

Effect of salinity and environmental changes on the fish community of the St Lucia Estuarine System with focus on the salinity tolerance of *Oreochromis mossambicus* (Mozambique Tilapia).

by

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Declaration

I, Quintin Schutte, hereby declare that this whole thesis is my own original work, and to the best of my knowledge, it contains no material previously published or written by person or material submitted in any form for the award of any degree at another university. Where use of the work of others was made it has been duly acknowledged in the text.

Signature.....

Date.....

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Abstract

St Lucia, the largest estuarine lake system in Africa, has been closed since 2002, except for a brief opening in 2007 caused by Cyclone Gamede. Mouth opening in 2007 was preceded by five years of low lake levels and hypersaline conditions which greatly reduced marine fish species diversity. Regardless of this, the freshwater tilapia, *Oreochromis mossambicus* has been found in abundance in all parts of the system. This indicates that *O. mossambicus* is capable of surviving hypersaline conditions when no other fish species can. Mouth opening in March 2007 caused the system to partially fill, marine salinities were restored and also allowed for recruitment of marine species back into the system. Following re-closure in August 2007, salinities in North Lake became hypersaline during 2009-2010. In 2012 a 'beach channel' was dug to re-connect the St Lucia Narrows to the Mfolozi-Msunduzi Estuary, allowing water to enter the system and provide access to the ocean for recruitment of marine species.

The study investigated the effect of salinity and environmental changes on the fish community structure of the St Lucia system during periods of mouth closure as well as after opening of the new beach channel connecting St Lucia to the Mfolozi system. Sampling was conducted from May 2008 – Nov 2014 at six sites in the St Lucia system using small (10 m) and large (70 m) seine nets and CPUE's were calculated for each site as the number of fish, caught per meter of net, per haul. Fish were identified measured and returned to the system. The salinity tolerance of *O. mossambicus* from St Lucia was also investigated under laboratory conditions. Acclimation of *O. mossambicus*, was done at salinity intervals of five, with a 96 hour exposure trial to test for survival.

Spatial changes in the fish community were driven by the salinity gradient across the system, while temporal changes coincided with major changes in the salinity state of the system. Marine species dominated in terms of species number, but freshwater and estuarine species dominated the fish abundance, notably *O. mossambicus* and *Ambassis ambassis*. Prior to opening of the beach channel, the number of species decreased from 51 in 2008 to 37 in 2011. The abundance of marine species

decreased by >75% as the system became progressively more hypersaline and the closed mouth limited recruitment. Opening of the beach channel caused a decline in salinities and allowed for 12 marine species to re-enter the system in limited numbers. *Oreochromis mossambicus* was the most abundant species in the system, accounting for 48.8% of the catch between 2004-2014 and dominating the fish assemblage in salinities between 30-90 (highest recorded salinity). Estuarine species were dominant in salinities between 0-20, while marine species dominated the fish assemblage in salinities between 20-30. In the laboratory the salinity tolerance of *O. mossambicus* was found to be 0-105, with >70% survival in 105.

Freshwater deprivation and mouth closure had the biggest impact on the fish assemblage and a regular, more extensive connection to the ocean is, therefore, needed to maintain healthy fish populations in Lake St Lucia and off-shore marine populations.

Keywords: *Oreochromis mossambicus*, fish assemblage, drought, hypersalinity, recruitment, mouth closure, St Lucia, estuary

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Chapter 1: General Introduction

1.1 The St Lucia Estuarine System - History

The St Lucia system is the largest estuarine lake in Africa and was declared a World Heritage site in 1999. It is the most important estuary on the south east-coast of southern Africa and covers about 80% of the total estuarine area of the province of KwaZulu-Natal (Begg, 1978). Turpie *et al.* (2002) assessed the conservation importance of the St Lucia system and reported that it contributed almost 45% to the calculated estuarine biodiversity of South Africa, which, given that 246 estuaries were assessed, emphasizes the ecological importance of the system. It was also ranked 5th in terms of estuarine importance based on its size and habitat diversity and most importantly, 1st in terms of its fish importance rating.

St Lucia has a surface area of ~350 km², an axial length of 70 km, an average depth of only 0.9 m and an average volume of 322 Mm³ (Begg, 1978; Hutchison and Midgley, 1978; Stretch *et al.*, 2013). The system comprises four interconnected water bodies, False Bay, North Lake, South Lake and the Narrows (Figure 1.1). The Narrows is a 22 km estuarine channel that connects the lakes to the Indian Ocean. Due to St Lucia's large surface area to volume ratio, it is very susceptible to water loss through evaporation, decreased precipitation and river inflow during dry periods (Hutchison and Midgley, 1978).

Sugarcane farming on the Mfolozi River floodplain from the 1930-1950's, which largely destroyed the natural ability of the *Phragmites-Papyrus* swamp to trap river-borne sediment, raised concerns about increasing sediment deposition in the St Lucia mouth. As a result, the St Lucia system was separated from the adjacent Mfolozi-Msunduzi Estuary in 1952, with which it historically shared a common mouth (Taylor, 2006) (Figure 1.2). Historically, during periods of drought, when the combined St Lucia-Mfolozi mouth closed, water from the Mfolozi River, which has the second largest catchment within KwaZulu-Natal, and the Msunduzi River would flow into St Lucia, preventing extreme low lake levels and hypersalinity. Nearing the

end of a drought period increased river flow would cause water levels across the St Lucia system to rise and ultimately the mouth would breach (Whitfield and Taylor, 2009).



Figure 1.1: Map of the St Lucia estuarine system, situated in the iSimangaliso Wetland Park, South Africa (Figure from Perissinotto *et al.*, 2013a).

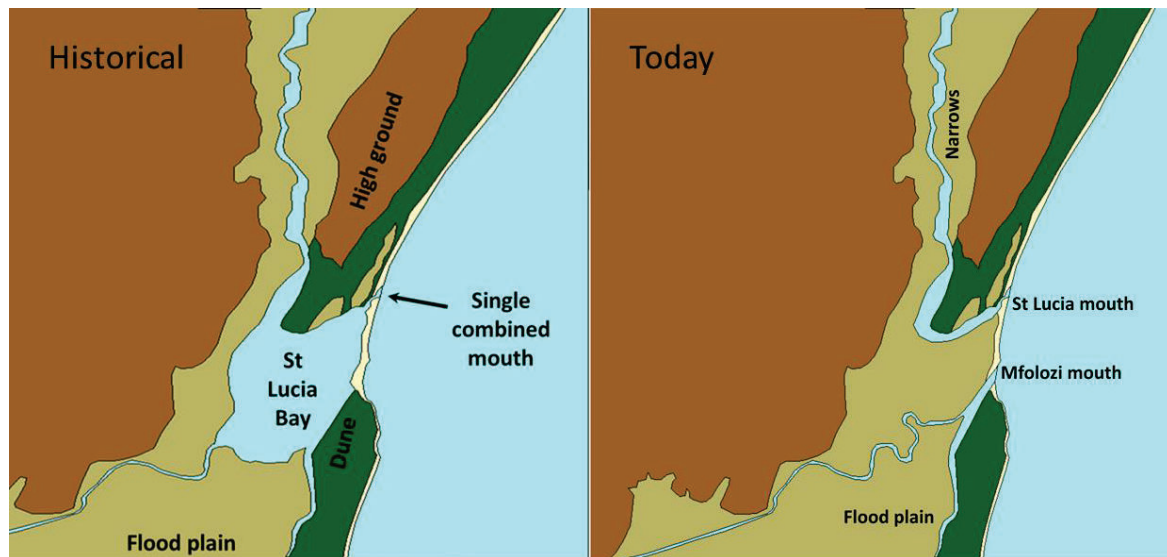


Figure 1.2: Historical (pre 1952) and current mouth states of St Lucia and Mfolozi-Msunduzi systems (Figure from Taylor, 2006).

Following the separation of the St Lucia and the Mfolozi estuaries in 1952, there appears to have been an increase in the frequency of drought driven mouth closures that lasted for longer periods (Cyrus *et al.*, 2010a). The first period of mouth closure after separation was recorded from 1955-1961, during which time the mouth was artificially breached on three occasions, with each open mouth period lasting approximately a year. Salinities did not exceed marine levels during this period (Kriel, 1966; Cyrus *et al.*, 2010a). The next two periods of drought related mouth closure occurred from 1967 to 1972 and 1980 to 1984. During these periods the St Lucia mouth was artificially kept open by dredging, however salinities within the system increased to 110 in False Bay and 55 in South Lake (Cyrus *et al.*, 2010a). During the period 1992 to 1996, the system closed and was dredged open on several occasions, which caused salinities in both South and North Lake to increase to 55 (Taylor, 2006). Since the separation of the St Lucia and Mfolozi systems, the St Lucia mouth has only breached naturally due to external influences of extreme weather events such as cyclones.

The onset of a regional drought in 2001 caused the St Lucia mouth to close in June 2002, as annual rainfall at the time was lower than the average evaporation of 1200

mm year⁻¹ (Hutchison and Midgley, 1978). At the time, Ezemvelo KZN Wildlife (EKZNW) decided not to open the mouth artificially and to let the system breach naturally. During 2003-2004, North and South Lake became hypersaline and compartmentalized with salinities exceeding 200 in False Bay and North Lake, while Charters Creek in South Lake reached over 120, the highest levels ever recorded in the system (Taylor, 2006) (Figure 1.3). By July 2006, lake levels had dropped so low that only 10% of the lake surface was covered by water (Cyrus *et al.*, 2010a). Then, in March 2007, the St Lucia mouth was opened by a storm surge caused by Cyclone Gamede, which passed offshore. The mouth remained open for almost six months (2 March - 24 August), allowing the system to fill to about 75% of full capacity and resetting salinities to marine levels (Vivier *et al.*, 2010a).

In an attempt to direct Mfolozi River water into St Lucia, conservation authorities dredged a channel from the Mfolozi mouth through the mangroves to Honeymoon Bend in the St Lucia Narrows (Figure 1.1). The channel, referred to as the 'back channel', was excavated in the 1960s and diverted water to the St Lucia system from 1970-1973, but has been left in disrepair since. (Whitfield and Taylor, 2009; Taylor, 2013). During periods when the Mfolozi mouth closes, water backs up onto the Mfolozi-Msunduzi floodplain, which allows a limited volume of sediment free water to flow through the back channel into the St Lucia system. In order to prevent a re-occurrence of the extreme low lake levels and hypersalinites experienced during 2003-2006, EKZNW reopened and widened the mangrove-lined back channel between the Mfolozi mouth and the St Lucia Narrows in 2008 (Cyrus *et al.*, 2008). The Mfolozi mouth closed during the low flow winter periods of 2008 and 2010. This allowed 17 Mm³ and 5 Mm³ of estuarine and freshwater to enter the St Lucia system during 2008 and 2010, respectively (Taylor, 2011). It was, however, not sufficient to prevent the lakes from becoming hypersaline again during 2009-2010, with salinities rising as high as 217 in False Bay (Carrasco and Perissinotto, 2012).

Following good rains during the summer of 2010/11 and increased estuarine water inflow through the back channel, water levels increased throughout the St Lucia system and during 2011, salinities returned to estuarine levels (<40 in South Lake).

Despite lake levels during 2011 being the highest since 2007, the mouth, however, remained closed. When Cyclone Irina failed to breach the mouth in March 2012, a new management strategy was introduced for breaching of the St Lucia mouth. This involved EKZNW opening a new channel along the beach from the Mfolozi-Mzunduzi Estuary mouth to the St Lucia Narrows to allow for increased inflow of water (estuarine and fresh) into the system in July 2012. It was anticipated that sufficient water would be diverted via this channel, known as the ‘beach channel’, into St Lucia to prevent a re-occurrence of the extremely low lake levels experienced during 2004-2006 and 2008-2010 as well as increasing the possibility of the mouth breaching naturally in the future. More importantly, it was anticipated that this channel would provide opportunity for recruitment of marine fish and invertebrate species into the St Lucia estuarine system when the Mfolozi mouth was open to the ocean.

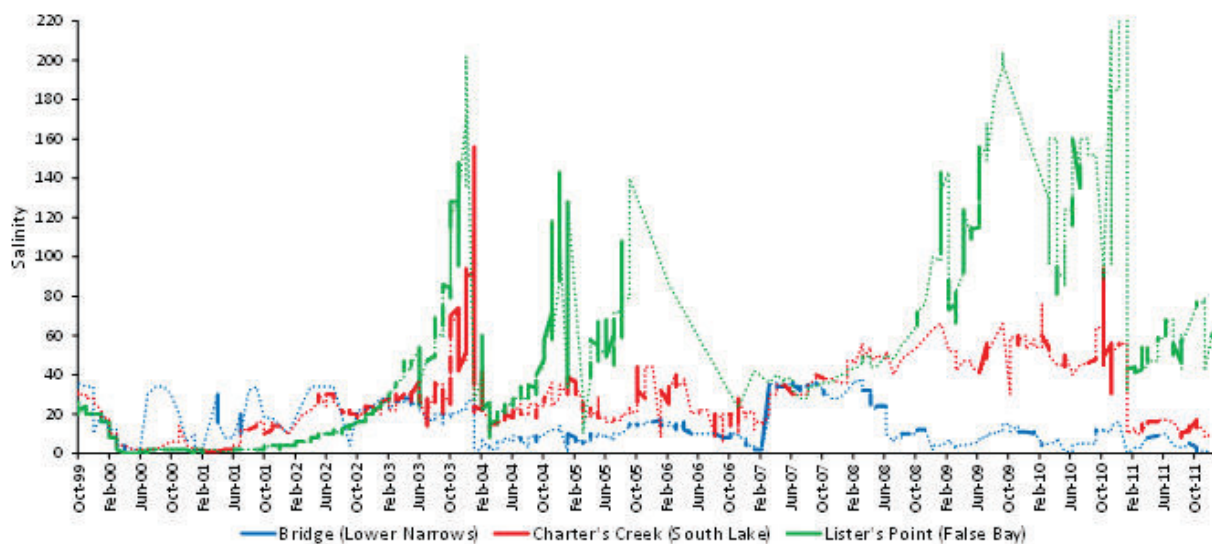


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1.2 Salinity in Estuaries

Within estuarine communities, salinity is considered to be one of the most important factors influencing survival, because estuarine organisms differ widely in their osmotic physiology and salinity tolerance (McLachlan and Erasmus, 1974; Matthews

and Fairweather, 2004). Changes in salinity affect almost all aquatic life forms with euryhaline species being able to tolerate a wide range of salinities, while stenohaline species are only capable of tolerating very narrow ranges.

The St Lucia System is considered as a 'low-inflow' system and is susceptible to becoming hypersaline during dry periods (Largier, 2010), this was even more so after it was separated from the Mfolozi system in 1952. Examples of estuarine systems that experience hypersaline periods are found along the arid coasts of Mexico, Iraq and Western Australia, the temperate west coasts of California (USA), Mexico, Western Australia, the west and south coast of southern Africa (examples include Langebaan, Milnerton Lagoon, Kleinriver Estuary, Heuningnes Estuary and the Kromme Estuary) and along subtropical coasts, of which the St Lucia Estuary system is a prime example (Largier, 2010). Other subtropical estuarine systems that undergo periods of hypersalinity include the Laguna Madre of Texas, Laguna Madre de Tamaulipas and Corpus Christi Bay in the Gulf of Mexico; Lagoa de Araruama and Patos Lagoon in Brazil; Saloum and Casamance Rivers in Senegal and Puttalam Lagoon in Sri Lanka (Largier, 2010). Fish population or community studies under extreme hypersaline conditions have, however, been limited to only a few systems, namely the Laguna Madre (Hedgpeth, 1967), the Beaufort Estuary (Lenanton and Hodgkin, 1985), the Wellstead Estuary (Young and Potter, 2002), the Sine-Saloum Estuary (Simier *et al.*, 2004), the Rio Largartos (Vaga-Cendejas and Hernandez de Satillana, 2004), Lake St Lucia (Vivier *et al.*, 2010a) and the Casamance Estuary (Kantoussan *et al.*, 2012).

The salinity regime of an estuarine system can be divided into different states according to their salinities. Large systems such as St Lucia can have more than one state present at any given time in different areas of the system. An 'estuarine state' is characterised by salinities between 13–35, but may reach up to 65. During this state the mouth is usually open to the ocean. According to Taylor (2006), this state can be subdivided into 'low' estuarine (13–25), 'marine' estuarine (26–45) and 'high' estuarine states (46–65). A 'hypersaline state' occurs when salinities exceed 65, this is usually due to drought conditions when evaporation exceeds precipitation and the

mouth closes. A 'freshwater state' occurs when salinities drop to below 13 and may occur due to significant rainfall events coinciding with a total flushing of the system (Cyrus, 2013).

During open mouth periods St Lucia generally has a salinity gradient much like most other estuaries with marine dominated salinities in the Narrows and southern parts of South Lake, due to the tidal influence. During dry periods, when limited freshwater inflow enters the system, this state may extend well into North Lake (Figure 1.1). During periods of heavy precipitation the system may become less saline due to increased freshwater input into the system, particularly via the Mkuze River in the north. When the St Lucia mouth is closed and cut off from the sea, a reverse salinity gradient is formed, with lowest salinities in the relatively deep Narrows, while hypersaline conditions develop in the shallow lakes due to excessive evaporation. This can also occur when the mouth is kept open artificially, the resulting hypersalinity may not be as severe as during closed mouth conditions but there is a constant input of salt into the system (Lawrie and Stretch, 2011a). During closed mouth conditions with limited freshwater input via the Mfolozi and Mpate Rivers, the salinity gradient in the system can stretch from near freshwater at the mouth to exceeding 200 in North Lake and False Bay (Perissinotto *et al.*, 2013b).

St Lucia has experienced quasi-decadal cycles as the salinity changes within the system according to wet or dry periods and whether the mouth remains open or closed (Day, 1981; Taylor, 1993). The development of hypersaline conditions alternating with limnetic states has happened at regular intervals in the past. In the lake region, major peaks in hypersalinity (salinity >100) have been recorded during the periods 1970-1971, 1983-1984, 2003-2006 and 2009-2010 (Whitfield and Taylor, 2009; Cyrus *et al.*, 2011). This is usually followed by oligohaline to limnetic conditions (salinity <5), due to extreme rainfall events as occurred during 1964, 1976-1978, 1984-1986, 1988-1992 and 2000-2001 (Whitfield and Taylor, 2009; Stretch *et al.*, 2013).

1.3 Effect of Salinity on Fish Community

The fish recorded in the St Lucia system can be classified according to their estuarine dependence, based on the classification by Whitfield (2005a) and revised by Potter *et al.* (2013) for sub-Saharan species (Table 2.1). Fish entering estuaries that breed in the marine environment can be grouped into marine species (M) and include marine estuarine-opportunists, marine estuarine-dependent fish and marine stragglers. Fish that breed in estuaries and are able to conduct their entire life cycle within the estuarine environment, or have a marine or freshwater aspect to their cycle, can be grouped as estuarine species (E). These include the solely estuarine, estuarine-marine, estuarine-freshwater and estuarine migrant species. Fish that occur in estuaries that usually breed in freshwater can be grouped as freshwater species (F) and include freshwater estuarine-opportunists and freshwater stragglers. These groups also have specific salinity ranges in which they occur (Whitfield *et al.*, 2006). The marine species are most abundant within salinities ranging from 10-40, but a large number of species can tolerate salinities up to 70. Freshwater and estuarine species are most abundant under oligohaline conditions. Estuarine species also occur in large numbers up to salinities of 40. The fish population becomes depauperate in salinities above 65 and of all the naturally occurring species within the St Lucia Estuary, only 12 can survive in salinities between 70 and 110, and of these only one (*Oreochromis mossambicus*) has been found to survive in salinities up to 120 (Whitfield and Blaber, 1979a; Costa-Pierce and Riedel, 2000).

The St Lucia system is the largest estuarine nursery on the east coast of southern Africa and is a very important area for many marine fish species with varying dependence on the estuarine environment for part of their life cycle when open (Whitfield, 2005b). The nutrient-rich, sheltered waters of estuaries have been reported world-wide to function as important nursery areas for many marine fish species (Blaber and Blaber, 1980; Young and Potter, 2002; Whitfield *et al.*, 2006), with larvae and juveniles often unable to develop or survive if prevented from recruiting into estuaries (Harrison, 2003; Whitfield, 2005b; Mann and Pradervand, 2007). The prolonged closure of the system prior to Cyclone Gamede, from June

2002 to March 2007, resulted in substantial declines in both diversity and density of a number of fish species, most notably marine breeding species (Cyrus and Vivier, 2006a; Vivier *et al.*, 2010a). The opening of the mouth in 2007 allowed the recruitment of at least 20 euryhaline marine species that were absent from the system during the previous five years (Vivier *et al.*, 2010a). This, combined with the associated increase in lake levels and return to estuarine salinities, allowed for an increase in both species diversity and density, indicating the potential of the fish community to recover to its former state with a regular connection to the ocean (Vivier *et al.*, 2010a).

1.4 *Oreochromis mossambicus* (Mozambique Tilapia)

The Mozambique Tilapia (*Oreochromis mossambicus*) (Figure 1.4) is a member of the Cichlidae family with a wide distribution in southern Africa. It is naturally found in closed and confined estuaries and coastal stretches of rivers on the east coast of southern Africa from the lower Zambezi system down the coast to the Bushmans Estuary in the Eastern Cape (Jubb, 1974; Trewavas, 1983; Skelton, 2001). Dorsally the head and body are greenish in colour and the flanks silvery with three or more distinct black blotches. They can reach a length of 400 mm Standard Length (SL) and mass of 3.3 kg (Smith and Heemstra, 1986). Sexual maturity is reached within one year (Bruton and Allanson, 1974) at a length of between 80 and 120 mm SL (Bruton and Kok, 1980). This tilapia species is highly invasive throughout the world's warm temperate and tropical regions. In southern Africa it has spread outside its natural ranges to inland regions of the south-west and west coast rivers (Skelton, 2001). However *O. mossambicus* is classified as 'Near Threatened' on the IUCN Red List of Threatened Species, due to hybridization with the equally invasive *Oreochromis niloticus* in its natural ranges.

Oreochromis mossambicus is an extremely euryhaline freshwater species. Within the St Lucia estuarine system, under estuarine conditions (salinities 13-35), *O. mossambicus* is normally rare due to competition with other estuarine and marine fish species (Wallace, 1975). However under hypersaline conditions during drought

periods it becomes the most abundant fish species within the system (Cyrus *et al.*, 2011). In a study of the fish community and juvenile recruitment in the St Lucia system, Cyrus and Vivier (2006a) reported that *O. mossambicus* was the most abundant fish species under closed mouth, hypersaline conditions. At the time of the study in 2004 the lake was partitioned into four isolated segments. These were the Narrows, South Lake, the area just north of Fannies Island and finally North Lake, with salinities ranging from 8 to 15 in the Narrows, to 71 at Hell's Gate in North Lake (Figure 1.1). *Oreochromis mossambicus* was found in all four segments of the system and mouth-brooded larvae were present in samples taken in North Lake, Fannies Island, Charters Creek and the Upper Narrows (Cyrus and Vivier, 2006a). This indicated that *O. mossambicus* was able to breed in salinities of more than twice that of seawater. *Oreochromis mossambicus* was also found to be the only fish species to survive in salinities over 110 in North Lake in 2006 (Whitfield *et al.*, 2006; Cyrus *et al.*, 2011). Whitfield and Blaber (1979a) reported that *O. mossambicus* was found in salinities of 117 in St Lucia, while Cyrus (*pers. comm*) observed them in salinities >180 and breeding in salinities >100 (Cyrus, 2013). Wallace (1975) found juvenile *O. mossambicus* in the northern parts of the lake during 1969 and 1970,

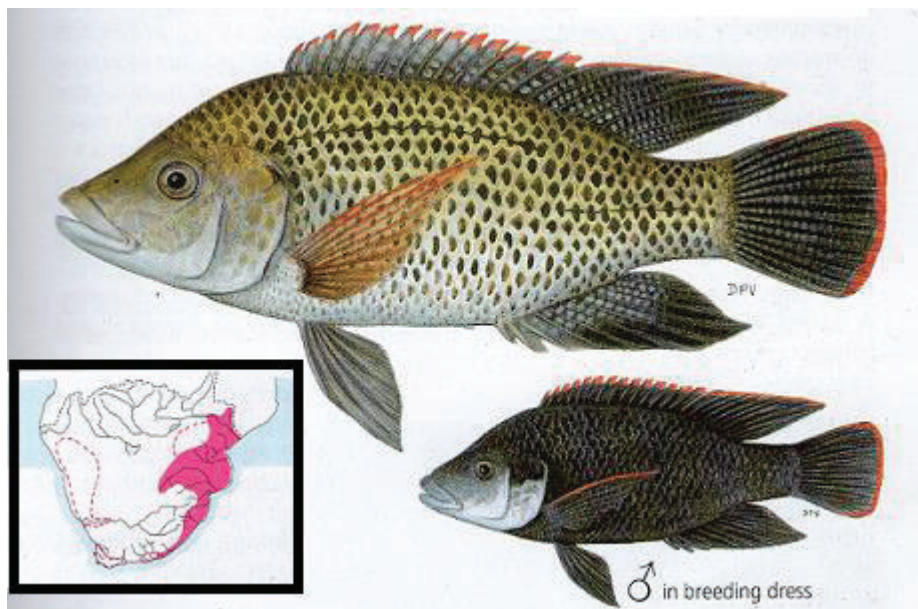


Figure 1.4: Illustration of *Oreochromis mossambicus* (Mozambique Tilapia) with its natural (colour) and introduced (dotted) distributions in southern Africa (Figure from Skelton, 2001).

when the system was also experiencing hypersaline conditions, indicating successful breeding of the species. This was also observed by Van der Elst (1972), with *O. mossambicus* breeding in salinities over 70.

Due to this extreme euryhalinity and ability to survive in captivity (Evans, 1984), *O. mossambicus* has provided a worthy study model for the mechanisms of osmoregulation in teleost fish (e.g., Foskett *et al.*, 1981; Foskett *et al.*, 1983). Under laboratory conditions many studies have been done on the physiological changes that occur within *O. mossambicus* during acclimation from fresh to saline water (Dharmamba *et al.*, 1975; Dange, 1985; Hwang *et al.*, 1989; Kültz *et al.*, 1992; Kültz and Onken, 1993; Borski *et al.*, 1994; Yada *et al.*, 1994; Sardella and Brauner, 2008). However, none have determined the salinity tolerance of *O. mossambicus* under laboratory conditions.

1.5 Motivation for the Study

The St Lucia estuarine system is considered the largest and most important nursery ground in southern Africa for juveniles of marine estuarine-dependent fish species which form the dominant component in large subtropical estuaries (Harrison, 2003). Loss of nursery function in St Lucia during periods of extended mouth closure had devastating consequences for regional off-shore stocks of marine breeding populations (Mann and Pradevand, 2007). Prolonged mouth closure prevents the recruitment of juveniles from the marine environment into the estuary and also prevents maturing adults from leaving the system to join offshore adult breeding populations (Cyrus and Vivier, 2006b; Cyrus *et al.*, 2010a). Mann and Pradervand (2007) showed that the offshore breeding population of *Rhabdosargus sarba* was aging and declining due to the prolonged closure of St Lucia and the associated loss of nursery function. *Rhabdosargus sarba* is only one of 20 marine fish species in regional waters which are totally dependent on estuarine nursery areas for completion of their life cycle. Closure of the mouth also leads to a decline in the number of fish species and abundances (Cyrus and Vivier, 2006a).

The construction of a beach channel will allow estuarine and freshwater fish to enter the St Lucia system when the Mfolozi mouth is closed, which will reduce salinities and increase water levels across the system and hopefully return it to a natural estuarine state. When the Mfolozi mouth is open, the St Lucia system will be reconnected to the ocean, albeit indirectly, and will to some extent resume its function as a nursery ground to marine species which will enter via the Mfolozi estuary. St Lucia will thus receive predominantly estuarine water during low tides from the Mfolozi River and marine water of high tides from the ocean. Many studies have shown that reconnection with the marine environment leads to both an increase in the number of fish species and abundance, especially in the marine group. In both the Wellstead and Beaufort Estuaries (Western Australia), Young and Potter (2002a) and Lenanton and Hodgkin (1985), recorded an increase in marine species after the mouth breached, following extensive periods of mouth closure. When the St Lucia mouth was breached by Cyclone Gamede in 2007, some 20 euryhaline marine species that were lost from the system due to drought related mouth closure were able to recruit back into the nursery area (Vivier *et al.*, 2010a).

This study will contribute to our understanding of the present and current state of the fish community structure within the St Lucia system. It will further provide information on how the fish community is affected by changes in salinity from hypersaline to near fresh, low water levels and the implications of freshwater and marine water input into the system via the beach channel connecting St Lucia to the Mfolozi Estuary and the ocean. The focus on *O. mossambicus*, which dominates the system under prolonged mouth closure and hypersalinity, will improve our understanding of how the population of *O. mossambicus* is altered with varying salinity states as well as to try and determine their salinity tolerance.

1.6 Aims of the Study

The first aim of the study is to assess changes in the fish community of the St Lucia system under different salinity states while the mouth remained closed during the

four year period May 2008 – November 2011, i.e. from after mouth closure following the Cyclone Gamede event, until before the beach channel was opened (Chapter 3*). Secondly, to assess recent efforts by EKZNW to increase freshwater flow from the Mfolozi-Msunduzi Estuary into St Lucia by comparing the fish community structure before (November 2010 - May 2012) and after (November 2012 - May 2014) opening of the beach channel in July 2012 (Chapter 4). Thirdly, to investigate the salinity tolerance of *O. mossambicus* under laboratory conditions (Chapter 5) and finally, to assess the effect of hypersalinity on the population structure of *O. mossambicus* within the St Lucia system over the total sampling period, November 2004, May 2006 – May 2014 (Chapter 5). The following hypotheses were adopted for the study:

- Closed mouth conditions within the St Lucia system causes a change in the fish community involving a decline in both the number of fish species and abundance.
- Salinity is the most important environmental variable responsible for changes in the fish community structure within the system during closed-mouth periods.
- The beach channel will lead to an increase in both the number of fish species and abundances within the St Lucia estuarine system.
- The beach channel is effective in allowing recruitment of estuarine dependent marine fish via the Mfolozi mouth into St Lucia.
- *Oreochromis mossambicus* can tolerate salinities higher than 120 under controlled experimental conditions.
- *Oreochromis mossambicus* from St Lucia has a greater tolerance for hypersalinity than those populations only reared in freshwater.

*Chapter 3 has been written up for publication in *Estuarine, Coastal and Shelf Science*, has been reviewed and resubmitted. It has therefore been formatted and edited according to the Journal's standards, which differ in some ways from the general formatting used in dissertations (and as used in chapters 4 and 5). Additional figures and tables not included in the publication are provided in Appendix 3.

Chapter 2: Materials and Methods

2.1 Study Area

The St Lucia estuarine system (mouth at 28°15'S; 32°30'E) on the east coast of southern Africa (Figure 2.1), is the largest estuarine lake system in Africa, has an axial length of 70 km and covers an area of 350 km² (Begg, 1978; Hutchison and Midgley, 1978). The system can be divided into four regions, the Narrows, a 22 km long channel that connects Lake St Lucia to the ocean, South and North Lake and False Bay. The system has a volume of 322 Mm³ and an average depth of 0.9 m with the deepest areas located within the Narrows and southern parts of the lakes, becoming shallower towards the north (Begg, 1978; Hutchison and Midgley, 1978; Stretch *et al.*, 2013).

The St Lucia system has five rivers providing it with freshwater, the Mpate River in the Upper Narrows, the Nyalazi, Hluhluwe and Mzinene Rivers in False Bay and in the north, the Mkhuze River enters through the Mkhuze swamps (Figure 2.1). Just to the south lies the Mfolozi-Msunduzi Estuary which was historically connected to the St Lucia Narrows, but has been artificially separated since 1952 (Taylor, 2006). Since then several man made channels have been created to connect the two systems, i.e. the link channel and the back channel, both entering in the St Lucia Narrows (when operational).

Recently (July 2012) a beach channel was dug (with a backactor) along the beach to connect the Mfolozi mouth to the St Lucia Narrows. The channel runs from the northern bend of the Mfolozi Estuary just before it enters the ocean and ends on the south side of the St Lucia Narrows where it is blocked from the ocean by the sandbar. It is ~200 m long with a width of 20-50m. The depth and water flow changes with the tides and over the study period the depth has decreased due to sediment build-up in the channel.

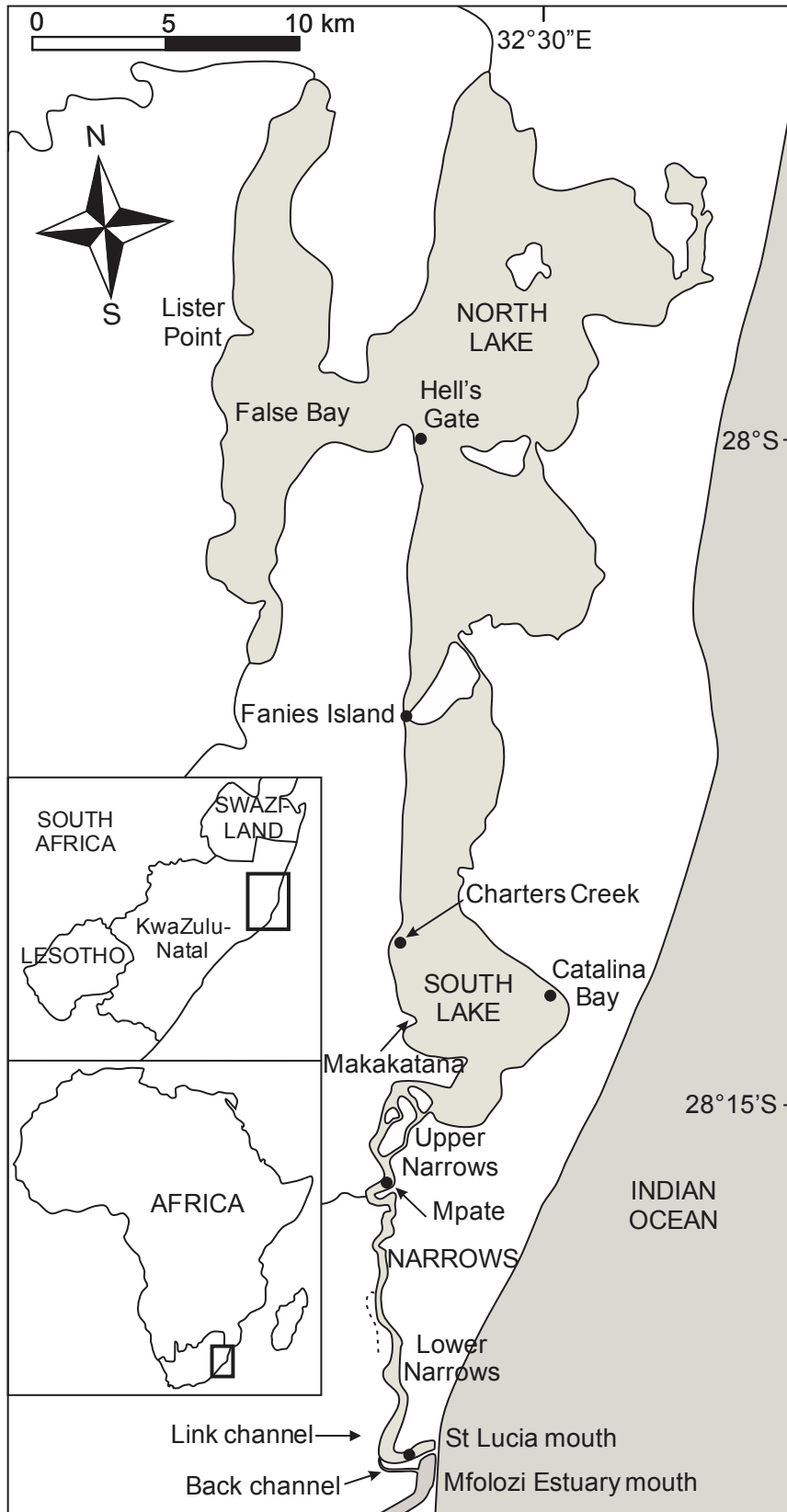


Figure 2.1: The St Lucia estuarine system and its tributaries with the six sampling sites used for large and small seine netting during the study period (Figure by L. Vivier, University of Zululand).

2.2 Sampling

The system was sampled biannually in late May (to represent winter) and early November (as summer) at six sites during the following periods; May 2008 - November 2011 (Chapter 3) and November 2010 - May 2014 (Chapter 4). In addition, historical data collected by researchers from the Zoology Department, University of Zululand, during the period November 2004 to November 2007 were combined with data collected during this study and analysed together in Chapter 5. Sampling was conducted at six sites, two each from the three (Narrows, South Lake and North Lake) majors regions in the system. False Bay was not sampled. The sites were, from the mouth towards the upper reaches, the Lower and Upper Narrows, Catalina Bay and Charters Creek in South Lake, and Fannies Island and Hell's Gate in North Lake (Figure 2.1).

Following Vivier *et al.*, (2010a), two sampling methods were used, small and large seine netting. The small seine net (10 x 1.5 m, 6mm bar mesh) and large seine net (70 x 1.5 m, 10mm bar mesh) were deployed from the shore and then pulled onto an exposed bank. All fish collected were identified, measured (Standard Length) and released. Identification of fish was done according to Smith and Heemstra, (1986). The catch per unit effort (CPUE) for large and small seine netting was calculated as the number of individuals caught per meter of netting per haul. The CPUE from all Small and Large seine nets were combined and a single value for each site was calculated. Where possible, fish samples were collected from all six sites using the two sampling methods. When low water levels prevented deployment of nets it was noted as a CPUE = 0 catch. Where nets could not be deployed due to lack of exposed banks, the decision was made to exclude the site during that sampling season (Catalina Bay, May – November 2013).

Physical water quality parameters were measured at each site using a YSI 6920 Sonde (YSI Incorporated), these included temperature (°C), pH, turbidity (NTU), dissolved oxygen (mg l^{-1}), oxygen saturation (%), depth (m) and salinity. For salinity measurements the Practical Salinity Scale (PSS) was used, which is a

dimensionless unit as recommended by the Intergovernmental Oceanographic Commission of UNESCO (McLusky and Elliott, 2004; UNESCO-IOC, 2009).

2.3 Estuarine Association

The fish recorded in the St Lucia system were broadly classified according to their estuarine dependence, based on the classification by Whitfield (2005a) and revised by Potter *et al.* (2013) for sub-Saharan species (Table 2.1).

- Fish entering estuaries that breed in the marine environment were grouped into marine species (M). This group includes marine estuarine-opportunists, marine estuarine-dependent fish and marine stragglers.
- Fish that breed in estuaries and are able to conduct their entire life cycle within the estuarine environment, or have a marine or freshwater aspect to their cycle, were grouped as estuarine species (E). These include the solely estuarine, estuarine-marine, estuarine-freshwater and estuarine migrant species.
- Fish that occur in estuaries that usually breed in freshwater were grouped as freshwater species (F) and include freshwater estuarine-opportunists and freshwater stragglers.

2.4 Salinity Tolerance

2.4.1 Fish collection

For the laboratory salinity tolerance trials on *Oreochromis mossambicus*, fish from both the University of Zululand hatchery (UniZulu) (hatchery reared, freshwater adapted) and from the St Lucia Estuarine System (wild stock, brackish water adapted) were used. A total of 60 fish from St Lucia (80mm – 100mm SL) (Bruton and Kok, 1980) were collected at Charters Creek and Fannies Island, following sampling methods by Vivier *et al.*, (2010a), described in section 2.2 of this chapter and transported back to the laboratory in a 500 L holding tank.

Table 2.1: Definitions of the different categories and guilds of the estuarine usage functional groups. O and F refer to obligate and facultative users of estuaries, respectively. A refers to species that ‘accidentally’ stray into estuaries. *Refers only to the estuarine population of the guild (Table adapted from Potter *et al.*, 2013).

Category and guild	Definition	Example
Marine Category (M)		
Species that spawn at sea		
Marine straggler	A Typically enter estuaries sporadically and in low numbers and are most common in the lower reaches where salinities typically do not decline far below - 35. Often stenohaline	Sand steenbars, (<i>Lithognathus mormyrus</i> , Sparidae) Colorado snapper (<i>Lutjanus colorado</i> , Lutjanidae)
Marine estuarine-opportuist	F Regularly enter estuaries in substantial numbers, particularly as juveniles, but use, to varying degree, coastal marine waters as alternative nursery areas	Bluefin (<i>Pomatomus saltatrix</i> , Pomatomidae) Flathead mullet (<i>Mugil cephalus</i> , Mugilidae)
Marine estuarine-dependent	O Juveniles require sheltered estuarine habitats and are thus not present along exposed coasts where they spend the rest of their life	Cape stummose (<i>Rhabdosargus holobi</i> , Sparidae) Oval moony (<i>Monodactylus falciformis</i> , Monodactylidae)
Estuarine Category (E)		
Species with population in which the individual completes their life cycles within the estuary		
Solely estuarine	O Found only in estuaries	Elongate hardyhead (<i>Atherinosoma elongata</i> , Atherinidae) Estuarine round herring (<i>Gilchristella aestuaria</i> , Clupeidae)
Estuarine & marine	O* Also represented in marine populations	Super klipfish (<i>Clinus superciliosus</i> , Clinidae) Longsnout piperfish (<i>Syngnathus temmincki</i> , Syngnathidae)
Estuarine & freshwater	O* Also represented in freshwater populations	Western hardyhead (<i>Leptatherina wallacei</i> , Atherinidae) River goby (<i>Glossogobius callidus</i> , Gobiidae)
Estuarine migrant	O Spawn in estuaries but may be flushed out to sea as larvae and later return at some stage to the estuary	Prison goby (<i>Caffrogobius gilchristi</i> , Gobiidae) Knysna sandgoby (<i>Psammogobius knysnaensis</i> , Gobiidae)
Freshwater Category (F)		
Species that spawn in freshwater		
Freshwater straggler	A Found in low number in estuaries and whose distribution is usually limited to the low salinity, upper reaches of estuaries	Goldfish (<i>Carassius auratus</i> , Cyprinidae) Redbreast tilapia (<i>Tilapia rendalli</i> , Cichlidae)
Freshwater estuarine-opportunist	F Found regularly and in moderate numbers in estuaries and whose distribution can extend well beyond the oligohaline sections of these systems	Mozambique tilapia (<i>Oreochromis mossambicus</i> , Cichlidae) Checked goby (<i>Redigobius dewaali</i> , Gobiidae)

At the Zoology Department hatchery, *O. mossambicus* were kept in indoor holding tanks (300 L) during the entire experimental period. Fish were kept at 22°C under natural photoperiod (14h:10h, light/dark) conditions in a through-flow system fitted with a biological (coral) filter system. Fish were kept at salinities similar to those in which they were caught prior to the start of the experiment and then increased up to 75% seawater. They were fed 2% body weight of Trout Feed twice a week.

2.4.2 Acclimation

Salinity tolerance was determined for *O. mossambicus* from the UniZulu hatchery stock and St Lucia to test the hypothesis that St Lucia fish had a greater tolerance for high salinities. Three aerated 300 L tanks (System 1-3) were divided into two halves using plastic mesh, each tank was filled with 13 UniZulu fish (Group A) in one half and 13 St Lucia fish (Group B) in the other half (Figure 2.2). Group A was placed in acclimation tanks with salinity of 0. The salinity of the three systems were then gradually increased to 75% seawater at which point Group B was placed in the acclimation tanks. Previous studies have indicated that *O. mossambicus* cannot tolerate an abrupt transfer from freshwater to full-strength seawater and require a gradual (one week) acclimation period (Stickney, 1986). Water temperatures were kept constant in each treatment tank at 22°C and aeration was provided to maintain dissolved oxygen level above 95% saturation. The salinity was then increased up to seawater (salinity of 35) and then by intervals of five every five days. During the time between salinity increases a 96 hour exposure trial to test survival was conducted. This procedure was repeated over a period of four months for the three systems until no fish remained. Artificial seawater (Seachem - Reefsalt), was used to raise the salinity throughout the experiments. Survival of fishes was determined on a daily basis. System, group and date were recorded whenever a dead fish was found.

Due to the nature of the experiment, death is the only way to determine the upper salinity tolerance of the species and from an ethics point, the minimum number of fish was used to allow for statistical comparison between groups throughout. Ethical certification was obtained from the University of Zululand's Research Ethics Committee (Certificate Number: UZREC 171110-030 PGM 2012/15).

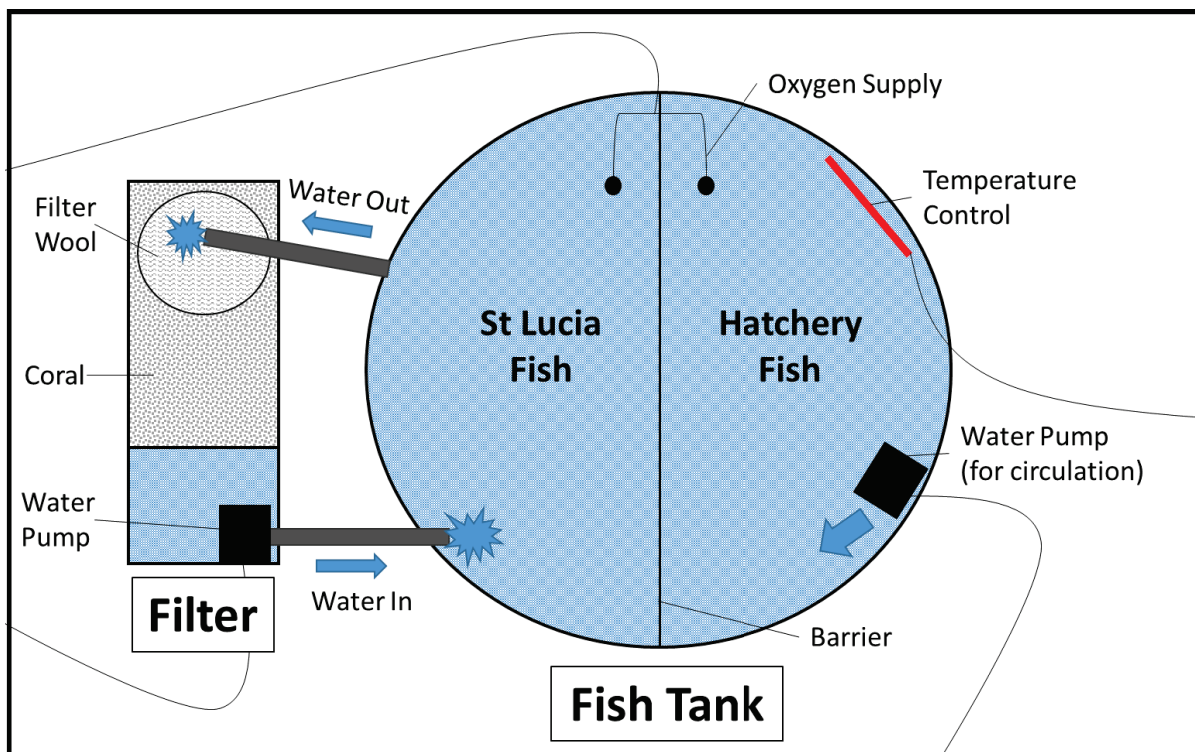


Figure 2.2: Diagram of acclimation fish tank set-up with photos of the biological filter and the holding tank.

2.5 Statistical Analysis

Variables were first tested for normality (Shapiro-Wilks test) and where variables were found to display a non-normal distribution, the Kruskal-Wallis test was used to test for significant differences between mean CPUE (N), number of species (S), species evenness (J'), species richness (D) and species diversity (H') collected during different sampling seasons and years and at different regions and sites.

Multivariate data analyses (PRIMER v6 Statistical Package) (Clarke and Warwick, 2006), were used to analyse for temporal and spatial changes in the fish community. The 4th root transformed averaged (regions, sites, years and sampling seasons) species CPUE data was used to calculate a Bray-Curtis similarity matrix, which was then subjected to hierarchical and agglomerative clustering, with group average linking, and ordination through non-metric multidimensional scaling (MDS). SIMPROF procedure was used in conjunction with Cluster investigated for significant structuring in the data. PERMANOVA (Anderson *et al.*, 2008) was used to test for significant differences in species assemblage between sampling seasons, years, sites and regions, and to test for interactions between these factors, two-way and nested analyses were used. The SIMPER procedure was used to determine the influence of individual species on the dissimilarities within sites and years.

Principal component analysis (PCA) in CANOCO (Ter Braak and Smilauer, 1998), was used to investigate the relationship between environmental variables and canonical correspondence analysis (CCA) was used to investigate the relationship between fish community composition and environmental variables. Pearson Product-Moment was used to correlated species abundance (CPUE) and salinity to investigate possible relationship between them.

Chapter 3: Effect of Mouth Closure and Hypersalinity on the Fish Community of the St Lucia Estuarine System (South Africa) after Cyclone Gamede.

3.1 Results

3.1.1 Physico-chemical Water Data

During May 2008, nine months after the St Lucia mouth closed, salinities in the Narrows had dropped to below marine levels (23.3-25.5) and continued to decrease from 2008 to 2011, reaching a low of 2.4 in November 2011. This was mainly due to freshwater inflow from the Mpate River and from the Mfolozi River via the back channel. In contrast, North and South Lake became hypersaline soon after the mouth closed in August 2007. During 2008, salinities were uniform throughout South and North Lake, ranging between 45.2-49.4. South Lake remained hypersaline (range 42.2-56.7) until 2010, but after good seasonal rains that year, it gradually decreased to a low of 11.1 in November 2011. In North Lake, salinity gradually increased from May 2008 to a maximum of 90 in November 2009 at Hell's Gate, followed by a gradual decrease to November 2011, with Fannies Island and Hell's Gate reaching salinities of 35.7 and 58.4, respectively (Figure 3.1).

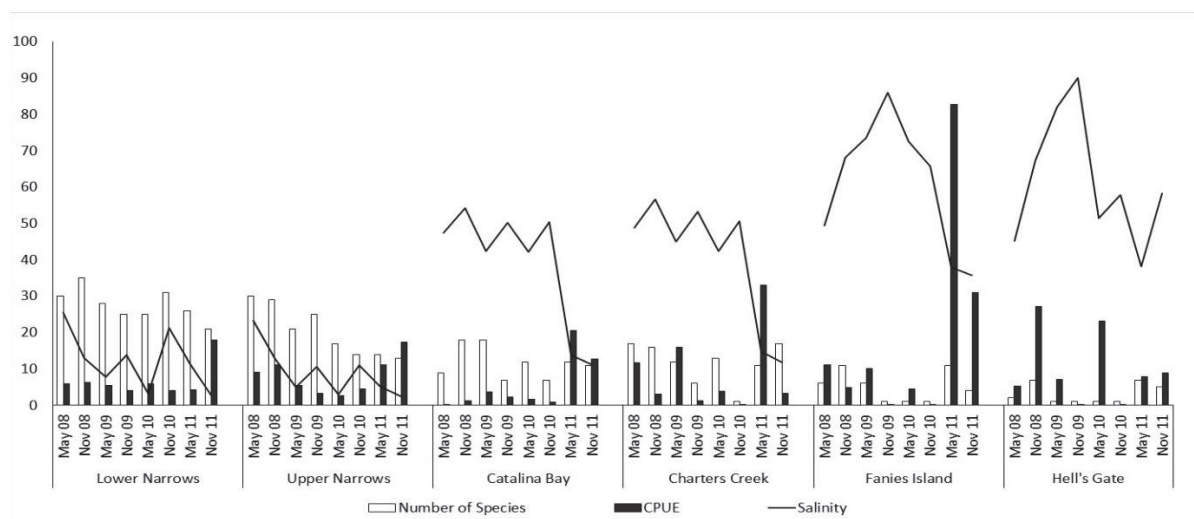


Figure 3.1: The salinity, number of species and abundance (CPUE) recorded biannually at six sampling sites in the St Lucia system during the period 2008-2011.

Water temperatures in May (19.9-26.2°C) and November (21.0-30.8°C) reflected typical winter and summer conditions. Dissolved oxygen concentrations (4.3-12.3 mg l⁻¹) and % oxygen saturation (60.0-126.5%) remained high throughout the study period, while a mean pH of 8.4 reflected the saline conditions throughout most of the system. Water turbidity was lower in May (3.7-101.6 NTU), compared to November, when generally windy summer conditions resulted in higher turbidities (23.1-512.7 NTU). Highest turbidities were recorded in Catalina Bay on the Eastern shore during 2008 (373.6 NTU) and 2010 (512.7 NTU).

3.1.2 Species Composition

A total of 19,726 fish representing 61 species was recorded in the St Lucia system during the period 2008-2011 (Table 3.1). The total number of species per site gradually decreased from the Lower Narrows (n = 54, range 20-35) towards Hell's Gate (n = 12, range 1-7) (Table 3.1; Figure 3.2). In contrast, fish abundance (CPUE) increased from the mouth (Lower Narrows) (CPUE = 6.7, range 4.0-18.1) towards the lakes, with the highest mean CPUE being recorded at Fannies Island (CPUE = 18.0, range 0.01-82.7) (Figure 3.2). The total number of species recorded gradually decreased throughout the study period, from May 2008 (n = 43, range 2-30) to November 2011 (n = 29, range 4-20) (Table 3.1; Figure 3.2). Mean seasonal CPUE decreased from 2008 to 2010, followed by a marked increase in 2011 (Figure 3.2).

Differences in the number of species, CPUE, species richness, evenness and diversity among regions, sites, years, sampling seasons and seasons (winter/summer) as determined by ANOVA are presented in Table 3.2. There were significant differences among region and sites for all five indices, which indicated a strong spatial gradient in species composition across the system (Table 3.2). In contrast, there were no significant differences among years, samples or seasons (Table 3.2).

Table 3.1: The fish species, estuarine association category (Est Ass) and total CPUE recorded per sampling season and sampling site from 2008-2011 in the St Lucia system. Species contributing >1% to the total CPUE are highlighted. (Sites: LN, Lower Narrows; UN, Upper Narrows; CB, Catalina Bay; CC, Charters Creek; FI, Fannies Island; HG, Hell's Gate. Est Ass: E, Estuarine species; F, Freshwater species; M, Marine species).

Species	Est Ass	2008		2009		2010		2011		SITES						Total %
		May	Nov	May	Nov	May	Nov	May	Nov	LN	UN	CB	CC	FI	HG	
<i>Acanthopagrus vagus</i>	M	0.53	0.20	0.14	0.06	0.01	0.03	0.03		0.28	0.68	0.01	0.01	0.01		0.22%
<i>Ambassis ambassis</i>	E	7.54	3.44	0.39	0.36	0.68	0.48	89.25	49.22	20.22	20.46	28.54	12.91	64.70	4.53	33.05%
<i>Ambassis dussumieri</i>	E			0.03						0.03						0.01%
<i>Ambassis natalensis</i>	E	0.07		0.45	0.01			13.35	0.07	0.33	0.21		13.40			3.04%
<i>Argyrosomus japonicus</i>	M	0.003		0.003				0.003		0.003		0.01				0.002%
<i>Arothron hispidus</i>	M	0.01											0.01			0.003%
<i>Arothron immaculatus</i>	M	0.01											0.01			0.003%
<i>Caranx ignobilis</i>	M	0.02	0.02							0.03	0.01					0.01%
<i>Caranx sem</i>	M		0.003							0.003						0.001%
<i>Caranx sexfaciatus</i>	M	0.02	0.01							0.02	0.003	0.003				0.01%
<i>Carcharhinus leucas</i>	M	0.003				0.003						0.003	0.003			0.001%
<i>Chanos chanos</i>	M			0.01		0.003						0.003	0.003	0.003		0.002%
<i>Chelon melinopterus</i>	M			0.23	0.03		0.10			0.15	0.10	0.11				0.08%
<i>Clarias gariepinus</i>	F				0.01			0.02	0.01	0.005	0.03					0.01%
<i>Drepane longimana</i>	M	0.01	0.003									0.01	0.003			0.002%
<i>Elops machnata</i>	M	0.02	0.02	0.10	0.02	0.03	0.01	0.02	0.02	0.03	0.05	0.07	0.04	0.04		0.05%
<i>Gerres filamentosus</i>	M	0.21	0.20	0.06	0.06	0.04	0.004	0.01		0.45	0.07	0.06				0.13%
<i>Gerres longirostris</i>	M	0.10	0.04	0.08		0.11	0.004		0.10	0.20	0.20	0.03	0.01			0.09%
<i>Gerres metheuni</i>	M	0.03	0.21	0.09		0.06	0.01		0.005	0.23	0.10	0.09				0.09%
<i>Gilchristella aestuaria</i>	E	0.07	9.96		0.05	0.35	1.88	0.07		1.12	1.49		0.17	0.20	9.40	2.70%
<i>Glossogobius callidus</i>	E		0.07	0.31	1.31	0.94	0.61	3.39	0.55	1.59	4.71	0.03	0.48	0.25	0.13	1.57%
<i>Glossogobius giurus</i>	F	0.01		0.56	0.06	0.04	0.01	0.08	0.01	0.06	0.63	0.03	0.03	0.01		0.17%
<i>Glossogobius tenuiformis</i>	E			0.14				0.20	0.10	0.14	0.13				0.17	0.10%
<i>Goby fry</i>	E			0.01				0.03	0.10	0.14						0.03%
<i>Hilsa kelee</i>	M	0.04	0.06	0.11	0.003	0.04	0.003			0.05	0.19	0.01	0.003			0.05%
<i>Hyporhamphus capensis</i>	E		0.61	0.24	0.25	0.04	0.78	0.43		0.28	0.18	0.21	0.95	0.58	0.15	0.51%
<i>Johnius dorsalis</i>	M	0.003	0.003						0.01	0.003		0.01	0.003			0.003%
<i>Leiognathus equula</i>	M	4.81	7.31	1.74	0.60	1.37	0.45	0.23	0.03	6.18	10.27	0.06	0.01		0.01	3.61%
<i>Liza alata</i>	M		0.003	0.09	0.003	0.003	0.003	0.02	0.01	0.03	0.01		0.09			0.03%
<i>Liza dumerilii</i>	M	0.30	1.35	1.74	1.18	2.21	0.52	1.30	3.60	1.84	0.98	1.14	5.87	2.37		2.66%
<i>Liza macrolepis</i>	M	0.08	1.22	0.51	1.61	0.06	0.15	0.20	1.58	0.73	0.59	1.73	0.82	0.02	1.53	1.18%
<i>Lutjanus argentimaculatus</i>	M		0.02	0.05	0.01	0.01				0.05	0.04					0.02%
<i>Lutjanus fulviflamma</i>	M	0.01	0.004	4.27	0.05	0.03				0.02	0.08		4.27			0.95%
<i>Megalops cyprinoides</i>	M		0.003				0.02	0.02		0.003	0.03					0.01%
<i>Monodactylus argenteus</i>	M	1.21	0.88	0.17	0.11	0.13	0.05			1.90	0.63			0.03		0.56%
<i>Mugil cephalus</i>	M	0.01	0.01	0.01	0.05	0.01	0.003	0.003	0.11	0.13	0.06	0.02	0.01			0.05%
<i>Muraenesox bagio</i>	M						0.003			0.003						0.001%
<i>Myxus capensis</i>	M	0.03		0.01	0.01					0.03	0.01	0.01				0.01%
<i>Oligolepis keiensis</i>	E				0.03	0.06				0.06			0.03			0.02%
<i>Oreochromis mossambicus</i>	F	26.43	24.91	33.38	2.87	34.24	4.91	41.66	31.59	12.44	15.28	7.53	32.48	68.89	63.38	43.67%
<i>Platycephalus indicus</i>	M	0.03	0.03	0.02				0.003	0.01	0.03	0.02	0.01	0.03			0.02%
<i>Pomadasys commersonnii</i>	M	0.03	0.07	0.10	0.54	0.10	0.05	0.06	0.08	0.28	0.53	0.08	0.01	0.05	0.08	0.22%
<i>Pomadasys kaakan</i>	M	0.08	0.02	0.003		0.003	0.01	0.003	0.01	0.07	0.04	0.01				0.03%
<i>Pomadasys olivaceus</i>	M	0.01		1.03	0.22		0.01	3.19		0.03	0.15	0.14	0.02	4.00	0.11	0.97%
<i>Pomatotus saltatrix</i>	M	0.01	0.01	0.003						0.003	0.003	0.01	0.003			0.003%
<i>Pseudocrenilabrus philander</i>	F						0.11	0.44	3.53	1.19	1.60	1.07	0.20		0.03	0.89%
<i>Pseudorhombius arsius</i>	M	0.08	0.02							0.03	0.07					0.02%
<i>Rhabdosargus holubi</i>	M	0.04	0.17	0.02	0.03	0.10	0.01	0.01		0.14	0.09	0.10	0.03	0.01		0.08%
<i>Rhabdosargus sarba</i>	M	0.32	0.19	0.63	0.04	0.26	0.02	0.02	0.01	0.33	0.31	0.69	0.10	0.05		0.32%
<i>Rhabdosargus thorpei</i>	M		0.01			0.003				0.003	0.003		0.003			0.002%
<i>Scomberoides lysan</i>	M	0.02	0.01			0.01				0.02	0.01	0.003				0.01%
<i>Silhouettea sibayi</i>	E	0.48	0.40	0.52	0.14	0.27	0.07	0.37	0.13	0.41	0.47	1.00	0.23	0.13	0.15	0.52%
<i>Sillago sihama</i>	M	0.03	0.07	0.08			0.03	0.01		0.11	0.03	0.08				0.05%
<i>Solea turbynei</i>	M	0.01	0.14	0.22	0.01	0.04	0.22	0.01	0.03	0.16	0.23	0.20	0.10			0.15%
<i>Sphyaena jello</i>	M					0.01					0.01					0.003%
<i>Stolephorus holedon</i>	M		0.03							0.03						0.01%
<i>Terapon jarbua</i>	M	0.18	0.15	0.01	0.08	0.48	0.48	0.06	0.02	1.20	0.26					0.32%
<i>Thyssa vitrirostris</i>	M	0.38	1.16	0.22	0.64	0.12	0.80	2.95	0.04	0.79	2.33	0.34	0.07	2.80		1.38%
<i>Tylosurus sp.</i>	M	0.003											0.003			0.001%
<i>Valamugil buchanani</i>	M			0.02	0.003		0.003	0.003		0.02		0.003	0.003			0.01%
<i>Valamugil cunnesius</i>	M	0.03	0.50	0.23	0.39	0.02	0.05	0.01	0.01	0.30	0.92	0.01				0.27%
<i>Valamugil seheli</i>	M	0.01	0.02			0.003			0.01	0.04	0.003					0.01%
Number of Species		43	42	39	33	35	34	33	29	54	48	38	36	18	12	61
Total CPUE		43.32	53.54	47.75	10.83	41.76	9.62	159.61	91.50	53.95	64.33	43.42	72.42	144.14	79.68	457.93
Average per Season or Site		7.22	8.92	7.96	1.80	6.96	1.60	26.60	15.23	6.74	8.04	5.43	9.05	18.02	9.96	

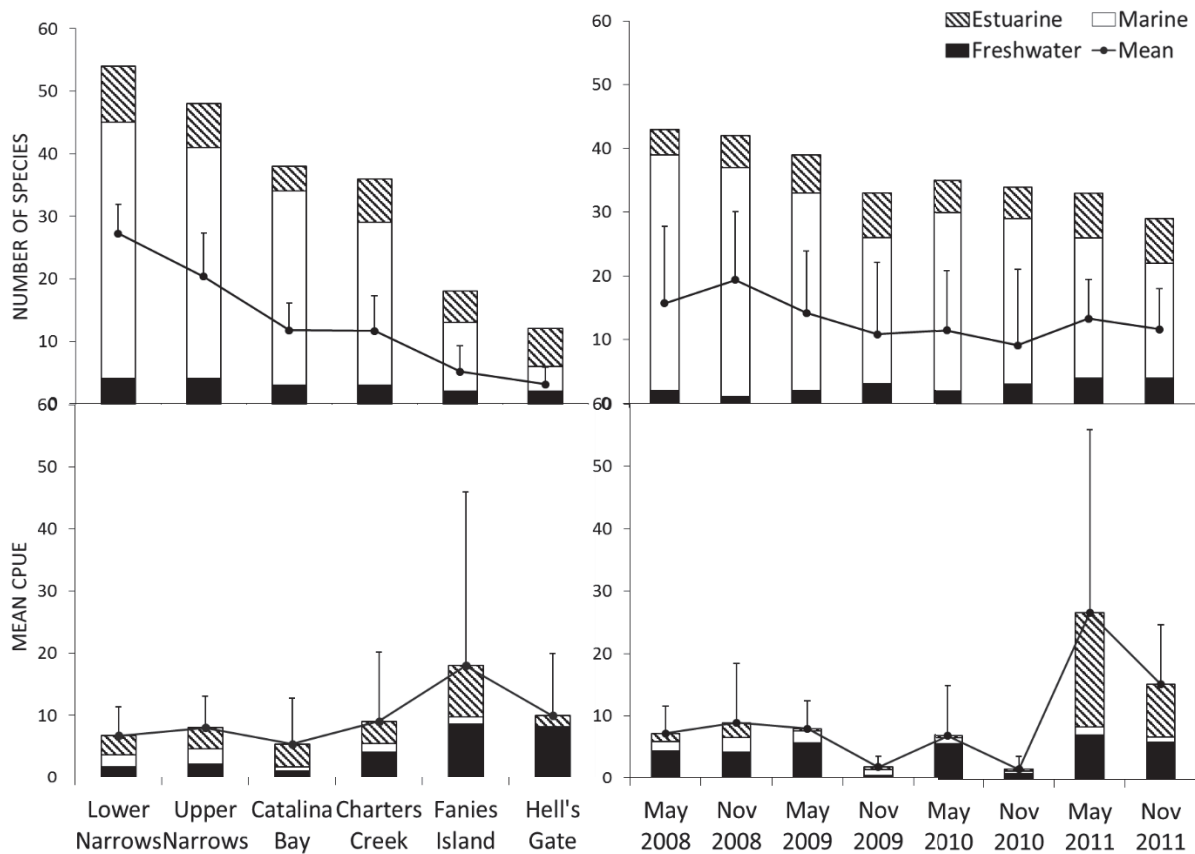


Figure 3.2: The total number of species, mean number of species (+1SD), mean abundance (CPUE) (+1SD) and estuarine association groups of the fish recorded at the six sampling sites and during the eight sampling seasons in the St Lucia system during 2008-2011.

The fish community was dominated by the freshwater species *Oreochromis mossambicus* and the estuarine species *Ambassis ambassis*, which accounted for 43.7% and 33.0% of the total catch, respectively (Table 3.1). The only other numerically important estuarine species included *Ambassis natalensis* (3.0%) and *Gilchristella aestuaria* (2.7%), while the only marine species that contributed more than 2% to the total catch were *Leiognathus equula* (3.6%) and *Liza dumerilii* (2.7%) (Table 3.1). *Oreochromis mossambicus* was the dominant species during 2008-2010, while *A. ambassis* became the most abundant species in 2011. During May 2010, *O. mossambicus* accounted for 76% of the fish sampled, completely dominating the system. Other numerically abundant species recorded per year included *Monodactylus argenteus* (2008), *Thryssa vitirostris* (2008 and 2010), *Lutjanus fulviflamma*, *Liza macrolepis* and *Pomadasys olivaceus* (2009), *Glossogobius callidus* (2009, 2010 and 2011), *Terapon jarbua* (2010) and *Pseudocrenilabrus philander* (2011) (Figure 3.3).

Table 3.2: ANOVA of univariate indices of the St Lucia fish community recorded during 2008–2011. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$ (Number of Species, S; Density (CPUE), N; Evenness (Pielou's), $D = (S-1)/\log(N)$; Species Richness (Margalef), $J' = H'/\log(S)$ and Diversity (Shannon), $H' = \sum(P_i \cdot \log(P_i))$).

Kruskal Wallis: Non-parametric ANOVA					
	Region (R)	Site (Si)	Year (Y)	Sample (Ss)	Season (Se)
<i>df</i>	2	5	3	7	1
S	27.6***	36.1***	3.3	2.9	4.3
N	24.5***	32.3***	3.9	2.2	6.7
D	25.3***	21.4***	2.8	4.2	3.1
J'	11.1**	35.7***	4.6	11.8	5.5
H'	27.6***	36.0***	3.1	3.6	4.6

Two-and Three way interaction							
	Y x Si	Si x Se	R x Ss	R x Se	R x Y	Y x Se	R x Y x Se
<i>df</i>	12	5	11	2	5	3	4
S	1.0	0.3	1.7	0.1	1.9	0.2	2.5
N	2.4*	0.2	2.1	0.4	3.3*	0.5	0.4
D	1.8	0.1	1.2	0.1	1.2	0.1	0.9
J'	1.5	0.2	1.1	0.7	2.1	0.9	1.5
H'	1.4	3.1*	0.9	0.2	1.2	0.5	0.2

Nested interaction						
	Region (R)	R(Site)	Year (Y)	Y(Sample)	Season (Se)	Se(Sample)
<i>df</i>	2	3	3	4	1	6
S	46.7	1.9	0.6	0.2	<0.1	0.6
N	34.0	2.2	0.1	0.4	<0.1	0.3
D	45.8	3.5	1.2	0.1	<0.1	0.4
J'	38.1	3.2	3.0*	0.8	<0.1	0.6
H'	5.8	1.3	0.6	0.4	0.9	1.9

3.1.3 Estuarine Association

In terms of numbers of species, the system was dominated by marine spawning species, but in terms of fish abundance (CPUE), freshwater and estuarine breeding species were most abundant (Table 3.1; Figure 3.2). Of the 61 fish species recorded in the system, 48 were marine species. Of the remaining 13 species, nine were estuarine species and only four were freshwater species (Table 3.1). The number of marine species in the system decreased markedly after the mouth closed in 2007, from 37 in May 2008 to 18 in November 2011 (Figure 3.2). At the same time, the number of freshwater and estuarine species increased from two to four and from four to seven, respectively (Figure 3.2). Only 26 of the 43 marine species recorded during 2008, were present in 2011. The marine species that were not recorded in the

system after 2008 included *Stolephorus holodon*, *Pseudorhombus arsius* and three kingfish species, *Caranx ignobilis*, *C. sem* and *C. sexfaciatus* (Table 3.1). Marine species comprised 72.8% of the species recorded at the six sampling sites, while estuarine and freshwater species accounted for 18.5% and 8.7% of the species, respectively. The total number of marine species recorded gradually decreased from 41 at the mouth to four at Hell's Gate, suggesting a very strong spatial gradient in marine species composition along the length of the system. Similarly, freshwater species ranged from four species at the mouth to two at Hell's Gate. Estuarine species ranged from nine species at the mouth to four at Catalina Bay.

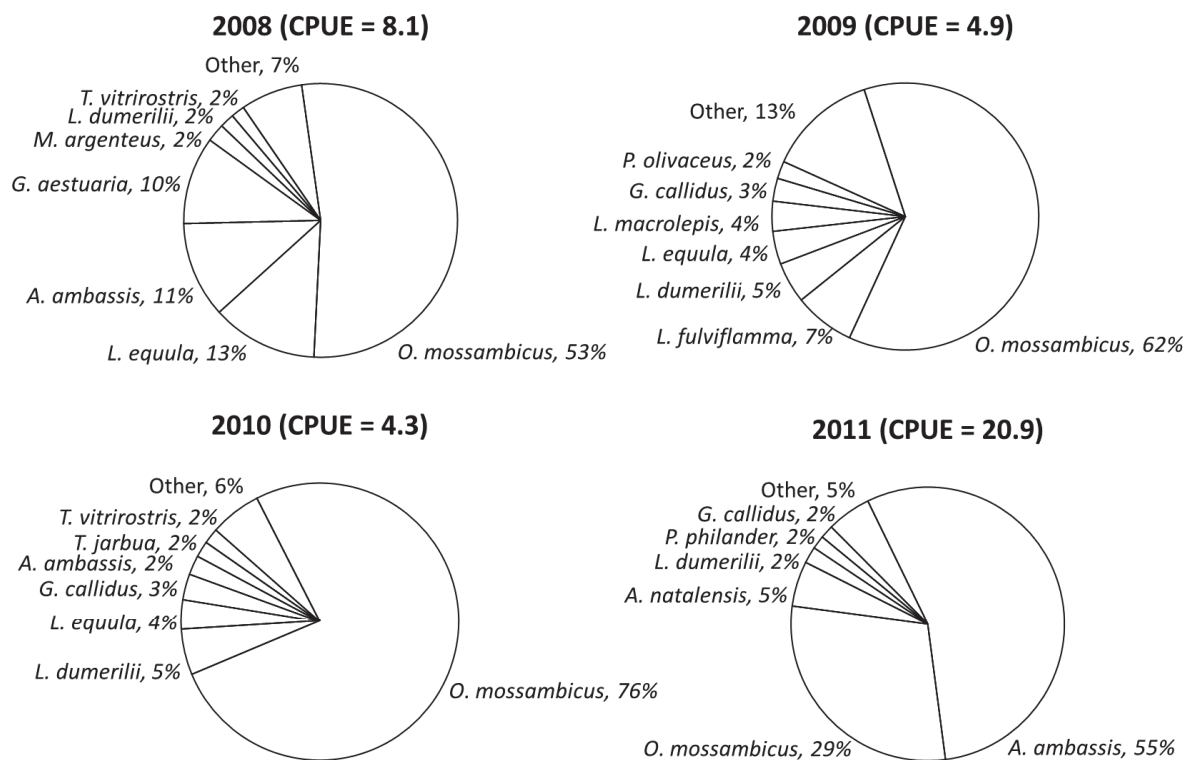


Figure 3.3: Percentage contribution (>2%) of the dominant fish species to the catch (mean CPUE) during the sampling year 2008-2011 in the St Lucia system (Full species names are listed in Table 3.1).

The opposite trend was observed with regard to fish abundance, with the mean CPUE of freshwater (CPUE = 4.3) and estuarine species (CPUE = 4.0) being markedly higher than that of marine species (CPUE = 1.3). Freshwater and/or estuarine species dominated the fish catch throughout the sampling period, except in November 2009, when the abundance of marine species exceeded the unusually low catch of freshwater and estuarine species (Figure 3.2). There was a gradual

decrease in the abundance of marine species throughout the sampling period, from a mean CPUE of 1.5 in May 2008 to 0.9 in November 2011 (Figure 3.2). There was however, a small number of marine species that increased in abundance from 2008 to 2011, these included; *L. dumerilii*, *T. vitrirostris*, *Pomadasys commersonnii* and *P. olivaceus*. At the same time, it is noteworthy that, of the 15 most abundant marine species recorded in 2008, all but *M. argenteus* and *L. fulviflamma* were still recorded in the system during 2011, indicating that very few of the numerically dominant marine species disappeared from the system after the mouth closed in 2007. In contrast, of the 15 least abundant marine species in the system during 2008, only three were still present in 2011 (Table 3.1). The abundance of estuarine species also decreased to very low levels during 2009-2010 (mean CPUE = 0.3), but increased dramatically in May 2011 (CPUE = 18.2). This rapid increase in estuarine species abundance in May 2011 was due to an unusually large catch (CPUE = 50.0) of *A. ambassis* at Fannies Island. The abundance of freshwater species (dominated by *O. mossambicus*) remained relatively stable throughout most of the study period, with the exception of low catches in November 2009 and November 2010.

3.1.4 Temporal and Spatial Changes in the Fish Community

Changes in the fish community during the study period were characterized by a strong spatial gradient in fish assemblage throughout the system, from the Lower Narrows through to Hell's Gate. Underlying this was a temporal shift in species composition from 2008 through to 2011 (Figure 3.4). Four main groups could be identified using the SIMPROF procedure in the cluster analysis. Group 1, consisted of the Lower and Upper Narrows samples, with a clear temporal progression from 2008-2011. Group 2, consisted primarily of the 2008-2010 Catalina Bay and Charters Creek samples, Group 3, consisted of most of the 2008-2010 Fannies Island and Hell's Gate samples, while Group 4, was predominantly the 2011 samples from all six sites; showing clear spatial distinction between them. There were significant differences in community structure between Groups 1 and 2 ($P_i = 3.65$, $p < 0.001$) and between Groups 3 and 4 ($P_i = 2.11$, $p = 0.03$), and also between Group 1+2, and Group 3+4 ($P_i = 4.12$, $p < 0.001$). A few samples from South Lake and North Lake did not fall into one of the four main groups. These were summer 2009 and 2010 samples which were characterized by very low fish catches.

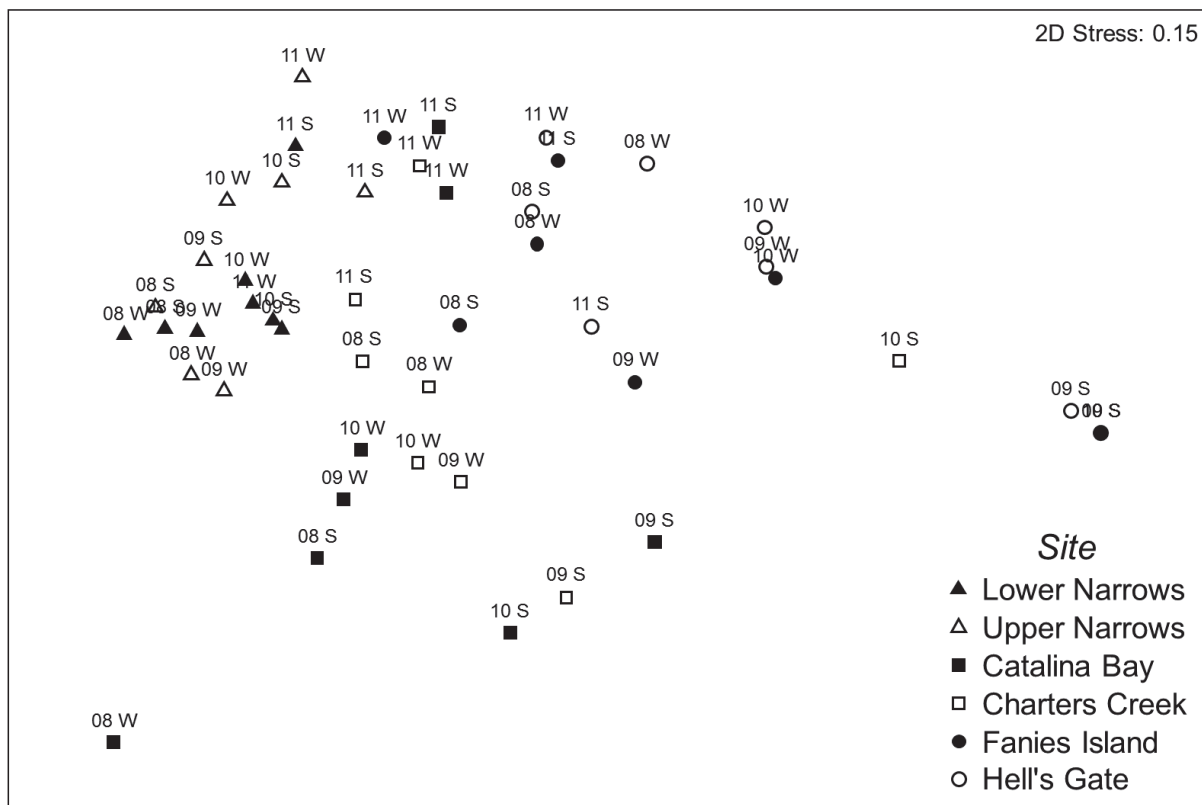


Figure 3.4: MDS ordination of the fish assemblage in the St Lucia system during the period 2008-2011 showing changes across sampling years and seasons (W, winter; S, summer) and sampling sites.

In order to better understand the underlying temporal and spatial patterns in the fish community during the study period, the fish data were averaged across the eight sampling seasons and across the six sampling sites (Figure 3.5). The cluster of sampling seasons confirmed the gradual temporal change in the fish community following mouth closure in 2007, through to November 2011 (Figure 3.5a). This was clearly shown by the separation between the 2008, 2009-2010 and 2011 samples, indicating that changes in the fish community occurred during late summer of 2008/09 and significant changes occurred during late summer of 2010/11 (Figure 3.5a). The analysis also confirmed the strong spatial gradient in the fish community along the length of the system, from the Lower Narrows through to Hell's Gate, with a similarity of less than 50% between Hell's Gate and rest of the system (Figure 3.5b). The two sampling areas in the Narrows showed a similarity of >85%, suggesting that the fish community along the Narrows remained relatively consistent.

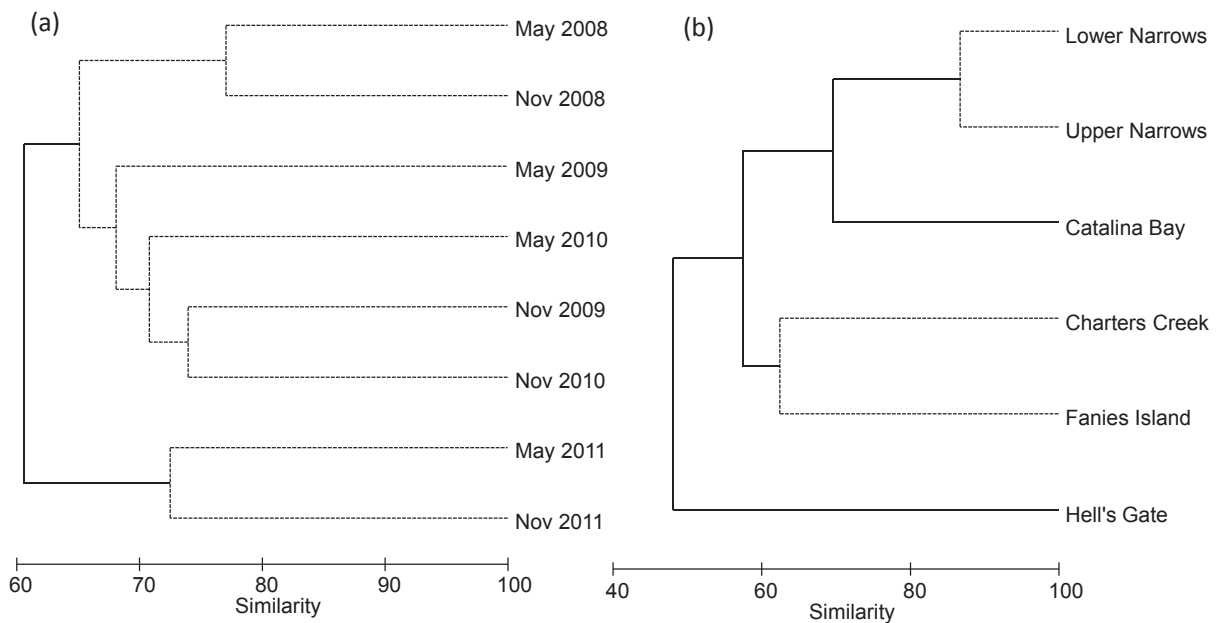


Figure 3.5: Cluster dendrogram of the fish assemblage recorded in the St Lucia system during the period 2008-2011, (a) averaged over sampling seasons; and (b) averaged over sampling sites. Solid line represent significant grouping as determined by SIMPROF.

PERMANOVA confirmed the strong spatial gradient in species composition throughout the system, revealing significant differences between the six sampling sites (Pseudo-F = 3.90, $p < 0.001$) and the three regions of the system (Pseudo-F = 8.77, $p < 0.001$) (Table 3.3). Pairwise comparison showed that the Lower and Upper Narrows communities differed significantly from the other four sampling sites, but there was no significant difference between the two Narrows regions (Table 3.4). Similarly, there were no significant differences between Catalina Bay and Charters Creek or between Fannies Island and Hell's Gate. The analysis also confirmed the strong temporal shift in species composition during the study period, showing significant differences across the eight biannual sampling seasons (Pseudo-F = 1.82, $p = 0.002$) and among sampling years (Pseudo-F = 2.62, $p < 0.001$) (Table 3.3). There were significant differences among all years except 2009 and 2010 (Table 3.4). There was however, no significant difference between winter (May) and summer (November) seasons (Pseudo-F = 1.65, $p = 0.11$) (Table 3.3). PERMANOVA two-way analysis indicated that there was a significant combined interaction between region x year (Pseudo-F = 1.77, $p = 0.005$), region x sampling season (Pseudo-F = 2.24, $p < 0.001$) as well as region x season (winter/summer)

(Pseudo-F = 1.61, $p = 0.05$), but not between site x year, site x season or years and season (Table 3.3). The nested analysis revealed that regions were significantly different from each other (Pseudo-F = 8.63, $p < 0.001$), but sites within them were not (Pseudo-F = 0.76, $p = 0.8$). Similarly, sampling years were significantly different from each other (Pseudo-F = 2.67, $p < 0.001$), but sampling seasons within them were not (Pseudo-F = 1.18, $p = 0.23$). There was no significant difference between summer and winter seasons (Pseudo-F = 1.82, $p = 0.08$) but there was between the samples (Pseudo-F = 1.82, $p = 0.006$) (Table 3.3). Three-way analysis reveal significant combined interaction between region x year x season (Pseudo-F = 1.79, $p = 0.001$) (Table 3.3)

Table 3.3: Mean squares and significance levels of the one-way, two-way, nested and three-way PERMANOVA of the fish composition in the St Lucia system from 2008-2011. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

One-Way PERMANOVA						
	Region (R)	Site (Si)	Year (Y)	Season (Se)	Sample (Ss)	
<i>df</i>	2	5	3	1	7	
Composition	15795.0	7147.4	5699.6	3889.5	3883.2	
Pseudo-F	8.8***	3.9***	2.6**	1.6	1.8**	
<i>df</i>	45	42	44	46	40	
Residual	1801.0	1830.9	2171.3	2364.1	2136.4	

Two-and Three-Way interaction							
	R x Se	R x Y	R x Ss	Si X Se	Si x Y	Se x Y	R x Y x Se
<i>df</i>	2	6	14	5	15	3	6
Composition	2747.8	2429.0	2178.2	1640.0	1597.8	2064.3	1737.6
Pseudo-F	1.6*	1.8**	2.2***	1.0	1.1	1.0	1.8***
<i>df</i>	42	36	24	36	24	40	24
Residual	1706.2	1371.5	973.7	1800.3	1493.0	2136.4	973.7

Nested interaction						
	Region (R)	R(Site)	Year (Y)	Y(Sample)	Season (Se)	Se(Sample)
<i>df</i>	2	3	3	4	1	6
Composition	15795.0	1382.6	5699.6	2520.6	3889.5	3882.1
Pseudo-F	8.6***	0.8	2.7***	1.2	1.8	1.8**
<i>df</i>		42		40		40
Residual		1830.9		2136.4		2136.4

Table 3.4: PERMANOVA results showing mean % similarity within (Bold) and between groups of community samples of the six sampling sites, the three main regions and the sampling years (2008-2011) in the St Lucia system. *denotes a significant difference.

	Lower Narrows		Upper Narrows		Catalina Bay		Charters Creek		Fanies Island		Hell's Gate	
	% Sim	t	% Sim	t	% Sim	t	% Sim	t	% Sim	t	% Sim	t
Lower Narrows	57.39											
Upper Narrows	53.94	1.06	51.58									
Catalina Bay	34.86	1.81*	30.10	2.00*	31.68							
Charters Creek	36.95	2.07*	33.33	2.09*	35.44	0.92	38.43					
Fanies Island	24.65	2.70*	26.07	2.40*	25.99	1.60*	33.47	1.29	35.00			
Hell's Gate	20.21	3.23*	22.22	2.88*	22.20	2.05*	30.02	1.77*	40.79	0.69	40.04	

	Narrows		South Lake		North Lake	
	% Sim	t	% Sim	t	% Sim	t
Narrows	54.20					
South Lake	33.81	2.65*	35.26			
North Lake	23.29	3.91*	27.92	2.29*	39.26	

	2008		2009		2010		2011	
	% Sim	t	% Sim	t	% Sim	t	% Sim	t
2008	39.98							
2009	30.87	1.45*	29.07					
2010	29.95	1.63*	31.84	0.71	30.09			
2011	38.05	1.83*	29.97	1.98*	30.25	2.03*	48.10	

3.1.5 Correlation between Species Assemblage and Environmental Variables

Canonical correspondence analysis (CCA) was used for testing the correlation between environmental variables and the fish assemblage during the study period (Figure 3.6). Salinity, depth and turbidity were the variables most responsible for structuring the fish community. Salinity ($F = 4.33$, $P = 0.002$) and depth ($F = 2.14$, $p = 0.008$) both showed a significant correlation with the fish assemblage during the study period. The biplot (Figure 3.6) showed an expected inverse relationship between depth and salinity, as the deepest areas of the system were found in the Narrows, where the salinity was lowest, while the highest salinities were recorded at Fanies Island and Hell's Gate, which are relatively shallow. Changes in turbidity were not correlated with salinity or depth, but with pH and temperature, suggesting that turbidity changes were seasonally driven. Temperature was not an important variable, suggesting that there were very limited seasonal (summer-winter) changes in the fish community.

The CCA also provided insight into the distribution of the fish species in relationship to environmental variables (Figure 3.6). There was a clear separation between species from the Lower and Upper Narrows (Group 1) and those from South and North Lake (Group 2) along the salinity/depth gradient.

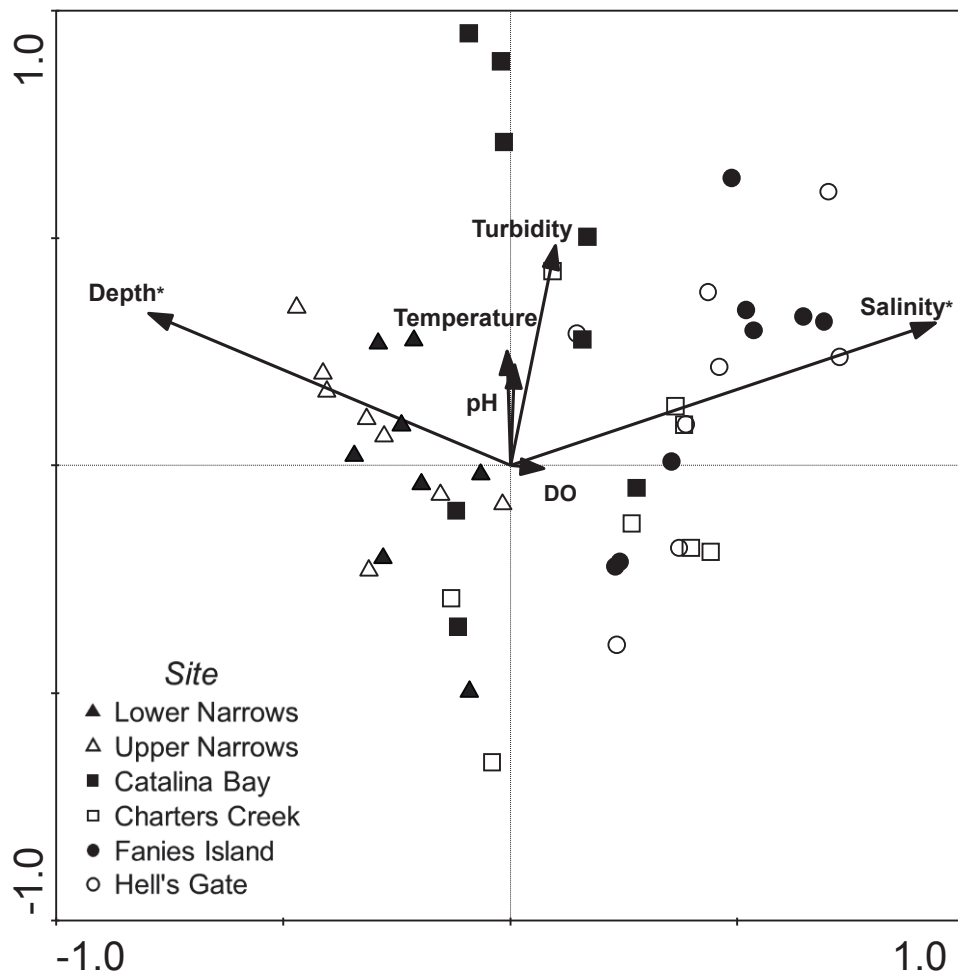


Figure 3.6: Canonical correspondence analysis (CCA) biplot of the relationship between the fish assemblage and environmental variables in the St Lucia system during the period 2008-2011. *denotes a significant environmental variable.

3.2 Discussion

Mouth closure of the St Lucia system in late 2007 led to a gradual decrease in species numbers, from 51 in 2008 to 37 in 2011. The loss related predominantly to marine species, with the largest decline being piscivorous marine species. No marine species were present in North Lake between May 2009 and May 2011, when the highest salinities were recorded. By November 2011, 22 marine and two

estuarine species had disappeared from the system. This decline in species richness closely matched events following mouth closure in 2002, when the species count decreased from 30 in November 2004 to 21 in May 2006, largely due to the disappearance of marine species from the system (Vivier *et al.*, 2010a). A similar decline in species richness was recorded in two Western Australian estuaries after extended periods of mouth closure. In the Wellstead Estuary, only 20 fish species were recorded after 47 months of mouth closure (Young and Potter, 2002a), while the Beaufort Estuary yielded only six species after being closed for three years (Lenanton and Hodgkin, 1985). Then after mouth breaching, species numbers in both systems increased as marine species returned to the system, with the species richness in the Beaufort Estuary double immediately following the mouth opening (Lenanton and Hodgkin, 1985). The status of an estuary mouth influences the distribution, abundance, and species composition of biotic communities (Whitfield *et al.*, 2012) and prolonged mouth closure has been shown worldwide to result in extensive fish mortalities due to salinity-induced osmoregulatory stress (Gillson, 2011).

Fish communities are regarded as indicators of ecological change in aquatic systems (Whitfield and Elliott, 2002). Estuarine fish communities include species with widely different tolerances and sensitivities to environmental change and functional guilds are thus likely to represent all components of such aquatic ecosystems that are affected by environmental disturbance. Whitfield and Elliot (2002) concluded that, depending on the tolerances of the fish species in a community, fish abundance and species richness can provide environmental managers with an indication of the environmental and ecological stress to which an estuarine system is being subjected and/or how the ecosystem will respond to such stress. This study, which assessed changes in the fish community of the St Lucia system over a four year period of salinity-induced changes, clearly showed dramatic declines in fish abundance and species diversity associated with hypersaline conditions, with marine species disappearing altogether from North Lake during the period 2009-2011.

The adverse impact of hypersaline conditions on the biota of estuaries worldwide (Largier, 2010; Gillson, 2011) and in St Lucia, has been well documented (Whitfield, 2005b; Whitfield, *et al.*, 2006; Whitfield and Taylor, 2009; Vivier *et al.*, 2010a).

Largier (2010) noted that estuaries which experience freshwater deprivation coupled with high evaporation rates, such as St Lucia, are susceptible to becoming hypersaline during periods of below-average rainfall, especially when the mouth closes for extended periods. Even though a closed mouth/hypersaline period may be part of the natural cycle of these systems, anthropogenic activities may prolong mouth closure or completely disrupt the cycle (Taylor, 2006), the consequences of which are often disastrous for off-shore marine fish populations (Mann and Pradervand, 2007). Gillson (2011) reviewed the effects of freshwater deprivation on estuarine environments worldwide and remarked that the provision of sufficient freshwater inflow in an estuary is a critical factor affecting every aspect of estuarine functioning, which ultimately affects species diversity in the estuarine and coastal environment. Although river flows are naturally and seasonally variable, river regulation or manipulation disrupts the structure and function of estuarine and coastal systems by forcing physico-chemical processes to deviate from natural patterns (Gillson, 2011).

Whitfield and Taylor (2009) reviewed the importance of freshwater inflow to the future conservation status of St Lucia and its biota and predicted that under continued low freshwater inflow conditions, hypersaline events will continue to occur as the system is being forced into extreme states such that it is unable to attain full recovery during intervening wet periods. It was also noted that some organisms may become permanently lost from the system and therefore recovery during wet periods becomes impossible. These predicted hypersaline events were related to reduced freshwater inflow, mainly from the Mfolozi River. Salinity fluctuations and extremes have always been a natural feature of Lake St Lucia, but Whitfield and Taylor (2009) remarked that unless the Mfolozi River is re-connected to the St Lucia Estuary, the amplitude and temporal scale of these salinity fluctuations are likely to increase in the future and hypersaline conditions can be expected to be higher and last longer than under natural conditions (Whitfield, 2005b). These changes were evident during the present study, with North and South Lake becoming hypersaline soon after mouth closure.

The return of hypersaline conditions following mouth closure in 2007, despite re-opening of the back channel in 2008, prompted conservation authorities to adopt a

new management strategy for maintaining water and salinity levels in the system. As a result, a new beach channel was opened in July 2012 between the Mfolozi mouth and the St Lucia mouth to increase the inflow of water (estuarine and fresh) into the system. It is anticipated that sufficient water will be diverted via this channel into St Lucia to prevent a re-occurrence of the extreme low lake levels and hypersaline conditions experienced during 2003-2006 and 2008-2010 and to increase the possibility of the mouth breaching naturally in the future. More importantly, this channel would also allow recruitment of marine fish species into the St Lucia estuarine system via the Mfolozi mouth. Continued monitoring will be required to determine the efficiency of the new channel and the extent to which juvenile recruitment of marine species occurs.

When the St Lucia mouth opened in 2007, juveniles of 20 marine fish species were recorded as having recruited into the system (Vivier *et al.*, 2010a), while 48 of the 61 species recorded during the present study were marine species. These results highlight not only the importance of the St Lucia system as a nursery area for marine fish species, but more importantly, the consequences of extended mouth closure and breakdown in recruitment for estuarine and coastal fish populations. Juveniles of marine species form the dominant component in large subtropical estuaries in southern Africa, such as St Lucia, comprising 71% of the fish species, 64% of the fish abundance and 96% of the total fish biomass under open conditions (Harrison, 2003). Similarly, in the large Sine-Saloum Estuary in West Africa, marine breeding species were found to comprise 79% of the abundance and 66% of the fish biomass (Simier *et al.*, 2004). The nutrient-rich, sheltered waters of estuaries have been reported world-wide to function as important nursery areas for many marine fish species (Young and Potter, 2002a; Gilson, 2011), with larvae often unable to develop or survive if prevented from recruiting into estuaries (Harrison, 2003; Whitfield, 2005b; Mann and Pradervand, 2007).

In 2008, marine species comprised only 23.6% of the fish abundance in the system, but this declined even further, to 5.5%, in 2011. In comparison, marine species comprised 61% of the fish abundance in the adjacent, seasonally open Mfolozi Estuary during the period 2007-2008 (Vivier *et al.*, 2010b), highlighting the extent to which extended mouth closure affected the abundance and recruitment of marine

fish species into St Lucia. The St Lucia system comprises 50% of the estuarine area along the South African coast. Extended mouth closure severely compromises the functioning of this single most important nursery area for marine estuarine-dependent fish in southern Africa and has deleterious consequences for regional offshore stocks of marine fish populations. Mann and Pradervand (2007) showed that the offshore breeding population of *Rhabdosargus sarba* was aging and declining due to the prolonged closure of St Lucia and the associated loss of nursery function. *Rhabdosargus sarba* is only one of 20 marine fish species in regional waters which are totally dependent on estuarine nursery areas for completion of their life cycle. The future state of marine populations of estuarine-dependent species along the east coast is therefore expected to be increasingly influenced by the frequency, timing and duration of connections between St Lucia and the marine environment.

Despite the decline in the number and abundance of marine species, new recruits entered the system to a limited extent through overtopping events from the Mfolozi Estuary during 2008 and 2009 and via the back channel, which was reopened in 2008 (Cyrus *et al.*, 2008; Whitfield and Taylor, 2009; iSimangaliso Wetland Park Authority, 2011). Large numbers of juvenile *Lutjanus fulviflamma* (20-30 mm SL) and *Terapon jarbua* (40 mm SL) entered the system during 2009 and 2010. Juvenile *Liza dumerilii*, recorded during 2009, 2010 and 2011, could only have recruited from the sea via the Mfolozi Estuary. Similarly, juvenile *Liza macrolepis* (length < 50 mm SL), *Thryssa vitirostris* (length < 50 mm SL), *Elops machnata* (length < 170 mm SL), *Pomadasys olivaceus* and *Johnius belangerii* were recorded in 2011, having been absent from the system during previous years. Recruitment densities of marine fish via the narrow back channel were however low compared to open-mouth conditions and insufficient for St Lucia to optimally function as a nursery estuary. The back channel was also not large enough to allow adult and sub-adult fish to migrate back to the ocean.

Salinity and depth were the most important environmental factors in the St Lucia fish community during the study period. Salinity has been shown to be an important factor structuring estuarine fish communities around the world (Blaber and Blaber, 1980; Harrison and Whitfield, 2006; Whitfield *et al.*, 2006; Largier, 2010). Salinity is particularly important for early life stages of fish in estuarine nursery grounds

(Gillson, 2011). In the Rio Llargartos, Mexico, which maintains a tidal connection to the ocean and has a constant freshwater input, both species richness and abundance declined from the mouth towards the upper reaches where salinities exceeded 80 during drought conditions (Vega-Cendejas and Hernandez de Santillana 2004). In the large, shallow Laguna Madre of Texas, USA, the number of fish species also declined under hypersaline conditions (Hedgepeth, 1967), while in the upper reaches of the Sine-Saloum Estuary, Senegal, Simier *et al.* (2004) found greatly reduced fish diversities at salinities exceeding 100. Many fish species that naturally occur in estuaries cannot tolerate hypersaline conditions and disappear from these regions of the system. In St Lucia, 20 fish species were shown to tolerate salinities between 70-95, but only one species can tolerate salinities greater than 95 (Whitfield *et al.*, 2006).

Salinity fluctuations between different regions led to changes in fish assemblages in the St Lucia system. Under hypersaline conditions in 2009-2010, North Lake was dominated by the freshwater tilapia, *Oreochromis mossambicus*, with no marine species being recorded. In 2011, however, marine species re-colonized this area due to a decline in salinity caused by increased freshwater input. A similar, salinity-induced fish migration was observed in the Wellstead Estuary, Western Australia, where hypersaline conditions in the lower reaches forced all fish species except the estuarine species *Atherinosoma elongata* to migrate into the upper reaches, where salinities were lower, or caused their mortality (Young and Potter, 2002a).

Fish abundance increased from the Narrows up to North Lake, which is in contrast to previous studies in which the highest fish abundance was recorded in the Narrows (Vivier *et al.*, 2010a; Cyrus *et al.*, 2011). During the present study, however, marine species were still most abundant in the Narrows, while freshwater and estuarine fish increased in abundance towards North Lake. The relatively high abundance of freshwater fish in North Lake was largely due to *O. mossambicus*, a highly euryhaline species and the only species found to survive and breed in salinities above 70 (Whitfield *et al.*, 2006; Vivier *et al.*, 2010a). Similarly, the lower reaches of the Casamance Estuary, Senegal, yielded a high diversity of marine species, while the hypersaline upper reaches were dominated by a small number of highly euryhaline species (Kantoussan *et al.* 2012).

Fish abundance in the system during November 2009 and November 2010 was relatively low, with very low catches in North Lake. This decline in fish abundance in North Lake was most likely due to a series of fish kill events that occurred during this period. Major 'fish kills' are most common during hypersaline periods and usually coincide with sudden changes in water temperature (Cyrus, 2013). A total of 15 such events were recorded between 2003 and 2011 (Whitfield *et al.*, 2006; Cyrus, 2013). The largest fish kill was recorded in July 2009 and involved an estimated 2.5 million fish belonging to 10 species, which consisted predominantly of *O. mossambicus*, including large numbers of juveniles (Cyrus, 2013). North Lake was hardest hit, but dead fish were found as far south as Makakatana Bay in South Lake. During 2011, however fish abundance throughout the system increased rapidly, with the overall CPUE increasing from 1.6 in November 2010 to 26.6 in May 2011, mostly due to increases in *O. mossambicus* (CPUE = 25.6) and *Ambassis ambassis* (CPUE = 50.0). This rapid increase in fish abundance during 2011 could be attributed to lower salinities in North and South Lake after good summer rains and higher lake levels, allowing species such as *O. mossambicus* and *A. ambassis* to rapidly re-colonize these areas. This also allowed marine species, including new recruits from the Mfolozi Estuary, to re-colonize the northern parts of the system. This was reflected in the fact that 75% of the recorded marine fish in the system during May 2011 was caught in North Lake at Fannies Island.

The freshwater species *O. mossambicus* was the most abundant fish species throughout the study period, with the exception of 2011, when it was second to the estuarine species *A. ambassis* and comprised 43.7% and 33.0% of the total catch, respectively (Table 3.1). But when looking at the biomass of these two species for 2011, the biomass of *O. mossambicus* far outweighs that of *A. ambassis*. Using length-weight relationships from Harrison (2001) to calculate the biomass of the two species it was found that the catch biomass of *A. ambassis* during 2011 was only 2.6% of that of *O. mossambicus*. *Oreochromis mossambicus* was clearly still the dominant species in the system. These two species were also found to be dominant in the system during 2004-2006 (Cyrus and Vivier, 2006a; Vivier *et al.*, 2010a), when hypersaline conditions were recorded in South and North Lake and water levels were very low. The overwhelming abundance of *O. mossambicus* in the St Lucia system

during the study period is indicative of how much of an impact the hypersaline and closed mouth conditions have had on the fish community of the system during the last decade, since under open mouth conditions, *O. mossambicus* usually is far less abundant than marine and estuarine species (Whitfield and Blaber, 1979a). This is reflected in the adjacent, seasonally open, river dominated Mfolozi Estuary, where *O. mossambicus* only contributed 0.5% of the total fish catch during 2007-2008 (Vivier *et al.*, 2010b).

Understanding the freshwater requirements of estuarine environments will in future become increasingly more important as climate change will result in increasing stress on aquatic resources and as demand for water increases with human population growth (Gillson, 2011). A Global Environment Facility (GEF) project, which will examine ways of supplementing freshwater input into Lake St Lucia, has been initiated by EKZNW. It is charged with identifying possible options for management to minimize human impacts on the St Lucia system.

Chapter 4: Effect of the New Beach Channel on the Fish Community Structure in the St Lucia Estuarine System.

4.1 Results

4.1.1 Physico-chemical Water Data

During November 2010, South and North Lake were hypersaline (50.5-65.8), while salinities in the Narrows remained below marine levels (11.0-21.4). Due to good rains during the summer of 2010/11, salinities throughout the system declined with a maximum salinity of 38.2 being recorded at Hell's Gate in North Lake in May 2011. By November 2011, salinities in the Narrows had dropped to 2.4 and the whole system was below marine salinities for the first time since the mouth breached in 2007. This was mainly due to freshwater inflow from the Mpate River and the reopened back channel connecting the Mfolozi River with the St Lucia Narrows.

During July 2012, when the Mfolozi mouth closed, EKZNW dug a new beach channel along the beach between the Mfolozi mouth and the St Lucia Narrows. The beach channel was aimed at diverting water from the Mfolozi River into the St Lucia system, reducing the water deficit and salinities in the system. During November 2012, salinities at Hell's Gate and the Upper Narrows had reached a low of 26.5 and 0.9, respectively. The Mfolozi mouth opened again during the summer of 2012/13 and the inflow of marine water into St Lucia via the beach channel caused a salinity reversal in the system. During May 2013, highest salinities in the system were recorded at the mouth (21.9), while lowest salinities were found in South Lake (8.5-9.7) and at Hell's Gate in North Lake (13.2). The salinities remained in this state until the end of the study (May 2014), with lowest salinities at the Mpate River mouth in the Upper Narrows, increasing towards the Lower Narrows and towards Hell's Gate in North Lake.

Water temperatures in May (15.7-23.2°C) and November (20.0-30.8°C) reflected typical subtropical winter and summer conditions. Dissolved oxygen concentrations (5.27-11.3 mg l⁻¹) and % oxygen saturation (60.0-125.9%) remained high throughout

the study period, while a mean pH of 8.0 was observed. Water turbidity was generally lower in May (5.5-101.3 NTU), compared to November, with windy summer conditions resulting in higher turbidities (13.1–512.7 NTU). Highest turbidities were recorded at Catalina Bay on the Eastern Shore during November 2010 (512.7 NTU). All physico-chemical data recorded during the study period are given in Appendix 1.

There was a gradual increase in water levels throughout the system during the study period. During November 2010 the average depth in the Narrows was 0.9 m and that of South and North Lake was 0.3 m and 0.2 m, respectively. Due to an increase in rainfall and freshwater inflow from the Mpate and Mfolozi River, via the back and beach channels, the average depth of the Narrows during May 2014 was 2.3 m, while the depth in the lakes was 1.8 m. The recorded depth measurements were correlated with data obtained from the Department of Water Affairs for Lister's Point and from EKZNW for the St Lucia Bridge, averaged per month to test its accuracy (Appendix 2).

4.1.2 Species Composition

A total of 23,369 fish representing 58 species were recorded from seine net catches in the St Lucia system during the period from November 2010 - May 2014. These can be divided into two groups, fish caught before the beach channel opened (i.e. pre-channel) in July 2012 and those caught after (i.e. post-channel). Of the 23,396 fish, 15,083 representing 45 species were caught prior to and the remaining 8,286 fish, representing 50 species, after the beach channel opened.

The highest total number of species ($n = 34$) caught in the system during this period were in November 2010 and May 2012 (both pre-channel) and the first two sampling seasons post-channel, in November 2012 and May 2013 (Table 4.1; Figure 4.1). The lowest number of species ($n = 29$) was recorded in November 2011. Although the total number of species caught per season remained relatively constant, there was considerable variability in the species composition, when compared to the total species ($n = 58$) caught during the study period. The total number of species caught

Table 4.1: The fish species, estuarine association category (Est Ass) and total CPUE recorded per sampling season before and after the St Lucia beach channel was opened in July 2012. Species contributing >1% to the total CPUE are highlighted (*one or **both periods) (Est Ass: E, Estuarine species; F, Freshwater species; M, Marine species).

Species	Est Ass	Nov 2010	May 2011	Nov 2011	May 2012	Total Before	Total %	Nov 2012	May 2013	Nov 2013	May 2014	Total After	Total %
<i>Acanthopagrus vagus</i>	M	0.03	0.03		0.01	0.07	0.02%	0.04	0.00		0.01	0.05	0.04%
<i>Ambassis ambassis</i> **	E	0.48	89.25	49.22	42.61	181.56	44.65%	12.99	3.37	16.67	11.51	44.55	30.56%
<i>Ambassis natalensis</i> **	E		13.35	0.07	9.14	22.55	5.55%	0.69	1.50	1.13	1.51	4.82	3.31%
<i>Argyrosomus japonicus</i>	M		0.00			0.00	0.00%						
<i>Arothron immaculatus</i>	M									0.05		0.05	0.03%
<i>Atherina breviceps</i>	M									0.00		0.00	0.00%
<i>Caranx sexfaciatus</i>	M								0.04		0.00	0.04	0.03%
<i>Carcharhinus leucas</i>	M							0.00				0.00	0.00%
<i>Chelon melinopterus</i>	M	0.10			0.01	0.11	0.03%						
<i>Clarias gariepinus</i>	F		0.02	0.01	0.04	0.07	0.02%	0.02	0.03			0.05	0.03%
<i>Elops machnata</i>	M	0.01	0.02	0.02	0.01	0.05	0.01%	0.01		0.01	0.03	0.05	0.04%
<i>Epinephelus malabaricus</i>	M				0.01	0.01	0.00%						
<i>Gerres filamentosus</i>	M	0.00	0.01			0.01	0.00%			0.01	0.01	0.02	0.01%
<i>Gerres longirostris</i>	M	0.00		0.10		0.10	0.03%		0.02			0.02	0.01%
<i>Gerres metheuni</i>	M	0.01		0.00		0.02	0.00%		0.01	0.02	0.01	0.05	0.03%
<i>Gilchristella aestuaria</i>	E	0.35	1.88	0.07		2.30	0.56%	0.02				0.02	0.01%
<i>Glossogobius callidus</i> **	E	0.61	3.39	0.55	0.40	4.96	1.22%	0.07	1.38	0.65	0.47	2.56	1.76%
<i>Glossogobius giurus</i>	F	0.01	0.08	0.01	0.21	0.32	0.08%	0.33	0.05	0.08	0.15	0.61	0.42%
<i>Glossogobius tenuiformis</i>	E		0.20	0.10	0.05	0.35	0.09%	0.10	0.03	0.13		0.26	0.18%
<i>Goby sp.*</i>	E		0.03	0.10		0.13	0.03%	1.60				1.60	1.10%
<i>Hilsa kelee</i>	M	0.00				0.00	0.00%						
<i>Hyporhamphus capensis</i> *	E	0.04	0.78	0.43	0.80	2.06	0.51%	0.98		0.30	0.12	1.40	0.96%
<i>Johnius dorsalis</i>	M			0.01	0.01	0.02	0.00%	0.03	0.00	0.01	0.06	0.11	0.08%
<i>Leiognathus equula</i>	M	0.45	0.23	0.03	0.11	0.83	0.20%	0.14	0.28	0.18	0.16	0.76	0.52%
<i>Liza alata</i>	M	0.00	0.02	0.01	0.01	0.04	0.01%	0.00	0.00	0.01	0.00	0.02	0.01%
<i>Liza dumerilii</i> **	M	0.52	1.30	3.60	18.66	24.08	5.92%	4.54	1.58	1.12	5.44	12.68	8.70%
<i>Liza macrolepis</i> *	M	0.15	0.20	1.58	0.14	2.06	0.51%	2.20	0.23	0.22	0.07	2.72	1.87%
<i>Megalops cyprinoides</i>	M	0.02	0.02		0.00	0.04	0.01%	0.01				0.01	0.01%
<i>Monodactylus argenteus</i>	M	0.05			0.01	0.06	0.01%		0.02	0.03	0.07	0.12	0.08%
<i>Monodactylus falciformes</i>	M										0.01	0.01	0.00%
<i>Mugil cephalus</i>	M	0.00	0.00	0.11	0.01	0.12	0.03%	0.01		0.00	0.02	0.03	0.02%
Mullet sp.	M				0.05	0.05	0.01%	0.27				0.27	0.18%
<i>Muraenesox bagio</i>	M	0.00				0.00	0.00%						
<i>Myxus capensis</i>	M								0.05		0.03	0.09	0.06%
<i>Oligolepis acutipennis</i>	E				0.00	0.00	0.00%	0.27				0.27	0.18%
<i>Oligolepis keiensis</i>	E								0.03			0.03	0.02%
<i>Oreochromis mossambicus</i> **	F	4.91	41.66	31.59	70.62	148.78	36.59%	8.07	14.51	27.05	11.15	60.77	41.69%
<i>Platycephalus indicus</i>	M		0.00	0.01		0.01	0.00%						
<i>Pomadasys commersonii</i>	M	0.05	0.06	0.08	0.26	0.45	0.11%	0.43	0.04	0.06	0.04	0.57	0.39%
<i>Pomadasys kaakan</i>	M	0.01	0.00	0.01	0.01	0.02	0.01%	0.00				0.00	0.00%
<i>Pomadasys olivaceus</i>	M	0.01	3.19			3.20	0.79%						
<i>Pomatomus saltatrix</i>	M							0.00				0.00	0.00%
<i>Pseudocrenilabrus philander</i> **	F	0.11	0.44	3.53	1.30	5.38	1.32%	1.51	0.27	2.18	0.95	4.91	3.37%
<i>Rhabdosargus holubi</i>	M	0.01	0.01		0.06	0.08	0.02%	0.00	0.18	0.21	0.03	0.43	0.30%
<i>Rhabdosargus sarba</i>	M	0.02	0.02	0.01	0.02	0.07	0.02%	0.01	0.01	0.29	0.02	0.33	0.23%
<i>Rhabdosargus thorpei</i>	M									0.15		0.15	0.10%
<i>Scomberoides lysan</i>	M								0.01			0.01	0.00%
<i>Silhouettea sibayi</i>	E	0.07	0.37	0.13	0.49	1.06	0.26%	0.10				0.10	0.07%
<i>Sillago sihama</i>	M	0.03	0.01			0.05	0.01%	0.01		0.01		0.02	0.01%
<i>Solea turbynei</i>	M	0.22	0.01	0.03	0.00	0.27	0.07%		0.05	0.21	0.08	0.34	0.23%
<i>Sphyaena barracuda</i>	M								0.00	0.01		0.02	0.01%
<i>Sphyaena jello</i>	M				0.00	0.00	0.00%		0.00		0.00	0.01	0.00%
<i>Stolephorus indicus</i>	M								0.10			0.10	0.07%
<i>Strongylura leiura</i>	M							0.01	0.00	0.01	0.00	0.03	0.02%
<i>Terapon jarbua</i>	M	0.48	0.06	0.02	0.15	0.71	0.17%	0.00	0.22	0.48	0.09	0.79	0.54%
<i>Thyssa vitirostris</i> **	M	0.80	2.95	0.04	0.68	4.48	1.10%	0.45	0.44	0.22	0.81	1.92	1.31%
<i>Trypanchen microcephalus</i>	E				0.01	0.01	0.00%						
<i>Valamugil buchanani</i> *	M	0.00	0.00			0.01	0.00%	1.70	0.00		0.02	1.72	1.18%
<i>Valamugil cunnesius</i>	M	0.05	0.01	0.01	0.03	0.10	0.02%	0.01	0.03	0.00	0.00	0.04	0.03%
<i>Valamugil seheli</i>	M			0.01	0.00	0.01	0.00%	0.10	0.00		0.14	0.25	0.17%
Nr of Species (Total = 58)		34	33	29	34	45		34	34	31	32	50	
Total CPUE		9.62	159.61	91.50	145.93	406.64		36.72	24.51	51.50	33.03	145.76	
Mean CPUE		1.60	26.60	15.25	24.32	16.94		6.12	4.90	10.30	5.51	6.71	

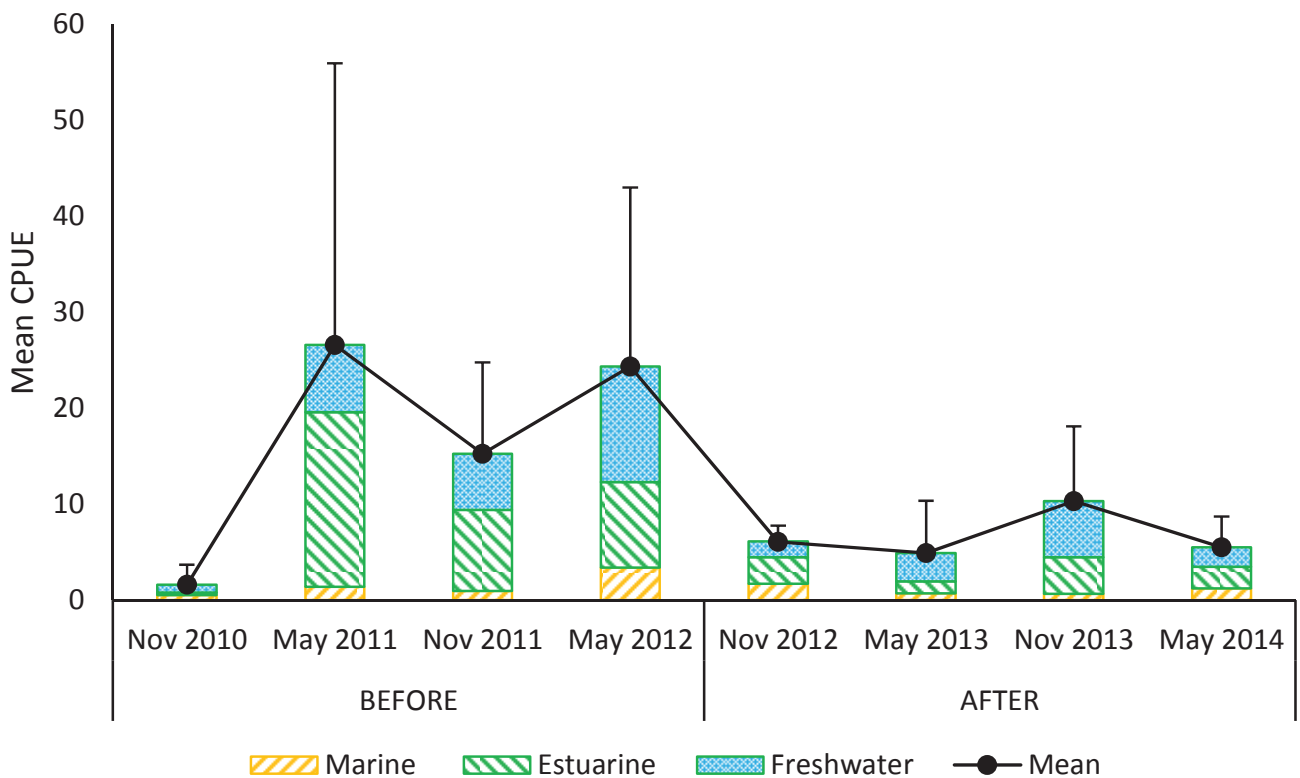
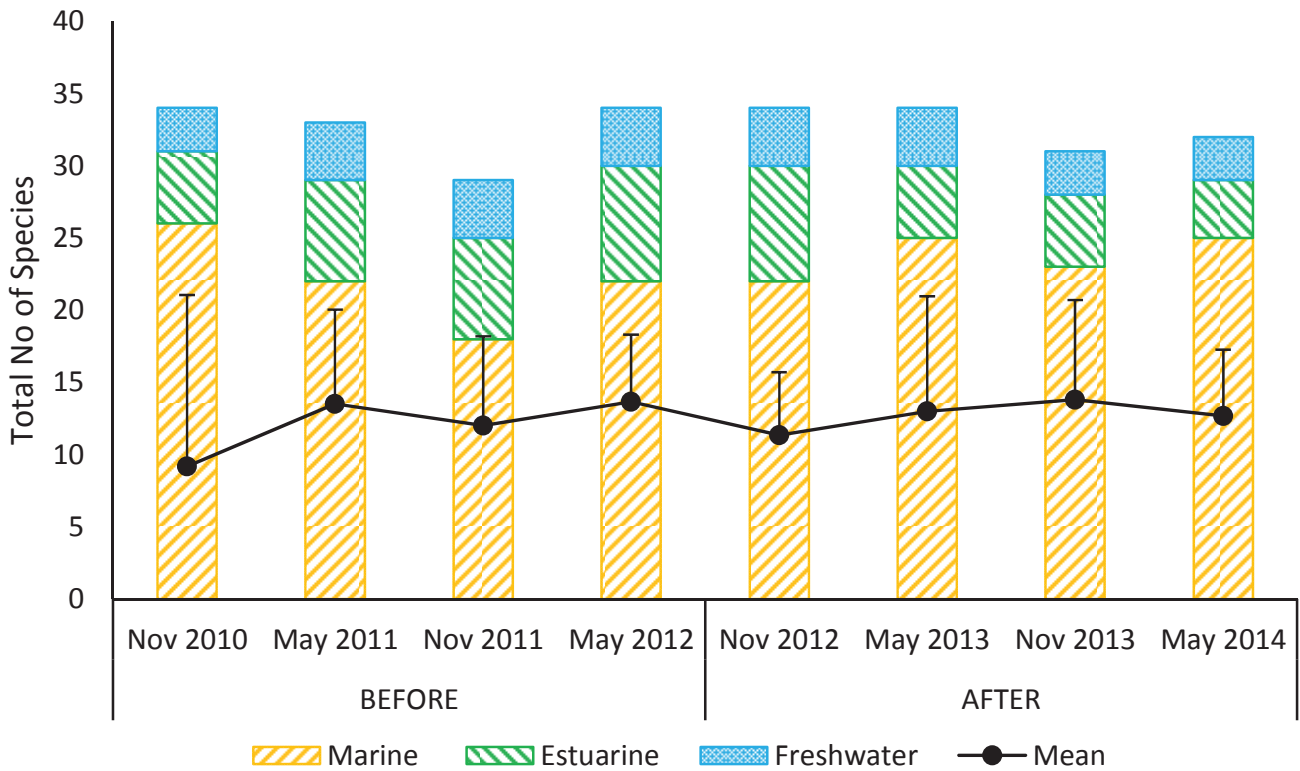


Figure 4.1: The total number of species, mean number of species (+1SD), mean abundance (CPUE) (+1SD) and estuarine association groups of the fish recorded during the eight biannual sampling seasons in the St Lucia system during Nov 2010 - May 2014.

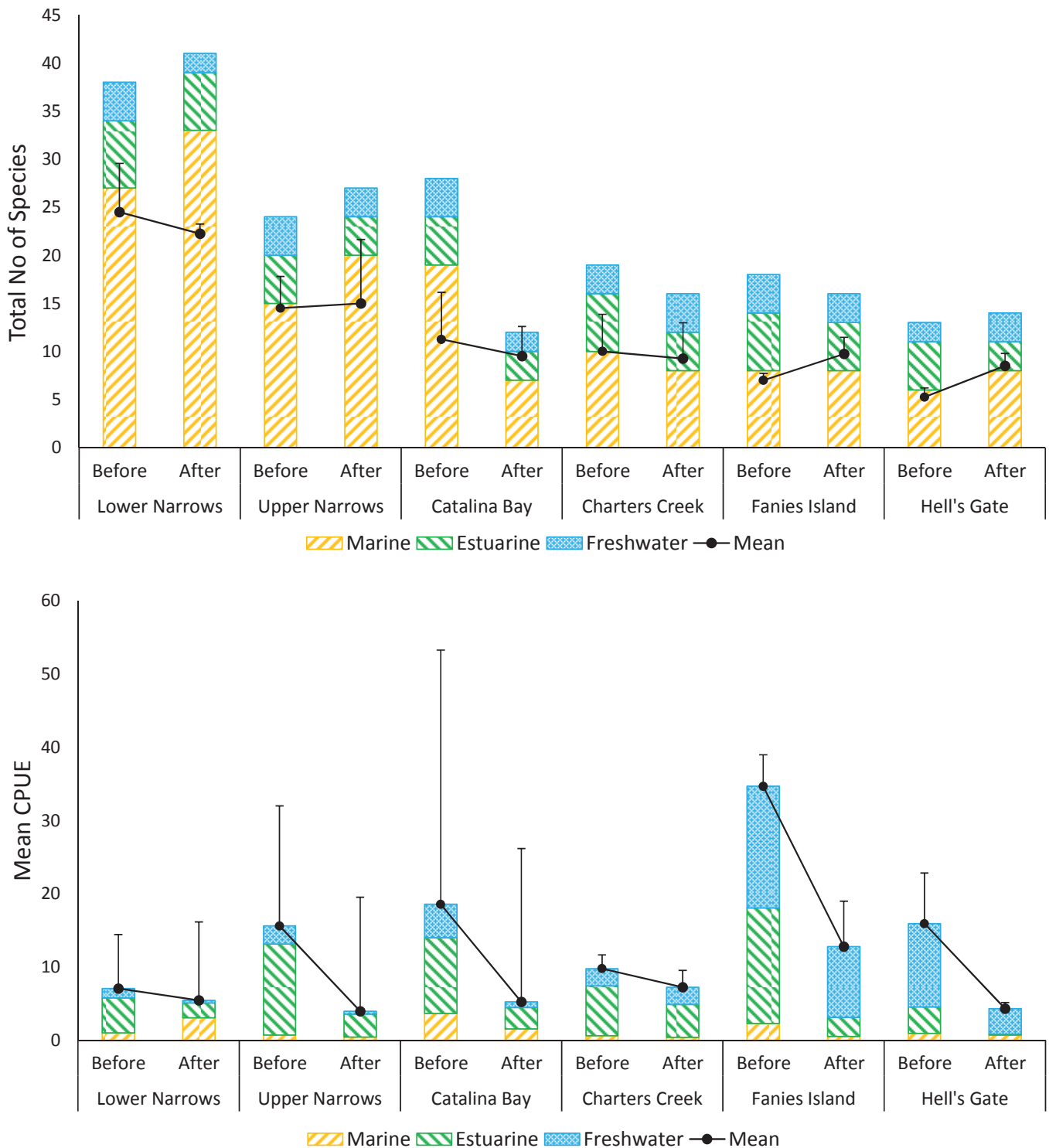


Figure 4.2: The total number of species, mean number of species (+1SD), mean abundance (CPUE) (+1SD) and estuarine association groups of the fish recorded at the six sampling sites before (Nov 2010 - May 2012) and after (Nov 2012 - May 2014) the beach channel opened, in the St Lucia system.

during the two years before the beach channel opened was 45, compared to 50 during the two years afterwards, indicating a higher species richness after St Lucia was connected to the ocean via the Mfolozi mouth (Table 4.1).

The greatest mean fish abundance (CPUE) was recorded in May 2011 (CPUE = 26.6) and May 2012 (CPUE = 24.3) both pre-channel, while the lowest was in November 2010 (CPUE = 1.6). There was a general decline in fish abundance after the beach channel opened, with catches (CPUE) ranging between 4.1-10.3 (Figure 4.1). There was a decline in the total and mean number of species from the mouth towards North Lake and an increase in fish abundance (CPUE) from the mouth to Fannies Island in North Lake, both pre- and post-channel. When comparing the number of species and CPUE of fish between channel states, at each of the sites in the system (Figure 4.2), there was an increase in species numbers in the Narrows after the beach channel opened, but a decrease in South and North Lake, with Hell's Gate being the exception here. At the same time, there was a decrease in fish abundance (CPUE) at each of the study sites after the beach channel opened (Figure 4.2).

Differences in the number of species, density (CPUE), species richness, evenness and diversity among regions, sites, years, sampling seasons, season (winter/summer) and pre- and post-channel as determined by ANOVA are presented in Table 4.2. There were significant differences among regions for all five indices. The same was shown for sites with the exception of species richness, which indicates a strong spatial gradient in fish composition across the system. Sampling seasons and pre- and post-channel periods showed significant difference only in species richness, while years and season showed none. Nested analysis revealed that there was significant differences between both regions and sites before and after opening of the beach channel as well as between the before and after region and site (Table 4.2).

The fish community during the study period was dominated by the estuarine species *Ambassis ambassis* and the freshwater species *Oreochromis mossambicus*, which accounted for 40.1% and 37.9% of the total catch (CPUE) from November 2010 - May 2014, respectively. During the two years prior to the beach channel being

Table 4.2: ANOVA of the univariate indices of the St Lucia fish community recorded during Nov 2010 - May 2014 (Channel separates the data into before (Nov 2010 – May 2012) and after (Nov 2012 – May 2014) the beach channel opened). *p<0.05, **p<0.01, ***p<0.001 (Number of Species, S; Density (CPUE), N; Evenness (Pielou's), D=(S-1)/Log(N); Species Richness (Margalef), J'=H'/Log(S) and Diversity (Shannon), H'=Sum(Pi*Log(Pi)).

Kruskal Wallis: Non-parametric ANOVA						
	Region (R)	Site (Si)	Year (Y)	Sample (Ss)	Season (Se)	Channel (C)
df	2	5	3	7	1	1
S	26.1***	33.0***	1.0	1.7	0.3	0.8
N	15.2***	25.2**	2.8	4.8	0.5	2.1
D	29.6***	34.0***	0.2	1.3	0.1	0.0
J'	8.4**	17.8	7.2	15.1*	<0.1	3.8*
H'	27.2***	32.8***	0.7	1.7	0.2	0.2

Two-and Three way interaction							
	Y x Si	Si x Se	R x Ss	R x Se	R x Y	Y x Se	R x Y x Se
df	15	5	13	2	6	3	5
S	1.3	1.4	0.5	0.3	0.7	0.4	0.6
N	1.4	1.5	0.5	1.1	0.3	0.5	0.6
D	1.6	1.1	0.7	0.3	1.2	0.6	0.6
J'	1.1	0.6	0.7	0.4	0.2	3.2	1.3
H'	1.0	1.5	1.0	1.0	1.1	0.5	1.1

Nested interaction						
	Region (R)	R(Site)	Year (Y)	Y(Sample)	Season (Se)	Se(Sample)
df	2	3	3	4	1	6
S	51.9***	12.3***	0.4	0.3	0.0	0.3
N	14.0***	6.1**	0.6	0.4	0.1	0.6
D	52.7***	9.3***	0.3	0.5	<0.1	0.4
J'	4.0**	1.2	3.9*	2.4	0.2	3.3*
H'	49.8***	7.2**	0.4	0.4	<0.1	0.4

	Season (Se)	Se(Channel)	Region (R)	R(Channel)	Site (Si)	Si(Channel)	Channel (C)	C(Year)
df	1	2	2	3	5	6	1	2
S	<0.1	0.1	27.4***	0.6	27.2***	0.8	0.4	0.4
N	0.2	1.4	9.9***	0.9	8.6***	0.7	1.7	0.4
D	<0.1	0.1	33.7***	1.1	30.5***	1.8	0.0	0.3
J'	<0.1	3.0	4.2**	1.8	2.2	1.3	4.0	2.1
H'	0.2	<0.1	35.0***	1.0	25.1***	1.2	<0.1	0.5

	Channel (C)	C(Season)	Channel (C)	C(Region)	Channel (C)	C(Site)	Channel (C)	C(Sample)
df	1	2	1	4	1	10	1	6
S	0.3	<0.1	0.3	13.8***	0.6	14.0***	0.5	0.3
N	1.3	0.8	2.2	5.2**	2.9	4.6**	1.4	0.4
D	<0.1	0.1	<0.1	17.2***	<0.1	16.0***	0.1	0.4
J'	4.3*	0.7	5.4*	2.1	4.9*	1.5	2.4	2.4*
H'	<0.1	0.1	0.1	17.8***	0.1	13.1***	<0.1	0.4

opened, *A. ambassis* contributed 44.7% and *O. mossambicus* 36.6% to the total catch (CPUE). After the beach channel opened *O. mossambicus* became the dominant species in the system, contributing 41.7% of the total catch (CPUE), while *A. ambassis* only contributed 30.6%. Other species contributing more than 1% to the total catch (CPUE) pre-channel include the estuarine species *Ambassis natalensis* and *Glossogobius callidus*, the freshwater species *Pseudocrenilabrus philander*, and two marine species *Liza dumerillii* and *Thryssa vitrirostris*. Post-channel these species all continued to contribute more than 1% of the catch, as did the two marine species, *Liza macrolepis* and *Valamugil buchanani* and the estuarine species *Hyporhamphus capensis* (Table 4.1).

There was a notable change in the number of numerically dominant fish species between May 2012 (last pre-channel sample) and November 2012 (first post-channel sample), increasing from four to eight species contributing more than 2% to the total catch (Figure 4.3; Figure 4.4). The highest number of species contributing more than 2% of the catch was recorded in November 2010, but this was due to very low overall fish catches, especially in *O. mossambicus* and *A. ambassis*, which dominated the rest of the pre-channel period. The freshwater species *P. philander* became abundant in the system from November 2011 after salinities in the North started to decrease.

The change in the species composition after the beach channel opened can be seen when comparing the dominant species at each site pre- and post-channel opening (Figure 4.5; Figure 4.6). There was a decline in *O. mossambicus* and *A. ambassis* abundance in the Lower Narrows, with the mullet species *L. dumerillii*, *L. macrolepis* and *V. buchanani* becoming the dominant species in this area. *Leiognathus equula* became abundant in the Narrows after the beach channel opened, while the estuarine species *Gilchristella aestuaria* was most abundant in the Narrows pre-channel. The freshwater goby *Glossogobius giurus* became dominant in the Lower Narrows post-channel. Before the beach channel was opened, *Pomadasys olivaceus* was most abundant at Fannies Island, while *Pomadasys commersonnii* was abundant afterwards at Catalina Bay. *Ambassis ambassis* greatly declined in North Lake after the beach channel opened while *L. dumerillii* increased in numbers.

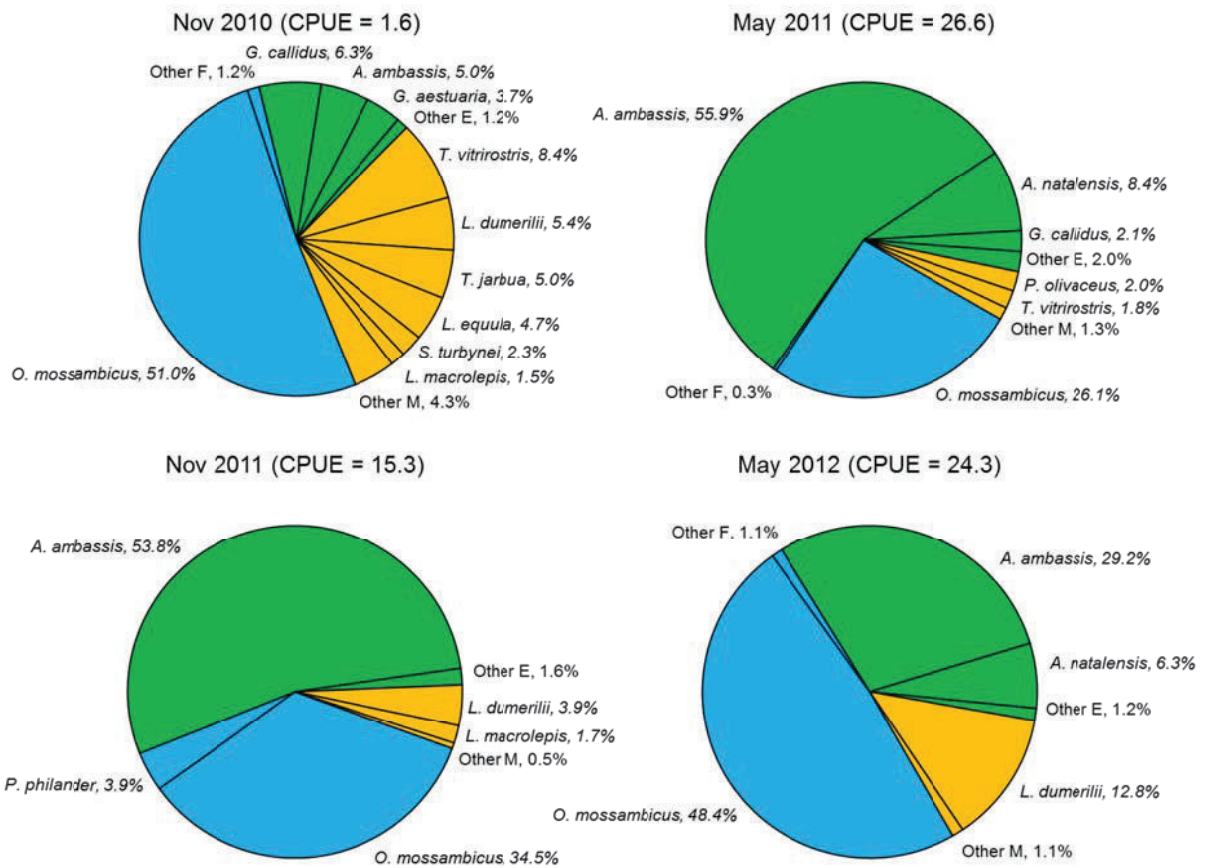


Figure 4.3: Percentage contribution of the dominant (>2%) fish species to the catch (mean CPUE) during Nov 2010 - May 2012 (Pre-channel) in the St Lucia system (■ Freshwater (F), ■ Estuarine (E) and ■ Marine (M) species) (Full species names are listed in Table 4.1).

4.1.3 Estuarine Association

In terms of numbers of species, the system was dominated by marine species, but in terms of fish abundance, (CPUE) freshwater and estuarine species were most abundant (Table 4.1; Figure 4.1; Figure 4.2). Of the 58 fish species recorded in the system during the study period, 44 were marine species. Of the remaining 14 species, 10 were estuarine and four were freshwater species. The number of marine species in the system decreased from 26 to 22 during the period November 2010 - May 2012, but increased after the beach channel opened from 22 in November 2012 to 25 in May 2014. The total number of marine species recorded before the beach channel opened was 32, compared to 37 species afterwards. Seven marine species that were present prior to the channel opening were not found again after it opened, these included *Argyrosomus japonicas*, *Chelon melinopterus*, *Epinephelus*

malabaricus, *Muraenesox bagio*, *Platycephalus indicus* and *P. olivaceus*, while 12 species not present during November 2010 - May 2012 were found in the system after the channel opened. Of these, nine occurred in the system after the mouth breached in 2007, but had subsequently disappeared prior to November 2010. A further three species have not been recorded in the system since before the mouth breached, these were *Atherina breviceps*, *Sphyræna barracuda* and *Stolephorus indicus*. The mean contribution of marine species to the total species count pre-channel was 67.7%, compared to 70.1% afterwards, while there was a decrease in the contribution of both estuarine and freshwater species from 20.0% to 18.4% and 12.3% to 11.5%, respectively.

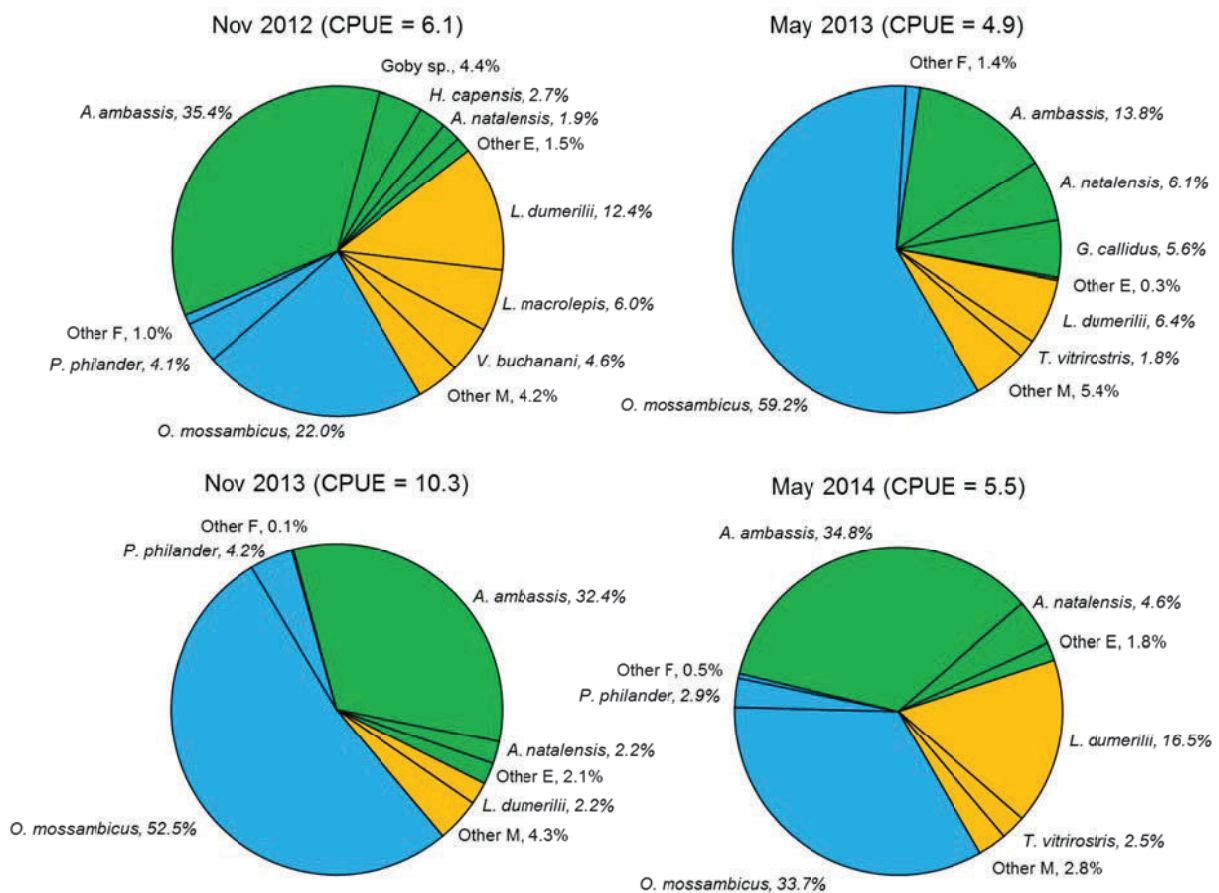


Figure 4.4: Percentage contribution of the dominant (>2%) fish species to the catch (mean CPUE) during Nov 2012 - May 2014 (Post-channel) in the St Lucia system (■ Freshwater (F), ■ Estuarine (E) and ■ Marine (M) species) (Full species names are listed in Table 4.1).

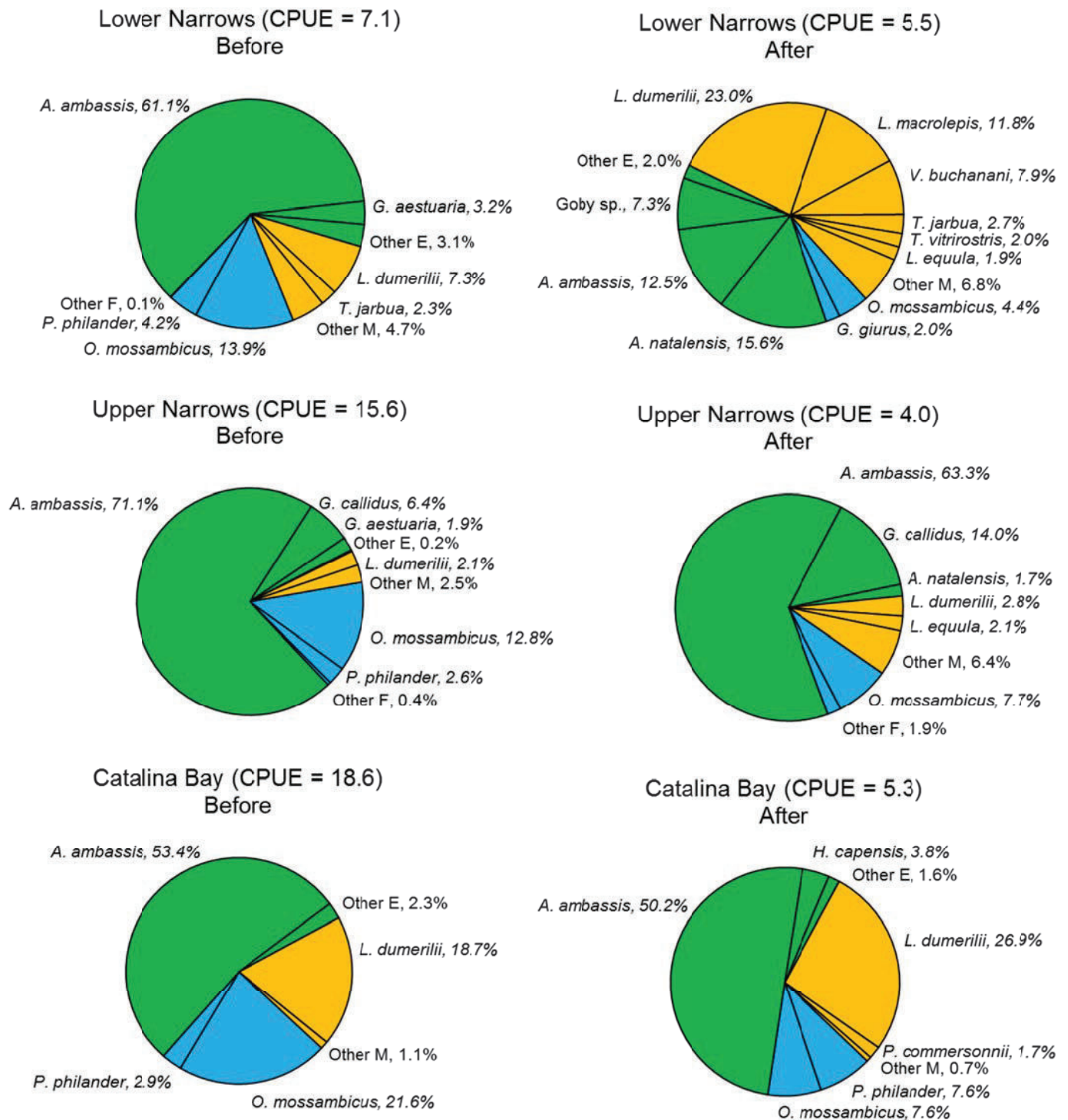


Figure 4.5: Percentage contribution of the dominant (>2%) fish species to the catch (mean CPUE) in the Lower Narrows, Upper Narrows and Catalina Bay before (Nov 2010 - May 2012) and after (Nov 2012 – May 2014) the beach channel opened (■ Freshwater (F), ■ Estuarine (E) and ■ Marine (M) species) (Full species names are listed in Table 4.1).

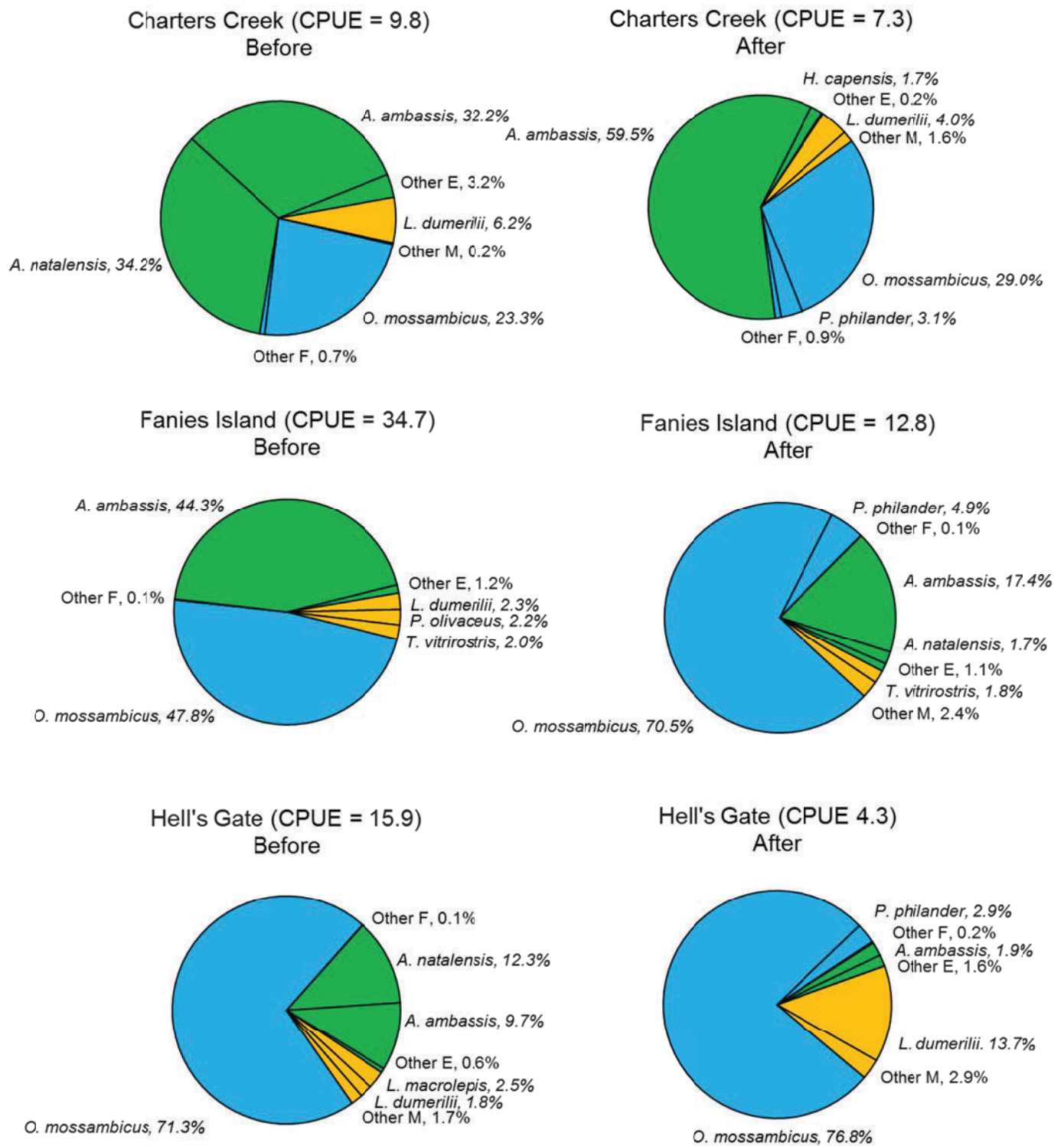


Figure 4.6: Percentage contribution of the dominant (>2%) fish species to the catch (mean CPUE) at Charters Creek, Fannies Island and Hell's Gate, before (Nov 2010 - May 2012) and after (Nov 2012 – May 2014) the beach channel opened (■ Freshwater (F), ■ Estuarine (E) and ■ Marine (M) species) (Full species names are listed in Table 4.1).

November 2010 had the lowest fish abundance (CPUE = 1.6; Marine Species CPUE = 0.5) recorded during this study, which was due to the low lake level and hypersalinity in large parts of the system as a result of drought conditions prior to 2011 (Figure 4.1; Figure 4.3). Due to the low catches of freshwater and estuarine species during November 2010, the contribution of marine species to the total catch was higher (31.5%) than during any other season, even though the total CPUE for November 2010 was the lowest. The highest CPUE for marine species was recorded in May 2012 (CPUE = 3.4), this was due to a large catch of *L. dumerilii* at Catalina Bay. The second largest catch (CPUE = 1.7) of marine species and the second largest contribution of marine species to the total catch (27.2%) was during November 2012, the first sampling season after the beach channel was opened (Figure 4.1; Figure 4.4). There was a decline in marine, estuarine and freshwater species abundance after the beach channel opened. The mean abundance (CPUE) of marine species decreased from 1.5 to 1.0, estuarine species decreased from 9.0 to 2.3 and freshwater species from 6.4 to 2.8. There was however an increase in the contribution of marine and freshwater species to the total abundance after the channel was opened, from 9.1% to 16.4% and 38.0% to 45.4% respectively, with a decline in the estuarine contribution from 52.9% to 38.2% (Figure 4.3; Figure 4.4). The dominant species in each estuarine association group for each season are shown in Figure 4.3 and Figure 4.4.

After the beach channel opened there was a general decrease in the total number of species from each estuarine association group at each site, with the exception of marine species in the Narrows and marine and freshwater species at Hell's Gate (Figure 4.2). The same trend was observed for fish abundance, with the exception of the Lower Narrows, where the abundance (CPUE) of marine species had tripled (1.0 to 3.1), after the beach channel opened (Figure 4.2). The dominant species in each estuarine association group for each site pre- and post-channel are shown in Figure 4.5 and Figure 4.6.

4.1.4 Temporal and Spatial Changes in the Fish Community

There was a distinct spatial separation in community species composition between samples from the Narrows (Lower and Upper) and from the lakes (Catalina Bay,

Charters Creek, Fannies Island and Hell’s Gate). Underlying this was a temporal gradient in the fish community during the study period, with the samples tending to separate into pre-channel and post-channel groups (Figure 4.7). In order to better understand the temporal and spatial patterns in the fish community associated with the opening of the beach channel, the fish data was averaged across the eight sampling seasons (Figure 4.8) as well as across the six sampling sites before and after the beach channel opened (Figure 4.9). SIMPROF was used to analyse for significant groupings in the fish composition and showed a significant difference between the Narrows and the lakes ($P_i = 3.17$, $p < 0.001$). The cluster ordination of sampling seasons confirmed the temporal change in the fish community associated with the beach channel opening. May 2011 - May 2012 was grouped with November 2012, while May 2013 - May 2014 samples formed a distinct post-channel group. November 2010 formed an outlier due to the hypersalinity and low water levels experienced across the system at the time (Figure 4.8). The cluster ordination of

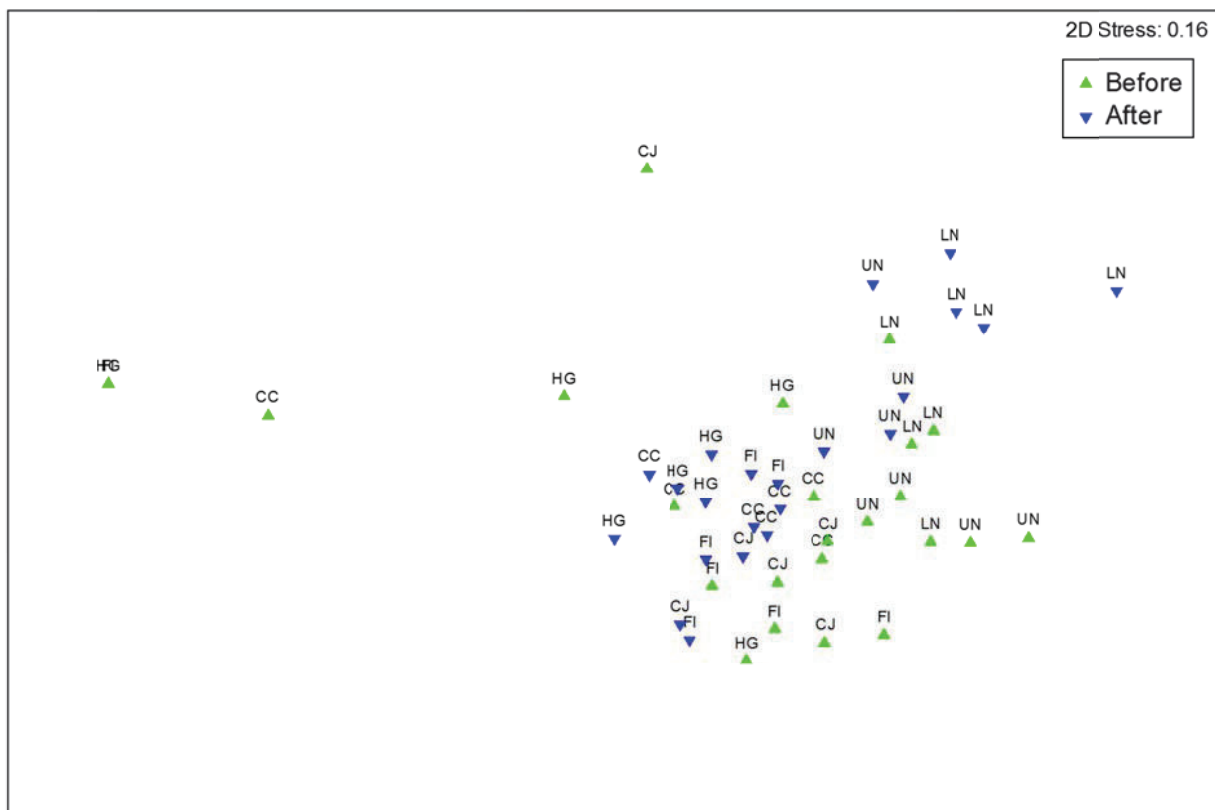


Figure 4.7: MDS ordination of the fish assemblage in the St Lucia system during the period Nov 2010 - May 2014 showing changes before and after beach channel opening and sampling sites (LN, Lower Narrows; UN, Upper Narrows; CJ, Catalina Bay; CC, Charters Creek; FI, Fannies Island; HG, Hell’s Gate).

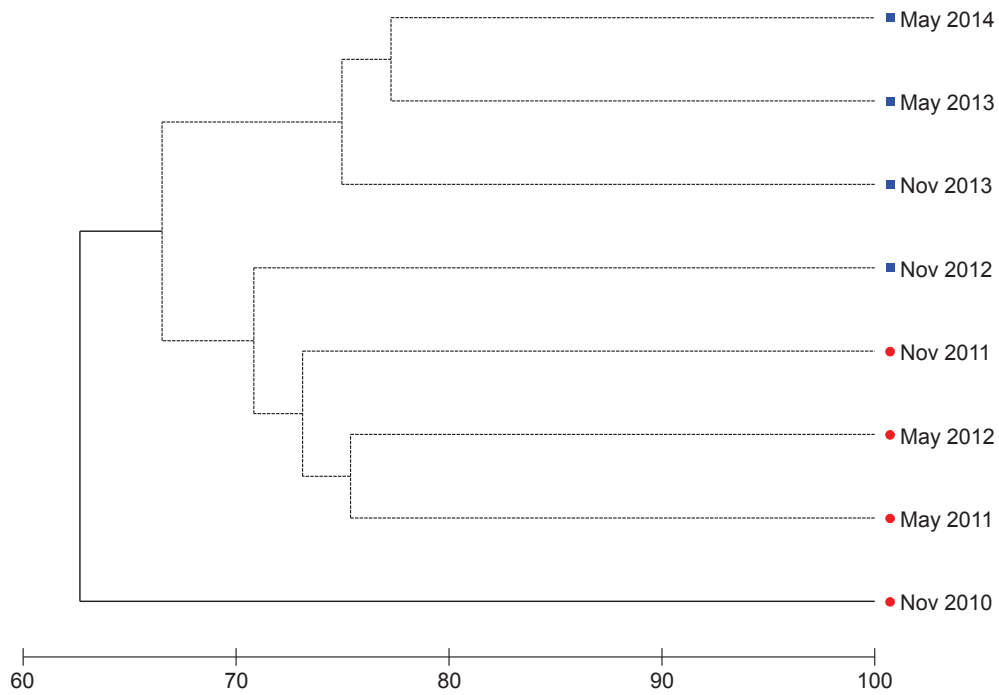


Figure 4.8: Cluster dendrogram of the fish assemblage recorded in the St Lucia system during the period Nov 2010 - May 2014, averaged over sample season. Solid line represent significant grouping as determined by SIMPROF (● Before and ■ After channel).

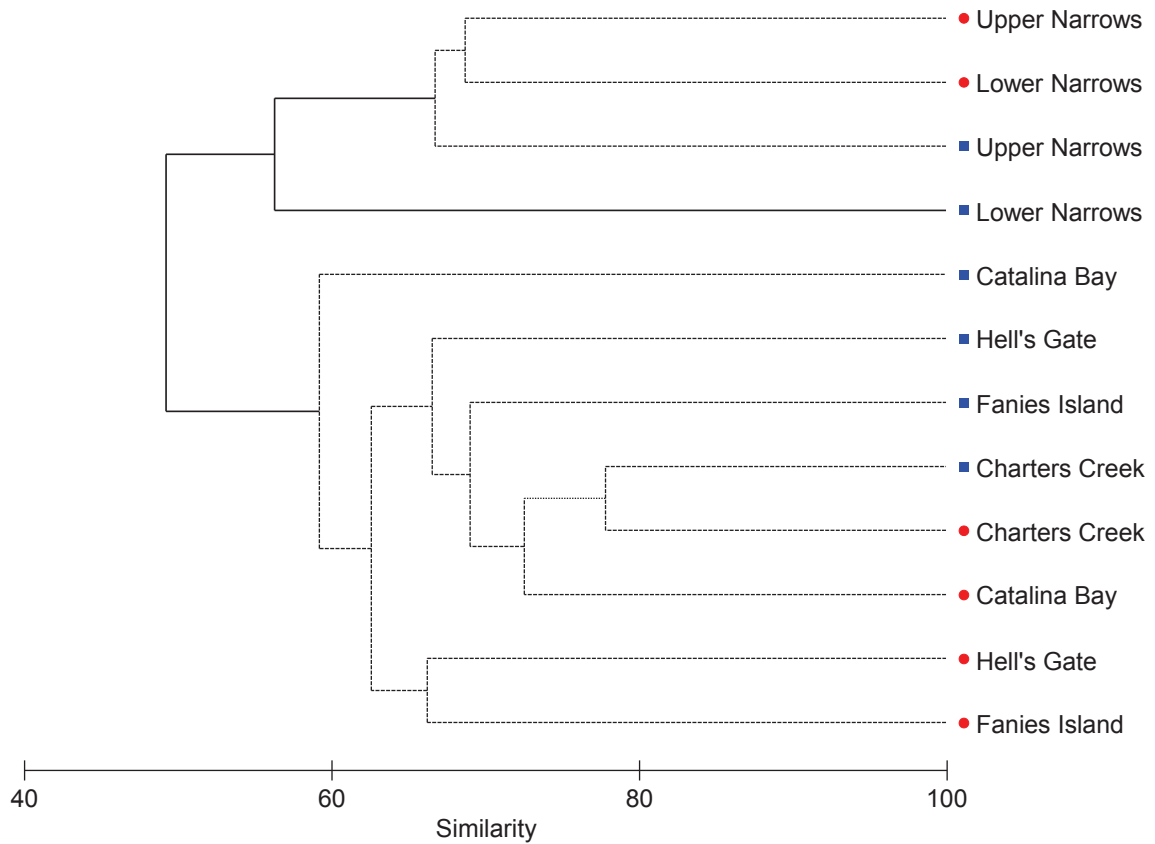


Figure 4.9: Cluster dendrogram of the fish assemblage recorded in the St Lucia system during the period Nov 2010 - May 2014, averaged over sample sites before and after opening of the beach channel. Solid line represent significant grouping as determined by SIMPROF (● Before and ■ After channel).

sites from before and after the beach channel confirmed that spatial changes occurred across the system after the channel opened. The spatial separation between samples from the Narrows and the lakes was not influenced by the opening of the beach channel, but there was greater similarity between sites in the Narrows (Lower and Upper Narrows) than site in the lakes (Catalina Bay, Charters Creek, Fannies Island and Hell's Gate) before the channel opened. However after the beach channel opened these similarities decreased but the lake had greater similarity than the Narrows (Figure 4.9).

PERMANOVA one-way analysis confirmed that there were significant differences between regions (Pseudo-F = 6.35, $p < 0.001$) and between sites (Pseudo-F = 3.43, $p < 0.001$) (Table 4.3). The nested analysis confirmed spatial differences in species composition before and after beach channel opened, with significant differences for sites (Pseudo-F = 2.59, $p < 0.001$) and regions (Pseudo-F = 4.52, $p < 0.001$). The nested analysis also revealed that sites (Pseudo-F = 1.64, $p = 0.02$) and regions (Pseudo-F = 2.29, $p < 0.001$) were significantly different before and after the beach channel opened (Table 4.3). Pairwise comparison showed that significant differences occurred between the Narrows, and South and North Lake, respectively, pre-channel and among all three post-channel regions. When comparing the pre- and post-channel regions it shows significant change within the pre- and post-channel Narrows and North Lake regions. The Lower and Upper Narrows were significantly different from all other sites in the system, with the exception of the Lower Narrows and Catalina Bay before the beach channel opened. The four sites that make up South and North Lake showed no differences among them in either channel state. The only change that occurred after the channel opened was that Catalina Bay was no longer significantly different from the Upper Narrows. When comparing pre- and post-channel site it showed significant change within the pre- and post-channel Upper Narrows and Hell's Gate sites (Table 4.4). The one-way analysis also confirmed the temporal change in the species composition during the study period, showing significant differences across the eight biannual sampling seasons (Pseudo-F = 1.57 $p = 0.01$), between years (Pseudo-F = 1.63, $p = 0.03$) and, most importantly, between the two years before the beach channel and the two years after the beach channel opened (Pseudo-F = 2.00, $p = 0.004$) (Table 4.3). The species composition during the first year (November 2011 - May 2011) of the study was

significantly different from the second (November 2011 – May 2012) and last year (November 2013 – May 2014) (Table 4.4). In contrast, there was little seasonal variation during the study (Pseudo-F = 1.20, $p = 0.29$), however nested analysis showed that there were significant differences between the before and after winter and summer seasons (Pseudo-F = 1.82, $p = 0.02$). PERMANOVA two-way reveal

Table 4.3: Mean squares and significance levels of the one-way, two-way, nested and three-way PERMANOVA of the fish composition in the St Lucia system from Nov 2010 – May 2014 (Channel separates the data into before (Nov 2010 – May 2012) and after (Nov 2012 – May 2014) the beach channel opened). * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

One-Way PERMANOVA						
	Region (R)	Site (Si)	Year (Y)	Season (Se)	Sample (Ss)	Channel (C)
<i>df</i>	2	5	3	1	7	1
Composition	9394.3	4948.8	2867.5	2163.3	2644.4	3582.7
Pseudo-F	6.3***	3.4***	1.6*	1.2	1.6**	2.0*
<i>df</i>	43	40	42	44	38	44
Residual	1479.9	1442.0	1757.7	1823.6	1682	1791.9

Two-and Three-Way interaction							
	R x Se	R x Y	R x Ss	Si X Se	Si x Y	Se x Y	R x Y x Se
<i>df</i>	2	6	14	5	19	2	6
Composition	2075.6	1793.1	1587.7	1127.5	1419.5	798.5	1232.1
Pseudo-F	1.5	1.4*	1.5**	0.8	1.6**	0.5	1.2
<i>df</i>	40	34	22	34	19	38	22
Residual	1432.5	1299.0	1039.9	1466.4	869.8	1682.0	1039.9

Nested interaction						
	Region (R)	R(Site)	Year (Y)	Y(Sample)	Season (Se)	Se(Sample)
<i>df</i>	2	3	3	4	1	6
Composition	9350.4	1985.1	2873.2	277.1	2000.0	2720.7
Pseudo-F	6.5***	1.4	1.7*	1.5	1.2	1.6**
<i>df</i>		40		38		38
Residual		1315.0		1357.9		1758.0

	Season (Se)	Se(Channel)	Region (R)	R(Channel)	Site (Si)	Si(Channel)	Channel (C)	C(Year)
<i>df</i>	1	2	2	3	5	6	1	2
Composition	2060.1	3201.6	9489.4	3107.2	4999.8	2162.1	3582.7	2509.9
Pseudo-F	0.6	1.8*	7.0***	2.3***	2.3**	1.6**	2.0*	1.4
<i>df</i>		42		40		34		42
Residual		1758.0		1357.9		1315.0		1757.7

	Channel (C)	C(Season)	Channel (C)	C(Region)	Channel (C)	C(Site)	Channel (C)	C(Sample)
<i>df</i>	1	2	1	4	1	10	1	6
Composition	3582.7	2503.4	3597.1	6131.9	2503.0	3413.4	3604.4	2488
Pseudo-F	2.0*	1.4	2.7**	4.5***	2.7**	2.6***	2.1*	1.5*
<i>df</i>		42		40		34		38
Residual		1758.0		1357.9		1315.0		1682.0

Table 4.4: PERMANOVA results showing mean % similarity within (Bold) and between groups of community samples of the six sampling sites, the three main regions and the sampling years (Nov 2010 - May 2014) in the St Lucia system. *denotes a significant difference (Grey-shaded indicates where before and after beach channel community sample are compared).

		BEFORE										AFTER													
		Lower Narrows		Upper Narrows		Catalina Bay		Charters Creek		Fanies Island		Hell's Gate		Lower Narrows		Upper Narrows		Catalina Bay		Charters Creek		Fanies Island		Hell's Gate	
		% Sim	t	% Sim	t	% Sim	t	% Sim	t	% Sim	t	% Sim	t	% Sim	t	% Sim	t	% Sim	t	% Sim	t	% Sim	t	% Sim	t
BEFORE	Lower Narrows	59.39																							
	Upper Narrows	52.39	1.66*	61.82																					
	Catalina Bay	41.62	1.31	40.65	1.49*	37.47																			
	Charters Creek	40.03	1.53*	36.56	1.73*	42.25	0.74	39.84																	
	Fanies Island	30.68	1.74*	35.54	1.59*	37.63	0.84	39.58	0.81	33.96															
	Hell's Gate	29.01	1.76*	31.33	1.72*	31.85	1.07	36.01	0.90	38.05	0.72	30.32													
AFTER	Lower Narrows	49.66	1.46	36.88	2.28*	30.73	1.70*	26.87	1.93*	20.78	1.99*	22.83	1.87*	52.11											
	Upper Narrows	53.26	1.60*	55.09	1.58*	39.36	1.53	38.86	1.62*	30.20	1.81*	32.42	1.67*	46.88	1.75*	61.80									
	Catalina Bay	42.32	1.91	44.26	1.93	45.23	1.00	47.88	0.88	38.65	1.07	32.62	1.22	23.07	2.38	45.03	1.94	59.34							
	Charters Creek	44.73	2.18*	47.10	2.19*	50.87	0.85	51.37	0.92	43.44	1.20	37.28	1.44	29.76	2.70*	48.15	2.15*	62.32	0.93	62.33					
	Fanies Island	41.31	2.42*	41.50	2.56*	47.60	1.11	48.08	1.16	45.42	1.15	40.27	1.34	30.14	2.72*	41.00	2.61*	55.80	1.39	61.75	1.16	62.82			
	Hell's Gate	39.32	2.92*	37.94	3.22*	46.12	1.31	51.02	1.14	42.39	1.41*	36.89	1.60*	27.12	3.20*	38.69	3.17*	53.46	1.94	64.15	1.26	62.10	1.52	71.79	

		BEFORE						AFTER					
		Narrows		South Lake		North Lake		Narrows		South Lake		North Lake	
		% Sim	t	% Sim	t	% Sim	t	% Sim	t	% Sim	t	% Sim	t
BEFORE	Narrows	55.91											
	South Lake	39.71	1.84*	40.71									
	North Lake	31.64	2.17*	36.27	1.10	35.52							
AFTER	Narrows	48.72	1.63*	33.95	2.08*	26.56	2.33*	51.20					
	South Lake	45.04	2.46*	49.60	1.10	38.79	1.68*	37.32	2.82*	62.13			
	North Lake	40.02	3.22*	48.20	1.37*	41.24	1.74*	34.24	3.38*	60.18	1.51*	64.33	

		BEFORE				AFTER			
		2 Year		1 Year		1 Year		2 Year	
		% Sim	t	% Sim	t	% Sim	t	% Sim	t
BEFORE	2 Year	31.87							
	1 Year	36.49	1.51*	48.93					
AFTER	1 Year	33.54	1.40	46.09	0.97	43.68			
	2 Year	35.93	1.53*	48.69	1.12	48.49	0.60	50.33	

significant interactions between region x year (Pseudo-F = 1.38, p = 0.05), region x samples (Pseudo-F = 1.53, p = 0.004) and site x year (Pseudo-F = 1.63, p = 0.004) while the three-way interaction between region x year x season, was not significant (Pseudo-F = 1.12, p = 0.22) (Table 3.4).

The fish species most responsible for the differences before and after the beach channel opened across all sites (Table 4.5) and for each site (Table 4.6) were analysed using SIMPER, which determines the contribution of each species to the average Bray-Curtis similarity within the group. The mean dissimilarity between the two years before and after the beach channel opened was 59.0% and the species most responsible for the dissimilarity were *A. ambassis*, *O. mossambicus*, *L. dumerilii* and *P. philander* (Table 4.5). These four species were also in the top five species most responsible for the dissimilarity within sites. The other species that contributed to the top five were *A. natalensis* in the Lower Narrows, Charters Creek and Fannies Island, as well as the overall system (Table 4.5; Table 4.6), *G. aestuaria* in the Upper Narrows, *H. capensis* at Catalina Bay and *L. macrolepis* at Hell's Gate (Table 4.6).

Table 4.5: SIMPER results showing the mean abundance, mean dissimilarity and % contribution of the fish species making the highest contribution to the mean dissimilarity before (Nov 2010 - May 2012) and after (Nov 2012 - May 2014) the beach channel opened in the St Lucia system.

Species	Before Mean Abundance	After Mean Abundance	Mean Dissimilarity	Diss/SD	Contribution %
Mean dissimilarity before and after = 58.94%					
<i>Ambassis ambassis</i>	1.18	0.97	6.08	1.23	10.32%
<i>Oreochromis mossambicus</i>	1.26	1.04	4.64	1.16	7.87%
<i>Liza dumerilii</i>	0.61	0.69	3.98	1.03	6.76%
<i>Pseudocrenilabrus philander</i>	0.35	0.49	3.53	1.07	5.99%
<i>Ambassis natalensis</i>	0.26	0.39	3.30	1.00	5.59%
<i>Glossogobius callidus</i>	0.34	0.22	2.73	0.94	4.64%
<i>Thryssa vitrirostris</i>	0.26	0.32	2.65	1.07	4.49%
<i>Hyporhamphus capensis</i>	0.27	0.23	2.37	0.95	4.03%
<i>Liza macrolepis</i>	0.25	0.20	2.19	0.89	3.72%
<i>Pomadasys commersonii</i>	0.18	0.30	1.92	1.12	3.26%
<i>Leiognathus equula</i>	0.15	0.20	1.69	0.86	2.87%
<i>Terapon jarbua</i>	0.14	0.16	1.48	0.86	2.52%
<i>Silhouettea sibayi</i>	0.19	0.03	1.43	0.67	2.42%
<i>Glossogobius giurus</i>	0.12	0.16	1.39	0.82	2.36%
<i>Gilchristella aestuaria</i>	0.19	0.02	1.18	0.60	2.00%

Table 4.6: SIMPER results showing the mean abundance, mean dissimilarity and % contribution of the fish species making the highest contribution to the mean dissimilarity before (Nov 2010 - May 2012) and after (Nov 2012 - May 2014) the beach channel opened at each site in the St Lucia system (For mean % similarities, see Table 4.4).

Species	Before Mean Abundance	After Mean Abundance	Mean Dissimilarity	Diss/D	Contribution %
<u>Lower Narrows: Mean dissimilarity = 50.34%</u>					
<i>Ambassis natalensis</i>	0.27	0.96	3.10	2.33	6.15%
<i>Pseudocrenilabrus philander</i>	0.63	0.00	2.86	2.52	5.69%
<i>Oreochromis mossambicus</i>	0.94	0.49	2.30	1.55	4.57%
<i>Ambassis ambassis</i>	1.09	0.83	2.26	1.03	4.49%
<i>Liza dumerilii</i>	0.76	0.79	1.92	1.40	3.82%
<u>Upper Narrows: mean dissimilarity = 44.91%</u>					
<i>Ambassis ambassis</i>	1.62	1.08	4.66	1.46	10.39%
<i>Liza dumerilii</i>	0.45	0.57	2.85	2.90	6.34%
<i>Oreochromis mossambicus</i>	1.17	0.73	2.81	2.65	6.26%
<i>Gilchristella aestuaria</i>	0.43	0.00	2.77	0.95	6.17%
<i>Pseudocrenilabrus philander</i>	0.28	0.28	2.68	1.08	5.96%
<u>Catalina Bay: Mean dissimilarity = 54.77%</u>					
<i>Ambassis ambassis</i>	1.42	1.23	7.03	1.76	12.84%
<i>Liza dumerilii</i>	0.82	0.65	6.28	2.12	11.47%
<i>Pseudocrenilabrus philander</i>	0.51	0.75	4.45	1.33	8.12%
<i>Oreochromis mossambicus</i>	1.17	0.76	3.46	1.24	6.33%
<i>Hyporhamphus capensis</i>	0.32	0.60	3.40	1.33	6.21%
<u>Charters Creek: Mean dissimilarity = 48.63%</u>					
<i>Ambassis ambassis</i>	0.81	1.27	8.28	1.14	17.03%
<i>Liza dumerilii</i>	0.66	0.70	4.52	0.93	9.30%
<i>Ambassis natalensis</i>	0.60	0.14	4.49	0.88	9.22%
<i>Pseudocrenilabrus philander</i>	0.39	0.67	3.52	0.82	7.23%
<i>Oreochromis mossambicus</i>	1.07	1.11	3.51	1.19	7.21%
<u>Fanies Island: Mean dissimilarity = 54.58%</u>					
<i>Ambassis ambassis</i>	1.38	1.12	7.52	1.40	13.77%
<i>Oreochromis mossambicus</i>	1.73	1.65	6.68	1.00	12.24%
<i>Pseudocrenilabrus philander</i>	0.16	0.79	5.77	1.31	10.58%
<i>Ambassis natalensis</i>	0.00	0.51	4.14	1.27	7.59%
<i>Liza dumerilii</i>	0.71	0.54	4.14	1.11	7.58%
<u>Hell's Gate: Mean dissimilarity = 63.11%</u>					
<i>Liza dumerilii</i>	0.26	0.86	8.85	1.45	14.03%
<i>Oreochromis mossambicus</i>	1.49	1.34	7.47	1.17	11.84%
<i>Ambassis ambassis</i>	0.74	0.42	6.31	1.69	10.00%
<i>Pseudocrenilabrus philander</i>	0.11	0.57	5.60	1.54	8.88%
<i>Liza macrolepis</i>	0.54	0.00	5.24	1.16	8.30%

4.1.5 Correlation between Species Assemblage and Environmental Variables

Canonical correspondence analysis (CCA) was used to test the correlation between environmental variables and the fish assemblage (Figure 4.10). For the pre-channel communities, turbidity ($F = 3.02$, $p = 0.008$) and salinity ($F = 2.35$, $p = 0.002$) were found to be most responsible for structuring the fish community, (Table 4.7). The principal component analysis (PCA) pre-channel biplot using environmental data only shows the expected inverse relationship between depth and salinity, as the deepest areas of the system were in the Narrows where salinities were lowest, while higher salinities were recorded in the shallow parts of the lakes. There was also an inverse relationship between water level and temperature, as higher evaporation occurred during summer months associated with increased salinities. The less pronounced relationship between depth and water level is due to the very small change in water level during this period. Turbidity was closely related to temperature, indicating the changes to be seasonally driven (Figure 10).

After the beach channel was opened, salinity ($F = 1.95$, $p = 0.034$) was only factor with significant correlation to the fish community (Table 4.7). The post-channel PCA showed that there was a close relationship between the depth and water level in the system, due to the increase in water level across the system. A positive relationship was observed between depth and salinity due to salinities in the lakes decreasing to below marine levels and the salinity in the Narrows increasing due to its connection to the ocean via the Mfolozi mouth. Temperature was also less related to water level even though greater evaporation occurred during summer months and there was also greater precipitation during the post-channel period (Figure 4.10) (Taylor *et al.*, 2014).

The CCA also provided insight into the distribution of the fish species in relation to the environmental variables (Figure 4.10). There was a separation along the salinity-and-depth gradient with samples in the Narrows forming a separate group from those in the lakes. The 15 most abundant fish species before and after the beach channel opened are illustrated in Figure 4.10. *Terapon jarbua*, *L. equula* and *G. callidus* were mostly associated with the Narrows, while *O. mossambicus*, *H. capensis* and *L. dumerilli* were mainly found in the lakes.

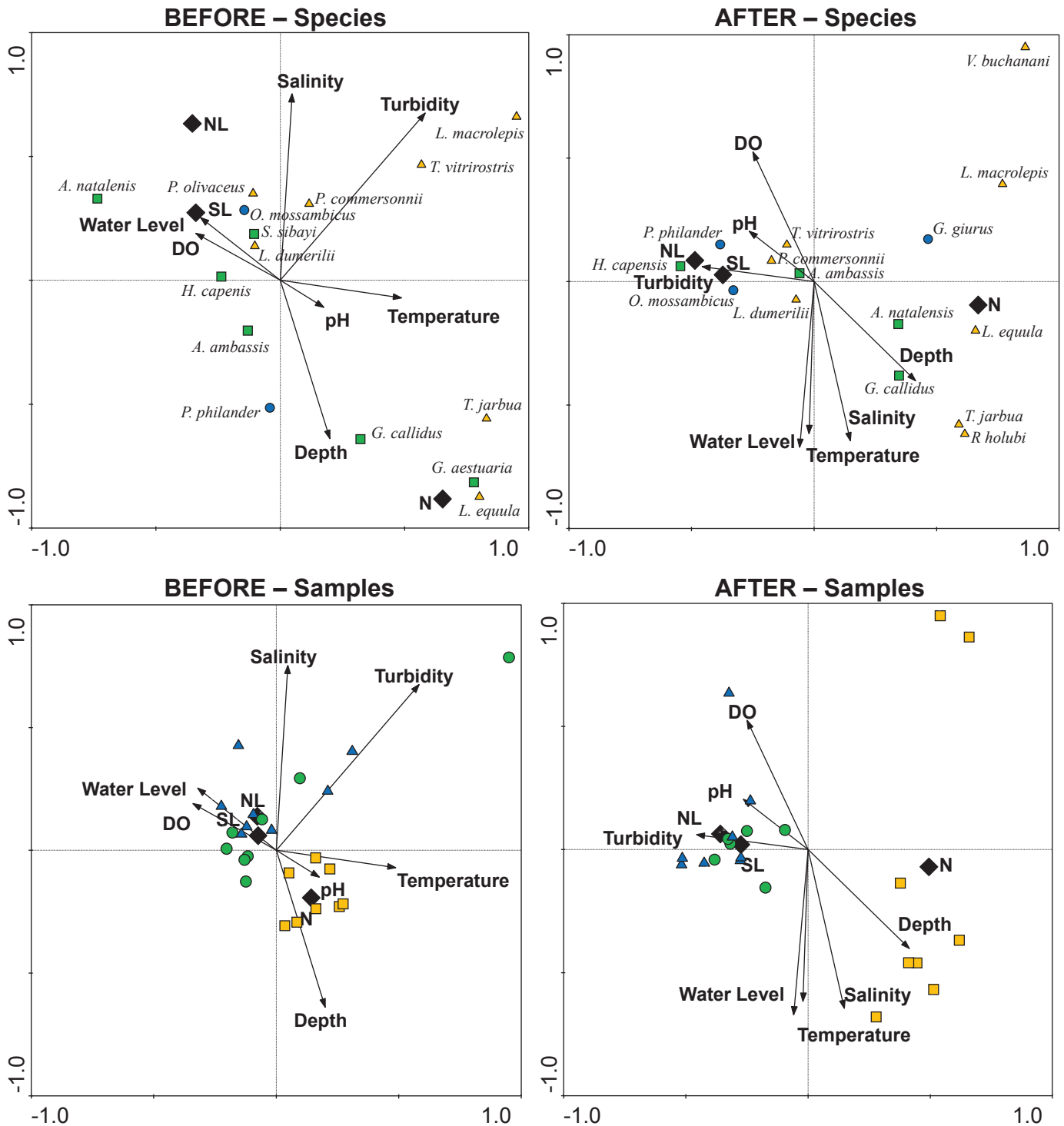


Figure 4.10: Canonical correspondence (CCA) analysis biplots (eigenvalues Table 4.8) of the relationship between the fish assemblage and environmental variables in the St Lucia system during the period before (Nov 2010 - May 2012), and after (Nov 2012 - May 2014) the beach channel opened. (Species: ■, Estuarine; ●, Freshwater and ▲, Marine species) (Samples: ■, Narrows (N); ●, South Lake (SL) and ▲, North Lake (NL)).

Table 4.7: Canonical correspondence analysis (CCA) showing the environmental variables and their contribution to the total variance in the fish community structure in the St Lucia system before (Nov 2010 - May 2012) and after (Nov 2012 - May 2014) the beach channel opened. *Variable contributing significantly to the total variance in the fish community.

	<u>BEFORE</u>			<u>AFTER</u>		
	Variance	F	P	Variance	F	P
Salinity	0.15	2.35	0.002*	0.18	1.95	0.03*
Turbidity	0.21	3.02	0.008*	0.14	1.74	0.11
Depth	0.06	1.04	0.40	0.13	1.54	0.11
Dissolved Oxygen	0.10	1.58	0.07	0.09	1.23	0.25
Water Level	0.08	1.29	0.19	0.15	1.73	0.06
Temperature	0.07	1.10	0.36	0.05	0.64	0.78
pH	0.08	1.21	0.26	0.14	1.72	0.06
Before/After Channel						

Table 4.8: Canonical correspondence analysis (CCA) eigenvalues and cumulative % contribution to the total variance of the first four axes of the correlation between environmental variables and the fish community structure in the St Lucia system during the period (a) before (Nov 2010 - May 2012) and (b) after (Nov 2012 - May 2014) the beach channel opened. Species-environment correlations depict the correlation between environmental variables and the fish community for each of the first four axes of the CCA plot.

	<u>AXES</u>				<u>Total (All Axes)</u>
	1	2	3	4	
<u>BEFORE</u>					
Eigenvalues	0.23	0.18	0.13	0.09	0.75
Cumulative %	30.00	53.80	70.60	82.00	
Species-environment correlations	0.93	0.87	0.87	0.85	
<u>AFTER</u>					
Eigenvalues	0.31	0.24	0.11	0.09	0.88
Cumulative %	34.90	62.10	74.50	84.80	
Species-environment correlations	0.88	0.76	0.79	0.78	

4.2 Discussion

4.2.1 Mouth Condition

Most South African estuaries are extensively utilized by marine fish species which rely on the warm temperatures, rich food supply and sheltered environment provided

by estuaries as nursery areas for their larvae and juveniles (Wallace, 1975; Wallace and Van der Elst, 1975). The recruitment of juvenile fish is subsequently dependent on a regular connection with the marine environment. However, many estuaries along the KwaZulu-Natal coast have been altered by anthropogenic activities, influencing their connectivity with the ocean (Gillson, 2011). The St Lucia mouth was altered in 1952 when it was separated from the Mfolozi system. Over the last 60 years, this has led to an increase in the frequency and duration of drought related mouth closures (Cyrus *et al.*, 2010b).

Following the recent mouth closure in 2002 and the decision by management not to dredge it open, the St Lucia estuarine system has experienced extremely low water levels, compartmentalisation and hypersalinities during 2003-2006 and 2008-2010. EKZNW needed a new strategy to manage the St Lucia mouth and in 2010, a workshop was held to investigate the possibility and implications of re-connecting the St Lucia and Mfolozi estuaries (Bate *et al.*, 2011). The most ambitious outcome of the 2010 Indaba was the recommendation to excavate a channel along the beach to connect the mouths of the two systems. The beach channel, completed in July 2012, allowed Mfolozi water to be diverted into the St Lucia mouth. The aim was that the Mfolozi would eventually breach into the St Lucia Narrows due to the natural migration of the Mfolozi mouth to the north and that the water inflow over time would allow the combined mouths to breach naturally. This would re-establish the connection between the St Lucia and Mfolozi systems to its historical condition, prior to separation in 1952.

The effect of closed mouth conditions on the fish population has been well established in the literature (Whitfield, 2005b; Whitfield, *et al.*, 2006; Hoeksema *et al.*, 2009; Whitfield and Taylor, 2009; Vivier *et al.*, 2010a). Studies of the St Lucia fish community have shown a decline in fish abundance and number of species, especially marine species, as recruitment potential in and out of the system was lost (Cyrus and Vivier, 2006b; Vivier *et al.*, 2010a). In the Nhlabane Estuary south of St Lucia, changes in composition and abundance of fish species were observed during extended mouth closure caused by drought conditions. The system changed from a marine-dominated fish community in 1992 to a freshwater/estuarine-dominated fish community by 1995 (Vivier and Cyrus, 2001).

4.2.2 Change in the Environment

The primary influence of the beach channel was on the physical environment. Low saline water entered the St Lucia system while the Mfolozi mouth was closed, which led, in conjunction with increased rainfall since 2010/11, to a rise in water levels and decreases in salinities across the St Lucia system. Both salinity and depth were significant factors responsible for structuring the fish community during the period November 2010 to May 2014 (CANOCO, Table 4.7; Figure 4.10). Before the St Lucia and Mfolozi systems were connected there was a reverse salinity gradient in the St Lucia system caused by the drought related mouth closure, with lowest salinities at the mouth and highest salinities in North Lake. The relatively low salinity water entering the St Lucia system from the Mfolozi, combined with increased rainfall, lowered the salinities to such an extent that during November 2012, the highest salinity of 26.5, well below marine water, was recorded at Hell's Gate, while the salinity in the Lower Narrows was as low as 6.2. By May 2013, a salinity reversal had occurred in the system, due to the Mfolozi mouth being open during the summer and autumn high flow period and predominantly marine water being pushed into St Lucia. The highest salinities were now found in the Lower Narrows, due to the connection to the ocean via the Mfolozi mouth. The lowest salinities during the study period have always been in the Upper Narrows where the Mpate River enters the Narrows and with increased rainfall, the freshwater inflow has decreased salinities in this region to just above freshwater.

Water levels across the system increased by 1-1.5 m during the study period, covering previously dry areas of the lakes, re-establishing habitats for fish and improving connectivity between the lakes and the Narrows thus allowing for better fish movement between different regions of the St Lucia system (Appendix 1 and 2).

4.2.3 Species Composition

Numerous studies, particularly from South Africa and Australia have shown that in intermittently open estuaries, mouth breaching events result in an increase in fish species diversity (Bennett, 1989; Griffiths and West, 1999). During periods of

extended mouth closures in two Western Australian estuaries a decline in species richness was recorded prior to breaching. Species numbers in both the Wellstead and Beaufort Estuaries increased after mouth breaching, as marine species re-entered the systems (Lenanton and Hodgkin, 1985; Young and Potter, 2002a). Even though the beach channel re-established a connection between the St Lucia Estuary and the ocean via the Mfolozi system, it was not nearly as effective as a mouth breaching event. However, a connection between the St Lucia system and the marine environment will in the long term lead to further increases in the number of marine species.

During this study a total of 23,369 fish representing 58 species were recorded from seine net catches, 15,083 fish during the two years (November 2010 - May 2012) prior to the beach channel and 8,286 fish during the two years (November 2012 - May 2014) after the beach channel opened. During the two periods the total number of species caught increased from 45 to 50 species, indicating that some recruitment occurred after the beach channel opened. Prior to the beach channel opening 32 marine species were recorded in the system. After the beach channel opened, the marine group increased from 32 to 37 species, while estuarine and freshwater species numbers remained the same. Of the 32 marine species present in the system prior to the beach channel, seven were lost from the system and did not occur after the beach channel was opened, while 12 species not present during November 2010 – May 2012 were found in the system after the channel opened. Nine of these occurred in the system after the mouth breached in 2007, but have subsequently disappeared, prior to the start (November 2010) of the current study period (Vivier *et al.*, 2010a). A further three species had not been recorded in the system even before the mouth breached in 2007, these were *Atherina breviceps*, *Sphyraena barracuda* and *Stolephorus indicus*.

The total number of species recorded per season ranged from a low of 29 in November 2011 to a maximum of 34 in November 2010, May 2012, November 2012 and May 2013. As shown in Chapter 3 (Figure 3.3), there was a general decline in species numbers over time due to the loss of marine species and the absence of a connection with the ocean. November 2010 had the lowest number of species recorded during 2008-2010. However, during the two years prior to the beach

channel, it was the season least influenced by prolonged mouth closure before opening of the beach channel and therefore the number of species during November 2010 was higher than those recorded during 2011. Two estuarine species not recorded in the system since mouth closure in 2002 were found in May 2012, indicating movement towards a normal estuarine state, these were the gobies *Oligolepis acutipennis* and *Trypanchen microcephalus*. The high species numbers in November 2012 and May 2013, the first two seasons after the beach channel opened, were directly due to the connection to the ocean. In July 2012, when the two systems were joined, the Mfolozi mouth was closed and the indirect connection between the ocean and the St Lucia system was only established several months later. Fewer newly recruited marine species were recorded in November 2012 than in May 2013, with only two new marine species being recorded, i.e. *Carcharhinus leucas* and *Pomatomus saltatrix*, which were only present in the system during November 2012 when the channel was at its deepest. In May 2013, six previously absent species were recorded in the system, five marine and one estuarine species. The marine species included *Caranx sexfaciatus*, *Myxus capensis*, *Scomberoides lysan*, *S. barracuda* and *S. indicus*. Most of the marine species that entered the system during the first year after the beach channel was opened were piscivorous species that have been absent from St Lucia due to the system being closed to the ocean.

In the adjacent Mfolozi-Msunduzi Estuary, 50 marine species were recorded by CRUZ (Coastal Research Unit of Zululand, unpublished data) during 2009-2012, including 31 of the marine species recorded in the St Lucia system after opening of the beach channel and six of the seven species that were lost from St Lucia prior to the start of the study period. This means that 19 other marine species could potentially have entered St Lucia after the channel between the two systems was connected, although most of these were marine stragglers (Whitfield, 2005a; Potter *et al.*, 2013). Similar number were also recorded during 2007-2008 (Vivier *et al.*, 2010b). During St Lucia's mouth breaching event in 2007, 59 species were recorded in the system, of which 49 were marine (Vivier *et al.*, 2010a). During the year after the beach channel was opened, only 32 marine species were recorded in St Lucia, which is considerably lower than the 49 species recorded after the mouth opened in 2007. The similarity in the number of marine species found in the Mfolozi-Msunduzi

Estuary and in the open mouth St Lucia system illustrates that with a direct link to the ocean, marine fish can recruit to a much greater degree into the estuarine environment. This indicates that the beach channel was not nearly as effective in allowing recruitment of marine species into St Lucia, compared to a direct connection to the ocean, even though the number of marine species within the system increased from 22 in November 2012 to 25 species in May 2014. In a study to compare the fish composition in the natural (Mandurah) and artificial (Dawesville) channels in the Peel-Harvey Estuary (Western Australia), Young and Potter (2002b) found that there was no difference in the fish diversity between the two channels. However according to Perissinotto *et al.* (2010) artificial breaching of a system is not as effective as natural breaching events because freshwater input plays an important role in the productivity of larval fish, as well as allowing for necessary recruitment cues to enter the marine environment (Strydom, 2003). While the study in the Peel-Harvey Estuary was conducted under normal flood and ebb tide exchange, the St Lucia beach channel breach into the Mfolozi Estuary, not the ocean and had very little outflow due to system recovering from the recent drought.

The Lower and Upper Narrows both showed an increase in species numbers after the beach channel was opened, as marine species entered the system via the Mfolozi mouth. Most marine species kept to the Narrows as the highest salinities (still below marine levels) were found in this region after the beach channel opened. Catalina Bay, Charters Creek and Fannies Island showed declines in the number of species recorded. The decline at Catalina can, however, be attributed to difficulty in sampling due to the absence of exposed banks to pull seine nets. The increased water level and thick vegetation growing along the shoreline, resulted in a reduced sampling effort at this site during 2013. Despite the slight decline in the number of species at Charters Creek and Fannies Island, these sites still showed higher species numbers than Hell's Gate, where there was an increase in species number after the beach channel opened. This region was most affected by drought conditions and was the most inhospitable area for fish survival prior to the channel opening. The increased water levels and decline in salinities after the beach channel opened made it a more hospitable environment for species that could not previously survive there. Higher water levels also made it more probable for fish to move between South and North Lake.

4.2.4 Fish Abundance

The beach channel was efficient in diverting Mfolozi-Msunduzi Estuary water into the St Lucia system and allowing some marine species to recruit via the Mfolozi mouth. There was, however, a decline in overall fish abundance (CPUE) throughout the system after the beach channel opened. The fish abundance in the system decreased from a mean CPUE of 16.9 before (two years before) to a mean CPUE of 6.7 after the channel opened (two years after), a decline of 60.4%. This decline should be considered in view of the exceptionally large fish catches made during the pre-channel period, May 2011 - May 2012, which were considerably larger than those recorded during the preceding three years 2008-2010, as shown in Chapter 3 (Figure 3.3). One could ask why this sudden increase in abundance during 2011-2012? This was due to exceptionally large catches of the freshwater species *Oreochromis mossambicus* (CPUE = 25.6) and the estuarine species *Ambassis ambassis* (CPUE = 50.0), particularly at Fannies Island, and a number of factors contributed to their population explosion. Declines in salinities in the northern parts of the system and the concomitant higher lake levels not only made breeding easier for estuarine and euryhaline freshwater species, particularly *O. mossambicus* and *A. ambassis*, but also provided abundant habitat for marine immigrants, especially the mullet *Liza dumerilli*, which entered the system via the back channel and re-colonized the northern parts of the St Lucia system. This was evident in that 75% of the total marine fish abundance in the system during May 2011 was recorded at Fannies Island.

During the study period, marine species dominated the system in terms of species numbers, but in terms of fish abundance (CPUE), freshwater and estuarine species dominated (Figure 4.1). *Ambassis ambassis* and *O. mossambicus* were the two most abundant species in the St Lucia system, accounting for 40.1% and 37.9% of the total catch (CPUE) from November 2010 - May 2014, respectively. Although *O. mossambicus* dominated the system under closed mouth, hypersaline conditions (Cyrus *et al.*, 2011), its abundance was surpassed by *A. ambassis* during May 2011 and November 2011. This was most likely due to the diet of *Ambassis* species. They are zooplanktivores that individually select their prey out of the water column.

According to Martin and Blaber (1983), *Ambassis* species in the St Lucia system feed mainly on isopods and mysids such as *Pseudodiaptomus stuhlmanni* and *Mesopodopsis africana*. They documented that juvenile *A. ambassis* (<30 mm SL) feed predominately on Copepod nauplii, which have been shown to be abundant in the St Lucia system (Carrasco *et al.*, 2013). Carrasco *et al.* (2013) recorded a substantial increase in zooplankton densities between November 2010 and May 2011, with the most common species being *P. stuhlmanni* and *M. africana*. The relative abundance of *A. ambassis* during 2011 could thus be attributed to high food availability across the system (Carrasco *et al.*, 2013) and the absence of competing marine zooplanktivore species due to continued closed mouth conditions. *Oreochromis mossambicus* on the other hand has been found to have an extremely variable diet and they exhibit great flexibility under harsh environmental conditions (Carrasco *et al.*, 2012), which greatly contributes to their dominance in the system under 'stressful' conditions.

In May 2012, *O. mossambicus* again became the most abundant species, with the largest catches of *O. mossambicus* being made in North Lake, at Fannies Island (CPUE = 21.9) and Hell's Gate (CPUE = 32.9). These two sites accounted for 77.4% of the total *O. mossambicus* catch during this sampling season. As previously mentioned, Hell's Gate was the sampling area most severely affected by drought conditions and at the time, the mouth had been closed for more than four years. Good rains during summers of 2010/11 and 2011/12 raised the water level at Hell's Gate to the extent where it could again sustain large fish populations and the only species recorded in any numbers in the area up to that point was *O. mossambicus*, which could exploit these conditions in the absence of competing marine species.

There was a notable change in the number of dominant fish species in the St Lucia system between the sampling season immediately prior to (May 2012) and after (November 2012) the beach channel opened. The system changed from four dominant species (contributing more than 2%) in May 2012 to nine the next season, indicating a greater diversity of species after the channel was opened (Figure 4.3; Figure 4.4).

After the beach channel opened, fish abundance in the system (CPUE) was, unexpectedly, lower than during the 2008–2010 period (Chapter 3), when the system was hypersaline and not connected to the ocean. It was expected that fish abundance would increase after the beach channel opened. *Oreochromis mossambicus*, for example, changed from its highest catch in May 2012 to its lowest catch in November 2012. It was also expected that under 'normal' open mouth conditions, which, after the beach channel opened is the closest the St Lucia system has come to 'normal' in several years, the abundance of *O. mossambicus* would be much lower than that of marine and estuarine species (Wallace, 1975; Whitfield and Blaber, 1979a). But, *O. mossambicus* remained the most abundant species in the system from May 2013 - May 2014, even though its abundance declined after the channel opened. A similar decline in abundance was also observed in estuarine and marine species after the channel opened. Freshwater fish abundance (CPUE) decreased from 6.4 before to 2.8 after the beach channel opened, while marine and estuarine fish abundance decreased from 1.5 to 1.0 and from 9.0 to 2.3, respectively. Marine species showed the smallest decline in abundance, as this was the only group in which recruitment from elsewhere could occur. There was however an increase in the relative abundance of marine and freshwater species after the channel opened. The contribution of marine species to the total catch increased from 9.1% to 16.4% after the channel opened and freshwater species increased from 38.0% to 45.4%, while there was a decline from 52.9% to 38.2% in the contribution of estuarine species to the abundance. This relatively large change in the contribution of freshwater and estuarine fish abundance to the total catch was largely due to the change in dominance of *O. mossambicus* over *A. ambassis* after the channel opened.

The decline in fish abundance (CPUE) after the beach channel opened was observed at all sites within the St Lucia system in the freshwater and estuarine groups. The CPUE of marine species also decreased at most sites, except in the Lower Narrows, where it increased from 1.0 before the channel, to 3.1 after the channel opened, an increase of 67.0%. The beach channel was thus responsible for an increase in the contribution of marine species within the St Lucia system, particularly in the Narrows. This indicates that even though marine specie recruited

into the system after the beach channel opened, they mostly remained in the Lower Narrows where salinities were the highest.

The eight most abundant marine species recorded (Vivier *et al.*, 2010b) in the adjacent Mfolozi-Msunduzi Estuary during 2007-2008 were all present in the St Lucia system after the beach channel opened. Six of these species (*Acanthopagrus vagus*, *Leiognathus equula*, *L. dumerillii*, *L. macrolepis*, *Terapon jarbua* and *Valamugil cunnesius*), accounted for 39.0% of the total catch (2009-2012) in the Mfolozi-Msunduzi system (CRUZ, unpublished data). However, apart from the two mullet species *L. dumerillii* and *L. macrolepis*, none of these marine species contributed >1% to the total catch within the St Lucia system after the two systems were connected. *Liza dumerillii*, the most abundant marine species in the St Lucia system, showed no increase in abundance after the Mfolozi and St Lucia systems were re-connected. *Liza macrolepis* and *T. jarbua* were the only two of the six species that increased in abundance after the beach channel opened. Apart from the 12 previously mentioned marine species that re-entered the St Lucia system after the beach channel opened, in addition to *L. macrolepis*, 12 more marine species showed a similar pattern of increased abundances, with only *V. buchanaani* contributing >1% to the total catch (Table 4.1). Of the 25 marine species that increased in abundance after the beach channel opened, 20 also occurred in the Mfolozi system, indicating that some dispersal occurred between the two systems. However, the Mfolozi supported a large population of marine species that could have dispersed into the St Lucia system (Vivier *et al.*, 2010b; CRUZ, unpublished data), but did not, either due to the channel size not allowing large numbers to disperse or the wrong cues being received from the St Lucia system due to the reversed salinity gradient present at the time.

It is clear from the data collected that the beach channel had a positive effect on the fish community of the St Lucia system, which to summarize, included:

- In conjunction with increased rainfall, it contributed to an increase in the water level of the system, leading to a decline in salinities to below marine levels and a salinity reversal in the Narrows.

- For the first time since 2008, the St Lucia system was linked to the marine environment and marine fish could recruit into St Lucia through the open Mfolozi mouth.
- There was an increase in total species numbers in the system, especially in marine species. However, many marine species present in the Mfolozi-Msunduzi system did not enter the St Lucia system. The lack of direct access to the ocean also excluded many marine stragglers from entering the system, thus lowering the species richness of the St Lucia system.
- There was a large decline in fish abundance after the beach channel opened across the system, particularly in freshwater and estuarine species.

The beach channel was largely responsible for altering the environmental state of the St Lucia system, from a hypersaline state to a more 'normal' estuarine state. The fish population had to adapt to this change in the environment. Remmert (1983) proposed that abiotic factors (salinity, depth, temperature, turbidity, dissolved oxygen, etc.) are responsible for the large-scale fish distribution patterns observed in estuaries, while biotic interactions (predation, competition, etc.) determine the local community structure (Sanders, 1968; Menge and Olson, 1990). In the St Lucia system during November 2010 - May 2014, spatial changes in the fish community were driven by the salinity gradient across the system, while temporal changes coincided with major changes in the salinity state of the system, which were largely influenced by the opening of the beach channel.

4.2.5 Future of the Fish Community and the Beach Channel

There remains one unanswered question with regard to the beach channel's functionality, i.e. the overall decline in fish abundance across the system after the beach channel opened. There is no definitive answer to this question with the current data available, but it may be due to limited recruitment in combination with the large increase in water volume leading to an increase in habitat availability over a relatively short period of time and the fish populations not increasing rapidly enough to occupy all the new habitats that became available. The fish density in the system may thus have decreased, leading to lower fish catches. If the fish density decreased

due to the increased water volume in the system, then it is possible that the abundance of marine species in the system actually increased during the post beach channel period and continued monitoring is therefore necessary to assess the continued response of the fish community to the changes in the system. Another possibility that should be considered is the exodus of fish after the beach channel opened (Whitfield, 1998), with adult and sub-adult marine fish being able to emigrate back into the marine environment for the first time since late 2007. In the Wellstead Estuary (Western Australia), Young and Potter (2002a) found a decline in the abundance of *Mugil cephalus*, *Rhabdosargus sarba* and *Aldrichetta forsteri* due to natural exodus back to the ocean after the mouth breached. However in the current study this would only account for loss in marine abundance, which only contributed 3% to the total decline in fish abundance after the beach channel open. It is also possible that freshwater and estuarine species emigrated to the adjacent Mfolozi-Msunduzi Estuary, therefore both systems will need continued monitoring to see how the beach channel has affected the Mfolozi Estuary and whether there has been any dispersal from the St Lucia system.

The future of the beach channel is in the balance without regular maintenance. Soon after it opened, it started filling up with sediment from the Mfolozi Estuary and over the past year (2014) has only carried water into the St Lucia system during spring high tides through over-topping (Taylor *et al.*, 2014). This has severely restricted the movement of fish between St Lucia and the marine environment. However, juvenile marine species are still able to enter the St Lucia system via the back channel during spring tides but this probably only occurs in small numbers. The lack of regular maintenance on the beach channel will increasingly impair its efficiency as a means of diverting water from Mfolozi into St Lucia and as an avenue for marine fish recruitment between St Lucia, the ocean and the Mfolozi-Msunduzi system. It will most certainly affect marine fish populations of the St Lucia Estuary and the off-shore adult populations of marine-estuarine dependant species that use the system as a nursery area. Therefore, to ensure healthy and viable fish populations in the future, a more extensive, regular connection to the ocean is required (Whitfield, 2005b).

Chapter 5: Effect of Salinity on the Fish Community Structure in the St Lucia system with focus on the Salinity Tolerance of *Oreochromis mossambicus* (Mozambique Tilapia).

5.1 Results

The aim of the study was to determine the salinity tolerance of *O. mossambicus* and the effect of various salinity states on its population structure, by analysing the fish community from 2004-2014 in the St Lucia system.

5.1.1 Physico-chemical Water Data

Physico-chemical water quality parameters were measured biannually (May and November) from November 2004 - November 2007, excluding November 2005. During 2004, two years after the St Lucia mouth closed, the system experienced low water levels and hypersalinity in certain areas. Salinities in the Narrows and South Lake remained below marine levels, ranging from 4.9-29.0. During the same period, North Lake became hypersaline, with salinities reaching highs of 72.0 and 90.0 at Hell's Gate in November 2004 and May 2006, respectively. When the mouth breached in 2007, salinities throughout the system returned to marine levels (range 33.9-37.2). After the mouth re-closed at the end of 2007, salinities in the Narrows gradually decreased again (range 27.6-28.4), while salinities in the lakes started to increase (range 36.2-39.4).

Water temperatures in May (15.9-31.7°C) and November (21.9-31.8°C) reflected typical summer conditions. The high maximum temperatures recorded during winter was due to very shallow water levels in the lake. Dissolved oxygen concentrations (6.4-10.9 mgl⁻¹) and % oxygen saturation (85.5-131.0%) remained high throughout the study period, while a mean pH of 8.1 was observed. Water turbidity was lower in May (0.7-120.0 NTU), compared to November (1.7-1350.3 NTU), when generally

windy summer conditions resulted in higher turbidities. All physico-chemical data recorded during the study period are given in Appendix 1.

Physico-chemical water quality parameters measured from 2008-2011 were presented in Chapter 3, Section 3.1.1 (Physico-chemical Water Data) and from 2012-2014 were presented in Chapter 4, Section 4.1.1 (Physico-chemical Water Data).

5.1.2 Salinity and Fish Community with focus on *Oreochromis mossambicus*

*The layout of this section was done in a way to firstly recapitulate the importance of salinity in the fish community and secondly to show its importance as the most significant factor responsible for the changes in the *O. mossambicus* abundance in the St Lucia system. The next section (5.1.3) investigate the relationship between salinity and *O. mossambicus*.*

5.1.2.1 Correlation between Species Assemblage and Environmental Variables

Canonical correspondence analysis (CCA) was used for testing the correlation between environmental variables and the St Lucia fish assemblage from November 2004 - May 2014. Salinity ($F = 3.36$, $p = 0.002$), depth ($F = 1.92$, $p = 0.004$) and temperature ($F = 1.93$, $p = 0.01$) showed a significant correlation with the fish assemblage and were most responsible for structuring the overall fish community.

The freshwater species *O. mossambicus* was the most abundant species during the 2004-2014 study period and therefore was most responsible for structuring the fish community in the system. It was followed by the three estuarine species *Ambassis ambassis*, *Ambassis natalensis* and *Hyporhamphus capensis*, and the marine mullet species *Liza dumerilii*. The five most abundant species together contributed 86.9% of the fish catch in the St Lucia system from November 2004 - May 2014. A CCA undertaken to determine which environmental factors most influenced the spatio-temporal arrangement of the five most dominant species, revealed that only salinity ($F = 6.84$, $p = 0.002$) showed a significant correlation (Figure 5.1; Table 5.1).

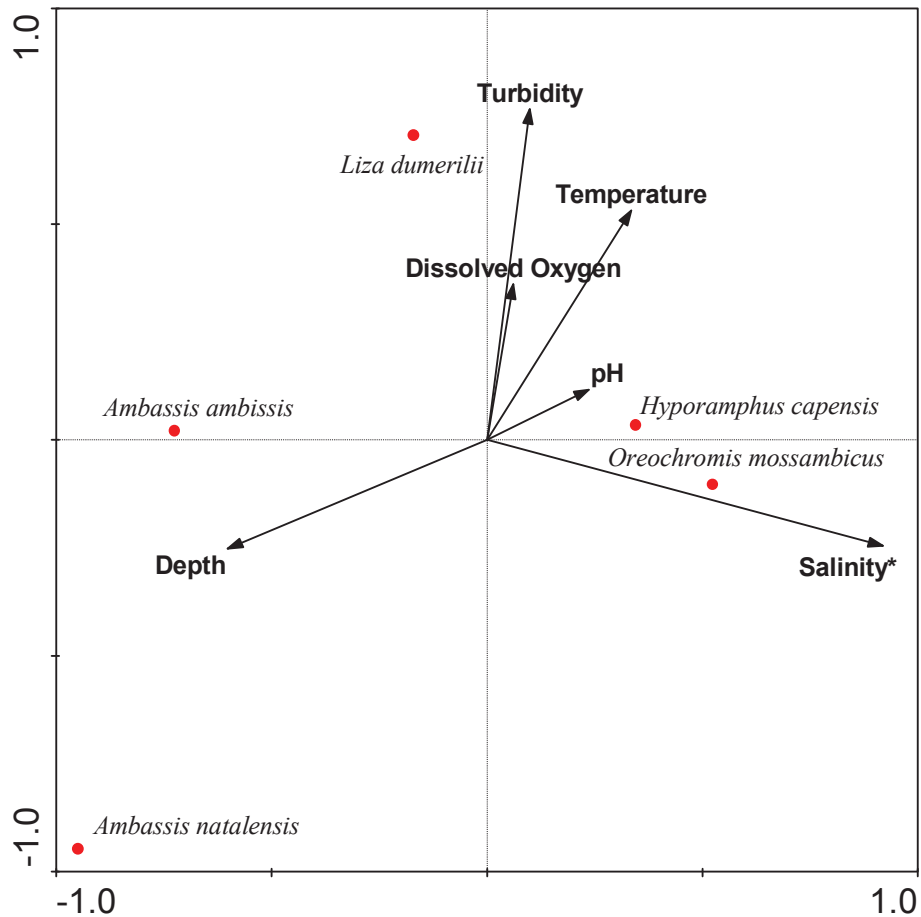


Figure 5.1: Canonical correspondence analysis (CCA) biplots (eigenvalues in Table 5.2) of the relationship between environmental variables and the relationship between the five most abundant fish species in the St Lucia system during the period Nov 2004 - May 2014 *denotes a significant environmental variable.

Table 5.1: Canonical correspondence analysis (CCA) showing the environmental variables and their contribution to the total variance of the five most abundant fish species in the St Lucia system during the period Nov 2004 - May 2014. *Variable contributing significantly to the total variance in the fish community.

	Top 5 Species		
	Variance	F	P
Salinity	0.06	6.84	0.002*
Temperature	0.02	1.90	0.11
Depth	0.01	0.22	0.91
Dissolved Oxygen	0.002	1.50	0.21
Turbidity	0.01	1.34	0.19
pH	0.002	0.21	0.94

Table 5.2: Canonical correspondence analysis (CCA) eigenvalues and cumulative % contribution to the total variance of the first four axes of the correlation between environmental variables and the five most abundant fish species in the St Lucia system during the period Nov 2004 - May 2014. Species-environment correlations depict the correlation between environmental variables and the fish community for each of the first four axes of the CCA plot.

	<u>AXES</u>				Total (All Axes)
	1	2	3	4	
<u>Top 5 Species</u>					
Eigenvalues	0.07	0.02	0.01	0.00	0.11
Cumulative %	65.90	88.10	98.30	100.00	
Species-environment correlations	0.53	0.35	0.22	0.09	

5.1.2.2 Temporal Changes in the Fish Community due to Salinity

The cluster analysis for fish data averaged across sampling seasons illustrates distinct temporal changes within the St Lucia fish community from November 2004 to May 2014 (Figure 5.2). Five periods that corresponded (qualitatively) with different environmental states (of which salinity was most significant) were identified using the SIMPROF procedure, these are; (i) November 2004 - November 2006: Before the mouth breached, the system displayed extremely low water levels and hypersalinities in South and North Lake, (ii) May 2007 - November 2008: The St Lucia mouth was breached by Cyclone Gamede, which allowed marine water to fill the system to 75% capacity and allowed for recruitment of marine species. Water levels were relatively high with marine salinities throughout 2008, (iii) May 2009 - November 2010: The continued drought led to low water levels and hypersalinities re-occurring in South and North Lake, (iv) May 2011 - November 2012: Increased rainfall leads to an increase in water levels and a decline in salinities and (v) May 2013 - May 2014: St Lucia indirectly re-connected to the marine environment via the Mfolozi mouth, highest water levels and lowest salinities recorded over the study period. PERMANOVA confirmed the significant temporal difference between the five periods shown in the cluster analysis (Pseudo-F = 4.10, $p < 0.001$) (Table 5.3).

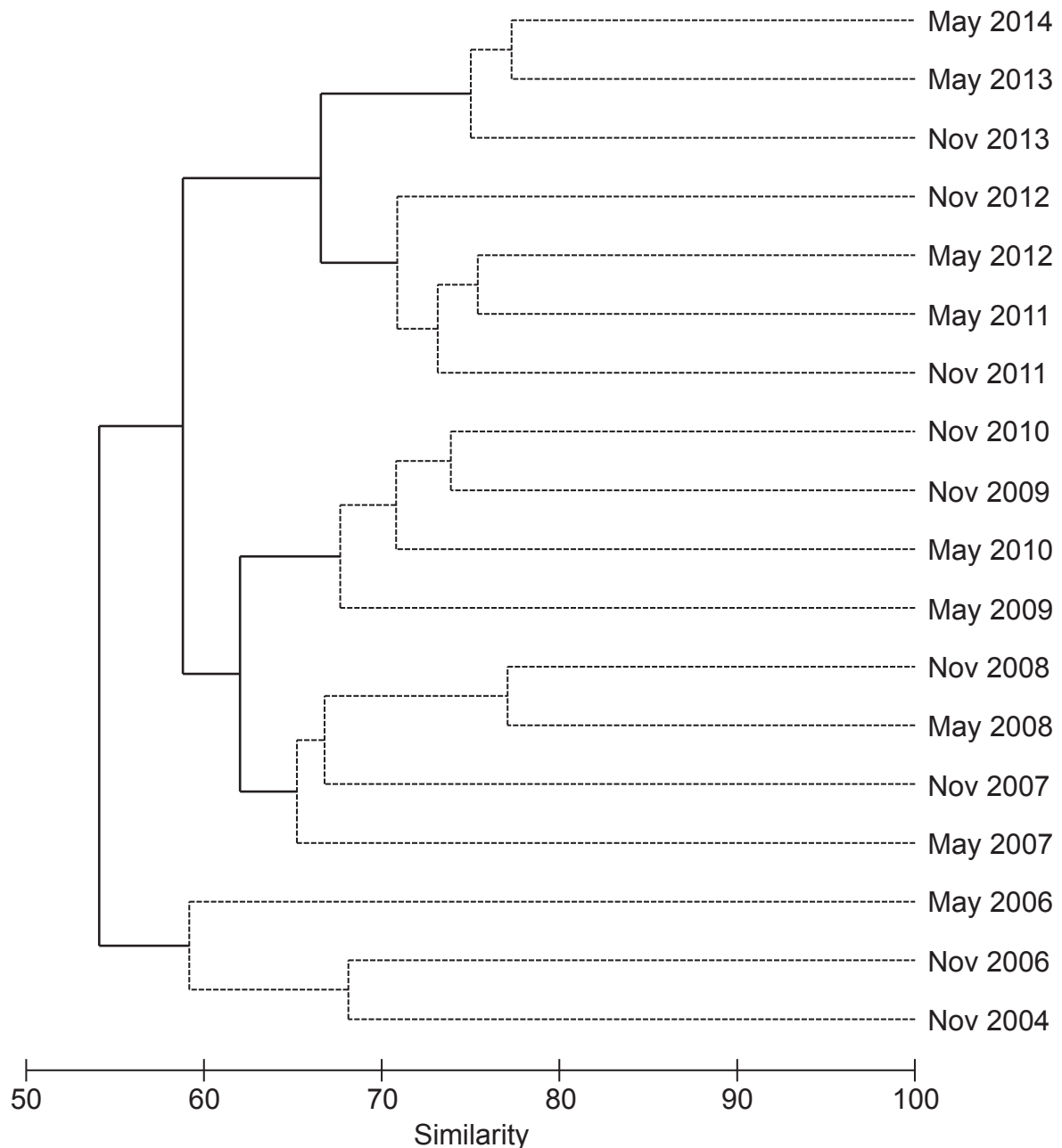


Figure 5.2: Cluster dendrogram of the fish assemblage recorded in the St Lucia system over the period Nov 2004 - May 2014, averaged over sampling seasons. Solid line represent significant grouping as determined by SIMPROF.

The SIMPER procedure was used to determine which fish species were most responsible for the similarity within the fish composition. *Oreochromis mossambicus*, *A. ambassis* and *L. dumerilii* were the three most important species accounting for 32.3% of the similarity in the fish community during the study period (Table 5.4).

Table 5.3: PERMANOVA results showing mean % similarity within (Bold) and between the groups identified in the cluster ordination within the St Lucia system from Nov 2004 - May 2014. *denotes a significant difference.

	(i) Before mouth breached		(ii) Open mouth and after		(iii) Hypersaline		(iv) Before beach channel		(v) After beach channel	
	% Similarity	t	% Similarity	t	% Similarity	t	% Similarity	t	% Similarity	t
(i)	62.12									
(ii)	52.15	2.00*	67.70							
(iii)	55.21	1.90*	62.01	1.70*	69.72					
(iv)	54.15	2.10*	55.97	2.34*	59.39	2.20*	72.37			
(v)	55.02	1.99	57.92	2.15*	62.54	1.94*	66.54	1.78*	75.75	

Table 5.4: SIMPER results showing mean similarity, % contribution and cumulative % of the fish species making the highest contribution to the mean similarity within the St Lucia system between Nov 2004 - May 2014 (Estuarine association: E, Estuarine species; F, Freshwater species; M, Marine species).

Species	Est Ass	Mean similarity	Sim/SD	Contribution %	Cumulative %
<u>St Lucia: mean similarity within seasons = 60.05%</u>					
<i>Oreochromis mossambicus</i>	F	9.21	4.49	15.3%	15.3%
<i>Ambassis ambassis</i>	E	5.66	2.75	9.4%	24.8%
<i>Liza dumerilii</i>	M	4.50	4.32	7.5%	32.3%
<i>Thryssa vitrirostris</i>	M	3.35	3.71	5.6%	37.8%
<i>Leiognathus equula</i>	M	3.07	4.10	5.1%	42.9%
<i>Glossogobius callidus</i>	F	3.03	1.89	5.1%	48.0%
<i>Liza macrolepis</i>	M	2.45	3.42	4.1%	52.1%
<i>Terapon jarbua</i>	M	2.15	2.52	3.6%	55.7%
<i>Pomadasys commersonii</i>	M	2.10	4.51	3.5%	59.2%
<i>Hyporhamphus capensis</i>	E	1.92	1.13	3.2%	62.4%

5.1.3 Changes in the *Oreochromis mossambicus* Population

5.1.3.1 Population Composition

From November 2004 - May 2014, a total of 50,791 fish representing 83 species were caught in the St Lucia Estuarine System. Of these, 24,792 (48.8%) were *O. mossambicus*, making it the most abundant species over the last 10 years in St Lucia. The second most abundant species was *A. ambassis*, which accounted for 18.6% of the catch, while the most abundant marine species (third overall), *L.*

dumerilii, accounted for 9.2% of the total catch. The remaining 23.4% was made up by the other 80 species recorded in the system during the period.

The mean CPUE of *O. mossambicus* per sampling season was 5.1, ranging from a very low catch of 0.5 in November 2009 to the highest catch of 11.8 in May 2012 (Figure 5.3). High catches were made under hypersaline, low water level conditions during 2004-2006, however there was a notably lower catch at the end of 2006, followed by a substantial increase in 2007 after the mouth opened. Low catches in November 2009 and 2010 were due to major fish kill events in the system, caused by a combination of hypersalinities and rapid drops in temperature. However during periods of extreme hypersalinities, such as during May 2006, May 2009 and May 2010, *O. mossambicus* generally dominated the St Lucia system, contributing >70% of the fish catch during these seasons. From 2011, increased rainfall and inflow of Mfolozi water via the back channel, led to higher water levels and declining salinities. The largest catch of *O. mossambicus* was recorded in May 2012 (CPUE = 11.8) under rising water level conditions. After the beach channel opened in 2012, there was a drop in *O. mossambicus* abundance with low catches up to May 2014 (Figure 5.3).

The mean CPUE per site of *O. mossambicus* was 5.0, ranging from 1.4 in the Lower Narrows to 9.3 at Fanies Island (Figure 5.4), indicating a gradual increase in mean abundance from the mouth towards to northern parts of the lake. The rest of the fish population showed the opposite trend, with a decline in abundance towards the north. The abundance (CPUE) of *O. mossambicus* and other species recorded at each sampling site in the St Lucia system is illustrated in Figure 5.5, together with the salinities measured at the time of sampling.

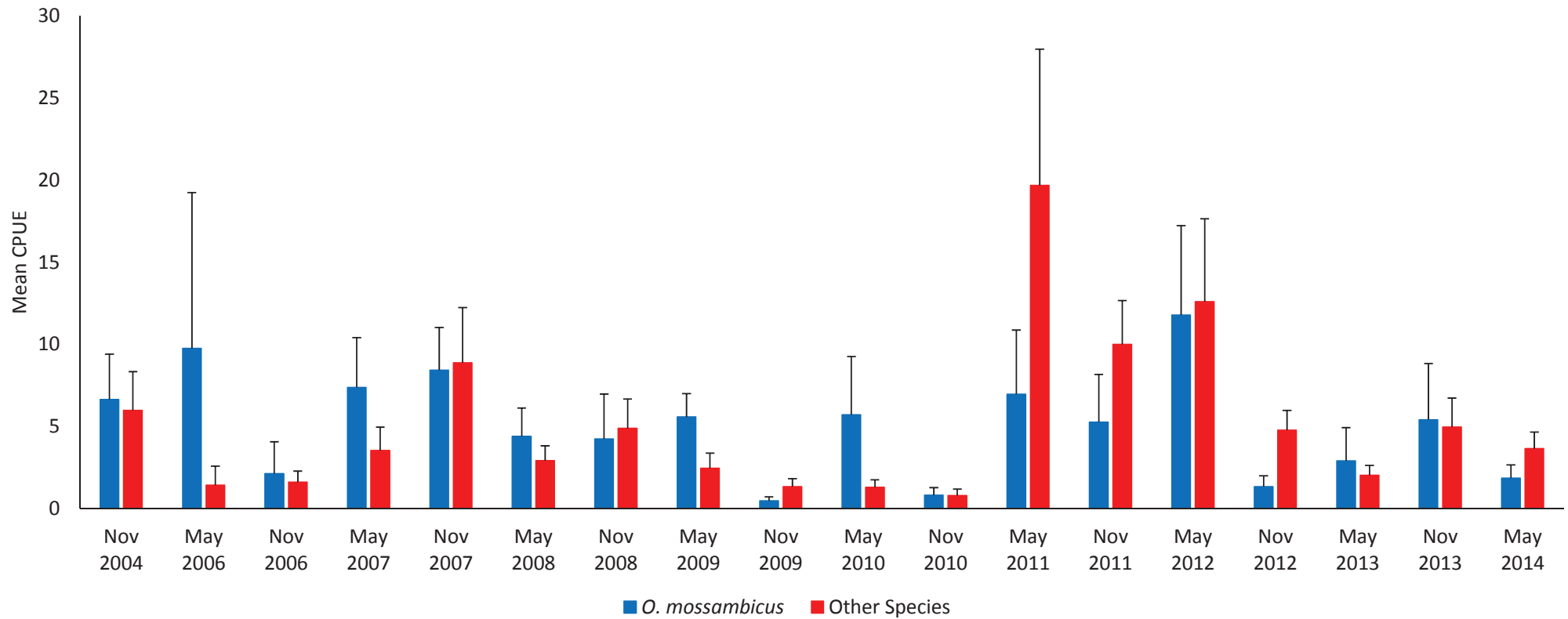


Figure 5.3 Mean abundance (CPUE) (+1SD) of *Oreochromis mossambicus* and other species recorded during 18 biannual sampling seasons from Nov 2004 - May 2014 (excluding 2005), in the St Lucia system.

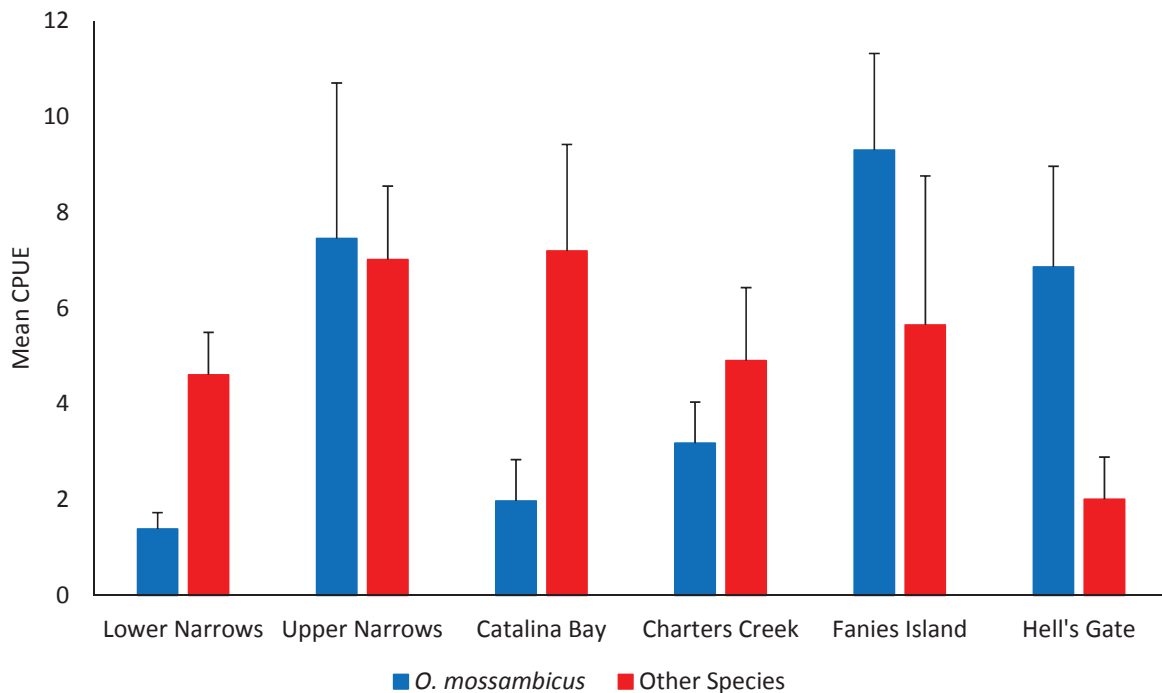


Figure 5.4: Mean abundance (CPUE) (+1SD) of *Oreochromis mossambicus* and other species recorded at each of the six sites, in the St Lucia system from Nov 2004 - May 2014 (excluding 2005).

a) The Narrows

The lowest mean abundance of *O. mossambicus* (CPUE = 1.4) relative to the other fish species (CPUE = 4.6) was recorded in the Lower Narrows. The abundance of *O. mossambicus* in the Lower Narrows only exceeded the combined abundance of the other species during May 2006 and May and November 2010, during which time the St Lucia system experienced very low water levels and high salinities. During times when the lake almost dried up, most fish were confined to the Narrows where water levels remained relatively high. The third highest mean abundance of *O. mossambicus* (CPUE = 7.5) in the system was recorded in the Upper Narrows, being slightly higher than the combined abundance of the other species (CPUE = 7.0). However, 89.7% of the total catch at this site was caught from November 2004 to May 2008 (6 sampling seasons), while only 10.3% was caught from November 2008 to May 2014 (12 sampling seasons).

b) South Lake

At Catalina Bay, the abundance of *O. mossambicus* was much lower (CPUE = 2.0) than the combined abundance of the other species (CPUE = 7.2), while at Charters

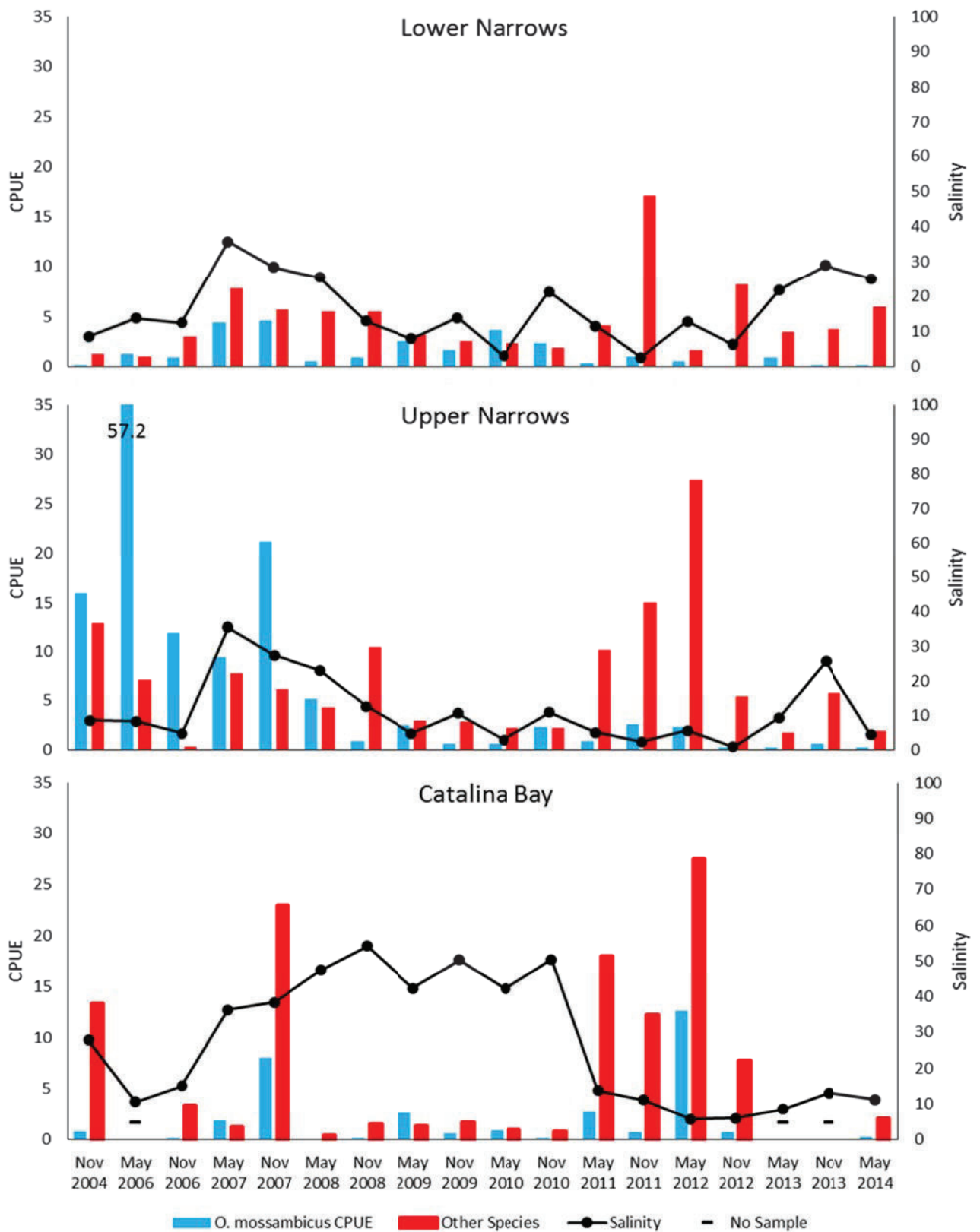


Figure 5.5: Abundance (CPUE) of *Oreochromis mossambicus* and other species, and salinity recorded for each of the six sites in the St Lucia system from Nov 2004 - May 2014 (excluding 2005).

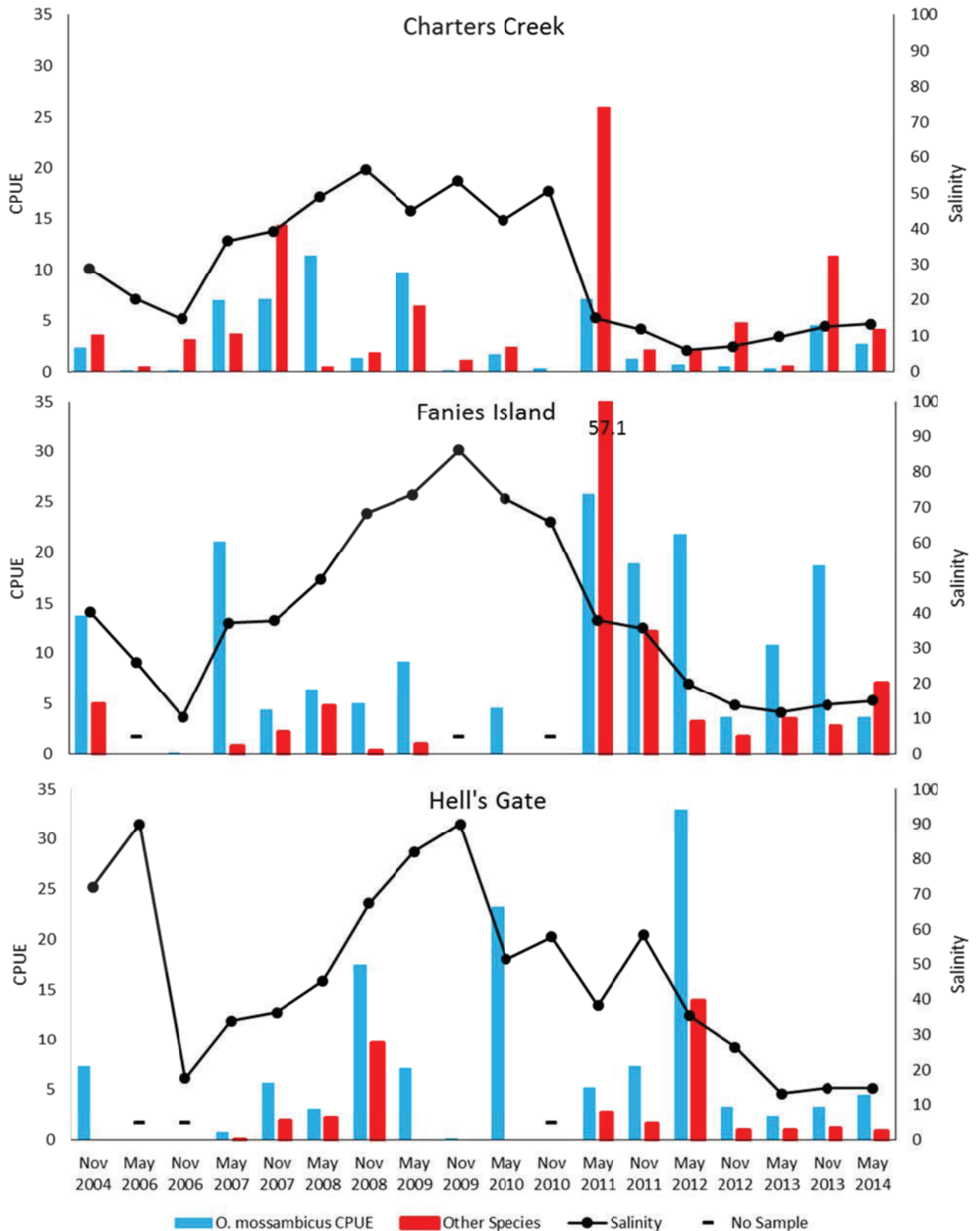


Figure 5.5 (Continued): Abundance (CPUE) of *Oreochromis mossambicus* and other species, and salinity recorded for each of the six sites in the St Lucia system from Nov 2004 - May 2014 (excluding 2005).

Creek, *O. mossambicus* abundance (CPUE = 3.2) was quite close to that of the other species (CPUE = 4.9). During periods of high salinities, however, *O. mossambicus* abundance exceeded the combined abundance of the other species, whereas during the period May 2011 to May 2014, the abundance of *O. mossambicus* was much lower than that of the other species at both Catalina Bay and Charters Creek.

c) North Lake

In North Lake (Fanies Island and Hell's Gate), the abundance of *O. mossambicus* completely outweighed that of other species during every sampling season except at Fanies Island in May 2011 and May 2014. The highest mean abundance of *O. mossambicus* in the system was recorded at Fanies Island (CPUE = 9.3), which was considerably higher than the combined abundance of the other species (CPUE = 5.6). However, the mean abundance of *O. mossambicus* at Hell's Gate (CPUE = 6.9) had the highest contribution to the total catch per site (77.4%), given that the combined abundance of the other species (CPUE = 2.0) at Hell's Gate was the lowest in the system.

There was a positive but not significant correlation (Pearson product-moment) between *O. mossambicus* abundance and salinity (Table 5.5). In contrast, there was a negative but not significant correlation between the abundance of the other fish species and salinity, indicating a decrease in fish abundance with higher salinities (Table 5.5). There was a significant correlation between the abundance of *O. mossambicus* and the combined abundance of the other species at Catalina Bay in South Lake and at Fanies Island and Hell's Gate in North Lake (Table 5.5). This suggests that favourable conditions within the lakes lead to concurrent increases in the populations of *O. mossambicus* and estuarine species. There was however no correlation between the abundance of *O. mossambicus* and the other species in the Narrows (Table 5.5). As shown in Chapter 3 and 4, marine species were most abundant in the Narrows, while freshwater and estuarine species were more abundant within the lakes. The numerically important species within the lakes, other than *O. mossambicus*, therefore mainly comprised estuarine species that respond to

the same stimuli as *O. mossambicus* to increase population size, while species in the Narrows were mostly marine, and their population was driven by different factors.

Table 5.5: Correlation (Pearson Product-Moment) between abundance (CPUE) of *Oreochromis mossambicus* and salinity, abundance (CPUE) of other species and salinity and abundance of (CPUE) of *O. mossambicus* against other species. *denotes a significant correlation.

Correlation	R ²	r	t	p
<u>O. mossambicus and Salinity</u>				
Lower Narrows	0.072	0.268	1.111	0.283
Upper Narrows	0.017	0.132	0.514	0.615
Catalina Bay	0.062	-0.249	0.890	0.391
Charters Creek	0.092	0.303	1.274	0.221
Fanies Island	0.011	-0.105	0.382	0.708
Hell's Gate	0.011	0.106	0.385	0.706
St Lucia (Overall)	0.014	0.120	1.179	0.255
<u>Other Species and Salinity</u>				
Lower Narrows	0.005	-0.068	0.273	0.788
Upper Narrows	0.006	-0.076	0.306	0.763
Catalina Bay	0.276	-0.526	2.227	0.044*
Charters Creek	0.045	-0.211	0.865	0.400
Fanies Island	0.001	-0.028	0.101	0.921
Hell's Gate	0.041	0.065	0.234	0.819
St Lucia (Overall)	0.024	-0.155	1.547	0.141
<u>O. mossambicus and Other Species</u>				
Lower Narrows ¹	0.000	0.019	0.077	0.939
Upper Narrows ¹	0.001	0.024	0.098	0.923
Catalina Bay ²	0.674	0.821	5.180	<0.001*
Charters Creek ²	0.197	0.443	1.979	0.065
Fanies Island ²	0.297	0.545	2.342	0.036*
Hell's Gate ²	0.566	0.752	4.119	0.001*
St Lucia (Overall)	0.081	0.285	2.923	0.010*
¹ Narrows	0.008	0.089	0.522	0.609
² Lakes	0.170	0.413	3.538	0.003*

5.1.3.2 Effect of Salinity on *Oreochromis mossambicus* in St Lucia

During the period November 2004 - May 2014, the highest salinity in which *O. mossambicus* was recorded was 90.0, at Hell's Gate (November 2009). A salinity of 90.0 was also the highest salinity recorded in the entire system over the period,

although salinities as high as >200 were reported by EKZNW in North Lake (Taylor, *pers. comm*) (Figure 1.3). In the literature, *O. mossambicus* salinity tolerance is given as 0-120 (Whitfield and Blaber, 1979a; Costa-Pierce and Riedel, 2000). The mean abundance (CPUE) of *O. mossambicus* and that of estuarine and marine fish species at different salinities during the study period are illustrated in Figure 5.6. The highest abundance of *O. mossambicus* was recorded in the 60-70 salinity range followed by the 30-40 range, while estuarine species were most abundant in the 30-40 salinity range and marine species in the 20-30 salinity range. No marine species were recorded at salinities above 80, or estuarine species above 70. Estuarine species had slightly higher abundances than *O. mossambicus* in salinities between 0-20, while marine species slightly dominated the 20-30 salinity range. When salinities exceeded 40, *O. mossambicus* was the most abundant fish in the St Lucia system, exceeding the combined abundance of estuarine and marine species (Figure 5.6).

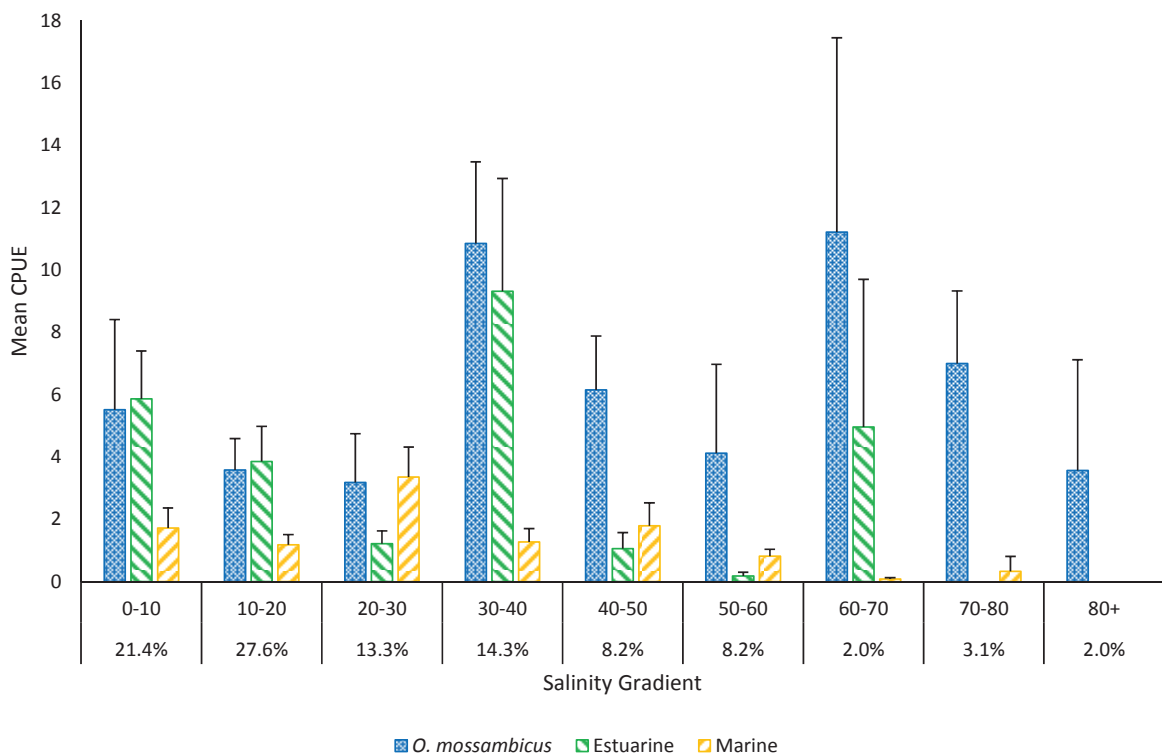


Figure 5.6: Mean abundance (CPUE) (+1SD) of *Oreochromis mossambicus*, estuarine and marine species at different salinities and the frequency (%) of each salinity state recorded in the St Lucia system over the study period Nov 2004 - May 2014.

5.1.3.3 Salinity Tolerance of *Oreochromis mossambicus* in the Laboratory

In order to determine the salinity tolerance of *O. mossambicus*, an experiment was conducted under controlled conditions in the laboratory. Three groups of St Lucia and hatchery reared *O. mossambicus* were exposed to salinities ranging from 35 to 110.

a) Laboratory Acclimation

Each of the three treatment tanks used in the experiment was acclimated to a salinity of 35 (seawater) and then thereafter, the salinity was increased by five units every five days. At a salinity of 45, several fish in tanks 1 and 2 died due to unexplained high ammonia levels. No fish in tank 3 died. All filters were cleaned and new water was added to all three tanks to reduce ammonia concentrations. Thereafter, survival rate in both groups of *O. mossambicus* remained at 100% or close to, up to a salinity of 100. At a salinity of 105, the ammonia levels became slightly elevated, and at 110 increased to very high levels in all three treatment tanks, which in combination with the high salinity, resulted in all the fish dying at 110. Results on the salinity tolerance of *O. mossambicus* in the laboratory are therefore inconclusive, but showed that the species can easily tolerate a salinity of at least 105, with >70% survival in 105 salinity (Figure 5.7).

b) St Lucia vs. Hatchery Fish

ANOVA (Kruskal-wallis test) results showed that there was no significant difference in the survival of *O. mossambicus* when comparing the three treatment tanks with St Lucia fish ($H = 0.71$, $p = 0.70$) or those containing fish reared in freshwater at the UniZulu hatchery ($H = 0.67$, $p = 0.72$), in salinities up to 110. Most importantly, there was no significant difference (Mann-Whitney test) in the survival between St Lucia and hatchery fish ($Z = 0.66$, $p = 0.51$), suggesting that even freshwater adapted *O. mossambicus* have a remarkable tolerance to high salinities.

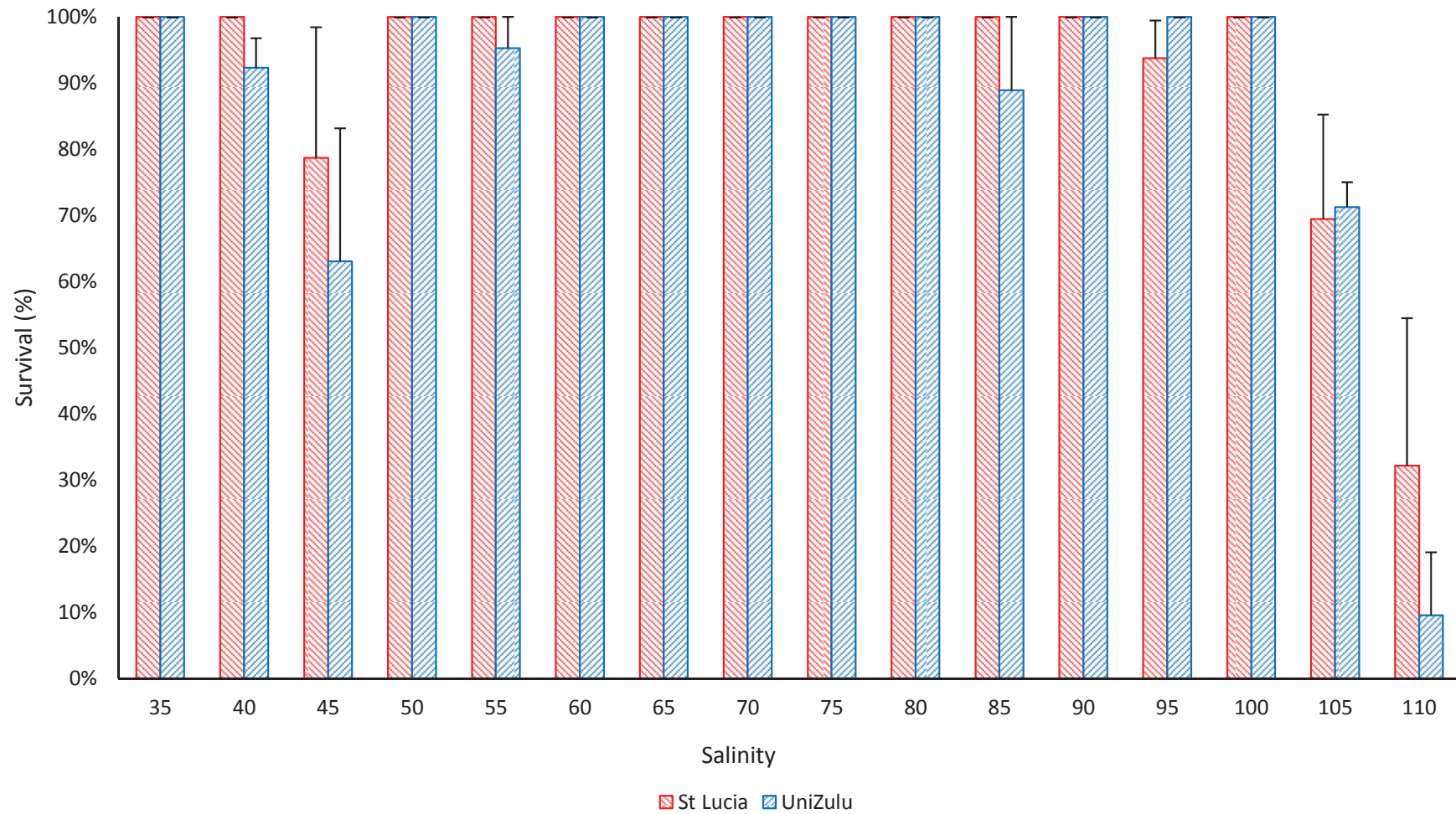


Figure 5.7: Salinity tolerance of *Oreochromis mossambicus*, mean survival (%) (+1SD) at salinity integrals of five, with 4 day (96 hours) salinity exposures in between, conducted from 28 July - 15 October 2014.

5.2 Discussion

The Mozambique Tilapia (*Oreochromis mossambicus*) is a widely distributed cichlid species that is naturally found in closed and confined estuaries, coastal lakes and rivers on the east coast of southern Africa, from the lower Zambezi River and its delta to Algoa Bay and the Bushmans system on the south coast (Jubb, 1974; Trewavas, 1983; Skelton, 2001). *Oreochromis mossambicus* is also highly invasive and is now widely distributed across five continents with established populations in 94 countries around the world (Fishbase, 2010). It is listed on the Global Invasive Species Database (2006) as one of the top 100 invasive species on the planet. Pérez *et al.* (2006) describes its success as an invader to its ability to tolerate a wide range of environmental conditions, flexibility in its diet and its ability to rapidly reproduce and provide maternal care. These factors also make them extremely tolerant to environmental changes in their natural habitat, as shown during this study in their ability to tolerate hypersaline conditions in the St Lucia Estuarine system.

Oreochromis mossambicus evolved from a marine ancestor (Kirk, 1972) and is considered to be one of the most saline tolerant of all the tilapia species, with a recorded salinity tolerance range of 0–120 (Whitfield and Blaber, 1979a; Costa-Pierce and Riedel, 2000). Wallace (1975) recorded *O. mossambicus* in salinities as high as 117 in the northern parts of the St Lucia system during 1969 and 1970, when the system experienced hypersaline conditions, and the presence of juveniles in the system at the time indicated that successful breeding was occurring. Similarly, Van der Elst (1972) observed *O. mossambicus* breeding in salinities over 70 in St Lucia. In Western Australia, an invasive population of *O. mossambicus* was recorded in a small salt lake adjacent to the Lyndon River, where salinities reached highs of 95 (Morgan *et al.*, 2004).

The upper salinity tolerance limit of *O. mossambicus* has never been established under laboratory conditions, even though many studies have been done on acclimation of *O. mossambicus* from freshwater to seawater (up to salinitie of 75) and from seawater back to freshwater (Dharmamba *et al.*, 1975; Dange, 1985; Hwang *et al.*, 1989; Kültz *et al.*, 1992; Kültz and Onken, 1993; Borski *et al.*, 1994; Yada *et al.*, 1994; Sardella and Brauner, 2008). Up to a salinity of 70, there is limited

change in plasma ionic and osmotic composition due to effective water replacement and excretion of Na^+ and Cl^- (Gonzalez, 2012). In the current study, an attempt was made to determine the maximum salinity tolerance of *O. mossambicus* in captivity. Fish from St Lucia, bred in brackish water, and fish from the University of Zululand hatchery stock, reared in freshwater, were used in the experiment. There was no significant difference in survival between the two populations of *O. mossambicus*, indicating that wild bred and hatchery reared fish tolerated extreme hypersaline conditions equally well. A maximum salinity tolerance of 105 was recorded. A number of fish died at the 45 salinity threshold, after a sudden increase in ammonia levels. The ammonia (NH_3) toxicity (96 hour LC_{50}) for marine fish species is 0.09-3.35 mg l^{-1} (Eddy, 2005). Sampath *et al.*, 1991 reported that *O. mossambicus* showed no negative effect to ammonia exposure up to 3 mg l^{-1} and their 96 hour LC_{50} toxicity was 32 mg l^{-1} . However the sudden increase in ammonia levels at the 110 salinity threshold, exacerbated by the high salinity, may have led to the death of the fish before the actual salinity tolerance level was reached. At salinities above 100, salt crystals started precipitating out in the biological filter, affecting its efficiency, thereby causing an increase in ammonia levels in the tanks. A more effective filtration system will be required for future attempts to acclimate *O. mossambicus* to higher salinities under laboratory conditions.

The St Lucia Estuarine System has experienced several changes in salinity state since 2002, after the mouth closed naturally due to a regional drought. The system transcended from a 'normal' estuarine state to hypersaline during 2003-2006, then to a marine state after the mouth breached in 2007, then became hypersaline again during 2009-2010 and finally changed to an estuarine state, with salinities below marine levels after the opening of the beach channel in 2012. At the end of the study, however, the system was only partly connected to the Mfolozi-Msunduzi system as siltation of the beach channel limited the frequency of water inflow to extreme high tides and flooding events, thereby also limiting the input of water from the Mfolozi system.

The extreme change in salinity and long periods of mouth closure has impacted the fish community in the system both in terms of species number and abundance. Since the mouth closed in 2002 and the system became hypersaline in 2003, *O.*

mossambicus, which is normally rare in open estuarine systems due to competition with marine and estuarine fish species (Wallace, 1975; Whitfield and Blaber, 1979a), became the most abundant species in the system (Vivier and Cyrus, 2006). During December 2004, the lake was partitioned into four isolated segments. *Oreochromis mossambicus* was found in all four segments and mouth-brooding larvae were present in samples taken at Hell's Gate in North Lake where the salinity at the time was 71 (Cyrus and Vivier, 2006). This indicated that *O. mossambicus* was able to breed in salinities more than twice that of seawater. *Oreochromis mossambicus* was also found to be the only fish species to survive in salinities over 110 in North Lake in 2006 (Whitfield *et al.*, 2006; Vivier *et al.*, 2010a; Cyrus *et al.*, 2011).

Oreochromis mossambicus dominated the fish community in salinities >30, even though it remained an important component of the fish community in salinities <30. In all salinities >40, its abundance was greater than the combined abundance of the estuarine and marine groups together (Figure 5.6). The highest combined fish abundance (estuarine, marine and freshwater) in the system was recorded in salinities between 30-40. Estuarine species were dominant in salinities between 0-20, while marine species dominated the fish community in salinities between 20-30.

Oreochromis mossambicus is one of a few species worldwide capable of tolerating salinities from 0 to over 100, while also becoming the dominant species in their respective environments. This group also includes the black-chinned tilapia *Sarotherodon melanotheron* (Family Cichlidae), the sheepshead minnow *Cyprinodon variegatus*, the mummichog *Fundulus heteroclitus* and the Arabian killifish *Aphanius dispar* (Family Cyprinodontidae), and the sailfin molly *Poecilia latipinna* (Family Poeciliidae) (Gonzales, 2012). *Cyprinodon variegatus* occurs in the Laguna Madre of Texas (USA), and has the highest recorded known salinity tolerance for fish species of 0-142 (Hedgpeth, 1967). *Sarotherodon melanotheron* from the Sine Saloum estuary in West Africa, where salinities can reach highs of 130 during dry periods (Panfili *et al.*, 2004), have been recorded in salinities of up to 102 by Lorin-Nebel *et al.* (2012) and acclimated in salinities of up to 120 by Lemarie *et al.* (2004).

During the study period, a total of 50,791 fish, representing 83 species, were caught in the St Lucia system, with *O. mossambicus* accounting for half of the catch. The

highest contribution by *O. mossambicus* to the catch was during May 2006 (87.2%) and May 2010 (81.5%). These two sampling dates fell within hypersaline periods, 2003-2006 and 2009-2010, when St Lucia was most affected by the drought with the highest recorded salinities and lowest water levels. There was a positive but not significant correlation between *O. mossambicus* abundance and field salinity measurements, even though salinity was the only significant environmental factor responsible for structuring the fish community (five most abundant species) in the system.

Very high fish catches were recorded from May 2011 to May 2012. The highest catch of *O. mossambicus* was recorded in May 2012, accounted for 48.4% of the total catch. The other 32 species recorded during this season made up the remaining 51.6%, this being the second largest catch of other species during the study. *Ambassis* species contributed 35.5% of the catch and the mullet *L. dumerilii* 12.8%. North Lake was extremely favourable for *O. mossambicus* and some estuarine species in 2011 and early 2012. Good summer rains caused a decrease in salinities across the entire system to below marine levels and higher water levels flooded previously dry fringing vegetation, substantially increasing the availability of suitable, sheltered habitat. The higher water levels could therefore support larger fish populations. In the absence of competing marine species, the populations of *O. mossambicus* and certain estuarine species expanded rapidly, notably in areas such as Hell's Gate.

The beach channel connecting St Lucia to the Mfolozi-Msunduzi system was opened in July 2012, at a time when the Mfolozi mouth was closed due to low winter river flows. As a result, low salinity water initially entered the St Lucia system through the beach channel. Seasonal rains caused the Mfolozi mouth to breach in early summer of 2012 and St Lucia was re-connected to the marine environment for the first time in five years, albeit indirectly through the Mfolozi mouth. The inflow of marine and river water from the Mfolozi Estuary resulted in a further increase in water levels across the system, while at the same time, allowing some recruitment of marine species. The connection to the ocean also caused a salinity reversal to occur in the St Lucia system, with higher salinity conditions developing in the Lower Narrows.

Despite the high water levels and favourable salinities in the lakes, much lower fish catches, notably of *O. mossambicus*, were recorded during November 2012 and May 2013 after the beach channel opened. The reason for this is not clear. The lowest contribution (22.0%) of *O. mossambicus* to the total catch was recorded during November 2012, during which time no *O. mossambicus* were caught in the Lower Narrows. Philippart and Ruwet (1982) argued that *O. mossambicus* prefers environments characterised by gradual changes in salinity, which is why they are almost always absent in the lower reaches of open estuaries where abrupt, tidally driven salinity changes occur. In the East Kleinmond Estuary, on the south coast of South Africa, *O. mossambicus* was only recorded in the lower reaches following seasonal closure of the system, whereas it was confined to the upper reaches under open mouth conditions (Whitfield and Blaber, 1979a; Vorwerk, 2000). Similarly, in the Mfolozi-Msunduzi estuarine system, *O. mossambicus* was most abundant in the upper reaches of the system when the mouth was open (Vivier *et al.*, 2010b). It can therefore be argued that *O. mossambicus* avoided the Lower Narrows in November 2012, where rapid salinity changes were caused by marine water tidally entering the relatively fresh St Lucia system. However, the highest catches of *O. mossambicus* in the Lower Narrows were recorded during May 2007 and November 2007, after Cyclone Gamede breached the St Lucia mouth. There is however one significant difference between the two periods during which the St Lucia system was connected to the ocean. During May 2006, St Lucia experienced its lowest recorded water levels and severe hypersaline conditions, with only 10% of the lake surface being covered in water (Cyrus *et al.*, 2010a). Water levels increased slightly over the 2006/07 summer due to increased rainfall, but when the mouth was breached by Cyclone Gamede in March 2007, the system filled with seawater to almost 75% capacity, resetting the hypersaline conditions to marine levels across the system. Due to the drought, there was limited freshwater inflow, therefore there was no difference in the salinity of incoming and outgoing tides and thus salinity conditions were stable for *O. mossambicus* to occur in the Lower Narrows when the St Lucia mouth was open.

Oreochromis mossambicus was most abundant in North Lake during the study (2004-2014). Under normal estuarine conditions, North Lake would be expected to have the lowest number of marine species due to distance from the mouth and low

salinities as this is where the freshwater-estuarine interface would occur. This is therefore the habitat where most *O. mossambicus* would be expected to occur (Nerves *et al.*, 2011; Dos Passos *et al.*, 2013). Under drought conditions, when the St Lucia mouth closes, North Lake is the first region to become hypersaline due to its large surface area and shallow depth. Hypersaline conditions then forces less adaptable species southwards towards South Lake and eventually into the Narrows, leaving large unoccupied regions for *O. mossambicus* to inhabit. The intrusion of *O. mossambicus* into the lower parts of the system is dependent on the severity of the drought. During 2003-2006, the system was severely affected due to hypersaline conditions in South Lake and North Lake, while water levels were so low that at one stage, only 10% of the lake surface was covered with water, and most fish were confined to the Narrows (Cyrus *et al.*, 2010a). This led to *O. mossambicus* completely dominating the Upper Narrows between 2003-2007.

Over the course of the drought period, *O. mossambicus* abundance peaked during 2003-2006. After the mouth opened in 2007, *O. mossambicus* abundance gradually declined, even though exceptionally large catches were recorded from May 2011 - May 2012, just before the beach channel opened. It can be argued that as the drought period reached its end and efforts were being made by management agencies to divert freshwater into the St Lucia system from elsewhere, the *O. mossambicus* populations was slowly returning to the low abundance expected under normal estuarine conditions. But even though there was a steady increase in the abundance of fish other than *O. mossambicus* during the study period, a substantial drop in most species occurred after the beach channel opened. One could ask why would there be such a large decline in fish abundance, particularly the hardy *O. mossambicus*? The abundance of *O. mossambicus* and other species (especially the estuarine group) were very closely related, in the lakes (Table 5.5). As the water levels increased after the beach channel opened and new areas of the system that was previously dry or shallow became available again, there should have been an increase in fish abundance, even with the limited connection the beach channel provided to the ocean, to fill all these unpopulated areas across the system as was found in 2007 (Vivier *et al.*, 2010a) and 2011 (Chapter 3). Cowley and Whitfield (2001) recorded a large increase in the fish abundance of the

temporally open/close East Kleinemonde Estuary after the system was open for an extended period.

Under favourable environmental conditions, several biotic factors may influence the abundance of *O. mossambicus*, including; predation, competition and food availability. Even under hypersaline conditions, food availability is not an issue, as *O. mossambicus* is an opportunistic omnivore with an extremely variable diet that has shown great flexibility under harsh environmental conditions in the St Lucia system (Carrasco *et al.*, 2012). Under normal estuarine conditions the abundance of *O. mossambicus* is usually low due to competition with other species, only becoming dominant in the absence of competing species. An example of this was recorded in the Nhlabane Estuary (KwaZulu-Natal), where drought conditions led to the estuary mouth closing in 1991. *Oreochromis mossambicus* became dominant in this system after a substantial decline in marine species abundance even though the mouth was closed and salinities near fresh (below >5) (Vivier and Cyrus, 2002). At St Lucia, after the beach channel opened, marine species were once again able to enter the system, however only in limited numbers, and they were mostly confined to the Narrows. As shown in Chapter 4, the only marine species that occurred in large numbers in South and North Lake was the mullet, *L. dumerilii*. Even though *O. mossambicus* and mullets such as *L. dumerilii* are grouped as iliophagous feeders (Blaber, 1997), *L. dumerilii*'s abundance was relatively low in comparison with *O. mossambicus* and due to the latter's flexible diet it could switch to other food sources to minimize competition. This was shown in that the largest catch of *L. dumerilii* was made in May 2012, coinciding with the largest catch of *O. mossambicus* during this study, thus competition for food with marine species, such as the mullet *L. dumerilii*, was not responsible for the decline in *O. mossambicus* population. Predation on *O. mossambicus* was also limited, as the numbers of piscivorous species in the system were low due to the prolonged closure of the mouth and limited access via the beach channel for larger marine piscivorous species. Predation by birds, such as pelicans, is dependent on fish abundance and water levels. Large numbers of pelicans were recorded in the St Lucia system during 2011-2012 when fish abundance was at its highest, notably of *O. mossambicus* and *A. ambassis*, and as such could at least partly be responsible for the decline in *O. mossambicus* and *A. ambassis* numbers. The numbers of birds have declined since in accordance with the fish abundance

(Taylor *et al.*, 2013). Another possibility for increased predation on *O. mossambicus* may be an increase in the crocodile population in South and North Lake due to the decline in salinities in these areas. However, it is unlikely that predation by birds and crocodiles could be sufficiently high to explain the large decrease in *O. mossambicus* abundance in the St Lucia system after the beach channel opened, given the limited competition and abundance of food.

The decline in fish abundance in the system after the beach channel opened could also be due to the large increase in water volume in the system associated with inflows via the beach channel, suggesting that *O. mossambicus* and the dominant estuarine fish species did not reproduce rapidly enough to occupy all the newly available habitat. The fish density was diluted into smaller populations, leading to a lowering of overall fish density within the system. But why would *O. mossambicus* not be able to reproduce rapidly enough to fill these unpopulated habitats? According to Riedel (1965), *O. mossambicus* is capable of spawning every two months, or even faster when environmental conditions are favourable. James and Burton (1992) calculated that *O. mossambicus* reared in ponds can spawn up to five broods per female during a 133 day period. In the St Lucia system, the abundance (CPUE) of *O. mossambicus* was observed to increase rapidly from 0.8 (November 2010) to 7.0 (May 2011) over a six months period (Figure 5.2).

The decline in fish abundance after the beach channel opened in July 2012 therefore remains a mystery and as mentioned in Chapter 4, monitoring of the system will need to continue if a satisfactory explanation to this question is to be found. It is however clear from the results that *O. mossambicus* has an exceptional tolerance to high salinities and an ability to proliferate under stressful environment conditions when few others species can survive. The response of *O. mossambicus* to changes in environmental conditions during the study can be summarised as follows:

- During drought induced mouth-closure, when the St Lucia system becomes hypersaline (>40) due to low water levels, *O. mossambicus* is capable of tolerating extreme hypersalinities and becomes the most dominant species in the system.

- However, 'dominant' does not necessarily mean that the abundance of *O. mossambicus* will increase in accordance with a rise in salinity, but that the percentage contribution of *O. mossambicus* to the total catch will increase.
- There was a positive relationship between the abundance of *O. mossambicus* and other species (mostly estuarine and freshwater) in the lakes but not in the Narrows, where marine species remained dominant.
- The decline in the abundance of *O. mossambicus* after the beach channel opened occurred despite favourable environmental conditions in terms of salinities, water levels, habitat availability, limited predation and competition.

There is one notable limitation to the study in that no data was recorded for the period from 2002-2004, and 2005, when the St Lucia mouth first closed and the system become hypersaline for the first time during the current drought period. There is thus no information on how fast, after mouth closure, *O. mossambicus* initially became dominant in the system or how the fish assemblage changed from 'normal' estuarine to the 'stressed' state.

Chapter 6: General Discussion and Conclusion

6.1 Mouth Condition and Salinity

Estuarine habitats and the fish assemblages associated with them, are increasingly impacted upon by anthropogenic influences, of which freshwater deprivation and its influence on natural mouth dynamics and the marine-estuarine link, is regarded as one of the greatest concerns worldwide (Whitfield, 2005b; Gillson, 2011). South African estuaries are mostly dominated by marine estuarine-dependant species which rely on the warm temperatures, sheltered environment and rich food supply provided by estuaries as a nursery area for their juveniles (Wallace, 1975; Wallace and Van der Elst, 1975) and recruitment of post larval and juvenile fish is dependent on a consistent connection with the marine environment. In 1952 the St Lucia mouth was separated from the Mfolozi-Msunduzi Estuary and over the last 60 years, this has led to an increase in the frequency and duration of drought related mouth closures (Cyrus *et al.*, 2010b).

Freshwater input is a primary determining factor contributing to the state of an estuary (Gillson, 2011). Marine water is always available as long as there is a connection between the estuary and the marine environment, which in itself is dependent on the freshwater input a system receives. Freshwater input into estuaries is under immense pressure from anthropogenic influences in river catchments, which are set to increase in the future as human populations and their activities require more water. Freshwater input is also dependent on regional climatic patterns, which directly impact the estuarine environment. Wet periods lead to higher freshwater input which lower salinities or even flood the whole system, while dry periods lead to low water levels. In estuaries that are considered as 'low inflow' systems and in which evaporation often exceed precipitation during dry periods, freshwater deprivation inevitably leads to mouth closure and hypersalinity (Largier, 2010).

Freshwater input affects a number of environmental processes occurring in estuaries and adjacent coastal areas, including estuary channel dimensions (Reddering,

1988), the mouth conditions (Roy *et al.*, 2001), the offshore extent of the riverine plume fronts (Grimes and Kingsford, 1996), tidal mixing (Hunter *et al.*, 2010), water temperature (Attrill and Power, 2002), salinity gradient (Kurup *et al.*, 1998), dissolved oxygen concentrations (Somville and De Pauw, 1982), nutrient input (Qu and Kroeze, 2010), sediment transfer (Eyre, 1998), turbidity (Laheta and Stramski, 2010), stratification of the water column (Schumann and Pearce, 1997) and the residence time of pollutants (Baird and Heymans, 1996). Modification of freshwater input through anthropogenic manipulation can also alter the environmental cues required for migration into and out of a system (Zale and Adornato, 1996), lower species diversity (Plumstead, 1990) and alter habitats to favour colonization of non-native species (Bunn and Arthington, 2002). In the St Lucia estuarine system, freshwater deprivation has had a number of impacts over the last 60 years and different managerial strategies have been implemented to deal with the water shortage, the effect of which can be most clearly observed during periods of drought. The largest concern is however, closure of the mouth.

Not only was the Mfolozi Estuary separated from the St Lucia Estuary, but increasing freshwater abstraction from the Mkuze, Mzinene, Hluhluwe and Nyalazi Rivers have contributed to lower freshwater input into False Bay and North Lake, all of which lead to a freshwater deficit during periods of below average rainfall, resulting in increased salinities (Whitfield and Taylor, 2009). Forestry on the Eastern and Western Shores also contributed to lower water input, but gradual removal of these plantations during the last decade, especially on the Eastern Shores, have partially restored ground water supply to the St Lucia system (Whitfield and Taylor, 2009). An increase in illegal informal cultivation in the Mkuze swamps could, however, compromise the sediment-retaining abilities of the swamp and lead to siltation of large parts of North Lake.

Following the decision by management not to artificially re-open the St Lucia estuarine system after its closure in 2002, the system has experienced extreme hypersalinites, compartmentalisation and low lake levels. EKZNW needed a new strategy to manage the St Lucia mouth and to address the continued freshwater deprivation in the system and in 2010 an Mfolozi-Msunduzi Indaba was held to investigate the possibility and implications of re-connecting the St Lucia and Mfolozi

Estuaries (Bates *et al.*, 2011). Lawrie and Stretch (2011a) investigated the water and salt budget of the St Lucia system under three different management scenarios; Scenario 1 corresponded to the management strategy that was followed from after the Mfolozi and St Lucia mouths were separated (1952) to the onset of the recent drought and mouth closure (2002), with the mouth kept artificially open and the two systems separated. Scenario 2 corresponded to the management strategy followed since the mouth closed in 2002 to date (2014), with no manipulation of the St Lucia mouth while the two systems remained separate. However, during 2008-2012, several attempts were made to direct water from the Mfolozi system into the St Lucia Narrows. Scenario 3 corresponded to the combined St Lucia-Mfolozi Estuary in its natural state before the two systems were separated in 1952, with no active manipulation by management. Lawrie and Stretch (2011a) found that the configuration of the St Lucia-Mfolozi connection played a significant role in the physico-chemical environment of the St Lucia system. Under Scenario 1, the open mouth would decrease the chance of drying of the lakes but increase salinities over 65 for about 17% of the time. Under Scenario 2, the closed mouth state would lead to about 50% of the surface area of the lakes becoming dry 32% of the time, this possibly lasting for up to 15 months. The low lake levels would also lead to hypersalinity in the lakes. Under Scenario 3, re-connection of the St Lucia and Mfolozi systems would decrease the frequency of periods of low water levels and hypersalinity and the system would naturally maintain a mostly open mouth.

A major concern associated with the re-connection of the St Lucia and Mfolozi systems is also the reason that they were separated in 1952, i.e. the large sediment load in the Mfolozi River being carried into St Lucia due to the loss of the Mfolozi swamps. Therefore, any water that enters the St Lucia system should ideally first have its sediment removed by a swamp filter, which will have to be recreated on the Mfolozi flood plain (Whitfield and Taylor, 2009).

Breaching of the St Lucia mouth would require a substantial input of water from rainfall and/or the Mfolozi system to overtop and breach the beach berm. The berm requires a few years to reach a maximum height of 3-3.5 m above mean sea level (amsl) (Whitfield and Taylor, 2009). Therefore the water required depends on the height of the berm. The longer the mouth remains closed the higher the beach berm

builds up and the larger the amount of water required to breach the St Lucia mouth. Breaching after longer closed mouth periods also leads to greater scouring of the mouth area and is therefore preferable to breaching soon after mouth closure.

A Global Environment Facility (GEF) project with the aim to examine ways of increasing freshwater inflow into Lake St Lucia was initiated in 2011. It is being run by iSimangaliso Wetland Park Authority and funded by the World Bank. The project also aims to establish new management procedures and ways to reduce human impacts on the St Lucia system. In addition, the role of sedimentology, hydrology, ecology and resource economics in the future functionality of the system will also be addressed (Whitfield and Taylor, 2009).

6.2 Fish Community States and *Oreochromis mossambicus*

A total of 155 fish species were recorded in the St Lucia system to date (Cyrus, 2013), but the most recent fish species list recorded during open mouth conditions was compiled in 1979 by Whitfield (1980), which contained 108 species. Between November 2004 and May 2006 - May 2014 (18 sampling seasons), 83 species were recorded in the St Lucia system, ranging from 21 in May 2006 during the worst part of the drought, to 50 in November 2007 after the mouth had been open for several months. The drought led to prolonged mouth closure due to freshwater deprivation, low lake levels and extreme hypersalinity, which adversely affected the species diversity in the system. The current post-beach channel species list contains a total of 50 species after two years of re-connection to the marine environment via the Mfolozi mouth, which is less than half of the species tally recorded by Whitfield (1980) under open mouth conditions.

After the mouth closed in 2002 and the system became hypersaline during 2003-2006, *O. mossambicus*, which is normally rare under open estuarine conditions due to competition with other marine and estuarine species (Wallace, 1975; Whitfield and Blaber, 1979a), became the most abundant species within the system (Cyrus and Vivier, 2006a). *Oreochromis mossambicus* was found to be dominant in salinities >40, with its abundance exceeding the combined abundance of all other estuarine and marine species together (Chapter 5). The combined fish abundance (estuarine,

marine and freshwater) was highest at salinities between 30-40. Estuarine species were dominant in salinities between 0-20 and marine species between 20-30. Several periods with different salinity states related to the fish communities of St Lucia were identified (Chapter 5; Figure 5.2). According to Remmert (1983), abiotic factors (salinity, depth, temperature, turbidity, dissolved oxygen, etc.) are responsible for the distribution patterns observed for estuarine fish species on a large scale, while biotic interactions (predation, competition, etc.) are responsible for the local composition of communities (Sanders, 1968; Menge and Olson, 1990). It has been shown that temporal changes in the St Lucia fish community were driven by large scale changes in the salinity state of the system over years, while spatial changes in the fish community were driven by the salinity gradient across the system. Chapter 3 showed that there was a decline in the number of species as well as the fish abundance with continued mouth closure, related to low lake levels and hypersalinity. The marine species that use the system as a nursery ground were most affected due to a lack of a connection with the marine environment. In July 2012, the beach channel between the St Lucia Narrows and the Mfolozi system was opened and this allowed water from the Mfolozi Estuary and marine environment to enter St Lucia, resulting in higher water levels and some recruitment of marine species. It has been shown in Chapter 4 that there was an increase in the number of marine species in the system after the channel opened but that recruitment was limited.

The limited recruitment of marine fish through the beach channel might be related to the lack of outflow from the St Lucia system, preventing migrating larvae and juveniles from receiving the necessary cue to migrate down the beach channel into St Lucia. Initially, freshwater from the Mfolozi Estuary and later saline water from the marine environment entered St Lucia, gradually filling the system. During this time, there was little outflow from St Lucia via the beach channel. Highest water levels since mouth closure in 2002 were recorded during early 2013, and normal tidal exchange occurred via the Mfolozi mouth. However, gradual sedimentation of the channel entrance eventually prevented all but spring tides from overtopping into the St Lucia system. Larval fish recruitment studies in Eastern Cape estuaries have shown that moderate water outflow into the surf zone is required for large migrations of marine fish into temporarily open/closed estuaries and that maximum recruitment

occurs during adult spawning periods, predominantly over spring and early summer months (Whitfield, 1998; Strydom 2003). During the 2012/13 spring spawning periods, there was very little, if any, outflow from the St Lucia system through the beach channel. Harrison and Cooper (1991) did however, argue that a mere trickle of water into the marine environment is sufficient to allow for successful recruitment of marine species into an estuary.

The biggest concern in maintaining a healthy estuarine fish population in the St Lucia system is the lack of a regular connection with the marine environment, with the mouth remaining closed for prolonged periods under low rainfall (drought) conditions as a direct result of reduced water input from the Mfolozi River. Although the beach channel allowed for some recruitment, it is clear from this study that a more extensive, and frequent connection is required between the St Lucia system and the marine environment in order for optimal recruitment to occur.

6.3 The Future of the St Lucia Estuarine System

In the St Lucia system, increased freshwater input seems to be what climate change models are forecasting. Various models predict increased summer rainfall, rise in sea level and an increase in the frequency of high intensity coastal storms for the sub-tropical east coast of South Africa (Tyson 1990, Tyson 1993, Schulze & Kunz 1993, Shackleton *et al.* 1996). There are positive and negative sides to this scenario as alteration in precipitation, river flow and storm intensity and frequency will affect the tidal exchange, occurrence and duration of mouth closure, salinity gradients, nutrient fluxes, occurrence and intensity of flood events and resulting sediment deposition/erosion and the dilution and/or flushing of pollutants (Alber, 2002). Rising sea levels and increasing rainfall are the two factors that will have the largest impact on the St Lucia system. Increased freshwater input will probably result in more sustained open mouth conditions, which will benefit species diversity and abundance (Mather *et al.*, 2013). However, too much water input may lead to northern parts of the system becoming very fresh, thus limiting its function as a nursery area for marine species. However Wasserman and Strydom (2011) showed that the young of euryhaline marine-spawning fishes are able to tolerate the low saline environments in the headwater of estuaries. Rising sea levels will result in the mouth migrating

inland by between ~26 to ~190 m and erosion of the shoreline. On a positive note, rising sea levels will lead to an increase in water levels across the whole system, increasing the surface area and depth of the system (Mather *et al.*, 2013). On a whole, climate change may have a beneficial impact on the biodiversity of St Lucia.

Under the GEF project, which is working towards establishing a natural functioning St Lucia-Mfolozi mouth, the current (2014) proposed plan is to remove the sand bank between the St Lucia and Mfolozi estuaries (which was built up from dredge spoil related to mouth separation) and re-establish the historical St Lucia Bay with a common mouth for both systems. It is theorised that this scenario will allow the St Lucia mouth to regulate naturally, while preventing sediment build-up in the system. However, implementation of the GEF project is still several years away as it is still in a modelling phase. In the meantime, the southern tip of the sand bank will be removed, which will increase water flow and connectivity between St Lucia and the Mfolozi system and the marine environment. Re-connection between the St Lucia and the Mfolozi system will have significant impact in several areas:

- Water and salt budget modelling has shown that a common St Lucia-Mfolozi mouth would stay closed for <30% of the time, compared to 80% experienced currently with the separate St Lucia and Mfolozi mouths (Lawrie *et al.*, 2011; Lawrie and Stretch, 2011b).
- During mouth closure, sediment will enter St Lucia, due to the absence of the Mfolozi swamp (Grenfell and Ellery, 2009), however when the combined mouth opens much of the sediment will be flushed directly out to sea (Van Niekerk and Huizinga, 2011).
- There will be a change in the marine sediment build up in the estuary mouth, as the combined flow from the St Lucia and Mfolozi systems into the estuary mouth will be much stronger than each system on its own (Lawrie and Stretch, 2011b).
- Sediment flushing when the combined mouth breaches would be substantially larger. In 1932, the head water at the time of breaching was approximately 4.6 m amsl (Van Niekerk and Huizinga, 2011) and this resulted in significant scouring of the combined St Lucia-Mfolozi mouth.

- Connection between the St Lucia and Mfolozi system is important for biodiversity, for example the freshwater caridean prawns that breed in the Mfolozi wetland (Bickerton, 2011). During small floods their larvae are carried into the St Lucia system.
- Prolonged mouth closure affects the abundance of marine estuarine-dependant fish (Mann, 1996; Vivier and Cyrus, 2009) and crustaceans (Forbes and Cyrus, 1991). It will take several years for marine populations to recover from the current low population densities. Abundance of key prey species in the St Lucia system such as *Mugil cephalus* will also affect the Nile crocodiles (Whitfield and Blaber, 1979b), African fish eagles (Whitfield and Blaber, 1978) and great white pelicans (Whitfield and Blaber, 1979c) populations.
- The Mfolozi Estuary is a relatively poor nursery area compared to St Lucia due to its small size and the limited food for juvenile zoobenthic foraging fishes (Owen *et al.*, 2010; Vivier *et al.*, 2010b). The combined mouth will allow recolonization of the St Lucia system by marine-estuarine species currently using the Mfolozi system as an alternate nursery.

6.4 Recommendations

The St Lucia system has experienced severe hypersalinity over the last decade, after the mouth closed in June 2002. Currently the system is experiencing a 'partly normal' estuarine state due to increased water input after the beach channel opened in July 2012. However, without regular maintenance, the long term prospects for the beach channel do not seem good. Over the past year it has slowly been filling up with sediment from the Mfolozi Estuary, which has limited the water input into the St Lucia system to over-topping during spring high tides (Taylor *et al.*, 2014). This has severely limited the movement of fish between the St Lucia Estuary and the marine environment. Juvenile marine species are still however able to enter the St Lucia system via the back channel during spring tides, albeit to a very limited extent. The lack of a properly maintained beach channel will further impair the vital marine-estuarine linkage and future research will be required on its role in maintaining fish abundance within the St Lucia system and recruitment between St Lucia, the ocean

and the Mfolozi-Msunduzi system. Closure of the channel will also affect the off-shore adult fish population of marine-estuarine dependant species whose juveniles are dependent on the system as a nursery area (Mann and Pradervand, 2007). Therefore, to maintain a healthy fish population in St Lucia as well as the marine environment in the future, a more extensive, regular connection to the marine environment is required (Whitfield, 2005b).

Future work on the fish communities of the St Lucia and Mfolozi Estuaries should include:

- Continued monitoring of the water flow in and out of the system as well as recruitment of both fish & invertebrates occurring over high tides when the beach channel is opened up again.
- Continued research on the fish population of the St Lucia system to determine whether fish abundance increases again with an open beach channel state.
- Comparative study of the fish assemblage of the St Lucia and Mfolozi systems after the beach channel has been re-opened (and in an optimal functioning state) to determine the extent of and differences in recruitment between the two systems.
- *Oreochromis mossambicus* is classified as 'Near Threatened' on the IUCN Red List of Threatened Species, due to hybridization with the rapidly spreading *Oreochromis niloticus*. Hybridization is already occurring throughout the northern part of the species' range (Cambray and Swartz, 2007; D'Amato *et al.*, 2007). Genetic work needs to be done to investigate whether hybridization has occurred in St Lucia and if not how to prevent the spread to St Lucia in the future.

Recommendations on the future management of the St Lucia-Mfolozi Estuarine System include:

- Understanding the freshwater requirements of estuarine environments will in the future become increasingly important as climate change (global warming) will apply increasing stress on aquatic resources and as human population growth increases the demand for water (Gillson, 2011).

- Increased input via St Lucia's other tributaries is also recommended and continued efforts to remove plantations on the Eastern and Western shore will help restore groundwater flows to the system (Whitfield and Taylor, 2009).
- Management of the informal settlements in the Mkuze floodplain, to prevent illegal cultivation of parts of the swamps which could compromise their sediment-retaining ability and lead to siltation of large parts of North Lake (Whitfield and Taylor, 2009).
- Reconstruction of the Mfolozi floodplains to re-establish the natural functioning of the swamps in removing river-borne sediment before entering the St Lucia system (Whitfield *et al.*, 2013).

Chapter 7: References

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Appendix 1: Physico-chemical Data

Table A: Physico-chemical parameters recorded in the St Lucia Estuarine System during the sampling periods. Codes for sites, are the year (2004-2014), season (N, November; M, May), alphabetic code (A-F) that corresponds to the site (LN, Lower Narrows; UN, Upper Narrows; CJ, Catalina Bay; CC, Charters Creek; FI, Fannies Island; HG, Hell's Gate).

Site	Temp	Salinity	DO (mg/L)	Oxygen %	pH	Turb (NTU)	Depth
04NALN	28.30	8.59	7.04	94.80	8.08	111.60	1.49
04NBUN							
04NCCJ	27.15	27.87	6.91	101.50	8.70	165.00	0.60
04NDCC	31.76	28.95	7.00	105.90	8.64	1350.30	0.50
04NEFI	28.99	40.27	7.53	123.00	8.39	157.90	0.50
04NFHG	27.78	72.04	7.53	103.70	8.61	250.60	0.99
05MALN	26.99	10.43	7.56	101.90	8.62	27.00	0.97
05MBUN	28.65	5.26	7.33	100.20	8.21	28.70	0.40
05MCCJ	25.91	26.17	6.95	99.20	8.72	22.80	0.80
05MDCC	29.87	21.18	8.14	120.80	8.78	55.40	0.49
05MEFI	31.70	24.03	8.09	125.50	8.55	44.80	0.36
05MFHG	24.90	32.47	9.02	131.00	8.70	7.90	0.20
06MALN	19.79	13.71	8.09	96.10	8.65	19.60	1.26
06MBUN	20.95	8.31	8.44	99.30	8.36	16.70	1.80
06MCCJ	15.89	10.51	10.51	113.20	8.74	120.00	0.30
06MDCC	16.42	20.22	9.37	108.20	8.66	65.10	0.58
06MEFI	26.87	25.93	10.91	114.90	8.67	2.80	0.40
06MFHG	28.60	90.00	8.90	119.40	7.90	0.70	0.10
06NALN	23.96	12.39	8.09	77.50	8.65	27.80	1.20
06NBUN	28.33	4.89	6.42	85.50	6.75	18.60	1.18
06NCCJ	24.80	15.00	7.24	95.10	8.16	130.00	0.90
06NDCC	28.60	14.72	7.19	100.90	8.30	133.30	0.60
06NEFI	23.37	10.47	8.75	109.00	7.95	14.10	0.50
06NFHG	23.18	17.60	9.10	118.60	7.91	1.70	0.25
07MALN	23.26	35.80	7.30	105.10	7.90	5.90	1.79
07MBUN	19.75	35.55	7.94	107.30	6.98	11.40	1.97
07MCCJ	17.39	36.26	8.67	112.60	8.12	2.20	0.63
07MDCC	18.86	36.56	8.62	115.20	7.70	20.50	1.00
07MEFI	18.56	37.22	6.81	91.20	7.87	11.20	0.41
07MFHG	20.36	33.90	9.01	122.40	7.37	23.10	0.54
07NALN	23.50	28.36	6.96	96.60	7.34	22.10	1.35
07NBUN	24.70	27.60	7.24	102.00	7.30	42.00	0.77
07NCCJ	21.87	38.44	6.70	96.00	7.75	33.00	1.33
07NDCC	24.29	39.35	6.35	95.10	8.23	254.30	1.02

07NEFI	27.55	37.84	6.42	100.90	7.51	231.00	0.81
07NFHG	23.08	36.20	7.75	111.70	7.82	96.90	1.01
08MALN	21.40	25.47	6.87	91.00	9.56	20.90	1.05
08MBUN	22.40	23.23	4.30	70.00	7.50	31.30	1.37
08MCCJ	20.25	47.48	6.34	92.70	9.39	27.00	1.37
08MDCC	21.67	48.89	6.58	99.60	9.25	75.40	0.85
08MEFI	22.08	49.40	5.84	89.20	7.75	29.20	0.91
08MFHG	21.68	45.20	7.88	116.70	9.11	3.70	0.85
08NALN	26.45	12.97	6.97	93.10	8.39	113.80	1.16
08NBUN	23.05	12.74	5.52	69.30	8.48	51.40	1.27
08NCCJ	23.83	54.28	6.45	104.30	8.36	373.60	0.90
08NDCC	21.26	56.69	6.66	104.50	8.34	57.10	0.64
08NEFI	24.41	68.26	6.16	108.90	8.33	54.40	0.59
08NFHG	23.75	67.30	4.98	86.50	8.22	172.80	0.40
09MALN	19.87	7.83	12.32	96.30	7.94	34.40	1.33
09MBUN	20.50	4.90	8.01	93.10	8.09	79.10	1.61
09MCCJ	21.99	42.36	11.99	94.60	8.11	46.70	1.12
09MDCC	20.93	45.10	11.45	106.60	8.03	23.40	0.38
09MEFI	22.40	73.60	9.55	118.30	8.52	9.90	0.47
09MFHG	20.50	82.00	6.68	120.30	8.45	22.50	0.49
09NALN	23.53	13.80	8.53	108.20	8.79	38.00	0.84
09NBUN	23.50	10.68	6.57	79.90	8.52	80.70	1.19
09NCCJ	20.96	50.27	6.52	97.70	8.39	121.80	0.44
09NDCC	25.47	53.34	8.92	126.50	7.88	210.00	0.22
09NEFI	21.65	86.05	5.88	96.90	8.82	108.10	0.22
09NFHG	29.41	90.02	3.12	63.00	8.89	148.90	0.19
10MALN	24.76	3.12	7.57	92.80	8.29	53.60	0.93
10MBUN	23.11	2.96	6.39	75.90	8.27	48.10	1.80
10MCCJ	25.60	42.18	5.51	83.50	8.13	71.50	1.00
10MDCC	24.12	42.35	6.28	95.20	8.22	55.60	0.52
10MEFI	26.20	72.54	8.87	108.80	9.09	101.60	0.35
10MFHG	23.20	51.45	4.23	66.60	8.51	20.30	0.46
10NALN	26.02	21.36	5.74	79.90	8.20	60.50	0.93
10NBUN	26.76	10.95	7.90	105.00	8.20	38.40	0.92
10NCCJ	30.77	50.45	5.36	94.70	8.26	512.70	0.50
10NDCC	26.75	50.63	6.64	110.30	8.21	73.00	0.12
10NEFI	29.45	65.82	6.68	125.60	9.02	29.30	0.24
10NFHG	27.53	57.88	11.33	125.90	9.04	29.80	0.22
11MALN	21.47	11.45	7.77	94.00	8.24	19.10	0.67
11MBUN	20.35	5.12	5.27	60.00	7.95	56.80	1.33
11MCCJ	21.99	13.76	7.36	91.20	8.32	46.00	0.73
11MDCC	20.79	14.88	6.63	80.60	8.42	26.50	0.45
11MEFI	22.18	37.90	8.73	125.30	8.51	30.80	0.38
11MFHG	19.80	38.23	6.55	89.90	8.28	34.40	0.48
11NALN	23.89	2.63	6.49	78.00	8.06	23.00	1.47
11NBUN	22.88	2.43	5.50	65.40	7.93	23.10	1.80

11NCCJ	26.16	11.14	8.56	112.60	8.01	30.40	0.94
11NDCC	23.93	11.84	7.42	94.10	8.19	56.10	0.76
11NEFI	27.95	35.73	6.78	99.70	8.00	101.90	0.27
11NFHG	24.25	58.38	5.38	89.70	7.76	213.00	0.40
12MALN	19.20	12.77	9.18	107.20	7.65	11.90	1.03
12MBUN	18.56	5.72	6.16	68.10	6.86	55.00	1.22
12MCCJ	17.75	5.73	9.33	101.30	7.68	101.30	1.12
12MDCC	15.71	5.87	9.36	97.80	7.68	33.60	0.58
12MEFI	18.93	19.95	9.74	118.00	7.20	54.40	0.45
12MFHG	15.66	35.30	7.25	90.70	7.12	30.30	0.78
12NALN	19.13	6.24	8.25	93.20	7.92	14.10	1.33
12NBUN	19.70	0.93	8.29	91.20	7.99	41.90	1.30
12NCCJ	21.31	6.04	9.15	110.00	7.07	64.30	1.26
12NDCC	20.76	6.99	8.89	98.70	6.65	182.00	1.11
12NEFI	21.02	13.76	7.86	95.60	8.13	65.60	0.54
12NFHG	20.95	26.49	6.87	90.00	7.77	13.10	0.85
13MALN	22.11	21.88	8.35	108.50	7.80	5.50	1.60
13MBUN	21.06	9.49	6.01	69.80	7.22	7.20	1.53
13MCCJ	20.81	8.47	9.09	106.70	8.14	13.70	1.12
13MDCC	20.06	9.67	8.24	96.10	8.10	8.30	1.57
13MEFI	20.60	11.91	7.10	83.70	8.33	13.10	0.90
13MFHG	19.70	13.20	5.40	67.80	8.33	8.20	1.70
13NALN	22.52	29.00	4.35	59.80	7.80	23.77	1.64
13NBUN	23.14	25.83	3.05	41.40	7.50	36.10	1.79
13NCCJ	21.76	13.00	7.19	97.20	8.45	35.18	1.86
13NDCC	21.61	12.54	7.95	97.10	8.45	48.88	1.50
13NEFI	23.60	13.90	8.09	103.30	8.39	77.20	0.84
13NFHG	21.89	14.81	7.45	92.70	8.32	56.00	1.50
14MALN	23.22	25.05	7.61	75.80	7.95	21.40	2.12
14MBUN	20.04	4.42	7.46	73.30	7.72	34.10	2.46
14MCCJ	19.43	11.26	8.51	98.90	8.46	35.90	2.12
14MDCC	18.65	13.20	8.33	96.40	8.42	22.20	1.77
14MEFI	20.63	15.09	8.33	101.30	8.41	29.20	1.19
14MFHG	18.90	14.83	7.73	91.00	8.40	16.50	1.94

Appendix 2: Water Level Data

Table B: Water level data obtained from the Department of Water Affairs for Lister's Point and from Ezemvelo KZN Wildlife for the St Lucia Bridge, averaged per month.

Date	Lister's Point	Bridge	Date	Lister's Point	Bridge	Date	Lister's Point	Bridge
Jan-04		0.768	Jul-07	0.529		Jan-11	-0.171	0.950
Feb-04		0.683	Aug-07	0.588	1.200	Feb-11	-0.140	0.671
Mar-04		0.605	Sep-07	0.568	0.880	Mar-11	-0.138	0.576
Apr-04		0.495	Oct-07	0.541	0.707	Apr-11	-0.113	0.595
May-04		0.573	Nov-07	0.541	0.690	May-11	-0.120	0.578
Jun-04		0.440	Dec-07	0.542	0.680	Jun-11	-0.111	0.652
Jul-04		0.539	Jan-08	0.486	0.626	Jul-11	-0.103	0.860
Aug-04		0.458	Feb-08	0.411	0.570	Aug-11	-0.104	0.724
Sep-04		0.530	Mar-08	0.343	0.495	Sep-11	-0.124	0.612
Oct-04		0.290	Apr-08	0.335	0.540	Oct-11	-0.122	0.805
Nov-04			May-08	0.319	0.593	Nov-11	-0.119	0.897
Dec-04			Jun-08	0.316	0.648	Dec-11	-0.112	0.775
Jan-05		0.608	Jul-08	0.351		Jan-12	-0.129	0.685
Feb-05		0.560	Aug-08	0.268	0.570	Feb-12	-0.135	0.715
Mar-05		0.600	Sep-08	0.158	0.610	Mar-12	0.166	1.016
Apr-05			Oct-08	0.088	0.590	Apr-12	0.188	0.643
May-05			Nov-08	0.042	0.540	May-12	0.132	0.563
Jun-05			Dec-08	0.004	0.575	Jun-12	0.131	0.545
Jul-05		0.515	Jan-09	0.001	0.540	Jul-12	0.143	0.708
Aug-05		0.463	Feb-09	0.001	0.605	Aug-12	0.211	0.631
Sep-05			Mar-09	0.004	0.662	Sep-12	0.278	0.949
Oct-05		0.335	Apr-09	0.005		Oct-12	0.343	1.078
Nov-05		0.295	May-09	0.006	0.505	Nov-12	0.470	0.960
Dec-05		0.258	Jun-09	0.006	0.490	Dec-12	0.677	1.169
Jan-06		0.345	Jul-09	0.006	0.440	Jan-13	0.785	1.148
Feb-06		0.577	Aug-09	0.004	0.395	Feb-13	1.071	1.294
Mar-06		0.570	Sep-09	-0.003	0.420	Mar-13	1.119	1.191
Apr-06		0.520	Oct-09	0.000	0.480	Apr-13	1.136	1.186
May-06		0.632	Nov-09	0.010	0.430	May-13	1.081	1.142
Jun-06			Dec-09	0.015	0.688	Jun-13	0.958	1.118
Jul-06		0.590	Jan-10	0.028	0.538	Jul-13	0.916	1.075
Aug-06		0.650	Feb-10	-0.034	0.640	Aug-13	0.849	1.135
Sep-06		0.620	Mar-10	-0.129	0.610	Sep-13	0.756	1.000
Oct-06		0.690	Apr-10	-0.155	0.625	Oct-13	0.990	0.928
Nov-06		0.605	May-10	-0.146	0.723	Nov-13		1.028
Dec-06		0.785	Jun-10	-0.126	0.510	Dec-13	0.395	1.079
Jan-07	0.015	0.655	Jul-10	-0.131		Jan-14	1.251	0.981
Feb-07	0.015	0.530	Aug-10	-0.128	0.450	Feb-14		0.971
Mar-07	0.015	1.043	Sep-10	-0.141	0.370	Mar-14		1.225
Apr-07	0.039		Oct-10	-0.123	0.408	Apr-14		1.177
May-07	0.109		Nov-10	-0.152	0.533	May-14		1.141
Jun-07	0.422		Dec-10	-0.180	0.800	Jun-14		

Note: To determine which set of water level data corresponded best with our depth measurements, the change in water level was determined and then correlated between the various data sources. May 2007 was used as the zero point and the change in water level was calculated for each sampling trip (Table C).

Table C: Change in Water Level with May 2007 as zero point.

Date	Lower Narrows	Upper Narrows	Catalina Bay	Charters Creek	Fanies Island	Hell's Gate	Lister's Point	Bridge
May-07	0	0	0	0	0	0	0	0
Nov-07	-0.448	-1.200	0.703	0.019	0.394	0.477	0.328	-0.355
May-08	-0.743	-0.600	0.745	-0.148	0.496	0.313	0.120	-0.427
Nov-08	-0.633	-0.700	0.272	-0.359	0.180	-0.135	-0.154	-0.475
May-09	-0.468	-0.360	0.492	-0.622	0.056	-0.047	-0.176	-0.500
Nov-09	-0.953	-0.780	-0.186	-0.778	-0.196	-0.350	-0.174	-0.565
May-10	-0.861	-0.170	0.372	-0.478	-0.064	-0.077	-0.336	-0.263
Nov-10	-0.862	-1.050	-0.128	-0.878	-0.174	-0.317	-0.326	-0.503
May-11	-1.125	-0.640	0.100	-0.549	-0.034	-0.059	-0.303	-0.458
Nov-11	-0.323	-0.167	0.310	-0.241	-0.143	-0.137	-0.299	-0.102
May-12	-0.768	-0.747	0.488	-0.419	0.038	0.238	-0.031	-0.460
Nov-12	-0.467	-0.670	0.633	0.116	0.126	0.317	0.191	0.110
May-13	-0.197	-0.441	0.493	0.576	0.486	1.163	0.896	0.140
Nov-13	-0.155	-0.183	1.235	0.498	0.429	0.964	0.808	-0.070
May-14	0.326	0.490	1.493	0.775	0.775	1.406	0.943	0.105

The best correlation (Pearson Product-Moment) was obtained between the average depth data and the water level data from Lister's Point (Table D), while the weakest correlation was between the Bridge water level and the Lister's Point water level data, indicating that there is a difference in water level between the two sites especially in periods of drought when the St Lucia system becomes compartmentalized. Therefore the water level data was also correlated against the average depth in the Narrows (Lower and Upper Narrows) and the Lakes (Catalina Bay, Charters Creek, Fanies Island and Hell's Gate). As expected the Lister's Point data correlated best with the Lakes while the Bridge data correlated best with the Narrows.

Table E: Correlation (Pearson Product-Moment) results between the Bridge, Lister's point and average depth (Narrows and Lakes).

Correlation	R ²	r	t	p
Bridge and Average Depth	0.579	0.761	4.230	0.001
Lister's Point and Average Depth	0.812	0.901	7.510	<0.001
Bridge and Lister's Point	0.453	0.673	3.280	0.006
Bridge and Average (Narrows) Depth	0.573	0.757	4.180	0.001
Lister's point and Average (Narrows) Depth	0.350	0.592	2.650	0.020
Bridge and Average (Lakes) Depth	0.464	0.681	3.350	0.005
Lister's point and Average (Lakes) Depth	0.889	0.943	10.180	<0.001

In conclusion, the data indicate that both the data from the Bridge and Lister's Point correlates to the change in water level we measured during our sample trips, but that Lister's Point is a more accurate fit and the Lister's Point data correlates better with the water level in the Lakes than with the Narrows.

Appendix 3: Figures & Tables (Chapter 3)

Chapter 3 has been written up for publication in *Estuarine, Coastal and Shelf Science*, has been reviewed and resubmitted. It has therefore been formatted and edited according to the Journal's standards. The following figures and tables have not been included in the publication.

Table E (3.5): SIMPER results showing mean similarity, % contribution (>5%) and cumulative contribution (%) of the fish species making the highest contribution to the mean similarity in the fish assemblage at each site in the St Lucia system during the period (2008-2011) (For mean % dissimilarities, see Table 3.4).

Species	Mean similarity	Sim/SD	Contribution %	Cumulative %
<u>Lower Narrows: mean similarity within group = 57.39%</u>				
<i>Oreochromis mossambicus</i>	7.22	4.95	12.6%	12.6%
<i>Ambassis ambassis</i>	5.39	3.86	9.4%	22.0%
<i>Leiognathus equula</i>	4.27	2.20	7.4%	29.4%
<i>Liza macrolepis</i>	3.41	2.90	6.0%	35.4%
<i>Terapon jarbua</i>	2.99	2.87	5.2%	40.6%
<i>Liza dumerilii</i>	2.97	1.57	5.2%	45.8%
<u>Upper Narrows: mean similarity within group = 51.58%</u>				
<i>Oreochromis mossambicus</i>	9.10	4.12	17.6%	17.6%
<i>Ambassis ambassis</i>	6.82	2.19	13.2%	30.9%
<i>Leiognathus equula</i>	6.20	4.09	12.0%	42.9%
<i>Glossogobius callidus</i>	3.87	0.94	7.5%	50.4%
<i>Valamugil cunnesius</i>	3.17	3.77	6.2%	56.5%
<i>Terapon jarbua</i>	2.91	3.80	5.6%	62.2%
<i>Thryssa vitrirostris</i>	2.64	1.00	5.1%	67.3%
<u>Catalina Bay: mean similarity within group = 31.68%</u>				
<i>Oreochromis mossambicus</i>	9.84	1.58	31.1%	31.1%
<i>Liza dumerilii</i>	4.94	1.56	15.6%	46.7%
<i>Silhouettea sibayi</i>	4.04	0.71	12.8%	59.4%
<i>Rhabdosargus sarba</i>	1.77	0.67	5.6%	65.0%
<i>Elops machnata</i>	1.62	0.71	5.1%	70.1%
<i>Liza macrolepis</i>	1.61	0.45	5.1%	75.2%
<u>Charters Creek: mean similarity within group = 38.42%</u>				
<i>Oreochromis mossambicus</i>	15.25	3.49	39.7%	39.7%
<i>Liza dumerilii</i>	8.12	1.36	21.1%	60.8%
<i>Silhouettea sibayi</i>	2.20	0.72	5.7%	66.6%
<u>Fanies Island: mean similarity within group = 35.00%</u>				
<i>Oreochromis mossambicus</i>	27.40	1.41	78.3%	78.3%
<i>Ambassis ambassis</i>	3.40	0.45	9.7%	88.0%
<u>Hell's Gate: mean similarity within group = 40.04%</u>				
<i>Oreochromis mossambicus</i>	36.13	1.70	90.3%	90.3%

Table F (3.6): SIMPER results showing mean similarity, % contribution (>4%) and cumulative contribution (%) of the fish species making the highest contribution to the mean similarity in the fish assemblage of each year (2008-2011) in the St Lucia system (For mean % dissimilarities, see Table 3.4).

Species	Mean similarity	Sim/SD	Contribution %	Cumulative %
<u>2008: mean similarity within group = 39.98%</u>				
<i>Oreochromis mossambicus</i>	11.14	1.23	27.9%	27.9%
<i>Ambassis ambassis</i>	5.30	0.96	13.3%	41.1%
<i>Silhouettea sibayi</i>	3.89	0.94	9.7%	50.9%
<i>Liza dumerilii</i>	2.60	0.89	6.5%	57.4%
<i>Elops machnata</i>	1.97	1.16	4.9%	62.3%
<i>Rhabdosargus sarba</i>	1.93	0.97	4.8%	67.1%
<u>2009: mean similarity within group = 29.07%</u>				
<i>Oreochromis mossambicus</i>	15.12	1.11	52.0%	52.0%
<i>Liza dumerilii</i>	1.97	0.57	6.8%	58.8%
<i>Liza macrolepis</i>	1.71	0.59	5.9%	64.7%
<i>Pomadasys olivaceus</i>	1.40	0.47	4.8%	69.5%
<u>2010: mean similarity within group = 30.09%</u>				
<i>Oreochromis mossambicus</i>	20.06	1.11	66.7%	66.7%
<i>Thryssa vitirostris</i>	1.24	0.48	4.1%	70.8%
<u>2011: mean similarity within group = 48.10%</u>				
<i>Ambassis ambassis</i>	15.53	2.20	32.3%	32.3%
<i>Oreochromis mossambicus</i>	14.37	2.46	29.9%	62.2%
<i>Liza dumerilii</i>	3.51	0.94	7.3%	69.5%
<i>Glossogobius callidus</i>	3.14	0.98	6.5%	76.0%
<i>Pseudocrenilabrus philander</i>	2.27	0.63	4.7%	80.8%

Table G (3.7): Canonical Correspondence Analysis (CCA) eigenvalues and cumulative % contribution to the total variance of the first four axes of the correlation between environmental variables and the fish community structure in the St Lucia system during 2008-2011. Species-environment correlations depict the correlation between environmental variables and the fish community for each of the first four axes of the CCA plot.

	<u>AXES</u>				Total (All Axes)
	1	2	3	4	
Eigenvalues	0.25	0.15	0.10	0.07	0.65
Cumulative %	37.80	60.30	75.30	85.50	
Species-environment correlations	0.92	0.73	0.80	0.71	

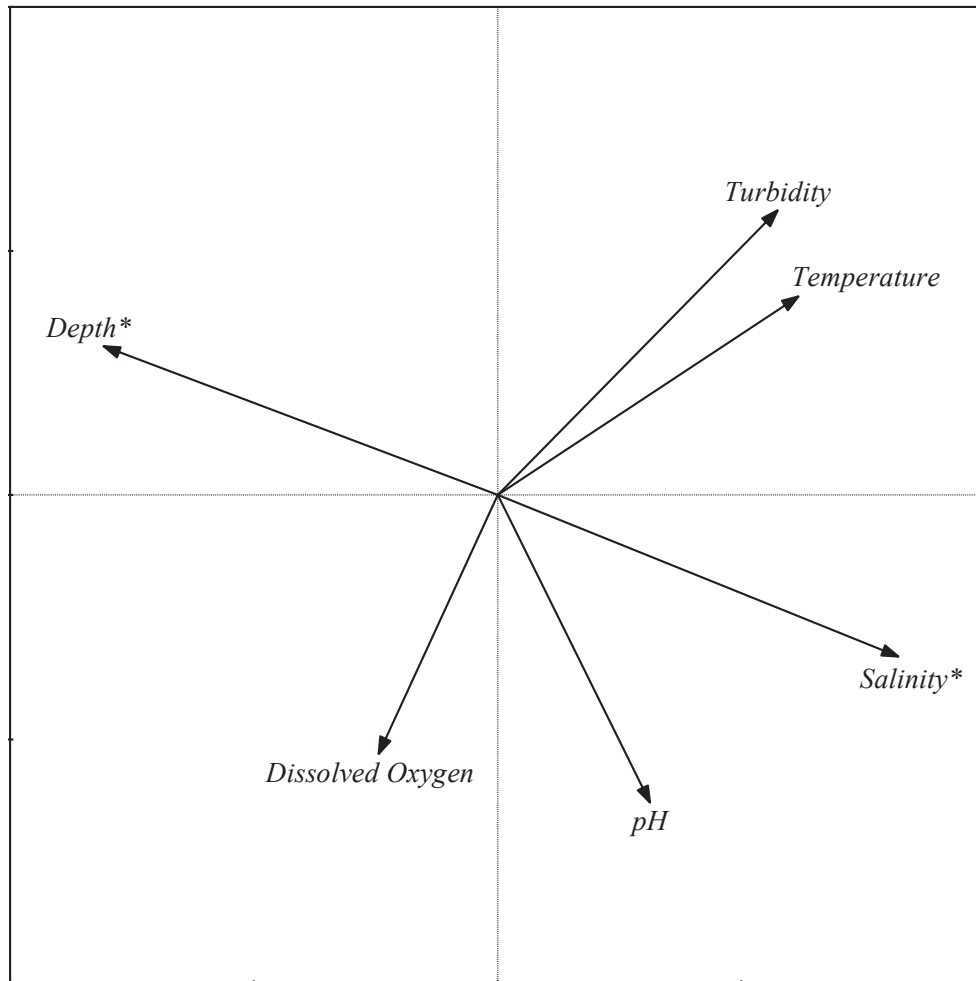


Figure A (3.7): Principal component analysis (PCA) biplot of the relation within the environmental variables in the St Lucia system during the period 2008-2011. *denotes a significant environmental variable.

Table H (3.8): Canonical Correspondence Analysis (CCA) showing the environmental variables in decreasing order of their contribution to the total variance in the fish community structure in the St Lucia estuarine system during 2008-2011. *Variables contributing significantly to the total variance in the fish community.

	Variance	F	P
Salinity	0.23	4.33	0.002*
Depth	0.11	2.14	0.008*
Turbidity	0.09	1.79	0.06
Dissolved Oxygen	0.09	1.63	0.06
Temperature	0.06	1.34	0.11
pH	0.07	1.32	0.17