi Estuary (rho = 0.52, p = 0.0001). Marginal tests in the distance-based redundancy model also suggested salinity explained the most significant variation in the fish community structure (18.13%), followed by dissolved oxygen (11.29%). Sequential tests identified salinity, temperature, and turbidity as the most important variables explaining the biological assemblages in the uMlalazi Estuary (30.71% cumulative total variation, Table 4.15). Axes 1 and 2 of the dbRDA plot explained 85.2% of the fitted model and 26.1% of the total variation in the resemblance matrix, providing an adequate representation of the data (Figure 4.14). The environmental variables in the uMlalazi Estuary explained more of the variation in the fish community than the uMgeni Estuary. However, other unmeasured factors may still be influential in the biological community patterns.

Differences in fish communities in different reaches were best explained by salinity (dbRDA 1), with higher salinities occurring in the lower and middle reaches (Figure 4.14). Dissolved oxygen was closely correlated with salinity. This may explain why dissolved oxygen was not considered as part of the sequential test, as it may not have altered the variation. Turbidity and temperature were influential over sampling trips, being warmer and more turbid in the lower, middle and upper reaches of Trips 2 and 3 (Table 4.1). Turbidity and temperature were more strongly associated with the lower and middle reaches along axis 2. As with the uMgeni Estuary, fish communities during Trip 1 differed from those during Trip 2 and 3. Chlorophyll-a did not contribute significantly to the biological community structure.

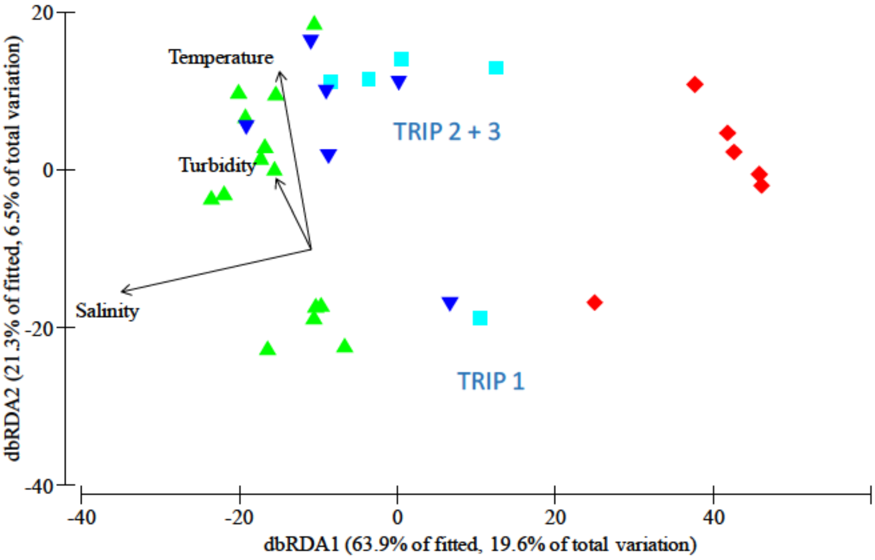


Figure 4.14 dbRDA plot of the fish community structure of the uMlalazi Estuary separated by reach. Overlaid vectors are environmental variables chosen from the DISTLM model, contributing significantly to the biotic community's variation. Reaches = ▲-Lower; ▼-Middle; ■-Upper; ◆-Riverine.

Table 4.15 DISTLM results (Marginal and sequential) for the relationship between fish community structure in the uMlalazi Estuary and environmental variables. Prop= proportion of variation explained. Asterisks denote significance at $p<0.05$.

MARGINAL TESTS			
Variable	**Prop.**	**Pseudo-F**	**P**
Salinity	0.181	6.420	0.0001*
DO (mg l^{-1})	0.113	3.692	0.0001*
Temperature (°C)	0.066	2.064	0.020*
Turbidity (NTU)	0.057	1.765	0.050*
Chlorophyll- a (µg l^{-1})	0.030	0.898	0.552

SEQUENTIAL TESTS					
Variable	**AIC**	**Prop.**	**Pseudo-F**	**P**	**Cum(%)**
Salinity	238.85	0.181	6.420	0.0001*	
Temperature (°C)	237.73	0.078	2.963	0.0001*	
Turbidity (NTU)	237.67	0.048	1.851	0.024*	30.71

Environmental variables which best explained the differences between the fish assemblages of the uMgeni and uMlalazi estuaries were salinity, dissolved oxygen, and temperature (rho = 0.36, p = 0.0001). Further permutational testing revealed that independently all variables except for chlorophyll-a explained some variation in the fish community structures (Table 4.16). Salinity was an important factor in determining fish community structures independently in both estuaries. Therefore, to prevent the dominance of this factor in differentiating the two systems fish assemblages, this variable was removed from the model.

Overall, the best solution from the model identified dissolved oxygen, turbidity and temperature as the best predictors of fish community structure variability (15.73% cumulative total variation, Table 4.16). Axes 1 and 2 of the dbRDA plot explained 87.9% of the fitted model and 13.9% of the total variation in the resemblance matrix, depicting a good representation of the data (Figure 4.15). Predictor variables that were not analysed (land-cover, nutrient concentrations) may also be responsible for assemblage differences.

Dissolved oxygen strongly separated the fish assemblage in the uMgeni Estuary from the uMlalazi Estuary along axis 1 (Figure 4.15). The uMgeni fish assemblage was associated with lower dissolved oxygen levels, whereas the uMlalazi fish assemblage was characterised by higher dissolved oxygen levels. Estuary assemblage differences were also driven by turbidity along axis 2, which was higher in the uMlalazi Estuary. The role of seasonal factors in determining fish community structures was observed. The dbRDA plot depicted the separation of samples according to trips driven by temperature differences. Winter fish assemblages for both estuaries (Trip 1) occurred primarily in the upper plot, whereas warmer spring and summer assemblages (Trip 2 and 3) occurred in the lower plot.

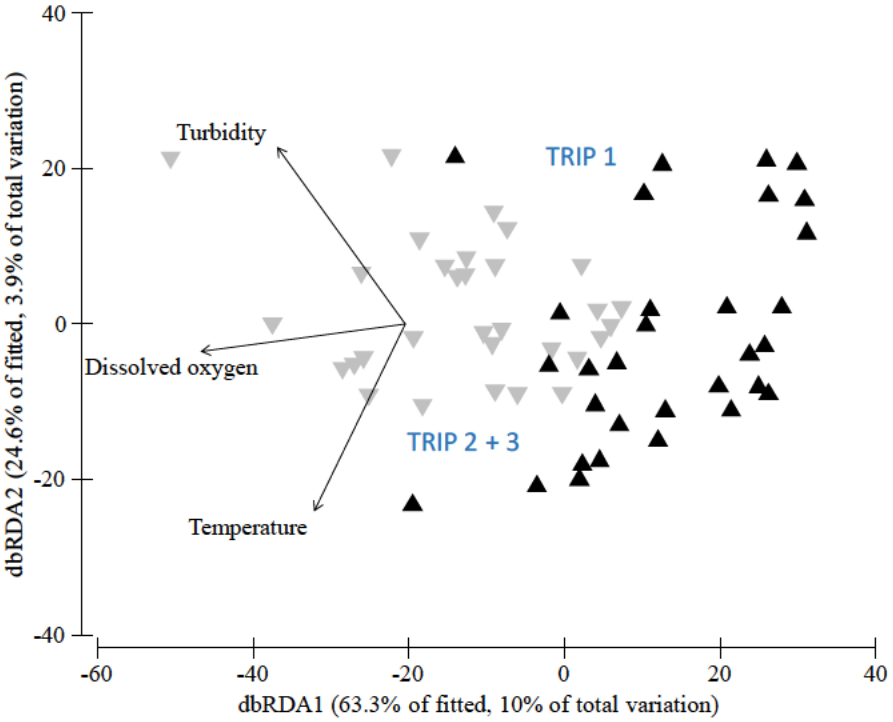


Figure 4.15 dbRDA plot of the fish community structure differences between the uMgeni (▲) and uMlalazi (▼) estuaries. Overlaid vectors are environmental variables chosen from the DISTLM model, contributing significantly to the biotic communities' variation.

Table 4.16 DISTLM results (Marginal and sequential) of the environmental variables which best differentiate the fish assemblages between the uMgeni and uMlalazi estuaries. Prop= proportion of variation explained. Asterisks denote significance at $p<0.05$.

		MARGINAL TESTS			
Variable		**Prop.**	**Pseudo-F**	**P**	
Salinity		0.079	5.168	0.0002*	
Temperature (°C)		0.040	2.473	0.002*	
Turbidity (NTU)		0.054	3.429	0.0004*	
DO (mg l^{-1})		0.073	4.742	0.0001*	
Chlorophyll-a (µg l^{-1})		0.047	1.436	0.167	
		SEQUENTIAL TESTS			
Variable	**AIC**	**Prop.**	**Pseudo-F**	**P**	**Cum(%)**
DO (mg l^{-1})	503.09	0.073	4.742	0.0001*	
Turbidity	502.04	0.045	2.982	0.0004*	
Temperature (°C)	501.2	0.039	2.272	0.002*	15.73

4.5 Discussion

As observed in several studies worldwide (Barletta et al., 2005; James et al., 2008; Kamrani et al., 2016), estuarine fish communities in the systems studied here were numerically dominated by only a few species. Compared to marine coastal systems, low species diversity results from the naturally stressed, highly variable conditions present in estuaries to which only a select few species are adapted (Elliott and Quintino, 2007).

The number of taxa recorded in the uMlalazi Estuary was twice that recorded in the uMgeni Estuary, although species richness still fell within the average range of previously sampled subtropical open estuaries (Harrison and Whitfield, 2006b). Likewise, diversity was lower in the uMgeni Estuary than in the uMlalazi. Although both estuaries are permanently open to the sea, allowing recruitment of marine associated species, differences may be influenced by estuarine area, water quality (Warry et al., 2018), habitat availability (Blaber et al., 1989) and food resources differences (França et al., 2011).

Valenti et al. (2017) proposed an urbanisation gradient role in reducing diversity, although ecological variables were essentially the determining factor. Species composition was also highly variable in an urban Australian estuary (Waltham et al., 2020). In this study, species richness was greater in the marine guilds, whereas estuarine guilds dominated in abundance. This is common in permanently open estuaries and has been identified in European estuaries (Maes et al., 2005; Nyitrai et al., 2012), Brazilian tropical Bays (Araújo et al., 2016; Ferreira et al., 2019), and South African estuaries (Whitfield et al., 1994; Vorwerk et al., 2003; Mbande et al., 2005). In contrast, marine species contribute less to species richness in temporarily open closed estuaries because recruitment opportunities into the system are limited by prolonged periods of closure (Vorwerk et al., 2003; James et al., 2008). Marine connectivity is therefore crucial in determining the species composition of an estuary, mainly through the contribution of marine species (Harrison and Whitfield, 2006b).

Marine straggler abundance was low in both estuaries and is typical of subtropical estuaries. These species are vagrants that enter estuaries in low numbers and are restricted to the lower reaches where salinities are higher (Potter et al., 2015; Whitfield, 2015). Lower densities of marine stragglers were also recorded in the Mondego Estuary (Portugal), with densities increasing during lowered precipitation periods (Nyitrai et al., 2012). Although abundances of these species are low, high species richness is generally associated with permanently open estuaries as observed in a northeastern Brazilian estuary (Ferreira et al., 2019) and two South African estuaries (Lamberth et al., 2008).

The majority of fish caught in the present study, especially those with marine associations, were juveniles. Various studies have reported dominant catches of marine estuarine opportunists and marine estuarine dependent species, all of which use estuaries as nurseries to varying degrees (Harrison and Whitfield, 2008; Selleslagh and Amara, 2008; Potter et al., 2016). Estuarine environments are favourable for juvenile fishes as they offer protection from predators, high densities of food supplies and optimum grow-out habitats (Blaber and Blaber, 1980; Vivier et al., 2010). Juvenile species that inhabit estuarine and marine inshore environments (MEOs) can be considered facultative users (Able, 2005). These species may move between estuarine and coastal environments during disturbance events to increase individual fitness (Selleslagh and Amara, 2008). Although the number of species belonging to the marine estuarine opportunist group was expected in the uMgeni Estuary, abundances were significantly reduced. The system has been heavily dammed, reducing its freshwater input and increasing salinity penetration (see Chapter 3). Naturally, marine estuarine opportunists are known to increase in abundance under such circumstances (Lamberth et al., 2008). Therefore, reduced abundances in the uMgeni may reflect reduced habitat and water quality associated with urbanisation (Whitfield and Elliott, 2002; Courrat et al., 2009).

Freshwater estuarine opportunists were relatively abundant in the uMgeni Estuary, and perhaps overly representative of what might be expected in a permanently open estuary. Instead, the contributions of these fishes to the total abundance more closely reflected closed estuaries and estuarine lakes (Harrison and Whitfield, 2008). *Oreochromis mossambicus* comprised most of the freshwater estuarine opportunists in the uMgeni Estuary and were recorded in the upper and riverine reaches. This species is usually present in estuaries with low water flow, stable salinities, sandy bottoms for nest building, high benthic floc, and few piscivorous predators (Whitfield and Blaber, 1979; de Moor, et al., 1986). *Oreochromis mossambicus* is extremely tolerant of poor water quality and can enter near-anoxic waters (Lamberth et al., 2010). Excessively high abundances of *O. mossambicus* were also recorded in the freshwater deprived St Lucia Estuary and were regarded as being indicative of an impacted system (Vivier et al., 2010). Their high relative abundance in the uMgeni Estuary, therefore, portrays the system's degraded nature.

The Mugilidae and Gobiidae families contained the highest species richness in both estuaries. Mullet species are well represented in South African estuaries (Whitfield et al., 1994; Mbande et al., 2005). Their occurrence is likely related to the year round availability of detritus and their ability to spawn over extended months, allowing greater recruitment into estuaries (Whitfield and Kok, 1992; James et al., 2008). Naturally, many Gobiidae species are estuarine residents, and their presence here was not surprising (Whitfield, 2019). Additionally, Mbande et al. (2005) hypothesised that the diversity of the Gobiidae species is testament to the colonisation of the system by species from freshwater and marine origins. More environments would therefore allow for the occurrence of a greater number of species.

The higher abundances of *L. equulus* in the uMlalazi Estuary and the near absence of the species in the uMgeni Estuary contributed the most to dissimilarities in fish communities between the two estuaries studied here. This species prefers warmer temperatures, intermediate turbidity (10 – 80 NTU), and feeds on zoobenthos (Cyrus and Blaber, 1987b). Turbidity and water temperature were higher in the uMlalazi, and previous studies have depicted a healthy, diverse zoobenthic community (Tagliarolo and Scharler, 2018). Zoobenthivores are also the first fish species affected by poor water quality (Franks and Dodds, 1997; Lamberth et al., 2010). The degraded water quality of the uMgeni Estuary has been reported in previous studies which showed reduced zoobenthos (DWA, 2011) and pollution tolerant species (Sheppard and MacKay, 2018). The absence of known subtropical zoobenthivore species may therefore reflect the effects of poor water quality and habitat degradation (refer to Chapter 3).

4.5.1 Longitudinal distribution of fishes

The present study confirmed that fish assemblages change along a longitudinal gradient. Species richness, as well as abundance, increased toward the estuary mouth. Fish assemblages were the most different between the riverine and lower reaches or upper and lower reaches. These trends have been observed in various estuaries (Neves et al., 2011; James et al., 2018; Medeiros et al., 2018) and are closely linked to salinity gradients and the occurrence of marine taxa in the lower reaches (Neves et al., 2011; Whitfield, 2019). Few species can survive in low salinities encountered in the limnetic zone (Selleslagh and Amara, 2008), resulting in the reduced abundance and species richness observed in the riverine reaches. Environmental heterogeneity is known to increase species diversity and influence the spatial distribution of fishes (Neves et al., 2011; Taddese and Closs, 2019). These heterogeneous environmental conditions in the uMlalazi Estuary produced a more distinct distribution of species, particularly for functional guilds. In comparison, the uMgeni Estuary was much less diverse in terms of habitat and physico-chemical conditions.

Trends in fish communities characterised by EUFG composition followed a similar pattern to that of species composition. This is expected considering the influence of salinity on both the study systems and follows the modified species diversity model (Remane model) proposed by Whitfield et al. (2012). The model suggests that marine species are dominant (in terms of number of taxa) in the mesohaline, polyhaline, and euhaline regions, with estuarine species most diverse in the mesohaline and polyhaline reaches (Whitfield et al., 2012). Similar results have been observed in Brazilian (Neves et al., 2011), European (Nicolas et al., 2010a) and New Zealand estuaries (Taddese and Closs, 2019). Most South African species are more adapted to lower (<5) rather than higher salinities (>65) and comprise mostly euhaline marine species (Whitfield, 2015). Therefore, it is not uncommon for marine taxa to be present in small numbers in riverine reaches as long as salinities are >3 (Whitfield et al., 2012). This was evident in the uMlalazi Estuary, where juvenile *A. vagus* (<60mm) and *P. capensis* (<60mm) were observed in the riverine and upper reaches. In contrast, most freshwater species, except for select members of the Cichlidae family, are unable to osmoregulate and are confined to oligohaline regions (Whitfield et al., 2012).

Boundaries between salinity reaches are not permanently fixed, and common species with greater salinity tolerances may overlap into freshwater or marine reaches (Jaureguizar et al., 2003). Species such as *A. gymnocephalus* and *A. natalensis* were common in more than one reach in the uMgeni Estuary, whereas *L. equulus* and *A. natalensis* were dominant in more than one reach in the uMlalazi Estuary. Of all the Ambassidae species, *A. natalensis* is most adapted to estuarine conditions (Martin, 1988), explaining its overlap within the study estuaries' reaches. *Ambassis gymnocephalus* prefer salinities above 28 and is therefore usually found in the lower reaches of permanently open estuaries (Martin, 1988). However, in the uMgeni Estuary, generally lower and variable salinities resulted in *A. natalensis* contributing more to the catch than *A. gymnocephalus*. Within the uMlalazi Estuary, higher contributions of *A. gymnocephalus* in the lower reaches reveal that the estuary is strongly influenced by tidal action and maintains a relatively stable, high salinity zone. During the study period, sampling was conducted over varying tidal ranges, which would have limited the distribution of some species, resulting in different assemblages. The result was particularly apparent in the uMgeni Estuary, which shared low similarities between fish communities in reaches. Sampling also took place over three seasons, namely winter, spring, and summer, and changes in rainfall, reproduction, and recruitment may have affected the species abundance in each estuary (Barletta et al., 2005; Nashima et al., 2021).

Detritivores dominated all reaches in the uMgeni Estuary. The lack of differences in feeding guilds between reaches suggests a detritus-based food chain (Whitfield, 2019). Detritus is an important component in all estuaries as it can often be found year round, providing a constant food source for many species (Whitfield, 2019). It is a food source that is persistent even in polluted systems. Detritus is derived from decomposing plant material transported into an estuary via river input, tidal action (seagrasses), or within estuary mangrove leaf litter (Flindt et al., 1999; Colombano et al., 2021). However, excessive nutrient input from anthropogenic activities may still create an imbalance in this detritus chain, resulting in nutrient and oxygen level fluctuations (Flindt et al., 1999).

No significant differences in feeding guild structure were observed between the uMgeni reaches, although the lower reach contained large abundances of the zooplanktivorous fish, *A. natalensis*. It is likely that *A. natalensis* was feeding on the marine derived zooplankton carried in on tidal inflow (DWA 2011), which is less polluted than freshwater inputs. Although diversity was low and feeding guild structures were relatively homogenous throughout the uMgeni, higher diversities may be present in the Beachwood Mangrove area. Mwandya (2019) documented the resilience of mangroves, reporting that disturbed sites had lower species numbers than undisturbed mangrove sites. The uMgeni's Beachwood

Mangrove Creek has also remained resilient to past pollution events, negatively affecting the system's estuarine species (Begg, 1984).

Zoobenthivores and zooplanktivores dominated the lower and middle reaches of the uMlalazi Estuary, whereas detritivores were dominant in the riverine reaches. Zooplankton densities are known to influence the distribution of zooplanktivorous fish species within estuaries (Mbandzi et al., 2018). Zooplankton diversity is fundamentally influenced by salinity, with contrasting studies revealing positive and negative relationships (Gao et al., 2008; Sutherland et al., 2013; Yuan et al., 2020). In the uMlalazi Estuary, zooplankton species richness increases along the salinity gradient, with marine taxa contributing to higher species richness at the mouth (DWS, 2015). In particular, increased densities of the ocypodid crab zoeae, *Paratylodiplax blephariskios*, in the lower reaches (DWS, 2015) may act as a primary food source for many of the zooplanktivorous fish species, allowing them to dominate the lower and middle reaches. Tagliarolo and Scharler (2018) also recorded increased macrobenthic abundances, particularly polychaetes, in the lower uMlalazi Estuary, which would serve as a food source for zoobenthivorous fish. The upper reaches of estuaries are characterised by slow moving waters where detritus and other materials from upstream may settle more easily, explaining the greater contribution of detritivores in this reach (Kaiser et al., 2011).

4.5.2 Linking environmental variables to fish community patterns

Salinity was identified as the most important variable influencing assemblage patterns in both estuaries, with various studies showing the same relationship (Barletta et al., 2005; Baptista et al., 2015; Kamrani et al., 2016; James et al., 2018). The importance of salinity in determining distributional patterns of fishes has been discussed above.

Turbidity was also proposed as an important factor affecting fish composition in the uMlalazi Estuary. The distribution of species preferring higher turbidities corresponded to results from Cyrus and Blaber (1987a). *Leiognathus equulus* and *M. cunnesius* were dominant in the more turbid middle and upper reaches of the uMlalazi Estuary. In contrast, species preferring less turbid waters such as *C. dumerili* were more dominant in the lower reaches (Cyrus and Blaber, 1987a). Turbid waters increase food availability, provide protection from predators, and assist fry in locating the estuarine area from the marine environment (Blaber and Blaber, 1980; Cyrus and Blaber, 1987a; Tigan et al., 2020). Reduced turbidity in the uMgeni Estuary may explain the reduced species diversity, although other water quality parameters are likely to have also played a role.

During the winter survey (Trip 1) of the uMgeni Estuary, waters were well-oxygenated (>5.89 mg l^{-1}) in comparison to spring (Trip 2) and summer (Trip 3) when waters were largely hypoxic (<3mg l^{-1}), indicating possible seasonal hypoxia of bottom waters. Higher temperatures and reduced windspeeds exacerbate water column stratification, resulting in the biological oxygen demand exceeding the ability of dissolved oxygen to replenish the bottom waters through mixing (Anderson and Taylor, 2001; Whitney and Vlahos, 2021). However, lowered oxygen levels in the uMgeni are more likely symptomatic of environmental degradation and pollution. Similar results were recorded in the Sundays Estuary, which is highly freshwater starved (Lemley et al., 2017). Hypoxia events are strongly correlated with allochthonous inputs of ammonia after heavy rains (Anderson and Taylor, 2001), suggesting that receiving waters to the uMgeni Estuary are high in organic matter and other contaminants associated with urban areas and wastewater treatment works (WWTW).

Although temperature was selected as a contributing variable to the fish assemblages of both estuaries, its influence was likely related to temporal factors (trip or season that the estuary was sampled) rather than spatial factors (longitudinal gradient differences). As with salinity, species may tolerate a particular temperature range (Kamrani et al., 2016). Excessively high or low temperatures compromise the metabolic rate of fishes, which affects their osmoregulatory abilities (Whitfield, 2019; Lefevre et al., 2021). Past studies have identified that endemic species such as *G. callidus*, *P. capensis* and *C. dumerili* are positively correlated with temperature, resulting in their frequent occurrence and increased abundance in subtropical estuaries (Harrison and Whitfield, 2006b). These species were present in both estuaries, although abundances were higher in the warmer uMlalazi Estuary. Although seasonal effects were not tested, fish communities during winter differed from those sampled in spring and summer. Temperature is often responsible for controlling seasonal patterns of fish assemblages and often coincides with rainfall (Wallace, 1975). On the east coast of South Africa, rainfall is higher during the warmer summer months. Nutrient-rich freshwater inputs from increased rainfall promote estuarine productivity, which is highly favourable for the recruitment of juvenile marine migrant species (Garcia et al., 2012; Whitfield, 2019; Kisten et al., 2020; Stewart et al., 2020). Recruitment patterns were evident in the present study in which juveniles were more abundant during the summer sampling trip in both estuaries.

Phytoplankton biomass in estuaries is often measured by chlorophyll-a concentrations and is strongly associated with water residence time, river discharge, flocculation, tidal exchange, and depth (Lemley et al., 2017; Odebrecht et al., 2017). Naturally, freshwater deprived estuaries contain low chlorophyll-a concentrations from reduced nutrient inputs. However, the uMgeni Estuary receives nutrient enrichment from surrounding land-cover activities. Tidal influence could therefore be limiting chlorophyll-a production in the uMgeni Estuary. On the oligotrophic KwaZulu-Natal coast, saltwater intrusion dilutes nutrient concentrations in estuaries, inhibiting nitrification and affecting nutrient uptake by phytoplankton (Niu et al., 2020). An estuary displaying a similar salinity gradient as the uMgeni found the highest chlorophyll-a concentrations where salinities were less than 10 (Kotsedi et al., 2012). Slightly higher chlorophyll-a concentrations in the riverine reach, most obvious during winter sampling, are likely linked to increased nutrient runoff from pollution sources, reduced flushing, and lower salinities, favourable for phytoplankton growth. Similar observations were noted in the water-deprived Nahoon Estuary, where nutrient concentrations increased along the salinity gradient during the winter months (Cotiyane et al., 2017).

Lower phytoplankton biomass directly affects zooplankton abundances and, subsequently, zooplanktivores in the uMgeni. Although *Gilchristella aestuaria* is usually abundant in permanently open South African estuaries, their contribution to this study's total catch was low. Reduced abundances in the uMgeni are likely related to hydrological issues mentioned above. Freshwater pulses have been deemed significant in triggering spawning evens of *G. aestuaria* (Strydom et al., 2002) and providing sufficient nutrient inputs to sustain phytoplankton and zooplankton stocks on which they feed (Allanson and Read, 1995; Adams et al., 1999). During periods of heavy rain, the estuary is subject to flash runoff from surrounding impervious surfaces, flushing zooplankton densities out to sea (Marques et al., 2007; DWA, 2011; Connelly et al., 2020). Reduced *G. aestuaria* may also indicate water column deterioration in the uMgeni Estuary, especially in the upper reaches where the species are likely to spawn (Wooldridge and Bailey, 1982). It is probable that zooplankton abundance in the polluted upper reaches do not support large abundances of *G. aestuaria* as zooplankton feeders.

In contrast, Chlorophyll-a concentrations were greatest in the middle reaches of the uMlalazi Estuary representing high biotic productivity in agreement with previous studies (DWS, 2015;

Mabaso, 2002). Higher chlorophyll-a concentrations during the spring and summer trips, coinciding with higher rainfall periods, illustrate increased nutrient availability from freshwater inflow, significantly influencing phytoplankton production. Nutrient input received from the fish farm and WWTW, situated in the middle reaches, may have also contributed to increased chlorophyll-a concentrations. During reduced freshwater inflow, high water residence time and stable physico-chemical conditions may be responsible for chlorophyll-a concentrations. The consistent food source in the uMlalazi Estuary is therefore accountable for greater zooplanktivore abundances and species richness compared to the uMgeni Estuary.

Although selected physico-chemical variables were correlated with fish distribution, the proportion of variance explained by the uMgeni Estuary was relatively low. Other factors such as vegetation type (Mbande et al., 2005), tidal exchange (Wilson and Sheaves, 2001), sedimentary characteristics (Richardson et al., 2006), habitat variability (Elliott and Dewailly, 1995), nutrient concentrations (Perkin and Bonner, 2014), food resource distribution (Whitfield 1980) or urbanisation (Osborne et al., 2021) may be responsible for the variation in the assemblage patterns. The greater proportion of variance explained in the uMlalazi Estuary suggests that the measured environmental variables more closely explain the assemblage composition, although other unmeasured variables may also be at play.

Although the DISTLM model depicted that dissolved oxygen was not important in determining the longitudinal distribution of fishes within each estuary, its role in differentiating the assemblages between the systems was highly significant. Dissolved oxygen concentrations may be influenced by temperature, mangrove presence, mixing processes or anthropogenic factors (Neves et al., 2011; Kamrani et al., 2016; Costa et al., 2017; Mattone and Sheaves, 2017; Valesini et al., 2017). The uMgeni and uMlalazi estuaries share the same biogeographically region and mouth state, influencing many of these environmental variables. Therefore, the significant difference in fish assemblages is likely a result of anthropogenic factors, namely the land-cover types surrounding each estuary (refer to Chapter 3).

The uMgeni Estuary is situated in a highly urbanised area with associated land-cover activities that contribute excessive nutrient and pollutant inputs to the system (DWA, 2011). These additions interfere with normal biological processes, resulting in reduced oxygen concentrations and the migration of fish species (Henriques et al., 2014; Costa et al., 2017; Adams et al., 2020). In contrast, the uMlalazi Estuary is largely natural and forms part of a protected area, with agricultural farming in its upper reaches (Van Niekerk et al., 2019). Reduced urbanisation and fewer associated activities have ensured good water quality and high dissolved oxygen levels. The significant differences between the two systems species richness, abundance and community structures are reflected through these water quality and land-cover influences. Chapter 5 will elaborate on these factors.

4.5.3 Conclusion

This chapter highlighted the longitudinal fish assemblage gradients in two permanently open South African estuaries, with salinity as the primary determining factor. Estuarine use functional guilds closely followed the revised Remane model (Whitfield et al., 2012), although reach overlaps were also common. In general, marine guilds occupied the lower reaches, estuarine guilds the middle and freshwater guilds the upper and riverine reaches. Longitudinal gradients in feeding mode functional guilds were only observed in the uMlalazi Estuary and were related to likely greater abundances of zooplankton in the lower estuary and detritus sinks in the middle and upper estuary. Distinct differences between fish assemblages suggest that the uMgeni and uMlalazi estuaries function differently, despite sharing similar mouth state characteristics and geographic location.

The uMgeni Estuary appeared to be less favoured by opportunistic marine species and perhaps even marine juveniles, which occurred in much lower numbers than the uMlalazi Estuary. Instead, the system currently supports high relative abundances of *O. mossambicus* and several marine estuarine dependents, particularly mullet species that feed directly on detritus food sources. In contrast, the uMlalazi Estuary supports a diverse fish assemblage with many marine opportunistic fishes and juveniles utilising the nursery function. Although detritus is an important component in the uMlalazi, energy transfers occur through the invertebrate food chain as opposed to direct detritivory as in the uMgeni. This is because zoobenthic food resources are vulnerable to environmental degradation compared to detrital food resources (Blaber et al., 1984).

These assemblage differences may have arisen from differences in mixing processes. Historically the uMgeni Estuary was a more river-dominated estuary with a limited tidal extent and a small or absent tidal delta (Cooper, 1993; Harrison et al., 2000). Subsequent to development of major dams in the catchment and water abstraction, the system experiences greater penetration of tidal saline water (DWA, 2011) and, hydrodynamically, is more similar to the uMlalazi Estuary as a permanently open estuary. However, with its large catchment, it is more freshwater dominated than the uMlalazi that maintains connectivity with the sea through tidal prisms, acts as a sink for marine sediment, is deeper further upstream, and has a well-developed flood tidal delta (Cooper, 2001). Physico-chemical parameters are also highly variable in the uMgeni and exhibit low dissolved oxygen in certain reaches compared to the uMlalazi Estuary, which is well oxygenated. Although natural estuary differences could be responsible, the role of anthropogenic pressures cannot be ignored considering the vast differences in land-cover usage surrounding each estuary.

CHAPTER 5: LONG TERM TRENDS IN FISH ASSEMBLAGES IN THE UMGENI AND UMLALAZI ESTUARIES

5.1 Introduction

Estuaries play a vital role in providing nursery grounds supporting resident and migratory fish species (Elliott and Quintino, 2007) that allows for the replenishment of marine stocks and thus influence coastal and marine fish assemblage structures (Wallace et al., 1984; Whitfield and Cowley, 2010; Vorsatz et al., 2021). These assemblages vary on daily to yearly timeframes depending on various factors such as salinity (Franco and dos Santos, 2018), temperature (Araújo et al., 2016), rainfall (Garcia et al., 2012), habitat availability (Blaber et al., 1989) and estuarine productivity (Correll, 1978). In addition to environmental factors, anthropogenic impacts alter estuarine condition and fish assemblage structures through climate change (Potter et al., 2016; Lefevre et al., 2021), overfishing (Whitfield and Cowley, 2010), water quality degradation (Ribeiro et al., 2008), aquatic food web alterations (de Jonge and Schückel, 2019) and habitat loss (Murase et al., 2017).

Habitat loss, associated with land-cover change, is a growing problem affecting more than 90% of South African estuaries and is primarily driven by human population and economic growth (McGranahan et al., 2007; Goble and van der Elst, 2013; Van Niekerk et al., 2019). Land-use/land-cover changes (LULC) alter various estuarine processes and characteristics (refer to Chapter 3 for details) (Lamberth et al., 2008; Kibena et al., 2014; Adams et al., 2016; Dala-Corte et al., 2016; Prosser et al., 2019; Dudley et al., 2020; Duque et al., 2020). Changes to estuarine water quality, from LULC changes, impact ichthyofauna community structures, species richness, diversity, and functional attributes (Wang et al., 1997; Selleslagh and Amara, 2008; Valesini et al., 2017; Flipo et al., 2020). Direct effects of land-cover change may also occur as physical barriers to migrating fishes and habitat alteration (Yi et al., 2010), reducing habitat availability for estuarine fishes (Strydom and Kisten, 2020).

Functional assessments are important when considering the responses of ecosystems or communities to anthropogenic pressures. Traditional taxonomic indices such as species richness and abundance are typically used to assess the ecological integrity of aquatic systems (O'Brien et al., 2016). However, these indices are strongly influenced by short-term environmental factors, making them highly variable, and they do not consider the functional role of species (Heino et al., 2007). Incorporating functional diversity indices in fish assemblage studies has allowed the impacts of environmental degradation at a functional guild level to be explored (Teichert et al., 2018). Typical functional groups of estuarine fishes include those based on estuary usage (Selleslagh and Amara, 2008; Ferreira et al., 2019), feeding modes (Possamai et al., 2018; Colombano et al., 2021), reproductive biology (Elliott and Dewailly, 1995; Potter and Hyndes, 1999) and body size (Waltham et al., 2020). These functional traits are more stable over long periods than typical metrics of community structure such as species richness and abundance. In the subtropics, generally, estuarine fishes exhibit high functional redundancy, with multiple fish species sharing similar functional attributes (Teichert et al., 2017; Whitfield and Harrison, 2021). Persistent species maintain key functional roles in the event of loss of species with shared functional attributes. Therefore, estuaries containing high species richness are more resilient to environmental perturbations than systems with fewer species and lower functional redundancy (Yachi and Loreau, 1999).

Phylogenetic diversity (taxonomic distinctness), in addition to traditional taxonomic and functional indices, has gained attention in community studies. Taxonomic distinctness (TD) measures incorporate the relatedness of species to one another within a community (Clarke and Warwick, 1999). They have proven robust, independent of sampling effort and are more sensitive in detecting anthropogenic disturbances than traditional taxonomic indices (Leonard et al., 2006; Can-González et al., 2021). Additionally, TD measures only require qualitative data (Clarke and Warwick, 1998, 1999), which is particularly useful for long term applications where only unstandardised data are available, and sampling effort is unknown or different (Clarke and Warwick, 1999; Rogers et al., 1999). Taxonomic distinctness measures have been employed in various studies of freshwater (Jiang et al., 2020), marine (de Azevedo et al., 2017), and estuarine (Tweedley et al., 2017; de Sousa Gomes-Gonçalves et al., 2020) fish assemblages. Impacted assemblages generally consist of closely related species, whereas un-impacted assemblages consist of less closely related species (Tweedley et al., 2017). Less taxonomically diverse assemblages are more likely to be negatively affected by environmental disturbances (Rogers et al., 1999).

Environmental disturbances are often a product of anthropogenic impacts such as altered habitats (Murase et al., 2017), hydrological manipulation (Baptista et al., 2015; Senecal et al., 2015), fishing pressure (Ferguson et al., 2013), climate change (Potter et al., 2016; Pfirrmann et al., 2021) and urbanisation (Valesini et al., 2017), which generally manifest over long time periods. For this reason, long term studies on fish assemblages are critical for detecting community changes and understanding ecosystem functioning to assist in effective environmental management (Ferguson et al., 2013; Araújo et al., 2016). These datasets are also valuable in determining if disturbances (natural or anthropogenic) result in community assemblage changes or if there is community resilience to change (Schrandt and MacDonald, 2020). For example, a study conducted on the Montego Estuary from 1988-2012 identified shifts in the fish community structure in response to human-induced hydrological manipulations (Baptista et al., 2015). In this instance, fish communities were unable to remain resilient to anthropogenic disturbances resulting in community changes.

Few studies have assessed the long term fish assemblage trends in subtropical South African estuaries (Van Niekerk et al., 2019). This is largely due to the lack of an appropriate "reference condition" and long term quantitative time-series data (Gatti et al., 2015), which may be overcome through the analytical approaches mentioned above. These studies are essential in addressing shifting baseline syndrome. Incorporating functional and phylogenetic indices in determining estuarine health may be more robust than traditional community metrics holding greater conservation importance, particularly when assessed on a long term scale (Elliott and Quintino, 2007). This chapter will contribute to understanding long term patterns of estuarine ichthyofauna at the taxonomic, functional and phylogenetic levels as outlined in the aims and objectives below:

5.2 Aims, Objectives and hypotheses

This chapter aimed to identify and compare long term patterns of fish assemblage change (species richness, functional, and TD) in the urban (uMgeni) and the rural, non-urban (uMlalazi) estuaries. Land-cover change and water quality trends investigated in Chapter 3 were analysed with fish assemblage changes to reveal any relationships.

Objectives

- In each estuary:
    - To identify changes in fish assemblages and functional guilds over time.
    - To investigate whether taxonomic distinctness indices are comparable to species richness and functional indices.
    - To identify relationships between land-cover, physico-chemical water quality variables and fish diversity.

- To compare changes in land-cover, water quality and fish assemblages in the uMgeni and uMlalazi estuaries.

Null Hypotheses

- Within an estuary, fish assemblages did not change over time according to the study periods.
- Within an estuary, functional guilds did not change over time according to the study periods.
- Fish community health (as reflected by diversity and TD) does not decline with increased anthropogenic pressure over time (as reflected by land-cover change).
- Changes in fish diversity are not correlated with changes in physical-chemical variables over time.

5.3 Materials and methods

General descriptions of the study estuaries, sampling approaches, historical data sources and statistical procedures can be found in Chapter 2.

5.3.1 Data acquisition

Land-cover and water quality data from Chapter 3, current fish assemblage data from Chapter 4 and newly introduced historic fish data were integrated in this chapter. Land-cover imagery was obtained from the National Geo-Spatial Information repository and used for classification against modified land-cover classes, specifically to the 20 m estuary contour. Classifications of polygons occurred at three hierarchical levels and were recorded as a percentage of the total area (see Chapter 3 for details). Level One, the lowest order of detail, classified an area as being natural, disturbed, or transformed. Level Two included eight higher-order classifications: cultivated, managed vegetation, artificial, waterbodies, bare, wetland, vegetation, and waterways. Level Three, the most detailed descriptor of land-cover types, included 29 classes that fall within the higher-order classifications.

Historical ichthyofauna and water quality data, together with data generated by field sampling conducted for this study in 2019 (Chapter 4), were used to analyse historical fish trends. Water quality and ichthyofauna estuarine data were taken from various sources (published and grey literature). Physico-chemical data included measures of depth (m), temperature (°C), salinity, dissolved oxygen (mg l^{-1}), turbidity (NTU), and chlorophyll-a (µg l^{-1}). A full spectrum of sources and data types can be found in Chapter 2. Alien fish species were removed but still noted from the historical analysis as their inclusion would contribute counter intuitively to diversity. Nomenclature was standardised to deal with taxonomic changes over the years, and, in some cases, species were grouped at genus level to deal with likely taxonomic inconsistencies. For example, gobies of the genus *Glossogobius* have not been consistently dealt with by various researchers, and all species in this genus were aggregated to *Glossogobius* spp. In most cases, published literature only presented species presence and not abundance data. Therefore, the analysis of historical ichthyofauna was conducted only on presence/absence data. The total species observed during a collection was taken as one sample. Each fish species was also assigned an Estuarine use functional guild (EUFG) and Feeding mode functional guild (FMFG) to identify any functional changes over time (see Chapters 1 and 4 for details).

5.3.2 Statistical analysis

To identify significant changes in fish communities over time, samples were categorised into periods. Land-cover groupings (identified in Chapter 3) were chosen as the "period" factor based on literature which suggested that major changes in land-cover correspond with changes in water quality and estuarine biota (Le Pape et al., 2007; Valesini et al., 2017). Period 1 represented all samples before 1989, whereas Period 2 samples occurred during and after 1989. Period 2 was extended to include the 2019 fish survey. To account for time correlations between the variables, linear interpolation was employed to correspond physico-chemical data points with land-cover data points. Water quality data points often proceeded the years in which land-cover data points occurred, accounting for time lags in environmental effects. Corresponding years were matched between water quality data and fish assemblage data based on known direct relationships between these variables (Hua, 2017). Lags could not be tested because of the small sample size of fish assemblages which would have resulted in a loss of earlier samples. To investigate whether fish assemblages had similar period groupings as land-cover derived periods, a similarity profile (using group averages, 1000 permutations and 999 simulations to calculate the departure statistic) and nonmetric multidimensional scaling plot (nMDS) was performed.

5.3.2.1 Univariate analysis

Some of the most common univariate diversity indices include the Shannon-Weiner diversity index (H'), Margalef's index (d), Pielou's Evenness index (J'), and the Simpson's index (λ) (Clarke and Warwick, 2001b). However, these indices are sensitive to varying degrees of sampling effort (Clarke and Warwick, 2001b; Clarke and Gorley, 2006), which render them inappropriate for use in long term studies where sampling efforts are variable. Moreover, they rely on some measure of abundance and therefore need quantitative data. To accommodate these sensitivities in the current study, taxonomic distinctness (TD) measures were used to analyse historical fish community data using Marine Ecological Research Software (PRIMER Version 6.0.3). These indices work on the principle that species may be taxonomically more closely or distantly related (according to the Linnaean classification) (Rogers et al., 1999). Generally, an assemblage with closely related species can be regarded as less diverse than an assemblage with more distantly related species (Clarke and Warwick, 2001b). Taxonomic distinctness measures have proven robust, independent of sampling effort and only require qualitative data (Clarke and Warwick, 1998, 1999; Leonard et al., 2006; Can-González et al., 2021). Two taxonomic biodiversity indices were computed:

The average taxonomic distinctness (AvTD, Δ^+) simplifies the taxonomic distinctness measure, which observes the average path length between two randomly chosen species in a sample, i.e. how closely related two species are to one another (Equation 5.1). This test is explicitly used for presence/absence data.

$$\Delta^+ = \left[\sum\sum_{i<j} \omega_{ij}\right] / [S(S-1)/2] \qquad (5.1)$$

The variation in taxonomic distinctness (VarTD, Λ^+) assesses the variability between pairwise distinctness weights, which make up the average distinctness (Equation 5.2). It represents the evenness of the distribution of taxa in the taxonomic tree (Clarke and Warwick, 2001b).

$$\Lambda^+ = \left[\sum\sum_{i<j} (\omega_{ij} - \Delta^+)^2\right] / [S(S-1)/2] \qquad (5.2)$$

Where (S) is species and ω_{ij} is the "distinctness weight", which links individuals *i* and *j* in the hierarchical classification (Clarke and Warwick, 1998; Rogers et al., 1999). Lowered AvTD and corresponding lowered VarTD values indicate a reduction in the number of higher order taxa with many taxa still represented in the lower orders (e.g., at the species level). In contrast, higher AvTD and corresponding elevated VarTD values may represent an assemblage which maintains its higher order taxa (e.g., order level) but which has a combination of well represented lower order taxa (e.g., at the species level) and poorly represented taxa (Clarke and Warwick, 2001b). Four taxonomic levels were included, namely species, genus, family, and order. Branch lengths were set to $W_k^{(1)}$, corresponding to increasing constant step lengths, with a standardised final step length of 100. Univariate diversity testing was run on total species (referred to in this chapter as species richness), AvTD, and VarTD using a T-test in SigmaPlot Version 12.5. If the assumptions of normality or equal variance failed, a Mann-Whitney U non-parametric test was performed. The same procedure was applied for within estuary data to test for differences between periods. These periods were determined via land-cover SIMPROF groups (Period 1=1937-1988, Period 2=1989-2018) defined in Chapter 3.

5.3.2.2 Taxonomic distinctness test

A Taxonomic distinctness test (TAXDTEST) was performed in PRIMER. The theory is that the AvTD or VarTD of a sub list does not differ from the taxonomic distinctness of the master list (Clarke and Warwick, 2001b). In this case, each sub list comprised all species recorded in a sample. For the purposes of this study, the species master list was taken from the work of Harrison et al. (2000), who derived representative fish communities for all South African estuaries based on their location in biogeographic areas and geomorphology. The expected average taxonomic distinctness and the observed AvTD were displayed as a funnel plot, with expected AvTD represented as 95% confidence intervals (Clarke and Gorley, 2006). Any samples plotted outside these confidence limits represented a deviation (decrease or increase) from the expected diversity (Clarke and Gorley, 2006). Likewise, the expected variation in taxonomic distinctness and the observed VarTD were displayed as a funnel plot, with expected VarTD represented as 95% confidence intervals. According to the known species pool, samples containing taxa that are over-represented or under-represented are plotted outside of the confidence limits and represent an unevenness in the distribution of taxa in the taxonomic tree.

5.3.2.3 Multivariate analysis

A Sorensen resemblance matrix was constructed as recommended for presence/absence species data (Clarke and Gorley, 2006) and was the input for further multivariate testing. Ordination plots (nMDS and CAP) were run to confirm *a priori* period groups defined in Chapter 3. A two-way PERMANOVA was performed with factors ‘estuary’ and ‘period’ (nested in ‘estuary’) using unrestricted permutations of raw data. Estuary differences were confirmed by assessing the sample dispersion (PERMDISP). Detailed explanations on PERMANOVA choices and PERMDISP are presented in Chapter 2. A similarity percentage (SIMPER) routine was used to identify species responsible for estuary and period differences based on the average species frequency of occurrence.

Functional group analyses were performed on species data to identify possible functional changes in each estuary over time. Species were summed across each sample to produce the total number of species occurring in each guild, per sample. This was performed for the estuarine use functional group (EUFG) and the feeding mode functional group (FMFG) analyses. A Nonmetric multidimensional scaling plot (nMDS) was used to visualise the *a priori* determined period groups based on the Bray-Curtis similarity matrix. Bray-Curtis measures were employed instead of Sorensen resemblance matrix as the number of species occurring in each guild, per sample was assessed instead of only the presence/absence of a guild in each sample. A two-factor PERMANOVA test and SIMPER analysis were run as described for the species presence/absence data above.

5.3.2.4 The relationship between historical biological data and predictor variables

Correlation analyses were used to reveal any relationships between diversity indices and physico-chemical variables, and diversity indices and land-cover classes over time (SigmaPlot version 12.5). Mean annual physico-chemical values and non-meaned annual land-cover data determined in Chapter 3 were correlated with diversity indices recorded in the same, or the closest year. Most land-cover variables were not normally distributed even after a 4th root or log transformation, therefore, a Spearman’s rank correlation was performed. Further simple linear regression analyses were performed on selected physico-chemical variables that met the regression analysis assumptions: normal distribution, independence of residuals, and constant variance of residuals.

Distance-based linear models (DISTLM) were used to identify combinations of predictor variables correlated to the diversity indices (refer to the explanation in Chapter 2). Significance values obtained from DISTLM were based on permutations, thus avoiding the assumption that errors are normally distributed (Anderson et al., 2008). Individual diversity indices were represented with a Euclidean distance matrix which produces R^2 values and F ratios equivalent to multiple regression and suitable for univariate indices (Anderson et al., 2008). Predictor variables represented via Euclidean distance included physico-chemical (dissolved oxygen (mg l^{-1}) and salinity) and land-cover variables (T-Artificial, N-Wetland, N-Bare and N-Waterbodies) which showed strong correlations with diversity and did not exhibit collinearity.

5.4 Results

5.4.1 Factor: period

Ordination identified broad groups of fish assemblages for the uMgeni Estuary (represented as dotted lines, Figure 5.1) at 51.67% similarity (pi = 2.68, p = 0.02). Fish assemblages in 1979 and 1987 were more similar to the fish assemblages of 1985 and 1986 (although still significantly different) than those from and after 1989. These fish assemblage broad groups conformed to the land-cover period groups of Period 1=before 1989, Period 2=during and after 1989. Throughout the chapter, these periods were used to represent fish assemblage changes over time and relationships with predictor variables. Although broad fish assemblage groups were evident in the ordination plot, statistical significance between groupings were only seen at 59.83% similarity as shown by SIMPROF testing (pi = 1.78, p = 0.031). Groups I and II were fish assemblages from 1979 and 1987, and group III comprised the assemblage years 1985 and 1986. Groups IV and V appeared closely clustered together in the nMDS, but were still significantly different and were representative of fish assemblages sampled from 1989 to the present.

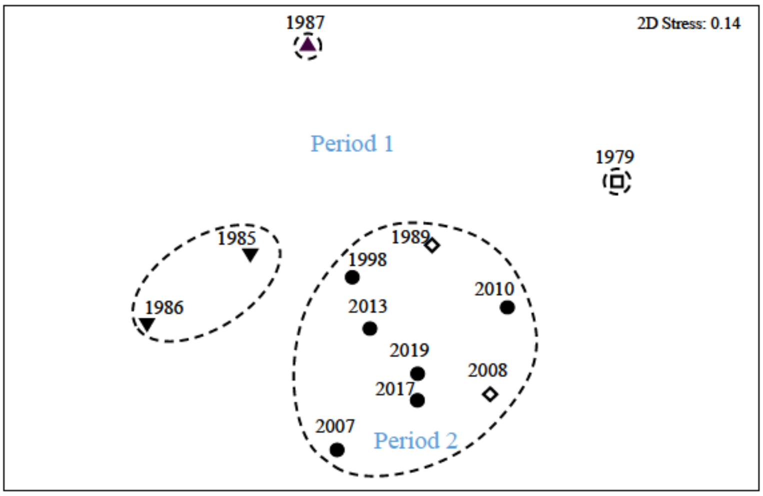


Figure 5.1 nMDS of historic fish assemblage samples for the uMgeni Estuary according to SIMRPOF cluster groups. Dotted line represents broader group similarities at 51.70%. Land-cover periods are overlayed (Period 1 and Period 2). Statistically significant SIMPROF groups at 59.83% similarity represented as symbols: Group 1=□, Group II=▲, Group III=▼, Group IV=◇, Group=●.

Four fish assemblage groups for the uMlalazi Estuary were identified at 64.08% similarity (pi = 1.70, p = 0.01) (Figure 5.2). Groups I and II were significantly different from group IV (Figure 5.2) according to SIMPROF testing. An nMDS subset showed that assemblage III separated distinctly from Group IV, although having seemed initially very similar (nMDS subset, Figure 5.2). Group IV fish assemblages, representing fish communities during and after 1989, were not significantly different from one another. In order to achieve a more balanced distribution of data points for further temporal analyses, samples from Groups I, II and III were assigned into Period 1 (before 1989), whereas the non-significantly different samples from Group IV were assigned into Period 2 (during and after 1989).

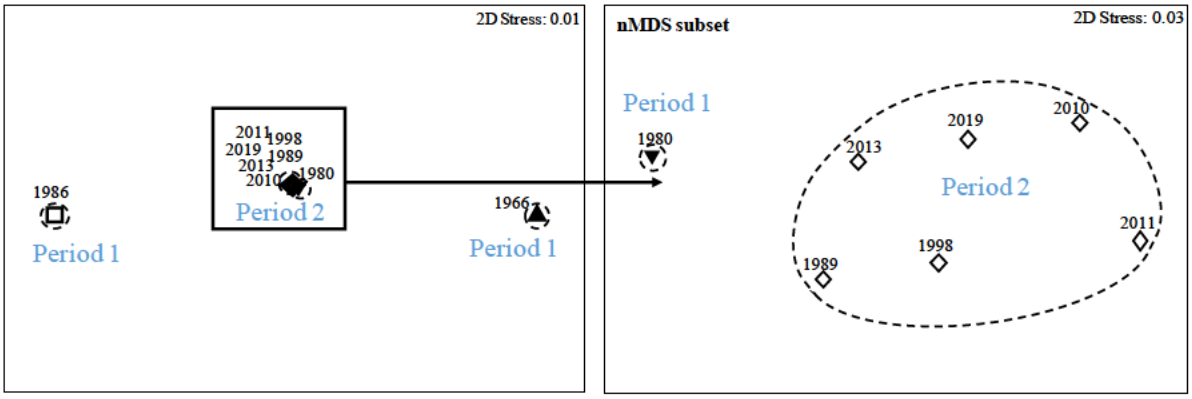


Figure 5.2 Names and nMDS subset of historic fish assemblage samples for the uMlalazi Estuary according to SIMRPOF cluster groups. Land-cover periods are overlayed (Period 1 and Period 2). Statistically significant SIMPROF groups at 64.08% similarity represented as dotted lines and symbols: Group 1=▲, Group II=□, Group III=▼, Group IV=◇.

5.4.2 Historic taxonomic composition

A total of 92 fish taxa have been recorded in the uMgeni Estuary to date. In contrast, 112 taxa have been recorded in the uMlalazi Estuary. Mean species richness increased from Period 1 to Period 2 in the uMlalazi Estuary (46.67 ± 21.50 to 50.50 ± 7.08 taxa, Figure 5.3). Although species richness in the uMgeni Estuary has only dropped slightly in Period 2 (29.25 ± 9.00 taxa, Figure 5.3), high variability between samples in Period 1 reduced the mean species richness (29.75 ± 18.23 taxa, Figure 5.3). Only three taxa were present in all uMgeni samples, all from the Mugilidae family: *Moolgarda cunnesius*, *Mugil cephalus,* and *Planiliza macrolepis* (Table 5.1). In contrast, 12 species were consistently present in all uMlalazi samples from 10 different families. Species represented were *Ambassis ambassis*, *Ambassis gymnocephalus*, *Arothron immaculatus*, *Chelon dumerili*, *Glossogobius* spp., *Leiognathus* *equulus*, *Moolgarda cunnesius*, *Platycephalus indicus*, *Pomadasys commersonnii*, *Sphyraena barracuda*, *Terapon jarbua* and *Thryssa vitrirostris*.

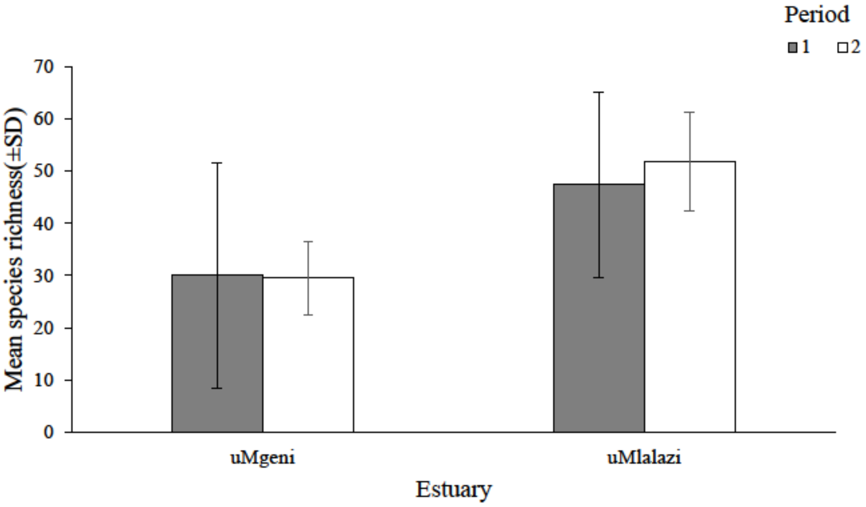


Figure 5.3 Mean species richness ± SD for Periods 1 and 2 in the uMgeni and uMlalazi estuaries.

Table 5.1 The number of fish species occurrences, per period in the uMgeni and uMlalazi estuaries. Estuarine use functional and feeding guilds indicated. Shading denotes species present in all samples of each period. Period 1= Before 1989, Period 2= During and after 1989 (n=number of datasets in each period).

			uMgeni		uMlalazi	
Taxa	**EUFG**	**FG**	**Period 1 (n=4)**	**Period 2 (n=8)**	**Period 1 (n=3)**	**Period 2 (n=6)**
Acanthopagrus vagus	MED	ZB	4	5	2	6
Ambassis ambassis	E&M	ZP	1	8	3	6
Ambassis gymnocephalus	E&M	ZP	1	5	3	6
Ambassis natalensis	E&M	ZP	3	6	2	6
Amblyrhynchotes honckenii	MEO	ZB	3	4	2	4
Antennarius hispidus	MS	PV	0	0	1	0
Antennarius maculates	MS	PV	1	0	0	0
Argyrosomus japonicas	MED	PV	3	2	2	3
Arothron hispidus	MEO	ZB	2	1	2	1
Arothron immaculatus	MEO	PV	2	3	3	6
Atherinomorus lacunosus	MEO	ZP	0	0	0	1
Awaous aeneofuscus	FEO	ZB	0	2	0	1
Bathygobius laddi	MEO	ZB	0	1	0	0
Bothus pantherinus	MS	ZB	1	0	1	2
Butis butis	SE	ZB	1	0	0	0
Caffrogobius natalensis	E&M	ZB	1	1	1	0
Callionymus marleyi	MS	ZB	1	0	0	0
Cantherhines pardalis	MS	ZB	0	0	1	0
Caranx heberi	MS	PV	0	2	1	3
Caranx ignobilis	MEO	PV	1	1	2	5
Caranx papuensis	MEO	PV	0	0	0	3
Caranx sexfasciatus	MEO	PV	1	6	2	6
Chaetodon sp.	MS	OP	0	0	1	0

			uMgeni		uMlalazi	
Taxa	**EUFG**	**FG**	**Period 1 (n=4)**	**Period 2 (n=8)**	**Period 1 (n=3)**	**Period 2 (n=6)**
Chelon dumerili	MED	DV	3	7	3	6
Chelon richardsonii	MEO	DV	1	0	1	0
Chelon tricuspidens	MEO	DV	1	1	1	4
Chelonodon laticeps	MS	ZB	0	2	2	4
Clarias gariepinus	FEO	OP	1	3	0	1
Coptodon rendalli	FS	HV	0	2	0	0
Crenidens crenidens	MS	HV	0	0	1	0
Diplodus sargus	MEO	OV	0	1	0	0
Drepane longimana	MS	ZB	1	0	1	2
Eleotris fusca	SE	ZB	1	0	2	0
Eleotris mauritiana	SE	ZB	0	1	0	0
Elops machnata	MED	PV	3	3	2	3
Engraulis japonicas	MS	ZP	0	0	0	1
Epinephelus andersoni	MS	ZB	1	0	1	0
Epinephelus coeruleopunctatus	MS	ZB	0	0	1	0
Epinephelus irroratus	MS	ZB	0	0	1	0
Epinephelus lanceolatus	MS	ZB	0	0	1	0
Epinephelus malabaricus	MS	ZB	0	1	0	4
Epinephelus marginatus	MS	ZB	0	0	1	0
Epinephelus tauvina	MS	ZB	0	0	1	0
Favonigobius melanobranchus	E&F	ZB	1	0	0	0
Favonigobius reichei	E&F	ZB	1	3	0	0
Fistularia petimba	MS	PV	1	0	0	0
Gazza minuta	MEO	ZB	0	1	0	1
Gerres filamentosus	MEO	ZB	0	3	1	6
Gerres longirostris	MEO	ZB	0	3	1	4
Gerres methueni	MEO	ZB	2	6	1	6
Gerres oyena	MEO	ZB	0	0	0	1
Gilchristella aestuaria	SE	ZP	1	4	0	6
Glossogobius spp.	E&F	ZB	3	8	3	6
Hemiramphus far	MEO	ZP	0	0	1	0
Herklotsichthys quadrimaculatus	MS	ZP	0	3	0	2
Hilsa kelee	MEO	ZP	1	0	1	6
Himantura uarnak	MEO	ZB	0	0	2	3
Hippichthys heptagonus	E&M	ZP	1	0	0	0
Hippichthys spicifer	E&M	ZP	0	0	1	1
Johnius dussumieri	MEO	ZB	1	0	0	0
Leiognathus equulus	MEO	ZB	2	7	3	6
Lichia amia	MED	PV	1	1	1	1
Lobotes surinamensis	MEO	ZB	1	0	0	0
Lutjanus argentimaculatus	MEO	PV	1	1	1	4
Lutjanus fulviflamma	MEO	ZB	1	1	2	2
Maculabatis gerrardi	MEO	ZB	0	1	0	1
Megalops cyprinoides	MED	PV	0	1	0	2
Mene maculate	MEO	ZB	0	0	1	0
Monodactylus argenteus	MEO	ZP	1	0	1	6
Monodactylus falciformis	MED	ZP	2	1	1	2
Moolgarda buchanani	MEO	DV	3	3	2	4
Moolgarda cunnesius	MED	DV	4	8	3	6
Moolgarda robusta	MED	DV	2	6	1	3
Moolgarda seheli	MEO	DV	0	1	1	4
Mugil cephalus	MED	DV	4	8	1	4
Muraenesox bagio	MEO	PV	0	0	2	0
Oligolepis acutipennis	SE	ZB	1	6	1	2
Oligolepis keiensis	SE	ZB	0	6	0	3

			uMgeni		**uMlalazi**	
Taxa	**EUFG**	**FG**	**Period 1 (n=4)**	**Period 2 (n=8)**	**Period 1 (n=3)**	**Period 2 (n=6)**
Oreochromis mossambicus	FEO	DV	1	6	0	4
Oxyurichthys opthalmonema	SE	ZB	0	0	1	0
Pelates quadrilineatus	MEO	OP	0	0	1	0
Pisodonophis boro	MEO	ZB	0	0	1	0
Planiliza alata	MED	DV	3	4	2	6
Planiliza macrolepis	MED	DV	4	8	2	6
Planiliza melinopterus	MEO	DV	0	1	0	3
Platycephalus indicus	MEO	PV	4	4	3	6
Plectorhinchus gibbosus	MS	ZB	2	1	0	0
Polydactylus plebeius	MS	ZB	0	0	1	0
Pomacentridae sp.	MS	OV	0	0	1	0
Pomadasys commersonnii	MED	ZB	3	8	3	6
Pomadasys kaakan	MEO	ZB	3	1	2	4
Pomadasys maculates	MEO	ZB	1	0	0	0
Pomadasys multimaculatus	MEO	ZB	1	0	0	1
Pomadasys olivaceus	MEO	ZB	0	0	0	1
Pomatomus saltatrix	MEO	PV	0	1	3	3
Psammogobius biocellatus	SE	ZB	1	0	0	1
Psammogobius knysnaensis	E&M	ZB	1	2	0	0
Pseudomyxus capensis	MED	DV	3	8	2	6
Pseudorhombus arsius	MS	ZB	2	1	3	4
Psuedocrenilabrus philander	FS	ZB	0	1	0	0
Pterois miles	MS	PV	0	0	2	3
Rhabdosargus holubi	MED	OV	3	8	1	5
Rhabdosargus sarba	MEO	ZB	1	5	1	6
Rhabdosargus thorpei	MEO	OV	0	0	1	1
Sardinella albella	MS	ZP	0	0	1	0
Scomberoides lysan	MEO	PV	0	1	1	6
Scomberoides tala	MEO	PV	1	0	1	1
Scomberoides tol	MEO	PV	0	1	1	1
Sebastapistes strongia	MS	PV	0	0	1	0
Secutor insidiator	MEO	ZP	1	0	0	1
Siganus sutor	MS	OV	0	0	2	0
Silhouettea sibayi	E&F	ZB	0	0	0	3
Sillago sihama	MEO	ZB	1	3	2	6
Solea turbynei	MED	ZB	3	8	3	6
Sphyraena barracuda	MEO	PV	0	1	1	4
Sphyraena jello	MEO	PV	0	1	2	5
Sphyraena qenie	MS	PV	1	0	1	3
Stethojulis sp.	MS	ZB	0	0	1	0
Stolephorus holodon	MEO	ZP	1	1	1	4
Stolephorus indicus	MEO	ZP	0	0	0	3
Strongylura leiura	MEO	PV	0	0	1	0
Strophidon sathete	MEO	PV	1	0	1	0
Syngnathus acus	E&M	ZP	0	0	0	1
Taenioides jacksoni	E&M	ZB	1	0	0	0
Terapon jarbua	MED	OP	2	8	3	6
Thryssa setirostris	MEO	ZP	0	0	0	2
Thryssa vitrirostris	MEO	ZP	1	0	3	6
Trachinotus blochii	MEO	ZB	0	0	1	0
Trachinotus botla	MS	ZB	0	0	1	0
Trichiurus sp.	MEO	PV	0	0	1	0
Upeneus vittatus	MS	ZB	0	0	1	3
No of samples			**4**	**8**	**3**	**6**
No of species			**69**	**68**	**90**	**83**

The percentage contribution (by number of species) of marine estuarine dependents (MED) has been highly variable within the uMgeni Estuary, with the greatest contributions occurring in 2008 (47.43%). More distinct decreases in the contribution of marine estuarine opportunists (MEO) and marine stragglers (MS) were observed over time (Figure 5.4a). In contrast, estuarine and marine (E&M), freshwater estuarine opportunists (FEO), solely estuarine (SE), estuarine and freshwater (E&F), and freshwater stragglers (FS) have increased over time. Feeding guilds have remained relatively constant in the uMgeni Estuary, except for the inclusion of herbivores (HV) in 2010 and 2017. Piscivores (PV) displayed the greatest decreases over time (Figure 5.4b).

Fish assemblages of the uMlalazi Estuary have been dominated by marine guilds (Figure 5.4a). Guilds that showed the greatest increases over time included the MEOs, and FEOs. The greatest decrease was among the MS from 23.08% in 1966 to 15.52% in 2019. Feeding guilds in the uMlalazi Estuary were relatively similar over time except for slight increases in ZPs (Figure 5.4b). Detritivore contributions were lowest during 1966 and highest in 1986 and 1989. More recent changes display an increasing trend for detritivores. Percentage contribution of opportunistic feeders was highest in 1966 (5.66%) and has declined since to between 1.5-4%.

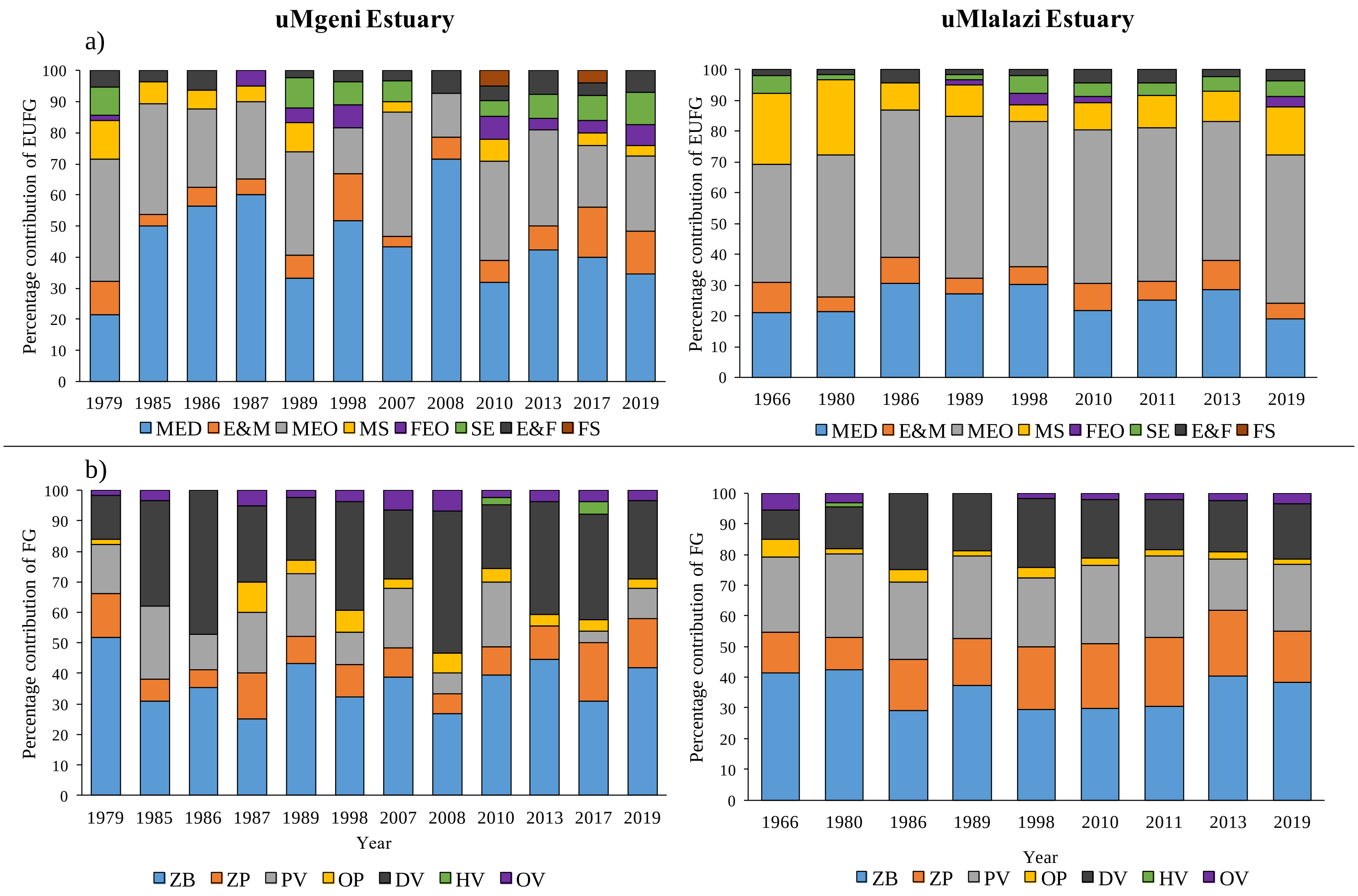


Figure 5.4 Average percentage contribution over time of a) estuarine use functional groups and b) feeding mode functional groups in the uMgeni and uMlalazi estuaries.

5.4.3 Univariate analysis

Fish species richness (t = -0.065, df = 10, p = 0.987), average taxonomic distinctness (t = 1.296, df = 10, p = 0.224), and variation in taxonomic distinctness (t = 0.07, df = 10, p = 0.945) did not differ significantly between Periods 1 and 2 in the uMgeni Estuary (Figure 5.5). No significant differences were found in fish species richness (Mann-Whitney Rank Sum test: U statistic = 8.5, p = 0.905), average taxonomic distinctness (t = 1.592, df = 7, p = 0.155), or variation of taxonomic distinctness (Mann-Whitney Rank Sum test: U statistic = 2, p = 0.095) between Periods 1 and 2 in the uMlalazi Estuary (Figure 5.5). High variability of fish assemblages, particularly in Period 1, in both estuaries, is likely responsible for the lack of significance. In a comparison between the uMgeni and uMlalazi estuaries, species richness (t = - 3.728, df = 19, p = 0.001), the average taxonomic distinctness (t = -2.712, df = 19, p = 0.014) and variation in taxonomic distinctness (Mann-Whitney Rank Sum: U statistic = 8, p = 0.001) were significantly different.

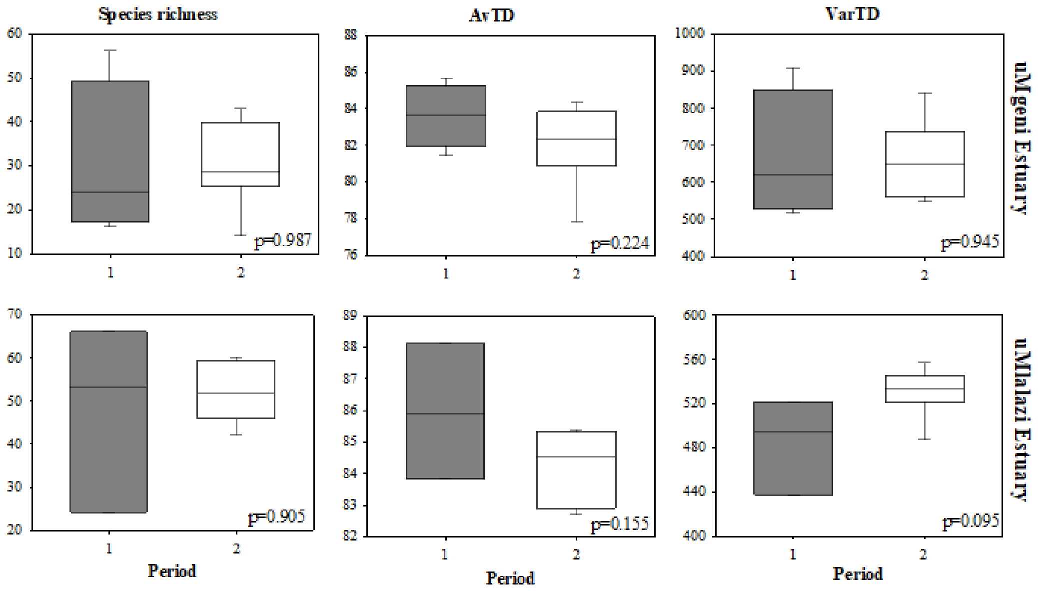


Figure 5.5 Boxplots of species richness, average taxonomic distinctness, and variation in taxonomic distinctness of fish assemblages in Periods 1 and 2 for the uMgeni and uMlalazi estuaries. Bands on the top, middle and bottom of each boxplot represent the 75th, 50th and 25th percentile, respectively. Whiskers represent minimum and maximum values.

5.4.4 Taxonomic distinctness analysis

All uMgeni and uMlalazi samples fell within the 95% confidence limits of the AvTD (Figure 5.6a). Most uMlalazi samples occurred above the theoretical mean value, whereas many uMgeni samples fell below the theoretical mean. The 2008 uMgeni sample occurred the furthest away from the theoretical mean with an AvTD of 77.8. All uMgeni samples except for 1979, 1987, and 2007 occurred above the confidence limit of the funnel plot for the VarTD (Figure 5.6b). In contrast, uMlalazi samples fell within the confidence limits for the VarTD and occurred primarily around the theoretical mean. uMgeni fish assemblages, particularly in 1986, 2008, and 2013, showed the greatest unevenness in the taxonomic spread, whereas the 1979 sample had the greatest evenness (Figure 5.6b).

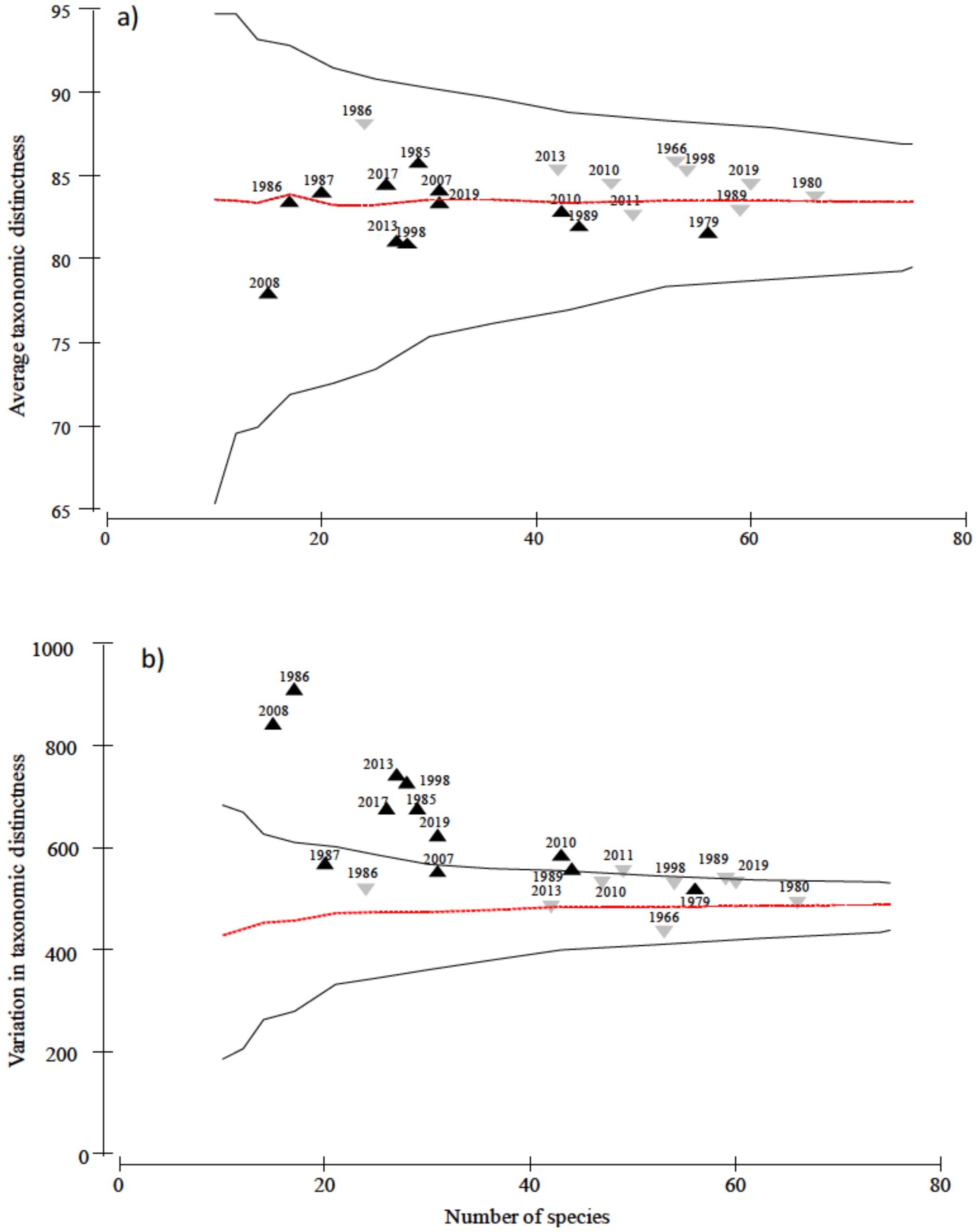


Figure 5.6 Funnel plots for the a) average taxonomic distinctness and b) variation in taxonomic distinctness of uMgeni and uMlalazi fish species lists, from different years, with weighted steps. The red dotted line is the expected mean taxonomic distinctness for the full master list (all permanently open subtropical estuaries). Solid lines are 95% confidence limits for the random selections from the master list. Samples occurring outside of these lines are deviations from the expected mean diversity. ▲=uMgeni, ▼= uMlalazi

5.4.5 Multivariate community analysis

To ensure *a priori* group patterns were represented as Period 1 (pre-1989) and Period 2 (1989 to recent), a canonical analysis of principal coordinates (CAP) was performed (Figure 5.7). A total of 80.95% of the variation in the original matrix was represented, exceeding the minimum suggested percentage of 60% (Anderson et al., 2008). Statistical PERMANOVA testing showed that fish assemblages were different between periods (PERMANOVA: df = 2, Pseudo-F = 1.986, p (perm) = 0.014, Table 5.2). These differences primarily occurred between uMgeni Period 1 and 2 assemblages (PERMANOVA pairwise comparison: t = 1.470, p (perm) = 0.012, Table 5.2, Figure 5.7).

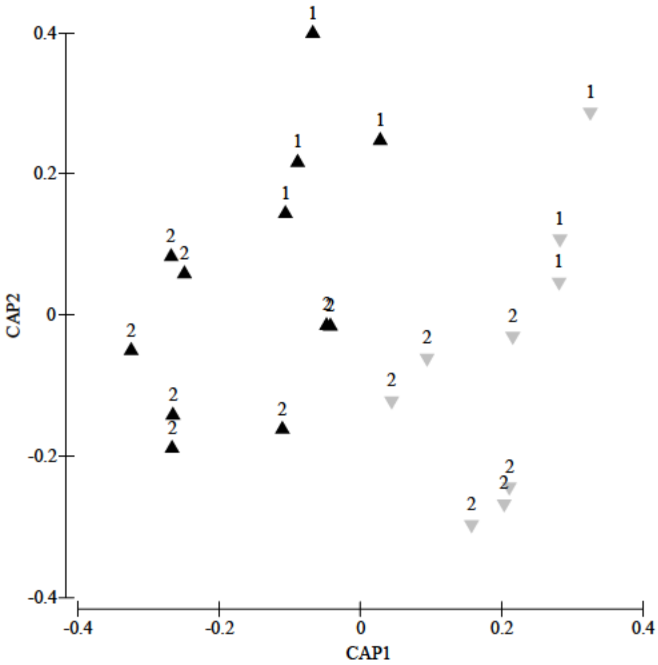


Figure 5.7 CAP of historically recorded fish assemblages in the uMgeni and uMlalazi estuaries. Period groups are represented as 1 (Before 1989) and 2 (During and After 1989). ▲=uMgeni, ▼ = uMlalazi.

Table 5.2 PERMANOVA results of estuary and period differences. MC denotes Monte Carlo test. Df = degrees of freedom, Pseudo-f = critical values. Asterisks denote significance at p<0.05

Source	**PERMANOVA**		
	Df	Pseudo-F	P(Perm)
Estuary	1	4.661	0.0001*
Period (nested in Estuary)	2	1.986	0.014*
Pairwise Comparisons	t value	Perms	P(Perm)
uMgeni 1, uMgeni 2	1.470	495	0.012*
uMlalazi 1, uMlalazi 2	1.365	84	0.126 MC

SIMPER analysis identified 45.01% similarity in fish assemblages present in uMgeni Period 1 samples. Each species's percentage contribution to this overall similarity was relatively small (<10%) as only presence/absence data was utilised. According to Clarke and Gorley (2006), this is expected of severely transformed data. The discriminating species included *Acanthopagrus vagus*, *M. cunnesius*, *M. cephalus*, *P. macrolepis*, and *P. indicus*, contributing 7.98% each to the within-group similarity. The average similarity of assemblages in Period 2 was 63.47%. Species contributing a cumulative total of 48% similarity included *A. ambassis*, *C. dumerili*, *Glossogobius* spp., *M. cunnesius*, *M. cephalus*, *P. macrolepis*, *P. commersonnii*, *Pseudomyxus capensis*, *Rhabdosargus holubi*, *Solea turbynei*, and *T. jarbua*. Taxa which increased in frequency of occurrence in the uMgeni Estuary and contributed the most toward period average dissimilarities (50.66%) included: *A. ambassis*, *Oligolepis keiensis*, *Oreochromis mossambicus*, *Caranx sexfasciatus*, *Oligolepis acutipennis* and *Rhabdosargus sarba*. Simultaneously species such as *Pomadasys kaakan*, *Elops machnata* and *Argyrosomus japonicus* decreased in frequency of occurrence in Period 2 (Table 5.3).

Table 5.3 Taxa contributing to the dissimilarity between fish assemblages in Periods 1 and 2 in the uMgeni Estuary. Only species contributing a cumulative total of 20% of the average dissimilarity are represented, due to the small individual taxon contribution. Av. Freq=Average frequency of occurrence, Av. Diss=Average dissimilarity, SD=Standard deviation, Contrib%=Contribution percentage, Cum%=Cumulative percentage.

	Period 1	**Period 2**				
Species	**Av. Freq**	**Av.Freq**	**Av.Diss**	**Diss/SD**	**Contrib%**	**Cum.%**
Ambassis ambassis	0.25	1.00	1.48	1.57	2.93	2.93
Oligolepis keiensis	0.00	0.75	1.26	1.53	2.48	5.41
Caranx sexfasciatus	0.25	0.75	1.17	1.17	2.31	7.72
Pomadasys kaakan	0.75	0.13	1.16	1.32	2.29	10.00
Oreochromis mossambicus	0.25	0.75	1.13	1.22	2.22	12.23
Oligolepis acutipennis	0.25	0.75	1.11	1.22	2.19	14.42
Elops machnata	0.75	0.38	1.11	1.03	2.18	16.60
Argyrosomus japonicus	0.75	0.25	1.07	1.16	2.11	18.71
Rhabdosargus sarba	0.25	0.63	1.01	1.06	2.00	20.72
				Average dissimilarity = 50.66		

The fish assemblages of the uMlalazi Estuary did not differ significantly between periods (t = 1.365, p (MC) = 0.126, Table 5.2). Rather, fish assemblages were more similar within each period, with an average similarity of 44.05% identified within uMlalazi fish assemblages of Period 1. Species contributing a cumulative similarity of 50% in this period included *A. ambassis*, *A. gymnocephalus*, *A. immaculatus*, *C. dumerili*, *Glossogobius* spp., *L. equulus*, *M. cunnesius*, *P. indicus*, *P. commersonnii*, *Pomatomus saltatrix,* and *Pseudorhombus arsius*. An average similarity of 71.87% was identified within fish assemblages of Period 2 for the uMlalazi Estuary. Contributions of each species were relatively small (2.70%), with a total of 19 species contributing towards a cumulative similarity of 50%. These species were present in all samples. Although fish assemblages were not significantly different between sampling periods, some species increased in frequency over time. These included *Gilchristella aestuaria, Gerres filamentosus, Gerrres methueni, Monodactylus argenteus, R. sarba, Scomberoides lysan, Epinephelus malabaricus, O. mossambicus, R. holubi, Stolephorus holodon,* and *Hilsa kelee*. Simultaneously *Eleotris fusca* and *Arothron hispidus* decreased in frequency of occurrence from Period 1 to 2 (Table 5.1).

Fish assemblages were significantly different between the uMgeni and uMlalazi estuaries (PERMANOVA: df = 1, Pseudo-F = 4.661, p(perm) = 0.0001, Table 5.2), although the contribution of individual species responsible for dissimilarities was small (Table 5.4). Most of these species were marine opportunists and occurred more frequently in the uMlalazi Estuary except for *Moolgarda robusta,* which was more dominant in the uMgeni Estuary (Table 5.4). The top five discriminating taxa between the estuaries were *T. vitrirostris, M. argenteus, S. lysan, H. kelee* and *Sphraena jello*.

Table 5.4 Taxa contributing to the dissimilarity between estuaries. Only species contributing a cumulative total of 24.06% of the average dissimilarity are represented due to the small individual taxon contribution. Av. Freq= Average frequency of occurrence, Av. Diss=Average dissimilarity, SD=Standard deviation, Contrib%=Contribution percentage, Cum%=Cumulative percentage.

Species	uMgeni Av.Freq	uMlalazi Av.Freq	Av.Diss	Diss/SD	Contrib%	Cum.%
Thryssa vitrirostris	0.08	1.00	1.17	2.55	2.32	2.32
Hilsa kelee	0.08	0.78	0.98	1.48	1.94	4.26
Sphyraena jello	0.08	0.78	0.96	1.47	1.91	6.16
Monodactylus argenteus	0.08	0.78	0.91	1.58	1.80	7.96
Scomberoides lysan	0.08	0.78	0.9	1.57	1.79	9.75
Caranx ignobilis	0.17	0.78	0.89	1.33	1.77	11.52
Pseudorhombus arsius	0.25	0.78	0.83	1.22	1.65	13.17
Chelonodon laticeps	0.17	0.67	0.82	1.15	1.63	14.8
Arothron immaculatus	0.42	1.00	0.82	1.11	1.63	16.42
Pomatomus saltatrix	0.08	0.67	0.82	1.21	1.63	18.05
Sillago sihama	0.33	0.89	0.82	1.26	1.62	19.67
Gerres filamentosus	0.25	0.78	0.81	1.28	1.61	21.28
Pomadasys kaakan	0.33	0.67	0.71	1.07	1.40	22.68
Moolgarda robusta	0.67	0.44	0.70	0.97	1.38	24.06
				Average dissimilarity = 50.41		

5.4.6 Functional guild analysis

No differences could be found between the fish guild structures of Period 1 and 2 in either estuary (PERMANOVA: df = 2, Pseudo-F = 1.296 p(perm) = 0.431, Table 5.5). Rather, a clear separation of overall EUFG structures was evident between the uMgeni and uMlalazi estuaries (Figure 5.8). Permutational tests confirmed guild differences between the estuaries (PERMANOVA: df = 1, Pseudo – F = 14.507, p(perm) = 0.0002, Table 5.5), although dispersion effects were also present (PERMDISP: df = 1, Pseudo-F = 17.343, p(perm) = 0.0006). Dispersion effects are likely responsible for the low percentage dissimilarity observed in the SIMPER analysis (31.35%). The EUFG structure of uMgeni assemblage was 75.76% similar. The most significant contributors to similarities in guild structure were MEDs (48.14%), MEOs (29.89%), E&M (8.04%), and E&F species (4.39%).

Estuarine use functional guild structures in the uMlalazi Estuary fish assemblages over time were highly similar (87.54%) and were dominated by MEOs (51.51%), MEDs (25.59%), MS (10.53%), and E&M (6.66%) functional groups. Marine estuarine opportunists (31.10%), followed by MED (32.45%) and MS (13.76%), were the main contributors of guild structure dissimilarities between the uMgeni and uMlalazi estuaries. Marine estuarine opportunists and MS were more frequently found in the uMlalazi Estuary whereas estuary associated guilds and MEDs were greater contributors to similarity in the uMgeni Estuary.

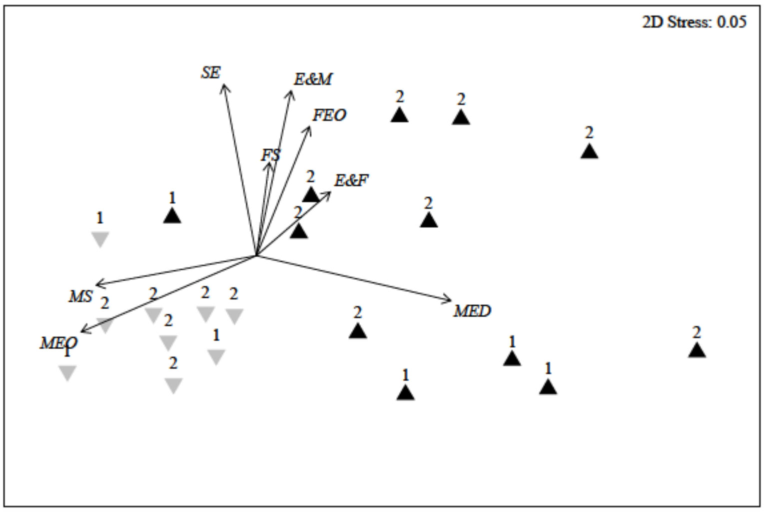


Figure 5.8 nMDS of fish assemblages based on the percentage contribution (species occurrence) of Estuarine Use Functional Guilds. Vector overlays represent the guild contribution to the total guilds present in each estuary, with longer vectors representing greater contributions. ▲ =uMgeni, ▼ = uMlalazi. Periods are represented as 1 and 2.

Table 5.5 PERMANOVA results of estuary and period differences for guild structures. Asterisks denote significance at p<0.05. Df = degrees of freedom, Pseudo-F = critical values.

Source	PERMANOVA		
	Df	Pseudo-F	P(Perm)
EUFG			
Estuary	1	14.507	0.002*
Period (nested in Estuary)	2	1.296	0.431
FMFG			
Estuary	1	6.021	0.003*
Period (nested in Estuary)	2	0.833	0.489

Feeding guild structures were comparable between periods, within each estuary (PERMANOVA: df = 2, Pseudo-F = 0.833, p(perm) = 0.489 Table 5.5) but were different between estuaries (PERMANOVA: df = 1, Pseudo-F = 6.021, p(perm) = 0.003, Figure 5.9, Table 5.5). Estuary differences, however, may be due to dispersion effects of samples and not location effects (PERMDISP: df = Pseudo-F = 14.373, p(perm) = 0.001). This suggested that the variability in feeding guilds was high among within estuary samples. Zoobenthivores (35.65%), DVs (35.51%), ZPs (10.80%) and PVs (10.80%) contributed the most to the similarity in guild structure in the uMgeni Estuary. In the uMlalazi Estuary, ZBs (35.27%), PVs (24.46%), ZPs (18.12%) and DVs (17.95%) contributed the most to the similarity in guild structure. Functional groups responsible for 93.70% cumulative dissimilarity between estuaries (although average dissimilarity was only 33.56%) included ZPs (16.10%), PVs (24.36%), DVs (30.40%) and ZBs (16.92%).

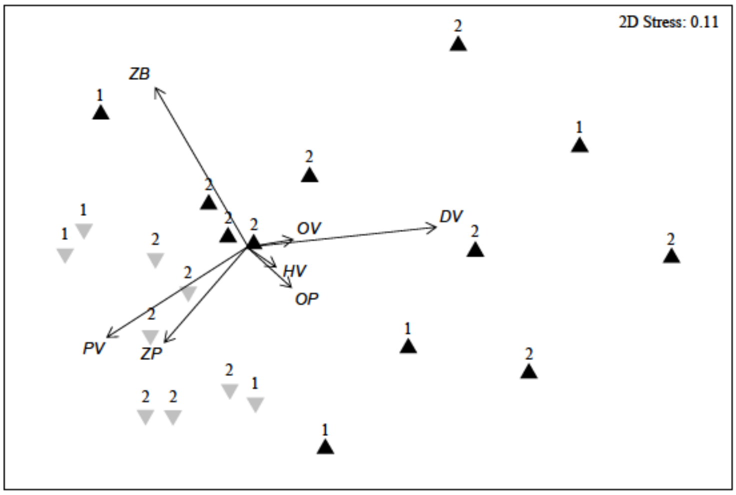


Figure 5.9 nMDS of historical fish assemblage samples based on the percentage contribution (species occurrence) of Feeding mode functional guilds (FMFG). Vector overlays represent the guild contribution to the total FMFG present in each estuary, with longer vectors representing greater contributions. ▲=uMgeni, ▼= uMlalazi. Periods are represented as 1 and 2.

5.4.7 Relationship between diversity indices and predictor variables: land-cover type and physico-chemistry

There were no significant relationships between individual Level One, Two, or Three land-cover types and species richness, AvTD, or VarTD in either the uMgeni and uMlalazi estuaries. Except for a negative relationship between uMgeni species richness and salinity (Linear regression: $r^2 = -0.44$, $p = 0.046$, Figure 5.10), no significant correlations were found between individual physico-chemical variables and diversity indices in either estuary. Permutational testing of the relatedness of the fish assemblage matrix and the predictor matrix showed no correlation, but it may have been that the available data were too sparse and the relationships too complicated to investigate this fully (RELATE: uMgeni rho=-0.168, p=0.68; uMlalazi rho=1, p=0.162). However, the individual analyses specific to land-cover, water quality (Chapter 3) or fish assemblages (Chapter 5) highlight the changes which have occurred within each estuary over time.

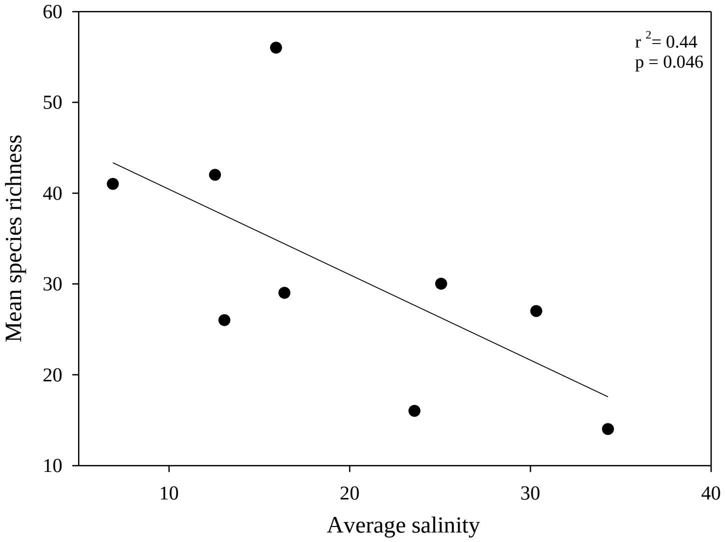


Figure 5.10 Correlation between mean species richness and average salinity in the uMgeni Estuary.

A summary of the most significant factors influencing the uMgeni Estuary and relative to this study are represented in Figure 5.11. Artificial land-cover in the 20 m contour increased drastically from 8.91% to 44.72%, with a concomitant decrease in natural vegetation from 48.58% to 26.92% (Figure 5.11a). Wetland land-cover showed an increasing trend from 1937-2018. These increases are largely a result of the expansion of mangrove area upstream and in the Beachwood Reserve (refer to chapter 3 for details). Over temporal scales, overall salinity has been highly variable, reaching over 30 in 1989 and 1992 (Figure 5.11b). Major droughts during these years are likely responsible for the increased estuary salinities as reduced freshwater flow allows for greater saltwater penetration in the system. A clear decreasing trend in dissolved oxygen was observed from 1972 (7.72 mg l^{-1}) to 2020 (4.81 mg l^{-1}). Salinity was an important variable influencing the longitudinal distribution of fishes in the uMgeni (Chapter 4), resulting in a variable total species count over time. Regardless, the present species richness in the estuary (29) is only approximately half that recorded in the earliest survey of 1979 (56) (Figure 5.11c). Guild composition has also changed (although not significantly), with the greatest differences occurring in the reduction of MS. Many of these marine stragglers were piscivorous species, resulting in a simultaneous decrease in this feeding guild (16.07% to 9.68%). Estuarine and marine species composition appears to be more variable depending on the sampling year, although their contribution to the fish assemblage appears to have increased.

Despite the increasing wetland area, which provides various benefits to an estuarine system, the water quality of the uMgeni has deteriorated over the years. Visual representation of the data depicts clear relationships and possible causative effects (Figure 5.11d). In earlier surveys, higher numbers of fish species were associated with higher dissolved oxygen levels and a significantly less transformed system. The large increase in artificial land-cover after 1989 saw significant decreases in dissolved oxygen, ultimately influencing the number of fish species which could make use of the degraded system.

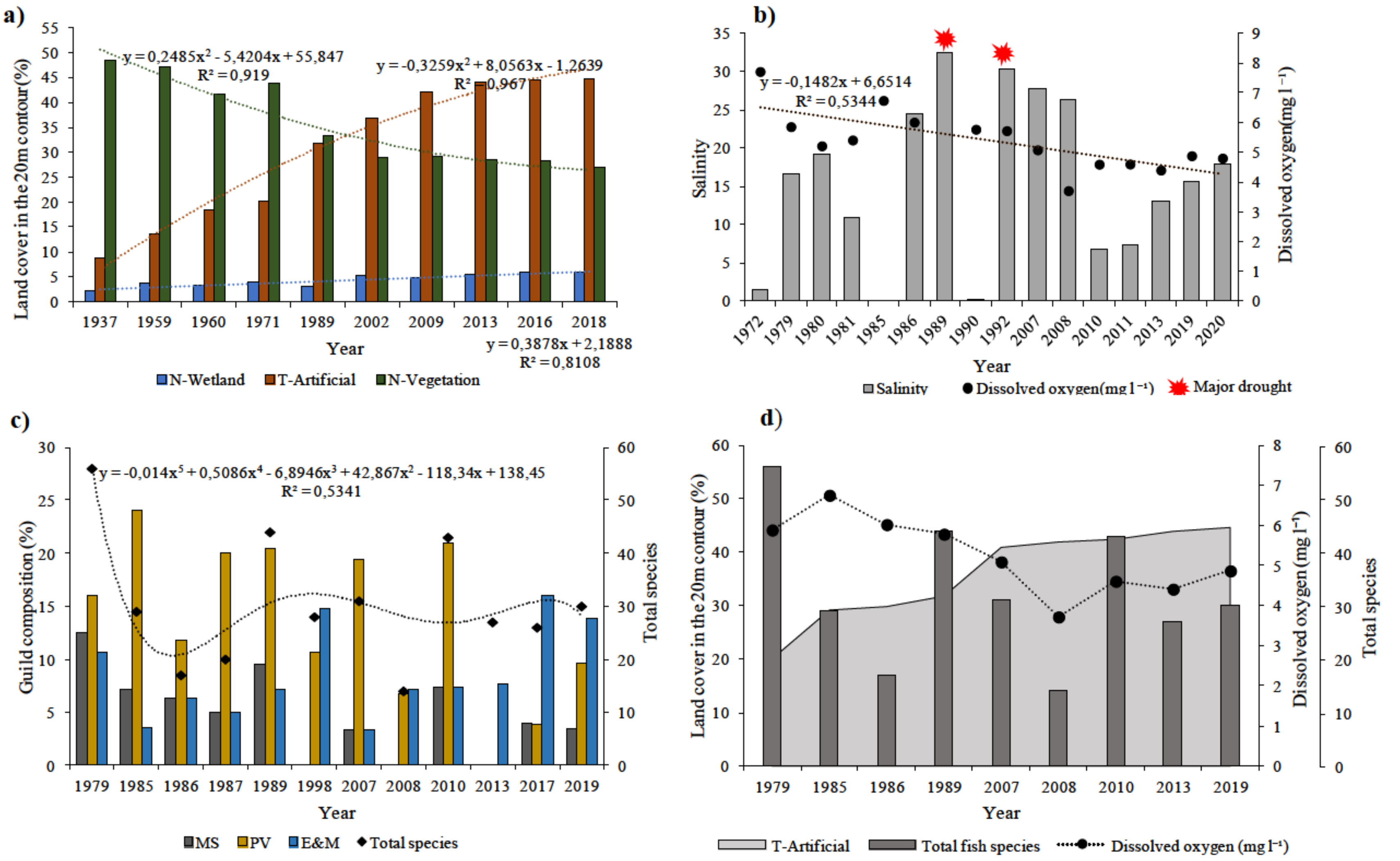


Figure 5.11 Summary graphs of the most relevant trends for the uMgeni Estuary from this study including a) land-cover change b) physico-chemical changes c) fish assemblage change and d) interactive effects.

In the uMlalazi Estuary, the greatest land-cover changes have been in increased cultivated area from 20.09% in 1937 to 47.86% in 2018 (Figure 5.12a). Although natural vegetation has simultaneously decreased, the present percentage contribution from the EFZ to the 20 m contour area (32.31%) is still higher than the in uMgeni Estuary. Wetland area has also decreased from 16.27% to 7.81%, despite the establishment of mangroves within the estuary. As with the uMgeni, salinity varied over time, although averages were usually > 20 due to the estuary's tide-dominated state (Figure 5.12b). Dissolved oxygen levels closely followed the salinity trend, increasing during periods of higher salinities and decreasing during more freshwater dominated periods. However, an overall weak, increasing trend is evident over time. The total species within the system appears to be unchanged (Figure 5.12c). More noticeable are changes in the contribution of specific guilds to the fish assemblage. Primarily, the contribution of DVs has increased from 9.93% to 18.33%, followed by increases in MEOs (38.46% - 48.28%) and ZPs (13.21% - 16.67%).

The interactive effects of all significant components within the uMlalazi (cultivated land-cover, dissolved oxygen and total species) are reflected in Figure 5.12d. The point of convergence of all three factors in 1986 showed a decrease in dissolved oxygen and total species when cultivated land-cover increased considerably. However, this trend did not persist and was likely a result of year-specific conditions in the estuary. Total species numbers have remained relatively high, corresponding to well-oxygenated waters. Overall increases in dissolved oxygen were also observed. Despite the noted land-cover changes, water quality and fish species richness have remained stable, especially compared to the water quality and fish community changes evident in the uMgeni. This suggests a greater impact of artificial land-cover, which has remained significantly lower in the uMlalazi than uMgeni Estuary 20 m contour.

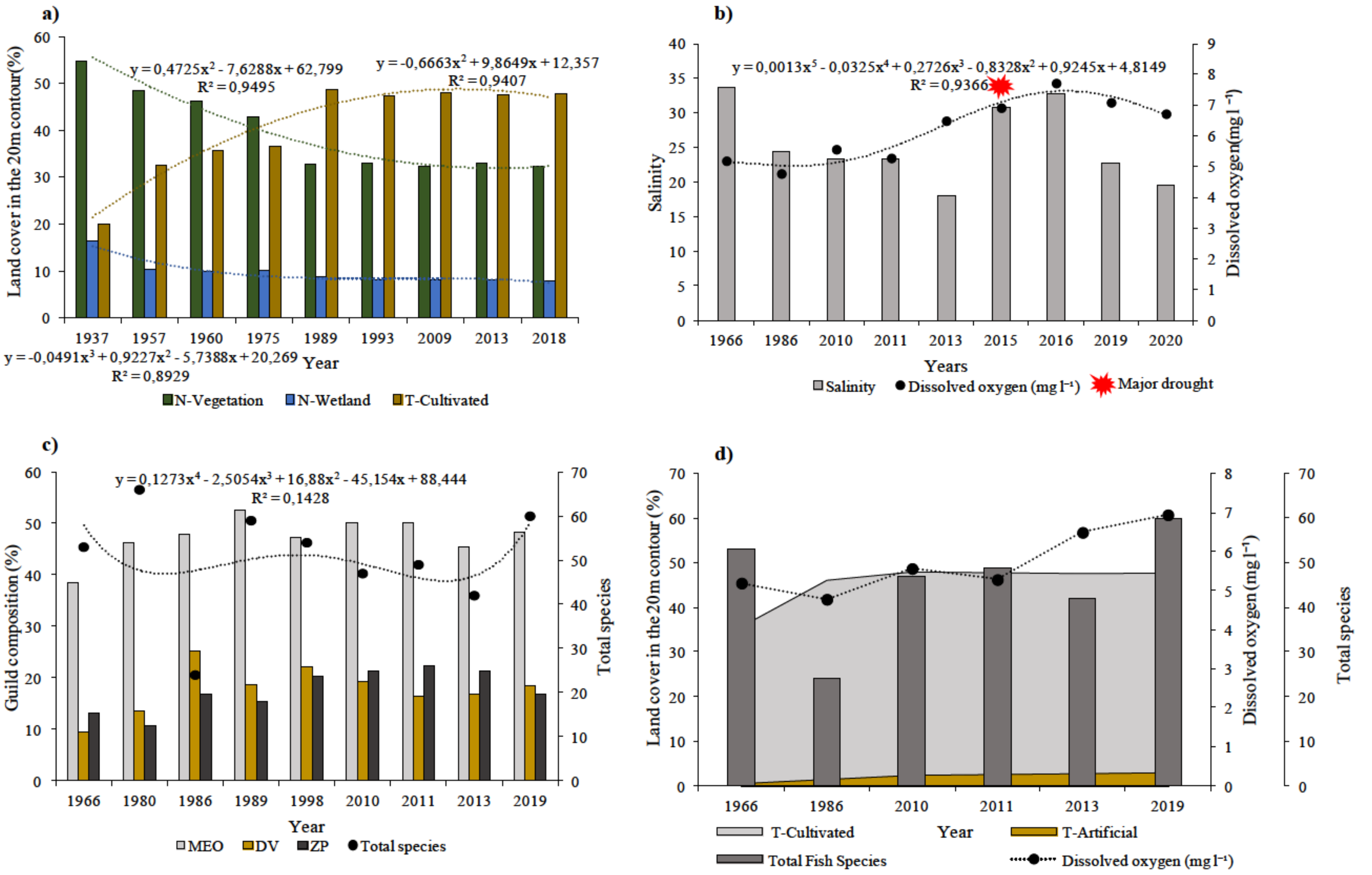


Figure 5.12 Summary graphs of the most relative trends for the uMlalazi Estuary from this study concerning a) land-cover change b) physico-chemical changes c) fish assemblage change and d) interactive effects.

5.4.8 Overall relationship between biological data and predictor variables

Distance-based linear models were performed on combined estuary data to determine any overall relationships between variables. In all DISTLM tests, only one variable was selected which best explained the variation in each diversity index. Species richness was best explained by dissolved oxygen concentrations (46% of the variation). Decreases in species richness were correlated with decreases in dissolved oxygen. In contrast to simple correlation analyses, permutational testing identified that artificial land-cover accounted for 50% of the variation in AvTD and 45% of the variation in the VarTD of the historical fish data (Table 5.6). Slight negative correlations were observed between AvTD and artificial land-cover, whereas VarTD appeared to increase with an increase in artificial land-cover.

Table 5.6 Best solutions from DISTLM for the significant relationships between univariate diversity indices and predictor variables (Predictor variables included dissolved oxygen, salinity and land-cover classes T-Artificial, N-Wetland, N-Bare and N-Waterbodies). Asterisks denote significance at $p<0.05$. N-Natural land-cover, T=Transformed land-cover

Diversity Index	Predictor Variable	AICc	Pseudo-F	P (perm)	r^2
Sp richness	Dissolved Oxygen (mg l^{-1})	63.766	9.534	0.010*	0.464
AvTD	T-Artificial	19.888	10.793	0.004*	0.495
VarTD	T-Artificial	-71.352	9.079	0.003*	0.452

5.5 Discussion

5.5.1 Historic univariate diversity changes

Fish diversity within each of the uMgeni and uMlalazi estuaries did not change significantly between periods which may be attributed to various factors. A major issue arises in the appropriateness of univariate indices in detecting biodiversity change, particularly when using species richness. Species richness is highly dependent on sample size, area and the abundance of individuals (Chase and Knight, 2013), all of which may vary from one ecological survey to the next. A lack of change in species richness over time does not necessarily imply that species composition has remained unchanged but may indicate immigration and extinction events that produce a neutral change in species richness (Hillebrand et al., 2018). Species that belong to single genera or families may be replaced by taxa that already have many genera within the system, maintaining the overall species richness (de Sousa Gomes-Gonçalves et al., 2020). The lack of change in univariate indices but obvious fish compositional changes over time suggests that, for this study, univariate measures may not be the best indicators of diversity changes.

Estuarine fish assemblages generally exhibit greater resilience to change than freshwater or marine assemblages (Teichert et al., 2017). These results may therefore highlight the stability and resilience of South African estuarine fish species to change. Previous studies have also recorded no long term changes in species richness (Ribeiro et al., 2008) or AvTD and VarTD (James et al., 2018). Alternatively, fish diversity in the uMgeni Estuary may have already been reduced at the first recorded fish survey of 1979. Historical records reveal that the system had undergone drastic land-cover changes before the 1970s (Chapter 3) and it may be that fish assemblages then would have presented a different species/abundance structure in the estuary, under a less disturbed state. This is common in monitoring systems that begin only after pressures manifest as impacts. For example, European biodiversity monitoring schemes on fishes, referred to as DaEuMon, began in the 1960s whereas land-cover changes had already begun in the 1700s (Mihoub et al., 2017). An inappropriate timeframe of biological data may, therefore, mask any negative anthropogenic impacts leading to a shifting baseline effect (Soga and Gaston, 2018).

On the other hand, the lack of change in uMlalazi Estuary diversity indices could reflect the positive impacts of estuarine functional zone protection. The reduced urbanisation and land-use activities surrounding the estuary have allowed the system to remain near a natural state with good ecological health (Van Niekerk et al., 2019). The diverse habitats and expanded resource availability in such systems allow the coexistence of distantly related species with different ecological niches, maintaining higher species richness and taxonomic diversity (Miranda et al., 2005).

5.5.2 Taxonomic distinctness of estuarine fishes

In this study, AvTD of fish assemblages in different years for the uMgeni Estuary remained within the expected range (in the 95% confidence intervals) of biodiversity according to the regional master list. However, AvTD values were lower than expected in particular years (e.g., 2008), emphasising that diversity has been reduced although not significantly so at this point. Degraded systems can be associated with increases in opportunistic species, often taxonomically related, reducing overall taxonomic diversity (Clarke and Warwick, 2001b;

Zhang and Hu, 2020). These genetically similar species will often share the same functional attributes and respond to disturbances in the same way (Schrandt and MacDonald, 2020). For instance, Mugilidae species are known to tolerate various conditions and contributed almost 45% of the uMgeni species composition for 2008. Highly elevated bacterial levels in the uMgeni in 2008 (Forbes and Demetriades, 2009) suggest high loads of wastewater inputs into the system that year and reduced water quality, a likely deterrent to the entry of many species resulting in a lowered AvTD. The earliest fish survey of 1979 was the only sample consistently within the range of the expected mean diversity for both AvTD and VarTD. This survey had the highest species richness (56 species), represented the greatest number of orders, and recorded species rare in South African estuaries (*Favonogobius melanobranchus* and *Butis butis*) (Begg, 1978). This observation likely reflects that water quality in the uMgeni Estuary during earlier surveys (1979) was better than during Period 2. Lowered AvTD has also been observed in commercial fishing areas (Rogers et al., 1999), environmentally polluted estuaries (Zhang and Hu, 2020), and in waters after red tide events (Schrandt and MacDonald, 2020).

Over time, fish assemblages in the uMlalazi Estuary have exhibited diversity patterns which are typical of healthy, subtropical permanently open estuaries, as determined by the master reference list. This suggests that the system is less affected by anthropogenic disturbances. Clarke and Warwick (2001b) highlighted that the taxonomic spread of species is greater in less impacted assemblages, whereas the taxonomic spread is reduced in impacted areas. For the study periods investigated here, the range of orders represented in the uMlalazi Estuary (6-12) was higher than the uMgeni Estuary (3-11). The number of families represented in the uMlalazi Estuary was also greater than the uMgeni Estuary, resulting in the reduced AvTD seen in uMgeni samples. Only three species were consistently present in all uMgeni samples, whereas 12 species were consistently present in all uMlalazi samples. Taxonomic distinctness is a measure that has been shown to reflect the response of fish communities to anthropogenic activities. Although not in the estuarine environment, a study conducted in Japan showed how average taxonomic distinctness was lower in lakes disconnected from the main river due to anthropogenic manipulations. These samples contained fewer orders and families than lakes not affected by hydrological manipulations (Jiang et al., 2020), an observation also evident in the estuaries studied here. The greater taxonomic spread in the uMlalazi Estuary corresponds to a higher taxonomic distinctness and therefore higher biodiversity.

Although diversity in the uMgeni Estuary was lower than the uMlalazi Estuary, AvTD tests revealed that fish diversity in both estuaries still fell within the range of expected biodiversity of the species master list used, taken as all ichthyofauna species recorded in KZN subtropical permanently open estuaries. Similarly, in the Alvarado Lagoon Estuary in Mexico, AvTD and VArTD of all assemblages from different periods remained within the confidence limits of the expected values, although year specific assemblages were reduced (Chavez-Lopez et al., 2005). It has been suggested that anthropogenic perturbations on biodiversity may be masked by natural environmental gradients, such as might occur in water quality, stream size and sediment characteristics, known to influence biotic organisms but not detected by taxonomic distinctness tests (Heino et al., 2007). In relation to estuarine fish, species may vacate an area of the estuary experiencing increased temperatures, anoxic waters, or pollution events and re-enter when conditions are favourable again (Whitfield, 2019). It is for these reasons that taxonomic diversity has been criticised as an appropriate measure for identifying biodiversity impacts (Bhat and Magurran, 2006; Stojković Piperac et al., 2016)

Most changes in the hierarchical structure of the uMgeni Estuary fish community were observed through the VarTD test. Fish assemblages in all years, except for 1979, 1987, and 2007, exhibited VarTD greater than the expected VarTD from the regional master list. This reveals that some lower taxonomic levels such as species, genus, or family may only contain one species, whereas others are regarded as species rich. The 2008 assemblage, for example, contained three different orders, one of which was dominated by members of a single family (Mugilidae). In comparison, Perciformes were dominated by five different families. Therefore, the combination of well-represented higher taxa and unevenness in lower taxa representation most likely resulted in the VarTD of many uMgeni samples appearing above the upper funnel limit. Similar results were observed in a coastal lagoon where salinity fluctuations and eutrophication lowered AvTD and increased VarTD, depicting an unevenness in the taxonomic tree (Mouillot et al., 2005).

Habitat and food availability greatly influences the diversity of certain taxa. The absence or degradation of particular habitats and associated food resources results in the loss of specific habitat-associated taxa, resulting in a more significant unevenness in the taxonomic tree (Clarke and Warwick, 2001b). In the uMgeni Estuary, the major higher order taxa associated with estuaries such as Mugilidae, Gobiidae and, Ambassidae are still represented. These species were largely MEDs and estuarine associated species which have no choice but to utilise the estuarine environment, regardless of its degraded nature. However, fewer species were present in taxa which can also utilise nearshore environments (MEOs), such as Haemulidae with losses occurring at the lower taxonomic levels first (with time), moving progressively up the taxonomic tree. In more stable environments, the taxonomic structure remains more regular with more distantly related species, allowing a greater variety of functions to be provided to a system (Mouillot et al., 2005). The VarTD of the uMlalazi assemblages remained within the confidence limits of the funnel plot, reflective of an even taxonomic spread and a more stable environment. Therefore, the system supports more functionally redundant species than the uMgeni Estuary. If one species is lost, another species may compensate for this loss because it performs the same functional roles. Functional redundancy therefore increases biological stability allowing the system to remain resilient against perturbations (de Sousa Gomes-Gonçalves et al., 2020).

5.5.3 Historic community assemblage

Variations in ichthyofauna composition may result from reduced recruitment pulses, alterations in food availability, and changes in larval transport and ichthyoplankton behaviour during specific periods (Pfirrmann et al., 2021). In this study, additional pressures such as degraded water quality, reduced freshwater runoff and habitat destruction are likely issues that affected fish community composition in the uMgeni. The increase in organic matter accumulation and anoxic bottom waters in the uMgeni Estuary (refer to Chapter 3) suggests that Gobiidae species, which occupy the benthic habitat would be negatively affected. A study in a Portugal Lagoon supports this assumption with results of reduced Gobiidae abundances in response to anoxic conditions above the sediment (Newton and Mudge, 2005; Ribeiro et al., 2008). However, the uMgeni Estuary has seen an increase in Gobiidae species from Period 1 to Period 2. Fewer Gobiidae species in Period 1 is unlikely an artefact of sampling gear as beam trawls, which are highly selective for bottom-dwelling species, were also used at the time. Rather, Gobiidae increases may be reflective of sampling further upstream the estuary and the general resilience of these species to hypoxic conditions (Nilsson et al., 2004).

Despite the increase in salinity in the uMgeni Estuary, the frequency of occurrence of *A. ambassis* has increased. *Ambassis ambassis* is primarily restricted to low salinities (<10) (Martin, 1988) and would occur in the upper and riverine reaches of the uMgeni Estuary. The apparent increased frequency of occurrence may be as a result of recent researchers sampling farther up the system into the tidal freshwater reaches than researchers in early years. The increased presence may also be linked to the species tolerance for high temperatures, which would be encountered in the riverine reaches (presented in Chapter 4), along with its varied diet (Martin and Blaber, 1983; Martin, 1988). *Ambassis ambassis* may have preyed upon invertebrates associated with floating *Pontederia* and *Pistia* mats in the upper reaches. Increases in *O. mossambicus* may also be attributable to better sampled upper reaches, along with the high adaptability of this species to varying conditions. *Oreochromis mossambicus* is usually present in estuaries with reduced water currents, varying salinities, sandy bottoms for nest building, high benthic floc, and few piscivorous predators (Whitfield and Blaber, 1979; de Moor, et al., 1986; Cyrus and Vivier, 2006; Whitfield, 2015); factors which were particularly prevalent in Period 2.

The reduced presence of *P. kaakan* is unlikely due directly to its dependence on macrobenthos abundance, as invertebrate numbers remain relatively high in the uMgeni (Sheppard and MacKay, 2018). Rather changes in zoobenthos composition associated with poor water quality in the uMgeni Estuary are more likely responsible for reduced *P. Kaakan* presence. Although not assessed in the current study, overfishing from shoreline anglers may have also reduced *P. kaakan* in Period 2. Van Niekerk et al. (2019) support this assumption by identifying the uMgeni Estuary's fishing pressure as very high, with 8.9 tons of fish caught per year.

The species assemblage of the uMlalazi Estuary did not show significant changes from Period 1 to 2. A large portion of the uMlalazi Estuary is located in a protected area which has limited the potential for intense developmental changes (Chapter 3), allowing the system to remain in a mostly natural state (DWS, 2015; Van Niekerk et al., 2019). Regardless of insignificant community assemblage changes, some taxa absent in Period 1 were recorded in recent years, namely *O. mossambicus, G. aestuaria* and Gerreidae species. Salinity decreases in Period 2 riverine reaches may explain the increased presence of *O. mossambicus*, which prefer the upper reaches of open estuaries (Whitfield and Blaber, 1979). Over time, detritus accumulation from slight flow reductions may have increased in the uMlalazi Estuary, resulting in more significant food supplies for *O. mossambicus.* Slight increases in nitrate and phosphate concentrations have also been recorded (DWS, 2015; Hemens et al., 1971), with sources arising from agricultural runoff, the overflow of the Mtunzini sewage works, and an aquaculture farm in the lower reaches (Peer et al., 2018). *Gilchristella aestuaria* is an important and highly prevalent estuarine species in southern African estuaries. Its apparent absence in earlier (Period 1) uMlalazi assemblages may be associated with more frequent floods (12% more than presently), which would have washed stocks of *G. aestuaria* out to sea, reducing their likelihood of being sampled during surveys (DWS, 2015; Whitfield, 2019).

The absence of common subtropical estuarine fish such as the Gerreidae in Period 1 cannot be fully explained. Bivalves, which constitute a significant component of their food resource (Cyrus and Blaber, 1983), were recorded as highly abundant in earlier surveys (Hill, 1966). Reduced food resources, therefore, cannot be considered as the cause. These slight differences in the occurrence of specific species in the uMlalazi Estuary over time is possibly a consequence of the natural variability of estuarine fish assemblages, which are dependent on a variety of factors at different points in time and space (Wilson and Sheaves, 2001; Sheaves, 2016; Kindong et al., 2020).

Despite fish assemblage differences between periods in the uMgeni Estuary, guild composition did not change significantly. A similar result was also observed in a eutrophic Australian open estuary (Potter et al., 2016). In contrast, other studies have found changes in guild structure over time in response to habitat modifications (Murase et al., 2017), anthropogenic activities (Araújo et al., 2016), overfishing (Ferguson et al., 2013) and increased tidal exchange (Potter et al., 2016). The uMlalazi Estuary also exhibited no significant differences in guild composition over time. This suggests that although different species have occupied the estuaries over time, these species share similar traits and utilise the estuary in the same way, rendering them functionally redundant (Baptista et al., 2015; de Sousa Gomes-Gonçalves et al., 2020). The occurrence of several species which share the same functional role is beneficial to a system as ecosystem functions can continue to be performed if disturbances affect specific species (de Sousa Gomes-Gonçalves et al., 2020).

Although significant guild differences were not observed over time, some fluctuations of certain guilds have occurred. Estuarine residents and freshwater species increased in the uMgeni Estuary. These observations conflict with those from other studies which have shown decreases in estuarine species under reduced freshwater inputs (e.g., Lamberth et al., 2008), although, in the case of the uMgeni changes have occurred to a system which was strongly river dominated to one that is more typical of a permanently open estuary. Sedimentation processes and habitat degradation associated with earlier land-cover changes (Begg, 1984) may have jeopardised the eggs of resident species. In particular, bottom-dwelling species such as Gobiidae lay their eggs along submerged rocks or other substrates (Araújo et al., 2016), which would have been greatly affected during the canalisation of the estuary during Period 1.

Increased occurrence of marine stragglers can be generally associated with increases in salinity. In the Peel Harvey Estuary, Australia, increased tidal action and reduced precipitation resulted in increased marine stragglers (Potter et al., 2016). In the case of the uMgeni, the construction of the Inanda Dam in 1989 is likely to have contributed to reduced freshwater inflow to the estuary altering mouth dimensions and the tidal prism. Although salinities in the uMgeni Estuary have increased over time, average salinities are still lower than seawater (25.18 ± 10.97 SD) and are highly variable (Chapter 4). This, along with reduced mouth dimensions, may prevent the occurrence of marine stragglers, which are stenohaline. Also, estuaries under severe anthropogenic stress may exhibit declines in marine stragglers due to changes in habitat attributes (Valesini et al., 2017). The role of notable land-cover changes within the 20 m contour of the uMgeni Estuary and affected estuary-associated habitats, therefore, cannot be ignored as a possible additional factor affecting the occurrence of marine stragglers.

Marine connectivity permits higher order predators such as piscivores to use the estuarine environment and associated food sources, resulting in greater species richness (Warry et al., 2018). A contrasting situation was found in the uMgeni Estuary, where species richness decreased as salinities increased. The reduction in piscivore species such as *E. machnata* and *A. japonicus* from Period 1 to Period 2 suggested that conditions such as food resources are not adequate for their utilisation of the estuary and this may be a result of the recent, poor environmental conditions. Harrison and Whitfield (2004) also found reduced piscivore numbers in the Sezela Estuary in response to environmental stress. Piscivores are also strongly targeted by recreational anglers. The estimated take for the uMgeni Estuary is 8.9 tons of fish per year (Van Niekerk et al., 2019). Therefore, in the uMgeni Estuary, poor water quality and prolonged overfishing has produced a predominantly detritus-based food chain, reducing the piscivore numbers and resulting in an overall shortening of the food chain length (Lin et al., 2007).

Zoobenthivores dominated the uMlalazi Estuary in contrast to the uMgeni. Previous studies have identified high abundances of macrobenthos, on which zoobenthivore fishes prey, in the uMlalazi Estuary (DWS, 2015). In contrast, the uMgeni zoobenthivore contributions were much lower. Reduced zoobenthivore contributions to fish assemblages have been shown to result from decreased habitat quality and reduced food resources (Araújo et al., 2016). This may have been the case in the uMgeni Estuary. Sediment movement in the lower uMgeni may have also prevented the establishment of macrobenthic stocks to support high abundances of zoobenthivore fishes (DWA, 2011). Surveys conducted in 2007/2008 in the uMgeni Estuary recorded low densities of amphipods, isopods, and tanaids known as pollution sensitive species. These low densities and polychaete dominance reflect poor water quality (DWA, 2011). Although detritus is present in the uMlalazi Estuary, detritivores contributed less than half of the uMgeni samples depicting that other food sources are also important in this system. The estuary is not as heavily dammed as the uMgeni and is not exposed to the effects of heavily transformed land (Chapter 3). Although agriculture does contribute nutrient input to the system, regular flushing and strong tidal mixing remove excess nutrients and detritus. Yabsley et al. (2020) showed that estuaries that receive high nutrient loads and simultaneously exhibit largely natural habitats such as mangroves contain high species abundances, characteristics also present in the uMlalazi Estuary.

Phytoplankton, followed by zooplankton stocks, are maintained through nutrient inputs from freshwater inflow coupled with tidal mixing (Allanson and Read, 1995; Adams et al., 1999). Although river inflow is reduced in the uMgeni Estuary, phytoplankton biomass remains low (Forbes and Demetriades, 2009). The system’s reduced water residence time from strong tidal action, turbid water and shallow depth prohibits the establishment of phytoplankton abundance (Paerl et al., 2014; Niu et al., 2020), zooplankton stocks and, therefore, the occurrence of zooplanktivorous fish. Additionally, the presence of floating invasive macrophytes may deplete nutrients in the water column and change habitat conditions which support zooplankton abundance (Adams et al., 2020). The presence of the freshwater diatom, *Aulacoseira granulate*, often associated with eutrophic systems, suggests that nutrient loading (pollution) is still an issue likely from reduced freshwater flows (DWA, 2011; Santiago et al., 2010). In comparison, the uMlalazi Estuary is associated with a smaller tidal range, greater light penetration, and longer water retention times promoting the natural growth of phytoplankton and providing adequate food supplies for zooplankton and, therefore, zooplanktivorous fish.

5.5.4 The relationship between fish assemblages and predictor variables

No direct correlations could be found between land-cover and species richness, AvTD or VarTD over time, except when permutational testing was implemented. Such direct relationships are often more easily identifiable in freshwater systems that are not exposed to extreme environmental variation, which typify estuarine systems (Warry et al., 2018). More direct correlations are also more prevalent in communities of less mobile organisms such as macrobenthos, which cannot avoid impacted areas. Changes in macrobenthic assemblages have been correlated to land-cover patterns in the Upper Roaneke River Basin, Virginia (Sponseller et al., 2001) and various estuarine systems in KwaZulu-Natal (Sheppard and MacKay, 2018). Distanced-based models using permutations revealed that artificial land-cover in the 20 m contour accounted for almost 50% of the variation for both the AvTD and VarTD. The results reveal that development (artificial land-cover) contributes to the lowering of biodiversity and increased unevenness in the taxonomic tree. Additional studies support the negative influences of urbanisation on fish assemblages at the estuarine extent (Wang et al., 1996) and the catchment level (Warry et al., 2018).

The more likely interaction between land-cover and fish assemblages is indirectly through water quality or stream habitat alterations (Hua, 2017). Fluctuations in physico-chemical variables influence water quality, driving the responses of fishes (Wang et al., 1996; Duque et al., 2020). Considering the large-scale land transformations to the 20 m contour over time and the correlated decreases in dissolved oxygen (Chapter 3), a decrease in the fish species richness, AvTD and VarTD of the uMgeni Estuary was expected. Direct correlations between individual univariate indices and dissolved oxygen, however, could not be found. Chapter 3 highlighted that temporal differences in physico-chemical variables were not as apparent across the entire estuary but instead occurred at the reach level over time. The lack of reach specific historical fish assemblage data prevented any analyses of changes in fish assemblages and water quality at the reach level, which may have revealed better correlations. It should also be considered that ichthyofaunal data and physico-chemical data were not always available for the entire timeframe of interest, and in some cases, statistical power was lower than recommended. Therefore significant correlations may have been overlooked. Valesini et al. (2017) also reported noticeable changes in fish species composition and dissolved oxygen independently over time but could not find any significant correlations between the two variables for similar reasons mentioned above. Therefore, attempting to correlate three different factors (land-cover, water quality and fish assemblages) which exhibit their individual influencers and confounding factors proved challenging. Regardless, individual analyses showed clear overlaps between land-cover changes, water quality degradation and changes to fish assemblages.

Distance-based redundancy models based on combined estuary data revealed a weak positive relationship between dissolved oxygen and species richness. Estuarine fish species will avoid areas experiencing depressed dissolved oxygen levels, only returning when levels are favourable again (Mattone and Sheaves, 2017). Reduced dissolved oxygen levels may be attributed to human pressures. Urbanisation can be associated with the increased runoff of nutrient-rich water from sewage treatment facilities, informal settlements, stormwater, and industries (Valenti et al., 2017; Adams et al., 2020). High nutrient-rich waters increase the water column's biological oxygen demand, resulting in depleted oxygen levels (Costa et al., 2017). Gallardo et al. (2011) revealed that distinctness metrics were not significantly related to abiotic factors but rather to trophic elements such as chlorophyll-a or phosphorous. These trophic elements were not assessed in this study because of the lack of historical data. However, nutrient concentrations are often a by-product of urbanisation (artificial land-cover), which was identified as the best predictor variable explaining changes in AvTD and VarTD in the overall study systems.

The negative relationship between salinity and mean species richness in the uMgeni Estuary adds to the weight of evidence that the system's fish community is showing signs of impact. This trend contradicts studies which show that increased salinities are associated with increased species richness by attracting more marine species that dominate permanently open estuaries. In this study, normal salinity and species richness relationships were likely offset by diversity losses associated with habitat alteration, sedimentation and water quality degradation from surrounding land-use activities and development (see Chapter 3 for details).

5.5.5 Conclusion

The role of land-cover, particularly related to urbanisation, and the associated adverse effects on water quality distinguished the uMgeni Estuary from the uMlalazi Estuary. The study provides evidence that artificially transformed systems are more severely impacted than agriculturally dominated systems. Although significant correlation effects were difficult to distinguish, clear land-cover changes, water quality changes and fish assemblage changes were observed individually over time. Dissolved oxygen was important in determining overall species richness, whereas the influences of artificial land-cover were better linked to AvTD and VarTD of fish assemblages. Although the AvTD of the uMgeni Estuary has not changed significantly between periods, fish assemblage patterns have been variable, resulting in unevenness in the taxonomic tree. The taxonomic distinctness test also revealed specific years in which biodiversity was lower than expected in the estuary, compared with other local subtropical permanently open estuaries.

The uMgeni Estuary has been subject to freshwater flow reductions, increased salinities, urbanisation, nutrient inputs, and significant habitat losses. These anthropogenic impacts are generally associated with a reduction in the spread of the higher order taxa, with species poor higher order taxa often the first to be lost (Clarke and Warwick, 2001b). Branch lengths between species are shortened, consequently lowering the AvTD of the assemblage (Jiang et al., 2020). Anthropogenic perturbations have therefore contributed to removing species and lowering the fish functional redundancy in the uMgeni Estuary, decreasing the system’s resilience to future perturbations (Miranda et al., 2005; Araújo et al., 2018). Reduced taxonomic diversity may also result in food web simplification, as related species generally consume the same resources (Miranda et al., 2005). Lowered species richness increases the chances of functional diversity changes, which reduce ecosystem functioning, stability, and resilience to environmental change (de Sousa Gomes-Gonçalves et al., 2020). These functional shifts jeopardise the goods and services provided by the estuary, such as coastal protection, recreational opportunities, carbon sequestration, and the restocking of marine fisheries. Monetary losses may occur as estuarine services in South Africa are valued at ZAR 972 million per annum (Turpie et al., 2017), contributing substantially to the economy.

The uMlalazi Estuary has remained largely natural with few artificial changes in the estuarine functional zone. This has ensured minimal water quality impacts, allowing fish taxonomic diversity to be maintained and preserving the system’s resilience to change. However, small changes in species composition and guild structure reveal that the system is not immune to environmental or anthropogenic effects and should be closely monitored

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CHAPTER 6: CONCLUSIONS AND RECOMMENDATIONS FOR FURTHER RESEARCH

6.1 Summary of findings

This study aimed to describe the spatial and temporal changes in fish assemblages in permanently open urban (uMgeni) and non-urban (uMlalazi) estuaries, and to determine the catchment-proxy and *in situ* factors influencing them. This was achieved in three parts. Chapter 3 described land-use/land-cover (LULC) patterns around each estuary, focussing on the Estuarine Functional Zone (EFZ) below the 20 m contour, and physico-chemical changes in each system over time. Chapter 4 assessed the current longitudinal distribution of fishes in each estuary, and Chapter 5 provided a holistic view of each system by assessing the relationships between LULC, water quality and fish assemblages over time. This final chapter aims to integrate the findings from Chapters 3, 4 and 5 from the perspective of the study aims. Contributions of the research to estuarine management are discussed as well as recommendations for future studies.

Land-use/land-cover analyses showed that the uMgeni Estuary had undergone significant land-cover changes as early as the 1930s. These included increases in commercial area, developed infrastructure and managed vegetation. Although the uMlalazi Estuary has also been subject to land-cover changes, these were primarily attributed to increased cultivated areas. Wider catchment land-cover types (e.g., natural vegetation) were relatively comparable between the estuaries; therefore, it was concluded that land-cover changes proximal to the estuaries (i.e., in the 20 m contour, including the full EFZ) are more dominant in revealing the estuary effects noted in this study. Urban runoff from wastewater treatment works (WWTW) and various other land-use activities associated with urban areas more severely affected water quality dynamics than agricultural runoff. This was reflected in the physico-chemical variability over time in the uMgeni Estuary and the strong negative correlation between dissolved oxygen and artificial land-cover types.

Fish assemblage composition was significantly different between periods in the uMgeni Estuary, whereas fish assemblages remained the same between periods in the uMlalazi Estuary. Periods represented temporal changes, taken as before 1989 (Period 1) and during and after 1989 (Period 2). Regardless of the community-level changes in the uMgeni Estuary, species richness, average taxonomic distinctness (AvTD), variation in taxonomic distinctness

(VarTD), estuarine use functional guilds (EUFG), and feeding mode functional guilds (FMFG) remained unchanged between periods. Likewise, no differences were observed in all metrics mentioned above for the uMlalazi Estuary. The lack of significant changes is likely due to the high number of functionally redundant species in subtropical permanently open estuaries compared to other estuary types (Whitfield and Harrison, 2021). Species redundancy is beneficial in an ecosystem as the functions performed by one species, which may be lost from a disturbance, can be compensated for by another species performing the same function (de Sousa Gomes-Gonçalves et al., 2020).

The hierarchical structure and functioning of estuary-associated species are generally quite resilient, with only drastic or long term changes resulting in taxonomic biodiversity differences (James et al., 2018). Studies have identified changes in hierarchical fish structure in response to prolonged red tide events (Schrandt and MacDonald, 2020), dystrophic crises from anthropogenic inputs (Xiujuan et al., 2010), long term overfishing and trawling (Zhang and Hu, 2020), extreme shifts in hydrological condition (Miranda et al., 2005), invasive species introduction (Jia et al., 2020) and climate change-induced weather extremes (Schrandt and MacDonald, 2020). The estuarine fish taxonomic distinctness test allowed biodiversity loss to be investigated by comparing sample selections to a regional master species list. Although taxonomic diversity has not yet changed significantly between uMgeni periods, diversity is still decreasing. Fish biodiversity during certain years, particularly in Period 2 (during and after 1989), was lower than other permanently open estuaries in KwaZulu-Natal. Similarly, the taxonomic spread in many year specific uMgeni fish assemblages was uneven, a phenomenon linked to degraded systems (Clarke and Warwick, 2001b; Miranda et al., 2005). This implies that the fish assemblage has lost some less resilient species whereas more resilient species and typical estuarine higher order taxa remain. These losses are more obvious in certain years and likely linked to more intense anthropogenic impacts exacerbated by environmental phenomena.

The uMgeni and uMlalazi estuaries were sampled during 2019-2020 to update information on recent urban development and the contemporary estuarine biophysical situation. Distinct longitudinal gradients in species richness, abundance, Shannon-Weiner diversity, and community analyses were present in the uMlalazi Estuary. In the uMgeni Estuary longitudinal fish assemblage gradients were more variable between sites resulting in fewer reach differences. Overall, as expected, salinity was the determining factor responsible for reach differences, with the riverine and lower reaches being the most different. Fish assemblages during winter (Trip 1) were also different from spring (Trip 2) and summer (Trip 3), with seasonal factors primarily controlled by temperature.

Geomorphologically similar estuaries also share similar fish community patterns and diversity (Harrison et al., 2000). Despite the uMgeni and uMlalazi estuaries being of the same type (permanently open) and in the same bioregion, differences between physico-chemical variables, diversity indices, and fish communities were evident between them. Moreover, distinct guild differences between the estuaries revealed that the uMgeni is primarily a detritus-based system that supports mostly small estuarine species (Ambassidae), detritivores (Mugilidae), and pollution tolerant freshwater opportunists (Cichlidae). In contrast, the uMlalazi Estuary is a more diverse system with fishes from various feeding guilds, including piscivores, and is utilised extensively by marine and estuarine species. Community differences in the uMgeni were directly related to water quality issues, namely lowered dissolved oxygen concentrations, likely linked to the indirect influences of artificial land-cover and land-use activities. A similar observation has been documented in the Seine Estuary, France, which has been subjected to intense development and organic contamination over the years. As a result, suitable nursery habitats for juvenile flatfish have been lost, which along with the contamination of remaining waters, has affected abundances of these fishes (Le Pape et al., 2007). A more recent study, Delaware Coastal Bays, depicted that species richness and densities of estuarine resident species decreased with lowered dissolved oxygen levels and that species preferred natural habitats to modified shorelines (Balouskus and Targett, 2018).

The major higher-order taxa associated with estuarine functioning is still represented in the uMgeni Estuary. However, changes have already occurred with reductions in species richness, abundance, diversity, and overall taxonomic spread, lowering the system’s resilience to change. Future perturbations are more likely to result in the loss of functionally redundant species and ecosystem function and services. Although the uMlalazi Estuary is relatively near-natural with few significant changes since earlier surveys, subtle species-level changes have occurred. Factors relevant to the estuary, such as nutrient input, fishing pressure, and alien species, should be closely monitored to prevent future degradation of the system. The current study addressed the need for updated information on individual permanently open estuaries and for identifying trends in LULC, water quality and fish assemblages over time.

6.2 Contributions and recommendations for estuarine management

Understanding of pressures on estuarine systems, and their consequences, is an important basis upon which management decisions can be made. The Drivers-Pressures-State change-Impact-Response (DPSIR) framework is a valuable integrated approach that has been used globally to assess the causes, consequences and responses to change (Wang et al., 2013; Elliott et al., 2017; Adams and Rajkaran, 2021). The framework has been used on estuaries (Caeiro et al., 2004; Wang et al., 2013), coastal beaches (de Sousa-Felix et al., 2017), freshwater (Skoulikidis, 2009; Pagan et al., 2020), and marine (Atkins et al., 2011) environments incorporating natural, social and economic aspects to provide a holistic viewpoint. Recent efforts have expanded the framework to include Drivers Activities - Pressures - State change - Impact - Human welfare - Response - Measures (DAPSI(W)R(M)), providing a more detailed cause and effect chain (Elliott et al., 2017; Elliott and O' Higgins, 2020). The revised framework identifies the demands of society for food, space or shelter from the environment (Drivers), which are achieved through the implementation of human activities. These activities impose pressures on the environment, resulting in changes to the natural ecosystem (State changes) and inevitably impacting human welfare (Elliott and O' Higgins, 2020).

Few South African studies have incorporated the DAPSI(W)R(M) framework. However, the approach has been applied to macrobenthic assemblages (Sheppard and MacKay, 2018), mangrove systems (Adams and Rajkaran, 2021), whole estuaries (Hamandawana et al., 2020) and coastal management governance (Goble et al., 2017). This study has identified some components that may serve as a starting point for analysing estuarine systems using the DAPSI(W)R(M) framework. Drivers of change are primarily population growth which leads to the transformation of land to accommodate human activities. Artificial land-cover and associated activities have significantly impacted water quality, reflected mostly in dissolved oxygen in this study, likely in response to nutrient loading, which has subsequently changed fish communities and estuarine function. These ecosystem changes may affect fisheries stocks, tourism-based activities, increase health risks to local estuary users, and reduce the ecosystem services derived from estuaries (de Groot et al., 2002; Wilson et al., 2005; Barbier et al., 2011).

Effective management must be implemented to ensure the continuous provision of these estuarine ecosystem services (Atkins et al., 2011). A "ten tenets" approach has been suggested for sustainable management to be successful. The approach considers ecological, technological, social, economic, legal, ethical, administrative, cultural, communicational and ethical aspects (Elliott et al., 2017). Each aspect contributes towards restoration, prevention, mitigation, protection and compliance. Applying the DAPSI(W)R(M) framework to the uMgeni and uMlalazi estuaries may prove useful for motivating and guiding management of the systems and their catchments. The baseline information provided by this study, and the understanding of relationships between land-cover, water quality and biological assemblage gains, will be useful in this regard.

Currently, South African estuaries are governed by the following legislation:

- The National Environmental Management: Biodiversity Act (Act 10 of 2004)
- The Marine Living Resources Act (Act 18 of 1998)
- The National Water Act (Act 36 of 1998)
- The National Environmental Management Act: Integrated Coastal Management Act (ICM Act 24 of 2008) (Van Niekerk et al., 2019; Whitfield, 2019).

Although these acts provide detailed guidelines for effective management, they use outdated information and often fail to integrate their work and enforce their policies (Strydom and Kisten, 2020). A significant contribution to these downfalls is the lack of human and financial capital needed to implement management strategies at the municipal level (Palmer et al., 2011). Human nature demands that value be added to objects or processes for their importance to be understood and their protection to be undertaken (de Groot et al., 2002). The Experimental Ecosystem Accounting approach by the United Nations aimed to encourage this investment in ecosystem protection (UN, 2017). This approach was recently piloted for the South African estuarine realm (Van Niekerk et al., 2020). Applying the accounting approach to South African estuaries may prove helpful in encouraging capital investment from the national government to local municipalities.

In this study, the importance of preserving the natural vegetation surrounding estuarine systems beyond the EFZ and as far as the 20 m contour extent was noted. Other studies have shown that the 5 m EFZ is inadequate for some systems and that land-cover up to the 20 m contour strongly influences the function, diversity, and health status of estuarine biota (Veldkornet et al., 2015; Sheppard and MacKay, 2018). The estuarine functional zone is a highly sensitive ecological area and urban development in this zone directly affects the integrity of the system (Masefield et al., 2014). Similarly, wider riparian zones around freshwater streams have been shown to reduce nitrate and phosphate concentrations from catchment agricultural activities, reduce bank erosion and positively influence stream macroinvertebrates (Weller et al., 2011; Sweeney and Newbold, 2014; Zaimes et al., 2021). A revision of the EFZ is needed to ensure long term protection of estuarine functioning as has already been implemented for some KwaZulu-Natal estuaries in which the 10 m contour delineates the EFZ (Van Niekerk et al., 2019). A correctly delineated EFZ also directly affects human wellbeing by protecting from back-flooding, sea-level rise, storms, pollution buffering and reducing development conflict (Van Niekerk et al., 2019).

Management should focus on preventing habitat degradation in the EFZ through land-use zoning (Hamandawana et al., 2020). The Integrated Coastal Management (ICM) Act was developed to ensure the coastal zone's effective management, in which Estuarine Management Plans are included. In addition to the ICM Act, local municipalities are responsible for developing land-use zonations as per the Spatial Development Framework (Palmer et al., 2011). Specifically for the uMlalazi Estuary, an estuarine management plan should be developed to keep the estuary functioning hydrologically and hydrodynamically as a permanently open estuary. This is vital to ensure the mangrove survival in the estuary (Adams and Rajkaran, 2021) and to maintain the salinity gradients and mouth conditions necessary to support recruitment and survival of estuarine biota.

In many cases, restoration and mitigation initiatives are required through ecoengineering. Ecoengineering can be referred to as manipulating the estuarine system to restore it to pre-impacted conditions or improve its current state to increase ecosystem functioning benefits (Elliott et al., 2016). The successful restoration of estuarine vegetation has been documented globally. In China, artificial afforestation and green space protection reduced turbidity in receiving waters to levels before significant urbanisation (Zhou et al., 2021). Although habitat degradation is irreversible in some areas of the uMgeni Estuary, potential still lies in restoring mangroves, reedbeds and intertidal habitats along the southern bank. Similar restoration initiatives and the development of an Estuarine Management Plan (EMP) have previously been suggested for the uMgeni Estuary. To our knowledge, no such recommendations have been implemented since their conception. Estuarine management plans are currently only available for four South African mangrove supporting estuaries, highlighting the gap between management plans and their successful implementation (Adams and Rajkaran, 2021).

Sowman and Malan (2018) suggested that the lack of capacity, resources, policy confusion, jurisdictional responsibility, and political support contribute to ineffective management plans. Public awareness and education increase the interests of communities, which may quicken the implementation of policies and management plans.

In areas where natural habitat restoration is impossible, artificial landscapes that mimic natural habitats may provide similar estuarine functions (Scyphers et al., 2015). A study conducted in a highly urbanised estuary in Australia showed that artificial structures provided settlement areas for invertebrate species, subsequently supporting zoobenthivorous fish species (Olds et al., 2018). Urban estuaries often support fish communities different from those in natural systems; however, key ecological functions may still be maintained by species more adapted to urbanised environments (Olds et al., 2018). In the uMgeni Estuary, mullet species constitute a significant percentage of the fish assemblage. Mullet species are particularly important in estuarine systems, ingesting and assimilating organic matter, contributing towards the turnover of microbial communities and energy fluxes (Ribeiro et al., 2008). Therefore, the conservation of these urban-tolerant species is essential to ensure the continued ecological functioning of the system. Although modified estuaries may still maintain ecosystem functioning, poor water quality significantly reduces their resilience (Yabsley et al., 2020). The current study clearly depicted the consequences of excessive nutrient input to the uMgeni Estuary via artificial LULC in the 20 m estuarine functional zone.

Highly developed catchments and flow reductions also significantly reduce the resilience of an estuary (Van Niekerk and Turpie, 2012). Population growth in the uMgeni catchment has increased the water demand, with current abstraction rates at 434 million m^3 per year (uMgeni Water., 2019). The catchment supplies water to various districts, interfering with land to sea connectivity, essential for estuarine resilience (Whitfield and Cowley, 2010; Van Niekerk et al., 2019). Diab and Scott (1989) suggested controlled flushing of the system to stimulate seasonal flows. Although releasing water from dams may allow an estuary to remain open, this does not accurately represent a system’s natural flow. Dam releases to the Great Brak Estuary created flow rates that were inadequate to remove excess organic matter or reset sediment levels (Adams et al., 2016). Although it is unlikely that baseflow can be restored to the uMgeni Estuary, other management interventions can prevent further water reductions and improve water quality in receiving waters. For instance, a wastewater reuse plant has been piloted at the Darvill WWTW in Pietermaritzburg. If successful, this will reduce water abstraction from the uMgeni River (uMgeni Water., 2019).

Urban stormwater runoff introduces various pathogens, heavy metals, nutrients and other contaminants into receiving waters, affecting water quality. A water sensitive urban design has been implemented in many Australian cities with the purpose of integrating artificial land-cover and the urban water cycle (Wong, 2006). Initiatives such as bioretention systems have proved successful in filtering pollutants such as nutrients and metals from stormwater runoff (Kim et al., 2003). Similar initiatives for the uMgeni Estuary may alleviate the impacts of an already highly transformed EFZ by improving the water quality of stormwater runoff. The concept of floating wetlands using non-invasive plant species at WWTW has also been considered. The non-invasive aquatic species would reduce nutrient input to receiving waters (uMgeni Water., 2019) and may be particularly useful in the Durban North WWTW identified as having a significant influence on the upper estuary.

Greater emphasis should be given to the Conservation of Agricultural Resources Act (CARA). Currently, guidelines to mitigate the impacts of agriculture on estuaries are not included in this act (Van Niekerk et al., 2019). In catchments that are primarily agricultural-based, as in the uMlalazi, fertilisers can be applied using the principle of “agronomic rates”, meaning reaching crop yields without using excessive fertilisers and modifying drainage canals to reduce nutrient loss into estuarine waters (Paerl et al., 2014). Some regulation of agricultural nutrient inflow may also be achieved by preserving fringing vegetation, as observed in the case of the uMlalazi Estuary Protected Area.

For estuarine management to be effective, adequate and updated information must be available on ecosystem functioning and the biology of ecologically and economically important species (Van Niekerk et al., 2019; Strydom and Kisten, 2020). Likewise, causes of assemblage change or deviation from the “normal” state require updated knowledge of ecological processes as baseline information (Sheaves, 2016). In many instances, system specific information is lacking. This can be problematic for effective management policies that base management initiatives on general estuarine conditions rather than individual estuaries (Sheaves, 2016). Therefore, the current study has bridged this knowledge gap by providing updated ecological information on individual systems of the uMgeni and uMlalazi estuaries.

Frequent sampling of an estuarine system also contributes to long term data sets, which have proven to be an essential resource in biodiversity research and are vital in preventing shifting baseline syndrome (Soga and Gaston, 2018), a phenomenon in which people cannot recognise the severity of environmental degradation because of a lack of memory of its past condition (Pauly, 1995). Study and interpretation of long term data may be challenging because of variations in sampling methodology, spatial extent, frequency, and taxonomic classifications (Magurran et al., 2010). Consequently, few studies have assessed long term ichthyofauna and environmental data (James et al., 2008). Most of these long term studies have not deviated from the use of traditional diversity indices such as the Shannon-Weiner diversity index or species richness (Magurran et al., 2010). This study provided some new insight into the application of new indices. It has shown that other metrics such as taxonomic distinctness may be useful in long term data analyses, particularly where sampling design and gear is variable.

6.3 Future research

Relationships between estuarine physico-chemistry and LULC were illustrated in this study; however, linkages and responses were not always clear, suggesting other factors at play. It is recommended that factors more closely associated with LULC changes such as nutrient concentrations and habitat types be assessed along with fish assemblages. Nitrates, phosphates and ammonia alter water quality dynamics, directly influencing fish distribution (Duque et al., 2020). Studies that assess nutrient concentrations and persistent organic pollutants can correlate fish assemblage patterns more easily to specific land-use activities such as agricultural farming or WWTW. Species diversity is generally greater in estuaries with a range of littoral plants and substrates (Whitfield, 1983). Analyses at this smaller scale will prove useful for identifying habitats that require protection or restoration because they support a large number of species or functionally important species (Mwandya, 2019).

Linked to habitat availability is food availability for fishes. A sound understanding of the structure and functioning of food webs is essential for understanding fish communities in estuaries and the successful management of estuarine systems (Fath et al., 2019). In light of the high species richness of zoobenthivorous fishes in healthy South African estuaries, future studies should investigate potential impacts of pollution events on estuarine zoobenthos and consequently zoobenthivore diversity.

Invasive alien vegetation is a large and increasing problem in the uMgeni Estuary. Floating macrophytes such as *Pontederia crassipes* and *Pistia stratiotes* were encountered during sampling trips. The excessive nutrient inputs and the slow flow rates in the system promote the growth of these species (Adams et al., 2020). Invasive species tolerate environmental stress, have fast growth rates, and outcompete native pioneer species (Legault et al., 2018). *Pontederia crassipes* is the most problematic aquatic species in South Africa. Its spread decreases water dissolved oxygen levels, reduces streamflow, obscures waterways, and alters nutrient cycling (Chamier et al., 2012). The inability of light to penetrate the water column reduces phytoplankton growth and zooplankton, affecting fish communities. Once the plant matter begins to decay, bacteria associated with the decomposition process deplete oxygen levels in the water column (Chamier et al., 2012). The decaying plant matter settles, sediments may become anoxic, and macrobenthic communities are affected (Coetzee et al., 2014).

Invasive alien fish species such as the largemouth bass (*Micropterus salmoides*), guppy (*Poecilia reticulate*), green swordtail (*Xiphophorus hellerii*) and the alien invasive gastropod (*Tarebia granifera*) have also been recorded in the uMgeni Estuary. Introduced fish species may form a barrier against upstream migrating endemic species. They may also predate on the eggs and larvae of marine estuarine dependent species as well as estuarine resident species (Van Niekerk et al., 2019). Estuaries under stress are more susceptible to invasive species than less disturbed systems (Whitfield et al., 2021). Therefore, the occurrence of invasive species in the study estuaries highlights the need to assess the impacts of invasive species on endemic estuarine fish species. This should include the role of invasive fish species as predators and competitors and invasive invertebrate species that alter food resources for indigenous fish species (Whitfield, 2019).

Indices presented in this study could be investigated for use in the National Estuary Health Index, where species richness, abundance and community composition are quantified to assess present ecological status. More specifically, the Estuarine Fish Community Index (EFCI) has value in determining the state of estuarine fish communities and overall environmental condition of the study systems over time. Although not presented in the current study, due to the lack of historical abundance data, it is an effective tool which can be used to communicate complex information in a more simplistic form to policy makers, managers and the public (Harrison and Whitfield, 2004).

Modern science and technologies are currently available which vastly increase the research opportunities within the ichthyological field. Stable isotopes and fatty acid analyses can provide information on energy flows in an estuary (Young et al., 2021), acoustic tracking allows the movement of fishes to be monitored (Dames et al., 2017), and genetic studies can assess the degree of connectivity of estuarine fish species (Phair et al., 2015). Many of these modern technologies such as eDNA and underwater video technology are also non-destructive in comparison to older sampling methodologies and are therefore highly attractive and relevant for future estuarine ichthyofaunal research.

6.4 Closing remarks

The uMgeni and uMlalazi estuaries are regarded as “important” and “highly important” estuaries respectively (Van Niekerk et al., 2019), yet variations in LULC and protection levels have resulted in the two systems having markedly different ecological conditions. The consequences of urbanisation and associated catchment inputs were well represented in the uMgeni Estuary. Comparisons with the uMlalazi Estuary serve as an indication of what can be lost because of habitat degradation in and beyond the current EFZ. The pressures exerted on the EFZs, the wider catchments, and consequently estuaries will increase as populations continue to grow. Therefore, future management should consider the implications of different land-use decisions, particularly in the EFZ, which acts as a buffer against impacts of development in the wider catchment around estuaries and take heed of initiatives that have resulted in the successful protection of estuarine services. Without appropriate protection, these estuaries’ vital ecosystem services and biodiversity may be lost.

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