Anthropogenic impacts and biophysical interactions in Lake St Lucia.

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As the candidates supervisor I have/have not approved this dissertation for submission.

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As the candidates co-supervisor I have/have not approved this dissertation for submission.

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Published peer reviewed journal paper

Publication 1
Lawrie, R.A. & Stretch, D.D., 2011. Anthropogenic impacts on the water and salinity budgets of St Lucia estuarine lake in South Africa. *Estuarine, Coastal and Shelf Science 93, 58 – 67.*

Publication 2
Lawrie, R.A. & Stretch, D.D., 2011. Occurrence and persistence of water level/salinity states and the ecological impacts for St Lucia estuarine lake, South Africa. *Estuarine, Coastal and Shelf Science 95, 67–76.*

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"And now we thank you, our God, and praise your glorious name."

1 Chronicles 29:13

Abstract

The St Lucia estuarine lake system in South Africa is part of a UNESCO World Heritage site and a Ramsar wetland of international importance. Like many estuarine systems worldwide St Lucia has experienced significant anthropogenic impacts over the past century including catchment land use changes, water diversions/abstractions and inlet manipulation. In addition, the system has recently suffered losses in species diversity and abundance following unprecedented hypersaline conditions and desiccation. Questions regarding its sustainability have motivated a reevaluation of management decisions made in the past and of options for the future. To understand the functioning of the system, it is necessary to analyse it holistically in terms of the physical processes and their interaction with the biology. This study focusses on aspects of the biophysical interactions in the estuarine complex, and aims to provide new knowledge to underpin the development of improved models for predicting the response of the system to anthropogenic interventions.

A model for the water and salt budgets was used to investigate what if scenarios in terms of past anthropogenic interventions, in particular the effects of diverting the Mfolozi River from St Lucia. Furthermore, the risks of hypersalinity and desiccation were assessed for each scenario. Integrating these modeled scenarios with observed biological responses to physicochemical changes suggested that large long-term changes in the ecological structure can be expected in the different management scenarios. To validate this, the ecosystem response to changing environmental responses was quantitatively assessed using ecological network analysis.

Long-term simulations show that the separation of the Mfolozi and St Lucia mouths had a significant impact on the functioning of the St Lucia system. The Mfolozi plays a pivotal role in maintaining a more stable mouth state regime and provides a vital source of freshwater during dry conditions. The configuration of the Mfolozi/St Lucia inlet plays a key role in the physico-chemical environment of the system and influences the system's susceptibility to desiccation and hypersaline conditions. Ecosystem indices revealed that the water level, salinity and mouth state have a significant impact on species abundance and diversity as well as the ecological structure and functioning of the system. In addition, ecosystem indices show that the system recovers rapidly during favourable conditions. The artificial separation of the St Lucia and Mfolozi inlets underpins the most significant impacts on the water and salt budget of the lake and its reversal is key to the sustainability of the system.

Preface

The work described in this thesis was undertaken at the School of Engineering as well as the School of Life Sciences of the University of KwaZulu-Natal under the supervision of Professor Derek D. Stretch and the co-supervision of Dr. Ursula M. Scharler. This research is intended to assist the iSimangaliso Wetland Park Authority and eKZN Wildlife in their quest to sustain the beautiful Lake St Lucia.

'Never doubt that a small group of thoughtful, committed citizens can change the world. Indeed, it is the only thing that ever has.

Margaret Mead

Contents

List of Figures

List of Tables

Chapter 1

Introduction

1.1 Estuaries

Estuaries comprise a small component of the Earth's surface yet they carry a disproportionate human load making them one of the most impacted ecosystems on Earth. Anthropogenic impacts including fresh water abstractions, sewage discharges, habitat alterations, eutrophication and overfishing have caused substantial degradation. In addition these impacts have altered the natural functioning of these systems and in turn have had a significant effect on species diversity and abundance. Estuaries are ecologically important due their high productivity and they play an important role in the sustainability of our fisheries as they provide a nursery area for juvenile fish and invertebrates. In addition rivers and estuaries are used as transport routes and recreation and contribute to economic and social development. The sustainability of these important ecosystems depends on well informed management decisions and policies based on scientific knowledge and research.

1.2 Problem Definition

Estuaries are among the most impacted ecosystems on Earth and therefore require sound management decisions and policies based on scientific understanding and research. Although there have been significant advances in the understanding of the different components that comprise estuarine systems, little is generally known about the biophysical interactions and functioning as well as the implications of anthropogenic impacts.

1.3 Research Questions

The ecology of St Lucia depends to a large degree on the extremely dynamic physico-chemical conditions that are associated with quasi-cyclic wet and dry climatic conditions. To understand the functioning of the estuary, it is necessary to analyse it holistically in terms of the physical processes and their interaction with the biological system. The aim of this thesis is to improve the understanding of the biophysical interactions in the estuarine complex, and to provide new knowledge to underpin the development of improved models for predicting the response of the system to changing climatic conditions. In order to achieve this, a set of research questions are discussed in the following sections.

1.3.1 Water and salt budget

The physico-chemical states of the system (e.g. water levels, salinity and turbidity) are determined by the water balance, which in turn is influenced by the mouth state and freshwater inflows. Govender *et al.* [2011] found that sites with low water depths and high salinities were dominated by benthic food webs and a reduced number of trophic positions. On the other hand, sites with deeper water levels and lower salinities sustained viable pelagic food webs. This illustrates the influence of salinity and water levels on the biological functioning of this system. The mouth state plays an important role in terms of the physico-chemical dynamics. A closed mouth prevents the recruitment and passage of fish and other invertebrates into and out of the system [Carrasco *et al.*, 2010; Forbes & Cyrus, 1993]. The mouth state, water level and salinity therefore form the basic drivers for the biological functioning of the system.

This thesis aims to improve the understanding of how mouth management strategies have influenced the natural functioning of the system in the past and how they should be used in the future. In terms of the physical dynamics, the key research questions include:

1. What was the effect of separating the St Lucia and Mfolozi systems on the water/salt budgets and mouth dynamics?
2. How does the system respond to extreme events under different mouth management scenarios?
3. How would importing additional fresh water into St Lucia change the functioning of the system?

1.3.2 Macroscale biophysical interactions

Due to the complexity of ecosystems, a great deal of effort has been given to ecological modelling and ecosystem analysis [Jørgensen & Bendoricchio, 2001]. It is anticipated that this aspect of the research could lead to the development of simple and efficient methods for modelling bio-physical interactions that are more useful for management applications than traditional mechanistic models based on complex non-linear dynamics. Some of the key research questions to be addressed are:

1. Can the overall biological structure and functioning of the system be characterized using a set of normalized ecosystem indices?
2. What are the biophysical responses of the system to changing mouth management scenarios?
3. What are the spatial and temporal scales for changes to the index spectra?

1.4 Motivation

The St Lucia estuarine-lake system was granted World Heritage Site status and is a Ramsar site of importance despite having undergone significant anthropogenic impacts over the past century. This important system makes up a substantial proportion of South Africa's total estuarine area and its sustainability is key in terms of its contribution to biodiversity. Substantial remedial measures have been undertaken in the past to recover the natural functioning of the system, however, these decisions were made without any detailed scientific understanding, the implications of which remain unknown even today. Lake St Lucia has recently experienced severe desiccation and hypersaline conditions thereby bringing its sustainability under question.

This thesis will aid the iSimangaliso Wetland Park Authority and Ezemvelo KZN Wildlife in understanding the biophysical responses to different management scenarios.

1.5 Aims and Objectives

In order to address the research questions outlined in the previous section, several aims and objectives were identified that would assist in understanding of the biophysical functioning of the St Lucia system. The aims of the study are listed as follows: followed by more specific objectives.

- To analyse the impacts of different mouth management options on the physicochemical functioning of the St Lucia system.
- To characterise the overall biological structure and functioning using a set of normalised ecosystem indices.
- To evaluate, simulate and assess the biological responses to physicochemical changes.

The aims are segmented into more specific objectives. The objectives of the study are:

- To update and simulate runoff data for the catchments surrounding Lake St Lucia from 1972.
- To construct a water and salt budget model for the St Lucia system that can be used to assess different mouth management options.

- To analyse the occurrence and persistence of water levels and salinities for the different mouth management scenarios.
- To characterise the overall biological structure and functioning using a set of normalised ecosystem indices.
- To assess the biophysical functioning of the St Lucia system by combining the water and salt budget model with the biological responses.

1.6 Research Approach

1.6.1 Water and salt budget modelling

A water balance model, building on previous work by Hutchison and Midgley [1978]; Hutchison & Pitman [1977] was developed and used to simulate the effects of fluctuating wet/dry periods and mouth management strategies. This modelling exercise incorporated recent advances in our understanding of estuary mouth dynamics and was used to critically evaluate the outcomes of the management strategies that have been implemented during the past 60 years. This knowledge was used to investigate and make recommendations concerning future scenarios. The model incorporates various physico-chemical parameters, namely water level and salinity. These parameters, together with the mouth state, inflows and other meteorological factors play a vital role in the biological functioning of this system.

1.6.2 Macroscale biophysical interactions

The St Lucia system is the most researched estuarine system in South Africa, however, little has been done to understand how the system functions as a whole. A qualitative assessment of the biological responses in terms of relative levels of biodiversity and abundance/biomass for various biological components was performed using various data sources. A more detailed quantitative assessment was later performed using data compiled for the St Lucia system during the recent drought. The St. Lucia estuarine system was depicted as networks of quantified trophic flows of which the direction and magnitude were analysed with ecological network analysis (ENA, e.g. Ulanowicz [2004]), using the software WAND [Allesina & Bondavalli, 2004]. The outcomes of these analyses provide a range of indices within which the St. Lucia system operates and demonstrates whether the indices reflect extreme climatic and other hydrodynamic conditions. The indices proposed for this study are indices of Odum [1969], Ulanowicz [2004] and Jørgensen and Fath [2004]. These all describe ecosystem functioning. These methods and findings coupled with the water balance model will contribute to providing an original management tool that will help decision makers gain a holistic understanding of the system and therefore be able to make management decisions based on all components of the system.

1.7 Technical and Scientific Contributions

The main technical and scientific contributions in this thesis are outlined below:

A water and salt budget of the St Lucia estuarine-lake system is presented and used to simulate various management scenarios. This management tool and findings have been used by management (EKZN-Wildlife and the iSimangaliso Wetland Park Authority) to simulate the effectiveness of different mitigation measures. The work is a new contribution, published in Lawrie & Stretch [2011a] and Lawrie & Stretch [2011b] and discussed in detail in Chapters 4 and 5 of the thesis.

1.8 Structure of the Thesis

This thesis begins with a literature review followed by seven chapters. Some of these chapters are reproductions of papers and are in their original form and are explicitly linked. A summary of all the key findings are given in Chapter 8. The following chapters included in this thesis are outlined as follows:

Chapter 2 presents a review of literature concerning the main subject areas.

Chapter 3 provides information about the case study, the St Lucia estuarine-lake system. It gives a brief overview of past anthropogenic impacts and management practices as well as a summary of the available research relevant to this study.

Chapter 4 includes the development of a model for the water and salt budgets of the St Lucia estuarine-lake system and includes the results of the long-term simulations used to evaluate past anthropogenic interventions.

Chapter 5 uses the long-term simulations of the water and salt budget to estimate the occurrence and persistence of water levels and salinities for different management scenarios. These modeled scenarios were integrated with observed biological responses to changes in salinity and water depth.

Chapter 6 presents the results of ecosystem network analysis of Lake St Lucia over the current dry period.

Chapter 7 discusses methods towards the development of a biophysical model of the St Lucia system.

Chapter 8 summarises the key results of the previous chapters and provides recommendations for future research in this field.

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Chapter 2

Literature Review

2.1 Environmental Sustainability of Estuaries

The realisation that environmental sources and sinks are finite has placed major emphasis on the need for environmental sustainability [Goodland, 1995]. Environmental change is inevitable; however, growing populations and infrastructure have placed significant pressure on natural resources. Throughout history, estuaries have attracted various human activities and stimulated development due to their abundant resources and economic value. Estuaries are transition areas between rivers and the sea and vary considerably in terms of geomorphology, hydrography, sedimentology, chemistry and foodweb dynamics. Physico-chemical conditions, such as salinities, temperature and turbidity fluctuate continuously creating a highly dynamic environment within which few species are able to adapt.

Estuaries are one of the most biologically productive ecosystems together with coral reefs and mangrove swamps [McLusky and Elliot, 2004]. They provide an array of ecosystem services including serving as nursery or refugia areas for euryhaline fish and invertebrates, providing feeding areas for migratory birds [McLusky and Elliot, 2004] and the provision of nutrients, detritus and sediment to the coastal environment [Van Niekerk & Turpie, 2012]. They are one of the most important coastal environments, but are also amongst the most severely impacted and exploited habitats on Earth [Kennish, 2002].

Anthropogenic impacts have severely compromised the ecological integrity of these systems placing them under significant pressure. McLusky and Elliot [2004] divided the key human impacts on estuaries into inputs and outputs. These inputs range from chemical contaminants to wastewater discharges to the development of harbours and bridges. Outputs comprise the removal of an available resource such as sand winning, freshwater diversions and fisheries exploitation. These anthropogenic perturbations are driven by economic and social pressures and affect the natural functioning of these systems thereby contributing to habitat modification and causing changes to the biodiversity and abundance of species. In addition, these impacts are expected to escalate with current growth projections unless appropriate mitigation measures are established to reduce them [Baird, 2005].

The ecological health of estuarine systems depends on the preservation, restoration and management of these systems, however, attempts to satisfy these requirements have not always been successful due to socio-economic constraints, the lack of policies and low-cost technologies, the belief that environmental degradation is inevitable and the failure to incorporate the whole river catchment in coastal management planning [Wolanski *et al.*, 2004]. The corollary to environmental sustainability is the need for ecosystem based management and restoration based on a sound understanding of these complex systems [Goodland, 1995; Lotze *et al.*, 2006]. In most cases the long-term sustainability of these important resources requires immediate corrective action to improve the health of these systems. In agreement with the old adage that "prevention is better than cure" Scheffer *et al.* [2001] states that in order to avoid catastrophic shifts in ecosystems, emphasis should be placed on maintaining the resilience of a system rather than controlling disturbances.

Ecosystem-based management and restoration efforts should be focussed on a desired endpoint and based on a thorough understanding of the biophysical functioning of that system. The overall objective is evidently a healthy and sustainable ecosystem, both of which are complex to define and measure [Constanza & Mageau, 1999; Mageau *et al.*, 1995]. Constanza & Mageau [1999] suggested that a healthy system is essentially a sustainable one i.e. "has the ability to maintain its structure and function over time in the face of external stress".

Estuarine habitats are not merely a combination of characteristics from the land and sea but comprise distinctive physical, chemical and biological features. Physical conditions in estuaries fluctuate extensively and as a consequence estuarine animals are subjected to severe physiological stress. Estuaries are characterised by relatively low diversity but high population abundance and estuarine species are generally able to tolerate variable physico-chemical conditions, but fluctuating and extreme salinities, turbidities and temperatures can diminish species diversity. In addition the tolerance of a species to salinity for example, may vary at different temperatures and/or at different stages of its lifecycle [McLusky and Elliot, 2004; Whitfield *et al.*, 2006]. Physico-chemical changes can also have a significant impact on food resources and availability [Whitfield *et al.*, 2006].

2.2 Tools for Evaluating Ecological Health and Integrity

Borja *et al.* [2008] state that the challenge for scientists is to develop simple and practical but scientifically sound techniques and tools that can be used by stakeholders, and in particular decision-makers, to define and monitor the health of these ecosystems. This includes, among others, a multidisciplinary approach, the integration of abiotic and biotic factors and methods for determining the ecological integrity and extent of potential human impacts. In addition Wolanski *et al.* [2004] suggests that ecohydrology principles should be adopted to guide management of the entire river basin, from upstream waters to the coastal zone. Borja *et al.* [2008] provide a global review of the present situation of integrative ecological assessment. Currently legislation exists in North America, Asia, Africa, Australia and Europe to address the ecological integrity and quality of estuarine and coastal systems with the intention of defining their status in an integrative manner. This legislation is, however, often based on studies carried out in single systems and therefore does not allow for generalisation.

There have been numerous advances in developing tools for assessing the different physico-chemical and biological elements in estuarine ecosystems, yet these methods often fail to evaluate an ecosystem as a whole entity. An integrative approach is vital for the long-term success of ecosystem-based management and restoration efforts due to the high level of complexity of these systems [Baird, 2005; Borja *et al.*, 2008; Naeem *et al.*, 2012]. For example, there can be significant shifts in the estuarine ecosystem as a result of changing fresh water inflows and salinity regimes [Wolanski *et al.*, 2004]. The dependence of food webs on hydrologic and human-induced changes therefore requires careful consideration in estuarine management.

2.2.1 Ecological indicators

Niemi and McDonald [2004] defined ecological indicators as quantifiable characteristics of the structure, composition or function of ecosystems. Ecological indicators have several purposes e.g. to assess the state of an ecosystem, to identify changes and/or trends, to diagnose the cause of an ecological problem, to establish possible remedial actions and to forecast future changes in an ecosystem [Dale & Beyeler, 2001; Niemi and McDonald, 2004]. Niemi and McDonald [2004] state that the primary role of ecological indicators is to monitor the ecosystem response to anthropogenic impacts. A good ecological indicator has the ability to describe numerous environmental factors by using a single value that is useful to both management and the public [Borja *et al.*, 2008]. Dale & Beyeler [2001] describe the importance of characterising ecological systems using a suite of indices in order to avoid oversimplification.

The Comprehensive Everglades Restoration Plan (CERP) in the United States is based on the use of conceptual ecological models. Ogden *et al.* [2005] describe conceptual ecological models as ”non-quantitative planning tools used to identify major anthropogenic drivers and stressors on natural systems, the ecological effects of these stressors, and the best biological attributes or indicators of these ecological responses”. Ecological indicators are often centered around indicator species and are based on the belief that a singles species is representative of other species with similar ecological requirements in addition to the overall ecological state [Niemi and McDonald, 2004]. Indicator species that respond to anthropogenic drivers and stresses are often identified and used in ecosystem modelling approaches (e.g. Barnes [2005]; Doering *et al.* [2002]; Whitfield & Elliot [2002];

Morrison [1986]; Ogden *et al.* [2005]; Schaeffer *et al.* [1985]). The use of indicator species is a contentious issue, nevertheless, there are a number of circumstances in which they can be useful [Carignan & Villard, 2002]. Alber [2002] highlights the importance of linking chosen ecological indicators to resources that are valued by society and providing this information to all stakeholders.

Ecosystem indicators are often focussed on ecosystem structural properties and fail to provide information about ecosystem functioning. Species-to-species interactions may, however, provide pertinent information about the ecological health or status of an ecosystem and therefore more comprehensive approaches should be adopted [Borja *et al.*, 2008]. Mageau *et al.* [1995] and Constanza & Mageau [1999] suggested that the sustainability or health of systems may be measured by quantifying three ecosystem characteristics, namely organisation, vigour and resilience. The organisation of a system refers to the diversity of trophic flows in an ecosystem (the structure), vigour describes the activity (the function) and resilience denotes the ability of a system to maintain its structure and function over periods of external stress.

Ecosystem Network Analysis (ENA) is a methodology from which a set of network indices can be derived that describes both ecosystem structure and functioning [Kay *et al.*, 1989; Ulanowicz, 2004; Wulff *et al.*, 1989]. A network flow model aims to include all ecological components and interactions as weighted links (who eats whom and at what rate) while the analysis provides information about the overall relationships and aspects of ecosystem functioning such as ecosystem resilience and stability [Fath *et al.*, 2007; Ulanowicz, 2004]. ENA has been performed on a number of systems around the world to describe ecosystem structure and functioning (e.g. Baird & Ulanowicz [1989]; Heymans & Baird [2000]; Leguerrier *et al.* [2007]; Rybarczyk & Elkaim [2003]; Scharler & Baird [2005]; Wolff *et al.* [2000]), to compare ecosystems [Baird *et al.*, 1991; Baird & Ulanowicz, 1993; Monaco & Ulanowicz, 1997] and to investigate mitigation measures [Chen *et al.*, 2010].

The need for ecosystem analysis has led to the development of numerous algorithms such as NETWRK [Ulanowicz & Kay, 1991], ECOPATH [Christensen and Pauly, 1992], Network Environ Analysis [Fath and Patten, 1999; Fath and Borrett, 2006], WAND [Allesina & Bondavalli, 2004], and MATLOD or MATBLD

Table 2.1: Four types of ecosystem network analysis and examples of the indices that they produce.

1. Total/Whole System Indices: define indices characteristic of the size and development of the ecosystem. [Ulanowicz, 1986, 2004; Ulanowicz & Kemp, 1979] *Total system throughput*(TST) - sum of all flows occurring in a system & is a measure of the size and activity of a system. *Development capacity* (DC) - reflects the systems potential to develop and is the product of TST and H. *Ascendency* (A) - describes size, growth and development. It is the product of TST and AMI. *Redundancy* (R) - provides a measure of parallel pathways *Average Mutual Information* (AMI) - avg constraint met by a measure of energy as it flows from a compartment to another. *Flow Diversity* (H) - measure of abundance & evenness of flows. Reflects the total uncertainty & complexity of an ecosystem.
2. Inputoutput analysis: quantifies the direct and indirect relationships between compartments. [Finn, 1980; Hannon, 1973; Szyrmer & Ulanowicz, 1987] *Partial Host* - shows where nutrients entering every compartment originated from. *Partial Feeding* - reflects the fate of nutrients that exit every compartment. *Total contribution coefficient* - gives percentage of total flow over all pathways that passes from compartments i to j. *Total dependency coefficient* - gives percentage of total amount ingested by j that passed through compartment i on its way.
3. Biogeochemical cycle analysis: evaluates the characteristics of cycles within the system. [Finn, 1976; Ulanowicz, 1986] *Cycles Count* - gives the number of cycles in the ecosystem. *Finn Cycling Index* (FCI) - gives the amount of flow that is recycled in the system. *Average path length* - shows avg number of links in a cycle i.e. number of steps taken to get from a compartment to another.
4. Lindeman trophic analysis: provides information based on the trophic concepts of Lindeman [1942] [Ulanowicz & Kemp, 1979] *Effective trophic level* - fractional value of a compartments trophic level that takes into account degrees of omnivory. *Trophic efficiency* - reflects the proportion of energy that enters a trophic level and is transferred to the next. *Herbivory:detritivory ratio* - quantifies the ratio of the flow along herbivorous and detrital food webs.

[Ulanowicz & Scharler, 2008]. These algorithms have the ability to automatically balance networks and/or calculate indices. Network analysis generally comprises numerous types of analyses, e.g. input-output analysis, trophic analysis, biogeochemical cycle analysis and the analysis of total/whole system level indices (e.g. Kay *et al.* [1989]; Ulanowicz [2004]). A few examples of the indices that these analyses produce are given in Table 2.1.

2.3 Ecosystem Response Modelling

Simulating and/or predicting the consequence of a given change is a vital tool for investigating the sustainability and restoration of ecosystems. Ecosystem response modelling is used to predict the impacts of management actions on a natural environment [Marsh & Cuddy, 2010]. Selecting an appropriate model or combination of models to represent an ecosystem depends on the desired outcomes of the modelling exercise. Stakeholders may, however, have varying requirements of the model i.e. a manager is more likely to be concerned about the ability of the model to predict different scenarios while a scientist would be more interested in processes. An important outcome of ecosystem modelling is to provide an understanding of how the system behaves as this is imperative for making informed management decisions [Jakeman *et al.*, 2006].

Sutherland [2006] provides a review of possible methods that can be used for making predictions of the ecological consequences of environmental change. These include (1) extrapolation which is simple and requires little data but does not consider changing conditions, (2) experimentation provides valuable information of the actual response and reveals unexpected interactions, however large-scale and long-term experiments are often slow, expensive and difficult to replicate and (3) phenomenological models that are based on empirically derived functions have been described as the backbone of ecology, even though their conclusions are mainly predictive. (4) Game-theory models can consider responses to novel conditions, (5) expert opinion e.g. in the form of rule based models or decision trees, can be used when there is no other information, however, there is no assurance that opinion has not been confused with knowledge, (6) outcome-driven modelling can be used for complex problems with limited outcomes and (7) scenarios are useful for exploring the best responses in complex environments and assessing decisions against possible alterations, however, they are subjective and cannot be easily applied to other systems.

It is often thought that complex models provide a more accurate and thorough representation of a system, but they are not necessarily the most effective [Jørgensen and Fath, 2004; Soetaert and Herman, 2009]. Soetaert and Herman [2009] state that "the largest intellectual challenge of modelling consists in the creative simplification of a scientific problem, in such a way that no great injustice is done to realism". The formulation of a model and its complexity depends predominantly on its intended use as the main objectives could get lost in additional and irrelevant details. The complexity is also determined by how much is known about the model i.e. the availability of data as well as the time available for the modelling exercise. It is also important to consider that more complex models can have a higher risk of uncertainty as they contain additional parameters [Jørgensen and Fath, 2004; Robinson, 2008; Stow *et al.*, 2003].

Simulation modelling requires an understanding of the system to be modelled and is essentially a simplification of the real world. Conceptual modelling is an important aspect of simulation modelling [Robinson, 2008, 2011]. It defines the different parameters (state/dynamic variables) of the problem and determines the correct relationships (flows/interactions) between them. Conceptual models provide a means of communication between the modeller, the experts, the clients and stakeholders and form the basis for quantitative modelling (e.g. Alber [2002]; Davis *et al.* [2005]; Rudnick *et al.* [2005]). These models can identify the requirements and can guide experimentation.

In terms of management and ecosystem modelling Zalewski [2002] and Wolanski *et al.* [2004] describe the importance of adopting Ecohydrology principles. The Ecohydrology concept was developed within the framework of the UNESCO International Hydrological Programme IHP-V [Zalewski *et al.*, 1997] and aims to integrate social, ecological and hydrological research to assist ecosystem managers [Zalewski, 2002]. The ecohydrology concept views the whole river basin as an ecosystem and acknowledges that ecosystem health requires a combination of physical and biological interventions to increase the resilience of a system to anthropogenic impacts. Wolanski *et al.* [2004] state that because changes in fresh water inflows and salinity regimes cause shifts in ecosystems, it is imperative for decision-makers to consider the impacts that natural physical processes and human-induced changes have on foodwebs. For example, alterations to fresh water inflows, eutrophication, habitat alterations, pollution, overfishing, increased turbidity and climate change. These factors can have a significant impact on the overall health of estuaries in terms of species diversity, abundance and productivity [Wolanski *et al.*, 2006].

2.3.1 Case studies: the implementation of integrative modelling techniques in estuarine systems

There have been numerous approaches to modelling ecosystem responses to environmental change ranging from simple qualitative methods to complex dynamic models. With the increase in the degradation of ecosystems due to anthropogenic impacts and uninformed management actions, models have become an important tool for understanding ecosystems and for seeking alternative ameliorative measures. A number of case studies will be discussed in this section to highlight some of the different approaches that have been used and in a few instances implemented.

The Everglades System, USA: The Everglades system is home to a rich array of fauna and flora including 68 species of special conservation concern, however, it has been drastically altered by anthropogenic impacts (e.g. Brown *et al.* [2006]). The Comprehensive Everglades Restoration Plan (CERP) aims to restore, protect and preserve certain areas of Florida including the Everglades. Crigger *et al.* [2005]; Davis *et al.* [2005]; Ogden *et al.* [2005] etc. focussed on different parts of the Florida ecosystem and used conceptual ecological models to define the ecosystem characteristics that have been altered by external drivers. Major working hypotheses of cause-and-effect relationships were defined for each of the chosen parameters. Ecological indicators were used for each defining characteristic to identify and monitor the status of the system.

Lake Ontario and St. Lawrence River system, North America: Indicators are a time- and cost-effective method to assess the impacts of environmental and ecological change on the state of a system. An indicator reflects the fundamental condition of the environment and generally portrays meaning beyond its measure [Whitfield & Elliot, 2002]. Desgranges *et al.* [2006] used an integrative ecosystem approach to evaluate potential impacts of water level fluctuations on selected indicator species of wetland birds in the Lake Ontario and St. Lawrence River system. Strong associations were found between and/or within a number of physical and biological parameters and were used to develop wetland bird performance indicators for use in a water review study of the system. They found that water regulations that influence the seasonal magnitude and frequency of water levels may have adverse effects on breeding bird populations. Many other biological groups have been used as indicators of the environmental state of ecological systems; for example Dennison *et al.* [1993] used submerged aquatic vegetation, McCormick and Cairns [1994] used algae, Fausch *et al.* [1990] and Whitfield & Elliot [2002] used fish while Morrison [1986] also used birds.

The Guadiana Estuary, South Portugal: Wolanski *et al.* [2006] developed an 1-dimensional ecohydrology model of the Guadiana Estuary to investigate the impacts of future anthropogenic changes and the effectiveness of possible mitigation measures. The Guadiana Estuary acts as a sink to various pollution sources and freshwater inflows are regulated by over 100 dams including the Alqueva Dam (Europe's largest reservoir). The model predicts the ecosystem health using a number of variables and integrates physical, biological and chemical processes in the system. It incorporates an ecological sub-model which is based on the Lotka-Volterra equation. Wolanski *et al.* [2006] found that the system requires remedial measures as ecosystem health depends on transient river floods and is adversely affected by flow regulation caused by the Alqueva dam.

Neuse River Estuary, USA: Stow *et al.* [2003] compared the important features of three different estuarine nutrient response models that were developed to inform the total maximum daily limit in the Neuse River Estuary. These models include a two-dimensional laterally averaged model [Bowen and Hieronymus, 2003], a three-dimensional hydrodynamic and water quality model [Borsuk *et al.*, 2003] and a Bayesian probability network model [Wool *et al.*, 2003]. Stow *et al.* [2003] found that accurate prediction is challenging even in a well-studied, data-rich system and that the predictive accuracy of the spatially detailed models were no better than the probabilistic model. They suggested adapting the concept of adaptive management which involves "learning by doing".

The Chilika Lake, India: The Chilika Lake has experienced a significant revival of its ecosystem after good management practices were introduced in 2000. In 1993 the lake was placed on the Montreux Record after the accumulation of sediment entering the lagoon from surrounding catchments caused the gradual narrowing of the mouth and a subsequent decrease in its salinity regime. As a result the surface area and depth of the lake decreased, the areal cover of freshwater macrophytes increased and biodiversity and fish catches declined. In 2000 operations began to restore the flow regime. This resulted in a dramatic improvement in lake salinities and the subsequent increase in fish catches, the recruitment in marine species, improved biodiversity and the reduction in weed coverage [Ghosh *et al.*, 2006]. Although challenges remain, the Chilika Lake provides an example of how the application of informed intervention measures based on scientific and technological methods can help to restore these system [Ghosh *et al.*, 2006; Mohanty*et al.*, 2009]. In terms of modelling of the system, Dube and Jayaraman [2008] developed a three-compartment (nutrients, phytoplankton and zooplankton) ecological model to explain the seasonal variability of plankton while Jayaraman *et al.* [2007] developed a a two-dimensional depth-averaged hydrodynamic model. Dube and Jayaraman [2008] suggested incorporating these two models to provide a complete and holistic understanding of the system. In more recent studies Panda *et al.* [2013] developed a numerical model to simulate hydrodynamic and salinity conditions for single and multiple inlets.

The Coorong Estuary, Australia: The Coorong Estuary is a long, shallow estuarine system which until the 1930s was connected to two freshwater lakes, Lakes Alexandrina and Lake Albert. A series of barrages were constructed between 1935 and 1940 to prevent the intrusion of saline water up the River Murray. The Coorong has recently experienced high salinities and variable water levels as a result of severe drought conditions which have been exacerbated by water resource development and past management of the Murray-Darling Basin [Webster, 2010]. This has had a significant impact on the biotic diversity of the system [Lester *et al.*, 2009]. With the recent knowledge gained and the development of a hydrodynamic and ecosystem response model of the system, a series of interventions have been proposed to alleviate the present stressed condition

[Lester & Fairweather, 2009; Webster, 2010; Lester *et al.*, 2009]. The ecosystem response model was constructed using a state-and-transition framework model. The states were defined by the biota and the transitions by classification and regression tree (CART) analysis of the environmental data of the area [Lester & Fairweather, 2009]. Webster [2010] incorporated the conceptual understanding of the physical dynamics of the system into a hydrodynamic model to investigate possible ameliorative measures.

Numerous ecosystem response modelling techniques have been applied to estuarine systems worldwide, however, these methodologies are often system specific or require large data sets. The St Lucia estuarine-lake in South Africa has experienced significant anthropogenic impacts over the last century and its sustainability relies on the implementation of informed management decisions. St Lucia has received considerable research attention over the past sixty years, but there has been insufficient progress made in terms of understanding its biophysical functioning. In addition, little is known about how the system behaved before human intervention. None of the ecosystem response models discussed here have been applied to this system, the only attempt was an incomplete rule-based model developed by Taylor [1987] and Starfield *et al.* [1989]. A brief overview of past anthropogenic impacts and a summary of the available research relevant to this study are provided in Chapter 3.

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Chapter 3

Case Study

3.1 Introduction

The St Lucia estuarine-lake in South Africa forms part of a UNESCO World Heritage Site and it is a Ramsar Site of importance. Despite this, the system has experienced significant anthropogenic impacts over the last century including freshwater reductions, the separation of the Mfolozi River from the St Lucia system and the subsequent manipulation of the mouth. As a result the current dry period has had severe repercussions on the health of the system including severe desiccation, hypersaline conditions and a subsequent loss in biodiversity. The system has received much research attention over the past sixty years, but there has been insufficient progress made in terms of understanding the biophysical functioning of the system and little is known about how the system behaved before human intervention. This chapter aims to highlight all the research and knowledge gained over the past sixty years to be later used in the development of a biophysical model of the system.

3.2 The St Lucia Estuarine Lake

The St Lucia estuarine lake is situated within the iSimangaliso Wetland Park on the north-east coast of South Africa and is located between $2742' - 2824'$ S, and $3221' - 3234'$ E. The lake spans about 328 km^2 at an average depth of only

1 m [Hutchison & Pitman, 1977]. The mean annual rainfall and evaporation at St Lucia is about 890 mm and 1470 mm respectively [Hutchison & Pitman, 1977]. This together with the high surface area to depth ratio makes the system vulnerable to freshwater losses, especially during drought conditions.

The lake is fed by several freshwater sources namely the Nyalasi, Mpate, Mzinene, Hluhluwe and Mkuze rivers as well as groundwater seepage from the eastern shores (refer Figure 3.1). The Mfolozi River, once a major contributor of freshwater was diverted from the system in the 1950s. The total supply of freshwater to the lake is estimated to be about 600 Mm^3 per annum, and the total loss due to evaporation about 450 Mm^3 [Hutchison, 1976]. Note that these values vary significantly depending on erratic wet and dry cycles. Episodic floods contribute an immense quantity of fresh water, most of which is lost to the sea when the mouth opens. These floods act to periodically reset the system by flushing out salt and accumulated sediments. Hutchison & Pitman [1977] estimated that fresh water inflows had decreased by about 20 % due to abstractions, afforestation and dams. Almost forty years later, the losses are certainly higher following continued changes in land use and development.

3.2.1 A brief history of human intervention

The Mfolozi floodplain and swamps were extensively altered in the early 1910s in order to ensure efficacious sugarcane farming. The Mfolozi swamps were drained and canals were excavated to divert floodwater away from the floodplain. Whitfield & Taylor [2009] state that before these alterations the Mfolozi swamps behaved as a filter thereby reducing the sediment load of the Mfolozi River. Shortly after the excavation of the main canal, Warner's Drain, sedimentation became particularly noticeable at the mouth.

It is widely believed that the extensive accumulation of sediments at the mouth by the early 1950s was caused by alterations to the floodplain which in turn increased silt loadings in the Mfolozi [Taylor, 2006]. It should be noted that the area experienced a prolonged drought starting in the mid 40s (one of the longest on record) which persisted until floods in 1956. In 1952 a separate Mfolozi mouth was dredged open to address the siltation issue and to protect sugarcane farms

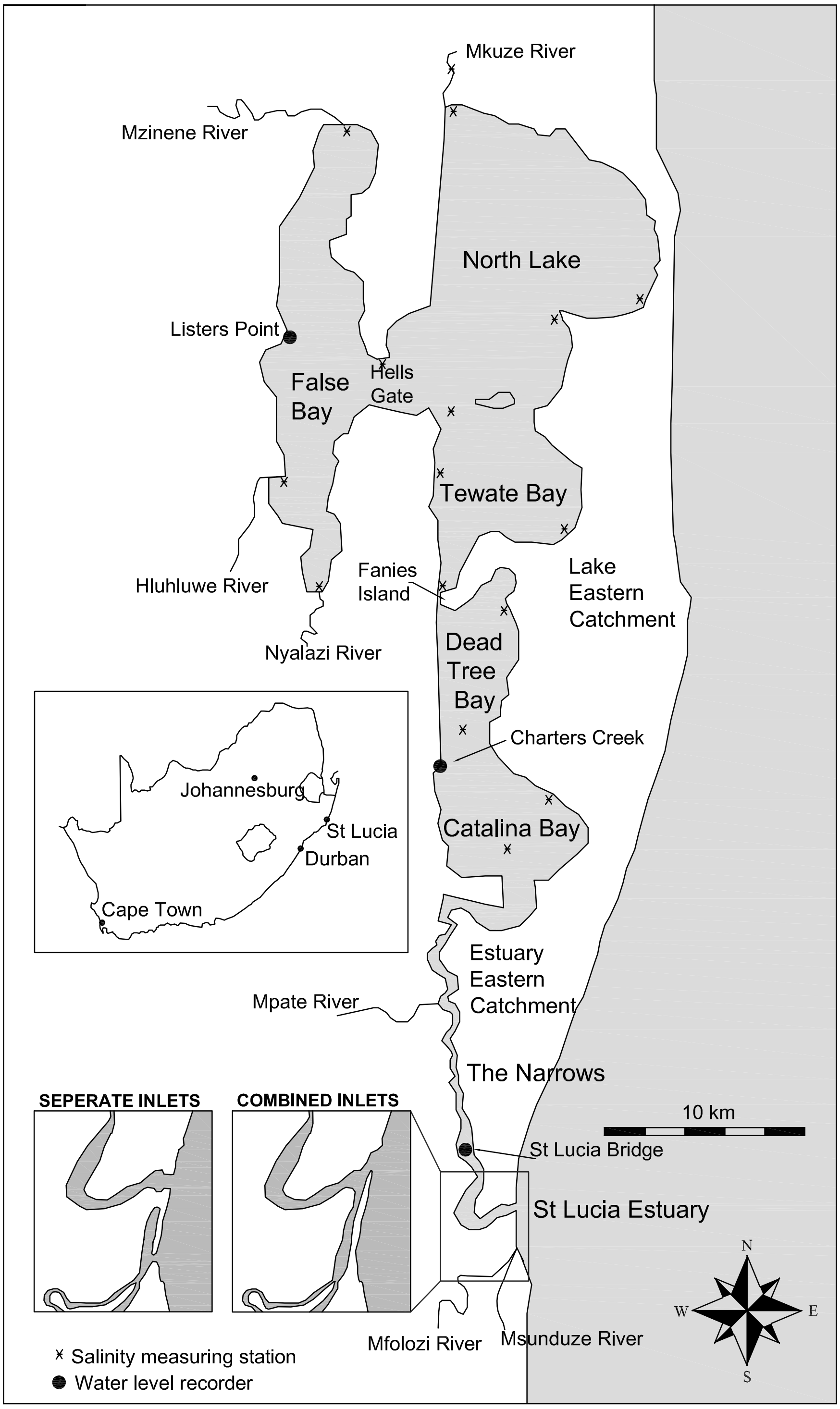


Figure 3.1: Location map for St Lucia on the east coast of South Africa. Also shown are the different mouth configurations i.e. with separate and combined Mfolozi/St Lucia inlets and also the positions of the salinity and water level measurement stations.

in the Mfolozi floodplain from flooding [Whitfield & Taylor, 2009]. With a mean annual runoff of more than 700 Mm^3, the Mfolozi was a major contributor of fresh water to the system. Note that while there appears to be a widely held perception that Mfolozi silts have been deposited into the main St Lucia lake basin there is no scientific evidence yet linking the two.

After 1952, the management strategy was, and still is, to keep the two mouths separate. This requires constant attention as the Mfolozi mouth has a tendency to migrate towards the St Lucia Estuary at a rate of about 2 m per day [Whitfield & Taylor, 2009]. Management actions were also directed at maintaining a sea-estuary link and the St Lucia mouth was kept open. In the 1970s extensive dredging operations took place in the Narrows to increase flows. The perception seems to have been that the removal of accumulated sediment from the Narrows would cause the St Lucia mouth to stay mostly open. A sand trap was also constructed at the estuary mouth to inhibit marine sediments from closing the mouth. The management strategy of maintaining an open mouth was changed in 2002 and the mouth was allowed to close in July 2002.

In the past, when St Lucia formed a combined mouth with the Mfolozi, a narrow north extending spit developed from the Maphelane bluff due to the prevailing littoral transport patterns. An aerial photograph of the combined Mfolozi and St Lucia mouth taken in the 1930s is shown in Figure 3.2. Note the constricted mouth with a well-developed flood delta. Large floods in the Mfolozi would generally destroy this spit and the Mfolozi would discharge out to sea. Littoral transport would then re-build the spit and the mouths would recombine. When the combined mouth was closed, fresh water from the Mfolozi would have flowed into St Lucia replenishing water lost due to evaporation and thus diluting salinities.

The current dry cycle has had a severe impact on St Lucia. The mouth has remained continuously closed with extreme hypersaline conditions and desiccation developing in the upper reaches of the lake. By May 2003 the surface area of the lake had decreased by 75 % and by July 2006 desiccation occurred in more than 90 % of the lake [Whitfield & Taylor, 2009].

Although the system has been extensively researched in the past, we believe that the re-current management crises, particularly concerning issues of mouth

Figure 3.2: An aerial photograph illustrating the combined St Lucia and Mfolozi mouth in the 1930s (provided by Ricky Taylor, original source unknown).

manipulation and catchment management, indicate a need for further research to develop our understanding of the physical and biological dynamics of this system with the aim of providing improved tools for the ongoing management of this key resource.

3.3 Previous Work at St Lucia

St Lucia is one of the most researched estuarine systems in South Africa [Whitfield & Taylor, 2009] with scientific studies dating back to the 1940s (e.g. Day *et al.* [1954]). Although an extensive amount of scientific research has been conducted at St Lucia most of it has been focused on the biology. The hydrology and physical dynamics of the system has received minimal research attention, the most significant of which has been the work at the Hydrological Research Unit (HRU University of Witwatersrand) reported by Hutchison and Midgley [1978];

Hutchison & Pitman [1977]. As a consequence there has been little effort in trying to understand how the system functions as an holistic entity, although this has been proposed numerous times (e.g. Starfield *et al.* [1989]; Hutchison & Pitman [1977]).

3.3.1 Hydrology and physical dynamics

In the 1970s, the Hydrological Research Unit (HRU University of Witwatersrand) carried out an extensive study on the hydrology and physical dynamics of the system. Hutchison & Pitman [1977] and Hutchison and Midgley [1978] devised mathematical models to simulate the water level and salinity regimes of St Lucia to quantify human impacts and test various ameliorative measures. The model was set-up to use simulated inflows for both virgin and present conditions. Virgin conditions refer to a state prior to significant anthropogenic influence. Present conditions include the effects of abstractions, dams and afforestation. Hutchison & Pitman [1977] suggest that these have led to a roughly 20 % reduction of fresh water inflows into the lake.

Freshwater inputs to the St Lucia Lake system comprise direct rainfall, river inflow mainly from the Mkuze, Hluhluwe, Mzinene and Nyalazi Rivers and groundwater seepage along the Eastern Shores. Flow gauges of the rivers that feed Lake St Lucia were located some distance from the lake and provided relatively limited or incomplete/unreliable data. Hutchison and Pitman [1973] used the rainfall-runoff model developed by Pitman [1973] to simulate monthly inflow from each of the surrounding catchments for the period 1918 to 1971. The morphology of the lake was analysed by Hutchison [1974] based on a bathymetric survey carried out in the 1970s. It should be noted that the HRU modelling did not include any attempt to predict the mouth state of the system: it was simply specified based on available historical observations.

Quibell [1996] found that during normal and wet conditions the freshwater contribution from groundwater seepage is negligible, however, in extremely dry conditions groundwater recharge is a vital resource. Groundwater recharge during dry periods creates micro-habitats which provide refuge sites for biota that do not tolerate high salinities. This is important for the recolonisation of species that are unable to survive adverse conditions through other adaptive methods [Taylor, 2006].

Simulation results showed that human impacts have had an adverse impact on salinities during drought conditions. Results also revealed that the salinity regime is predominantly dependent on the freshwater supply to the system and lake levels are dependent on the geometry of the estuary channel [Hutchison & Pitman, 1977].

3.3.2 Survey datum and bathymetry

The estuary mean sea level (EMSL) was first established by the Department of Water Affairs and then checked by Hutchison [1974]. The Survey Department of the University of Natal established a geodetic mean sea level (GMSL) of -0.446 m at Durban and the S.A. Navy estimated the actual mean sea level (AMSL) at Durban to be 0.20 m above GMSL. The actual mean sea level relative to the St Lucia estuary was therefore -0.25 m. The Hydrological Research Unit (HRU) used the estuary mean sea level datum for all work carried out on the system. The relationship between EMSL, AMSL and GMSL is illustrated in Figure 3.3.

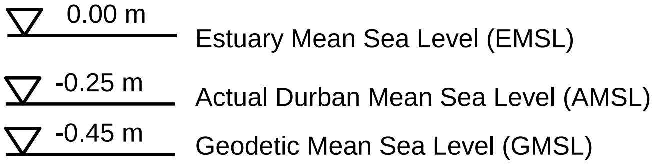


Figure 3.3: Schematic showing the relationship between estuary mean water level and the average mean sea level at Durban.

The lake bathymetry was first surveyed by the Department of Water Affairs in 1965 (see Figure 3.4). Results from this survey were not accurate between the -0.50 m and +0.50 m levels as the shoreline was steeper than the survey had indicated. A few years later (from 1969 until 1973) the Natal Provincial Administration surveyed cross-sections of the southern part of the lake (from Charter's Creek to Mitchell Island) and the estuary [Hutchison, 1976].

Hutchison and Midgley [1978] divided the lake into ten elementary cells and established depth-area and depth-volume curves for each of the cells. During

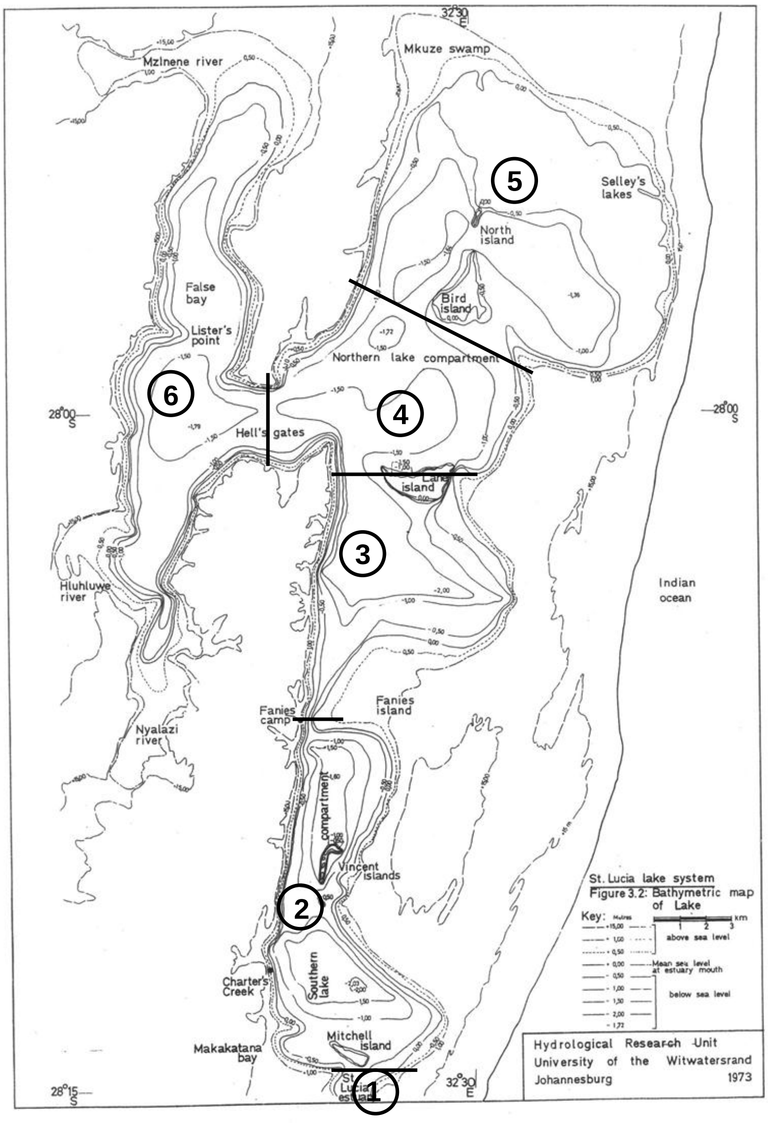


Figure 3.4: Map showing the bathymetry of Lake St Lucia [Hutchison, 1974] including an outline of the six cells used during the development of the water and salt budget model by Hutchison and Midgley [1978].

the development of the water and salt budget models, the number of cells was decreased to six (refer to Figure 3.4) in order to reduce computational effort and data organisation [Hutchison, 1976; Hutchison and Midgley, 1978]. The bathymetry has not been updated since then although significant changes are expected to have occurred.

3.3.3 Lake water levels and salinities

Salinity and water level fluctuations are common features of estuarine environments and the basic drivers for the biological functioning. Water level recorders deployed by the Department of Water Affairs at three different locations in the system (Charters Creek, Listers Point and at the St Lucia Bridge) provide measurements from 1960 (see Figure 3.5). Data show that the water level fluctuated depending on wet and dry conditions but remained at about the EMWL from 1960 until 2002 when the mouth was open. After the mouth was left to close in 2002, there was a gradual decrease in water levels (refer Figure 3.5) with the division of the system into several isolated compartments. This inhibited the movement of species within the lake and during 2003 and 2004 and a minimum of eight fish kills were recorded in the northern parts of the lake [Whitfield *et al.*, 2006].

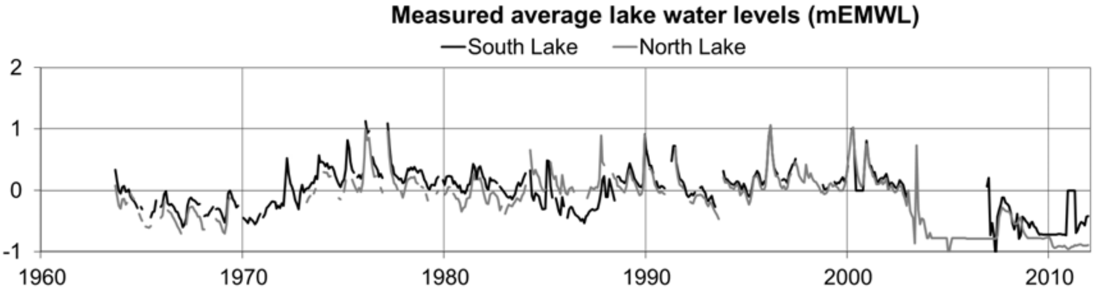


Figure 3.5: Measured monthly water levels in South and North Lake (provided by the Department of Water Affairs).

Average salinities of North Lake, False Bay and South Lake have been measured by EKZN Wildlife since 1958 and are shown in Figure 3.6. The dashed line represents the salinity of sea water (35) and the shaded area represents closed mouth conditions. Lake salinities vary spatially, the salinity gradient between the northern and southern parts of the lake are also shown in Figure 3.6. Note that a positive gradient indicates increasing salinities from South to North and vice versa. During drought periods hypersaline conditions are associated with a significant increase in the salinity gradient. During wet periods there is typically a negative salinity gradient (up to about 24). When conditions become intolerable, species are able to migrate to other sections of the lake where the biota can find refuge in area with lower salinities.

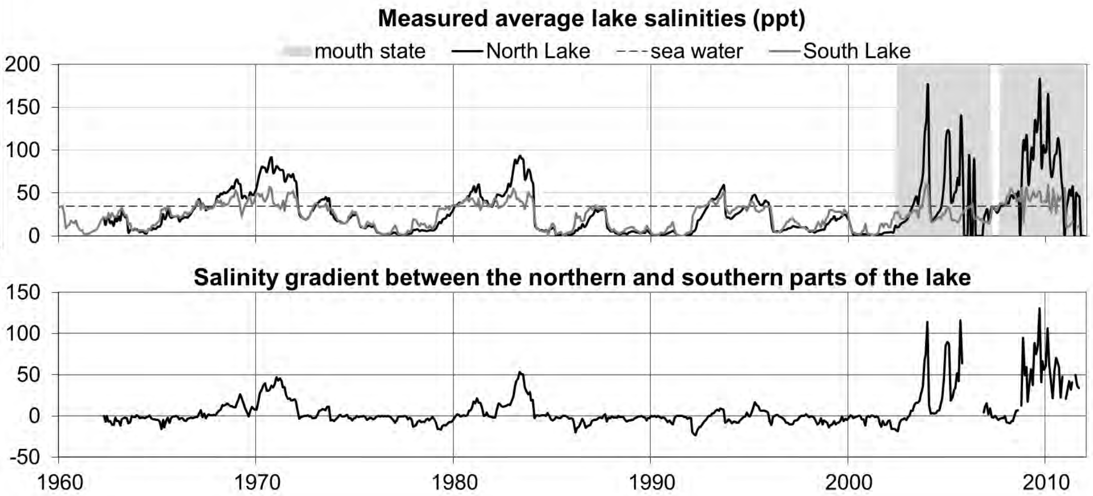


Figure 3.6: Measured monthly lake salinity with the salinity gradient between the northern and southern parts of the lake (provided by EKZN-Wildlife).

The salinity tolerance varies considerably between different species. Whitfield *et al.* [2006] documented the recorded salinity tolerances of the different fish species found in the St Lucia system. The Mozambique tilapia (*Oreochromis mossambicus*) was found to have the largest tolerance range and was most common under all salinity regimes. High salinities not only affect the osmoregulatory abilities of species but also impact the food resources. The main primary producers in St Lucia, namely phytoplankton, microphytobenthos and submerged macrophytes are all affected by the salinity regime of the system. However, [Whitfield *et al.*, 2006] found that microphytobenthos and detritus food chains were the least affected by increasing salinities. Studies have shown that mysids and macrozoobenthos are severely affected by hypersaline conditions [Carrasco and Perissinotto, 2011; MacKay *et al.*, 2010; Whitfield *et al.*, 2006]

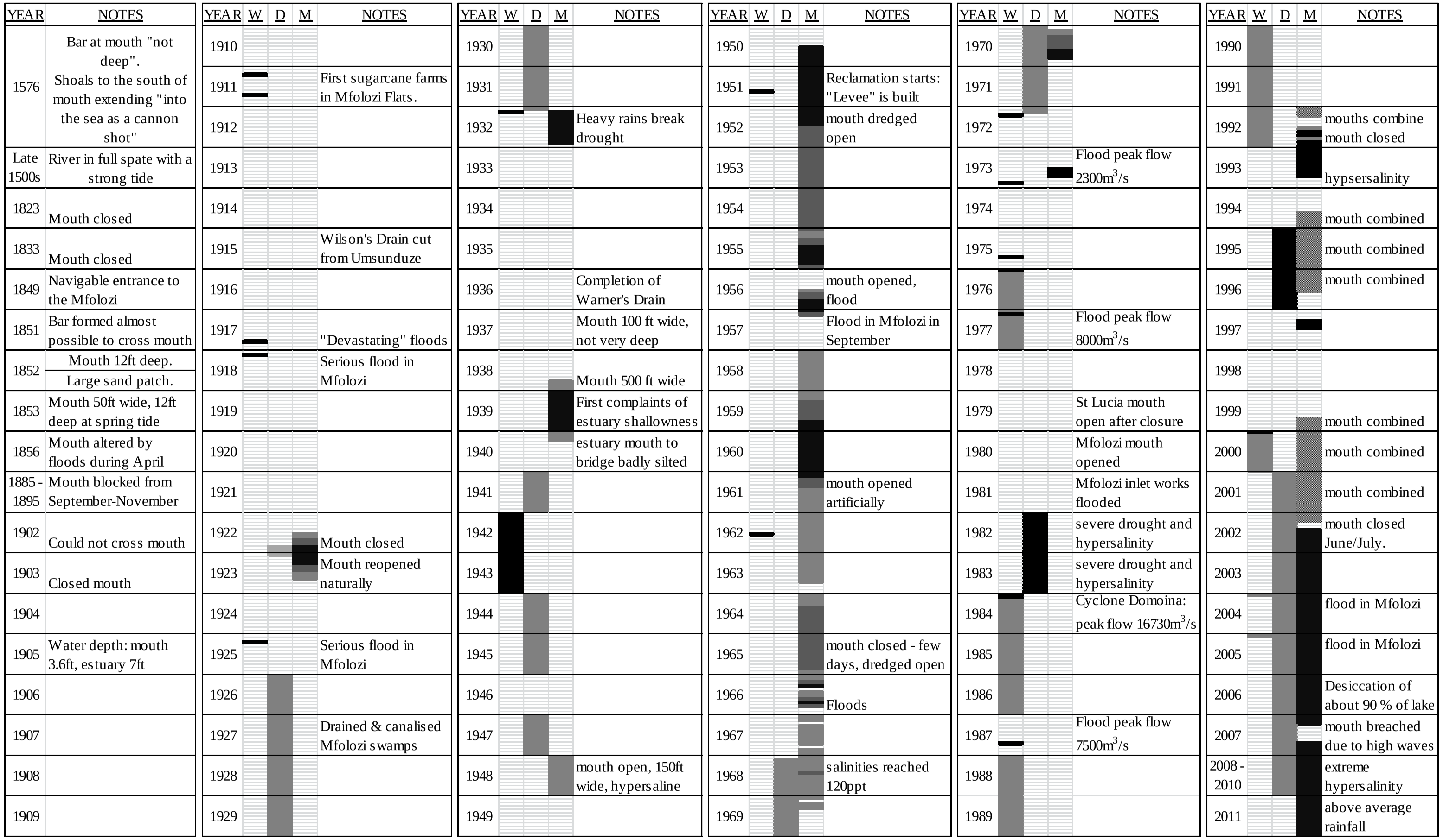
3.3.4 Sediment dynamics and turbidity at St Lucia

Grenfell and Ellery [2009] estimated the mean annual sediment load of the Mfolozi River to be 61 tons.km^2.yr^{-1} (about 600 000 tons.yr^{-1}), however, seasonal and annual variability in the load may occur. Stretch *et al.* [2013] used direct turbidity measurements to estimate the monthly distribution of suspended sediment yields and found that the sediment yield was highest in the wet season. In addition higher yields occurred at the start of the rainy season indicating that yields are limited by the sediment supply. Suspended sediment in the lower parts of the Mfolozi are composed mainly of silt [Grenfell *et al.*, 2009]. In the past sediment carried by the Mfolozi River was filtered out as it flowed through the Mfolozi swamps, however the natural sediment trapping function of the Mfolozi swamps was compromised when the swamps were drained and canalised.

The separation of St Lucia from the Mfolozi River was implemented to address the perceived threat of sedimentation due to the high silt loads carried by the Mfolozi. The sedimentation issue has been used to justify the artificial separation of the two systems since 1940 [Cyrus and Blaber, 1988; Grenfell and Ellery, 2009; Cyrus *et al.*, 2010; Day *et al.*, 1954; Taylor, 2006; Whitfield & Taylor, 2009], however, there remains no scientific evidence to substantiate this decision or quantify the impacts.

3.3.5 Mitigation measures

Possible mitigation measures have been investigated from the time the Mfolozi was diverted in the early 1950s [Blok, 1976]. Emphasis was initially placed on the siltation problem in the St Lucia Estuary and lower Mfolozi River but later shifted to possible ameliorative measures aimed at reducing lake salinities during drought conditions e.g. during 1965 to 1971. A time history of important events at St Lucia/Mfolozi have been summarised in Table 3.1. The shading depicts the intensity of the wet/dry period or how constricted the mouth was i.e. from fully open (white) to constricted (grey) to fully closed (black). Note that the hatching in the "M" column indicates that the mouths were temporarily combined. It has already been stated the mouths were previously combined but were separated in 1952.



YEAR	NOTES
1576	Bar at mouth "not deep". Shoals to the south of mouth extending "into the sea as a cannon shot"
Late 1500s	River in full spate with a strong tide
1823	Mouth closed
1833	Mouth closed
1849	Navigable entrance to the Mfolozi
1851	Bar formed almost possible to cross mouth
1852	Mouth 12ft deep. Large sand patch.
1853	Mouth 50ft wide, 12ft deep at spring tide
1856	Mouth altered by floods during April
1885 - 1895	Mouth blocked from September-November
1902	Could not cross mouth
1903	Closed mouth
1904	
1905	Water depth: mouth 3.6ft, estuary 7ft
1906	
1907	
1908	
1909	

YEAR	NOTES
1910	
1911	First sugarcane farms in Mfolozi Flats.
1912	
1913	
1914	
1915	Wilson's Drain cut from Umsunduze
1916	
1917	"Devastating" floods
1918	Serious flood in Mfolozi
1919	
1920	
1921	
1922	Mouth closed
1923	Mouth reopened naturally
1924	
1925	Serious flood in Mfolozi
1926	
1927	Drained & canalised Mfolozi swamps
1928	
1929	

YEAR	NOTES
1930	
1931	
1932	Heavy rains break drought
1933	
1934	
1935	
1936	Completion of Warner's Drain
1937	Mouth 100 ft wide, not very deep
1938	Mouth 500 ft wide
1939	First complaints of estuary shallowness
1940	estuary mouth to bridge badly silted
1941	
1942	
1943	
1944	
1945	
1946	
1947	
1948	mouth open, 150ft wide, hypersaline
1949	

YEAR	NOTES
1950	
1951	Reclamation starts: "Levee" is built
1952	mouth dredged open
1953	
1954	
1955	
1956	mouth opened, flood
1957	Flood in Mfolozi in September
1958	
1959	
1960	
1961	mouth opened artificially
1962	
1963	
1964	
1965	mouth closed - few days, dredged open
1966	Floods
1967	
1968	salinities reached 120ppt
1969	

YEAR	NOTES
1970	
1971	
1972	
1973	Flood peak flow 2300m^3/s
1974	
1975	
1976	
1977	Flood peak flow 8000m^3/s
1978	
1979	St Lucia mouth open after closure
1980	Mfolozi mouth opened
1981	Mfolozi inlet works flooded
1982	severe drought and hypersalinity
1983	severe drought and hypersalinity
1984	Cyclone Domoina: peak flow 16730m^3/s
1985	
1986	
1987	Flood peak flow 7500m^3/s
1988	
1989	

YEAR	NOTES
1990	
1991	
1992	mouths combine mouth closed
1993	hypsersalinity
1994	mouth combined
1995	mouth combined
1996	mouth combined
1997	
1998	
1999	mouth combined
2000	mouth combined
2001	mouth combined
2002	mouth closed June/July.
2003	
2004	flood in Mfolozi
2005	flood in Mfolozi
2006	Desiccation of about 90 % of lake
2007	mouth breached due to high waves
2008 - 2010	extreme hypersalinity
2011	above average rainfall

Table 3.1: Time history of important events at St Lucia/Mfolozi focusing mainly on the occurrence of wet/dry conditions (W and D columns respectively) and the mouth state (M column). The shading depicts the intensity of the wet/dry period (dark indicates floods/drought) or how constricted the mouth was i.e. from fully open (white) to fully closed (black). Information was sourced from Taylor [2006]; Hutchison [1974]; Wearne [1965].

The diversion of the Mfolozi River from St Lucia in 1952 was undertaken to address the siltation problem and to prevent further sediment deposition in the mouth. At the same time a dredging program was established to maintain an estuary-sea link, yet the St Lucia mouth closed regularly due to longshore sediment transport processes. In 1963 it was recommended that two groynes and a sand trap be constructed near the mouth to keep it open. Despite this the mouth had to be dredged open after it closed during the winter months of 1970 and 1973 and the sand trap had to be emptied numerous times [Blok, 1976]. Blok [1976] provided a number of possible improvements including the construction of hardened berms between the groynes and the construction of a narrow scour channel.

Sedimentation of the Narrows and Lake was another concern. In 1967 it was proposed that a channel 90 m wide by 1.8 m deep be cut from the bridge up the Narrows. By 1969, the channel was 13 km long and because of doubts of its effectiveness dredging ceased. Model tests later showed that the dredging had little effect on the average water level and salinity, but would rather raise the minimum lake level by 0.08 m [Blok, 1976]. Other options included reducing the surface area of the lake and/or deepening the lake, reducing catchment erosion or the construction of storage dams that would reduce silt loads and store freshwater that could be released during drought conditions [Blok, 1976].

In terms of freshwater addition, the HRU [Hutchison, 1976; Hutchison & Pitman, 1977] used their water balance model [Hutchison and Midgley, 1978] to investigate the efficacy of various management options to mitigate the effects of extreme hypersaline conditions that occur during drought conditions. These measures included the manipulation of freshwater supplies to the lake, the supply of sea water to the lake and possible changes to the geometry of the lake. Simulations showed that the importing of fresh water using various forms of link canal was the most effective in improving the salinity regime of the system. Those involving seawater supply and effecting lake geometry were not recommended. Blok [1976] added the possibility of introducing freshwater from the Mfolozi via a link channel that would link a proposed storage dam on the Mfolozi River with the Nyalazi River. Alexander [1973] on the other hand commented on the diversion of the Mkuze River into Lake St Lucia. There were however concerns that the canal may introduce sediment into the lake and that it may drain part of the Mkuze swamp, but these concerns were thought to outweigh the possible benefits.

From 1970 to 1971 a 4 km long channel was dredged to link the Mfolozi with St Lucia, but there was no head to drive the flow due to tidal influences from both ends of the channel. The only positive outcome was that when the St Lucia mouth was closed, it would act as an alternative link with the sea [Blok, 1976]. At the same time a 13.5 km long by 10 m wide channel was excavated from the Mkuze River near Mpempe pan to Demezane pan. Of this channel 4.5 km was through the Mkuze swamps. The channel was closed in 1974 due to significant erosion in the steep regions at the top of the channel [Blok, 1976]. The investigation by Alexander [1973] found that the diversion of water from the Mkuze River to St Lucia was an unlikely option to alleviate the conditions in St Lucia without serious implication for the Mkuze swamp and in the late 1970s the development of a link canal was initiated to reconnect the Mfolozi into St Lucia. The canal was later damaged by the floods associated with Cyclone Domoina in the early 1980s before the the initial stage of the canal was complete. It was later decided to close the canal due to concerns regarding high sediment loads [Whitfield & Taylor, 2009].

At the beginning of the drought in 2001 the decision was made to allow the St Lucia mouth to close based on experience gained from previous droughts. As a result the salt loading remained constant, however, evaporative losses caused a significant decrease in water levels. As a result Taylor [2006] posed two key management questions: should the mouth be kept open artificially or be allowed to remain closed during drought conditions; and should the Mfolozi mouth be linked back into the St Lucia system as it was in the past.

3.3.6 Biological responses to physico-chemical changes and food web studies

The St Lucia system is among the most studied estuarine systems in South Africa. A substantial amount of biological data have been collected at St Lucia over the past 60 years with most biological components having received some attention. These studies have, however, generally been in the form of short-term studies on specific components. The ecology of St Lucia was first documented by Day *et al.* [1954] and included the first comprehensive biological survey of the system (1948 - 1951). This survey was performed before the Mfolozi was diverted and the St Lucia mouth was kept open and is therefore the closest account of natural conditions. Day *et al.* [1954] discussed the effects of high salinities, turbidity and siltation on the biology and indicated the importance of maintaining an open mouth state for recruitment and migration of species.

During the period from 1952 to 2002 when St Lucia was artificially separated from the Mfolozi river and an open mouth was maintained, the system experienced significant salinity fluctuations depending on wet/dry seasons. Publications that deal with the responses of various biological components under these conditions include: (a) *Birds* – Berruti [1983]; (b) *Fish* – Forbes & Cyrus [1993]; Whitfield [1982]; (c) *Macrobenthic fauna* – Boltt [1975]; Blaber *et al.* [1983]; Forbes & Cyrus [1993]; Weerts [1993]; (d) *Zooplankton* – Grindley [1982]; (e) *Microalgae* – Fielding *et al.* [1991]; Johnson [1976]; (f) *Macrophytes* – Taylor [1987, 2006, 1993]; Taylor *et al.* [2006]; Ward [1982].

After 2002 when the mouth was allowed to close, physico-chemical conditions changed drastically. The closed system experienced low water levels, hypersaline conditions and a lack of recruitment from the ocean. Publications that deal with the responses of various biological components under these conditions include: (a) *Birds* – Whitfield *et al.* [2006]; (b) *Fish* – Whitfield *et al.* [2006]; Vivier *et al.* [2009]; (c) *Macrobenthic fauna* – MacKay *et al.* [2010]; Pillay & Perissinotto [2008]; (d) *Zooplankton* – Carrasco *et al.* [2010]; Jerling *et al.* [2010]; (e) *Microalgae* – Perissinotto *et al.* [2010]; (f) *Macrophytes* – Taylor [2006]; Taylor *et al.* [2006]. A number of these publications also include the response of the system to the brief 5-month interval from March to August 2007 after it was breached by high waves (e.g. Cyrus *et al.* [2010, 2011]; Whitfield & Taylor [2009]).

Data collection at St Lucia has generally been focussed on individual biological components with little attempt to understand the food web dynamics. In a three part series Whitfield and Blaber [1979]; Whitfield & Blaber [1978a,b] investigated the feeding ecology of piscivorous birds and Blaber [1979] investigated the food web of filter feeding fish. These studies highlighted several simple characteristics of the food web in St Lucia during the 1970s when the mouth was open and salinities were low. In 2006 Govender *et al.* [2011] investigated the food web structure of the system using carbon and nitrogen isotope analysis. Results showed that benthic carbon sources were predominantly utilised at sites with low water levels and high salinities while at sites with high water levels and lower salinities viable pelagic food webs were sustained. Furthermore, Scharler & MacKay [2013] depicted the major trophic pathways for False Bay and the lower Narrows using data collated by Day *et al.* [1954] from 1948 - 1951 and data from the recent dry period. These studies provide valuable insights into the food web dynamics of the system, but they do not provide a holistic and quantitative representation of the system.

3.3.7 Biophysical modelling

Researches and managers have tried many methods to simulate, predict and quantify biological responses to physical changes, but without a comprehensive and continuous biological data set and the coordination between studies it has been difficult to understand how the St Lucia system functions as a holistic entity.

In an attempt to predict biological responses to different management strategies Taylor [1987] and Starfield *et al.* [1989] developed a qualitative, rule-based model. Three main dominant trophic pathways were used to represent different salinity ranges. The dominance of the fauna in these pathways is influenced by the distribution of flora which in turn is driven by water level and salinity changes [Gordon *et al.*, 2008; Starfield *et al.*, 1989; Taylor, 2006]. The three main submerged macrophytes found in St Lucia are *Stuckenia pectinatus*, *Ruppia cirrhosa* and *Zostera capensis* [Taylor *et al.*, 2006]. The tolerance range to salinity varies with each species while optimal growth generally occurs within a smaller range. *Z. capensis* and *R. cirrhosa* tolerate salinities ranging from 2 to 40 and *P. pectinatus* occurs at salinities between 5 and 15 [Taylor *et al.*, 2006]. Salinity was used as the main physical determinant for the model, however, at that time very low water levels (and desiccation) were unprecedented.

A static interpretation of the biological response to changes in the physical determinant would be an oversimplification as species require time to establish themselves once the environment has changed. Therefore the persistence of these salinity regimes is an important factor [Taylor, 1993]. The main problem with this method is that there are insufficient data with which to calibrate these models.

3.3.8 Climate change

Taylor *et al.* [2006] suggested that the impact of climate change on St Lucia in this century would be minor when compared to the anthropogenic impacts over the last century. Climate change predictions suggest an increase in the frequency and/or intensity of extreme events [Hewitson *et al.*, 2005; Mason *et al.*, 1999]. More frequent and/or intense droughts and floods could have severe impacts on episodic hypersaline events, the risk of desiccation, breaching patterns, sediment loading etc. Mather *et al.* [2013] discussed the possible impacts of climate change on St Lucia. They suggested that the main impact on the system may be the large increase in rainfall predicted for the region and the increase in associated freshwater inflows. In addition sea level changes with expectations of a possible 30 - 50 cm rise [Mather *et al.*, 2010] and changes to the dominant wave direction and height [Corbella and Stretch, 2012] on the KwaZulu-Natal coastline may also affect the physical dynamics of the system. If drought conditions occur more frequently, there will be less time available for the ecosystem to recover. This would lead to the degradation of the system over time and the subsequent loss of resilience could cause significant shifts in the state of the system [e.g. Scheffer *et al.*, 2001].

3.4 Summary

The St Lucia estuarine-lake has undergone significant anthropogenic impacts over the past century, however, there has been insufficient progress made in understanding the physical dynamics of the system. Management decisions have been made and hard engineering methods have been implemented without sufficient scientific understanding. For example, little is known about the mouth dynamics of the St Lucia estuary and the impact of diverting the Mfolozi away from the system. In additions the effects of increased sediment loads has been a major concern, yet there remains no scientific evidence to substantiate this issue or quantify the impacts.

In terms of the biology, there has been significant progress made in understanding the different biological components of the system and how they respond to changing environmental parameters (e.g. to the current dry period). Research gaps however remain in terms of understanding the food web dynamics and how the system functions as a whole.

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Chapter 4

Anthropogenic impacts on the water and salt budgets of St Lucia estuarine lake: an evaluation using simulations of historical scenarios

This chapter is based on the paper: Lawrie, R.A. and Stretch, D.D, 2011. Anthropogenic impacts on the water and salt budgets of St Lucia estuarine lake: an evaluation using simulations of historical scenarios. Estuarine Coastal and Shelf Science 93, pp. 58–67.

Abstract

Lake St Lucia is part of a UNESCO World Heritage site and a RAMSAR wetland of international importance. Like many coastal wetlands worldwide, anthropogenic activities including catchment land-use changes, water diversions/abstractions, and manipulation of the mouth state have significantly affected its functioning over the past century. Questions concerning its sustainability have motivated a reevaluation of management decisions made in the past and of options for the future. A model for the water and salt budgets has therefore been used to investigate what if scenarios in terms of past anthropogenic interventions. In particular, simulations allow us to evaluate the effects of diverting the Mfolozi river from St Lucia on the functioning of the system and on the occurrence of various water level/salinity states that drive the biological functioning of the ecosystem. In the past, when the St Lucia estuary and the Mfolozi river had a combined inlet, the mouth was predominantly open. The lake had relatively stable water levels but variable salinities that increased during dry conditions due to evaporative losses and saltwater inflows from the sea. If the mouth closed, the Mfolozi flow was diverted into the lake which reduced salinities and maintained or increased water levels. Simulations indicate that without a link to the Mfolozi the lake system would naturally have a mainly closed inlet with lower average salinities but more variable water levels. During dry conditions water levels would reduce and result in desiccation of large areas of the lake as has recently occurred. We conclude that the artificial separation of the St Lucia and Mfolozi inlets underpins the most significant impacts on the water salt budget of the lake and that its reversal is key to the sustainability of the system.

4.1 Introduction

During the last century, water abstractions, eutrophication and other factors have begun to severely impact the natural biophysical functioning of estuaries on a global scale [e.g. Livingston, 2001; McLusky and Elliot, 2004; Wolanski, 2007]. The St Lucia estuarine lake, a focal attribute of the iSimangaliso Wetland Park in South Africa (Fig. 4.1) is an example. Despite its status as a UNESCO World Heritage and RAMSAR wetland of international importance, anthropogenic influences continue to drive major changes in the functioning and sustainability of this important system [Cyrus *et al.*, 2010; Whitfield & Taylor, 2009; van Vuuren, 2009]. Similar issues are faced by other large systems worldwide, such as the Coorong estuary in Australia and Chilika Lake in India [Gosh *et al.*, 2006; Webster, 2010].

Anthropogenic impacts on St Lucia began in earnest at the turn of the 20th century with the introduction of agriculture in the lower Mfolozi floodplain. This led to drainage of the Mfolozi swamps and partial canalization of the river [Taylor, 2006; Whitfield & Taylor, 2009]. It is widely believed that these changes contributed to increased silt loads in the Mfolozi which in turn led to extensive siltation of the mouth area during the 1940s [Whitfield & Taylor, 2009; Hutchison, 1974]. The situation was exacerbated by one of the worst droughts on record starting in the mid 40s and persisting until floods in 1956. In 1952, at the height of the drought, a separate Mfolozi mouth was dredged open to address the siltation issue and to protect sugarcane farms in the Mfolozi floodplain from back-flooding during mouth closures [Taylor, 2006; Whitfield & Taylor, 2009]. Since 1952 the management strategy has been to keep the inlets of the Mfolozi and St Lucia separate. This requires management interventions at about 1-year intervals to stop the Mfolozi inlet from migrating northward and rejoining the St Lucia inlet. The migration of the Mfolozi inlet is a natural consequence of the prevailing northerly littoral transport regime in the area.

One important consequence of the decision to change the Mfolozi/St Lucia inlet configuration was that it cut off a key supply of freshwater to the lake during drought conditions. Before 1952, when the combined mouth closed naturally during drought conditions, the Mfolozi flow was diverted into Lake St Lucia thereby mitigating losses to evaporation and reducing salinities. Mfolozi inflows also helped to maintain water levels in the lake and ultimately drive over-topping and breaching of the frontal sand berm to restore a functional link with the sea [Taylor *et al.*, 2006; Whitfield & Taylor, 2009].

A second important (and apparently largely unforeseen) consequence of the decision to separate the Mfolozi and St Lucia inlets was its effect on the stability of the St Lucia inlet. At the time it was considered desirable to have a continuously open mouth to facilitate biological exchanges between lake and sea. However, after the separation of the inlets it became apparent that the St Lucia inlet had a natural tendency to close and active management interventions were required to keep the mouth open. These interventions included dredging, artificial breaching, and the construction of groins at the St Lucia inlet [Taylor *et al.*, 2006; Whitfield & Taylor, 2009]. The management strategy was changed in 2002 and the mouth was allowed to close after the onset of dry conditions. The closure of the mouth in June/July 2002 was followed by ongoing dry conditions that ultimately led to extreme hypersaline conditions and desiccation of about 90% of the lake basin during 2006. This situation has persisted until the present with some temporary respite provided by seasonal rainfall. In addition, during March 2007, large storm waves coupled with very high tide levels breached the frontal berm and allowed seawater to flow into the lake. The re-closure of the mouth in August 2007 once again left the system vulnerable to desiccation and extreme hypersalinity.

In addition to the loss of freshwater from the Mfolozi link during drought conditions, Hutchison & Pitman [1977] estimated that river runoff from the lake's catchments have also been reduced by about 20% due to afforestation, irrigation and dams.

Previous research on the functioning of St Lucia has focused almost exclusively on the post-1952 configuration with the Mfolozi having a separate inlet. Moreover it has dealt mainly with the biological components of the system. The most significant previous research on the hydrology and physical dynamics of the system was by Hutchison [1976]; Hutchison and Pitman [1973]; Hutchison & Pitman [1977] and Hutchison and Midgley [1978]. They developed a water and salt balance model to simulate the functioning of the system and to investigate the efficacy of various options to mitigate the effects of extreme hyper-saline conditions that typically occur during drought conditions. Their work gave important insights into the effects of freshwater reductions on the state of the system. However, a major limitation in their approach was that it did not incorporate a model for the inlet mouth dynamics. Therefore a new model of the St Lucia system that incorporates the mouth dynamics and can contribute to developing our understanding of how the system functioned prior to 1952 is required.

The main objective of this study is to elucidate how mouth management strategies have influenced the natural functioning of the system and how they should be used in the future. Climate change is expected to result in an increasing frequency of extreme events, including droughts [Hewitson *et al.*, 2005; Mason *et al.*, 1999]. Therefore it is important to understand the way management strategies can change the response of the system to those events. Key research questions include: (1) What was the effect of separating the St Lucia and Mfolozi systems on the water/salt budgets and mouth dynamics; (2) How does the system

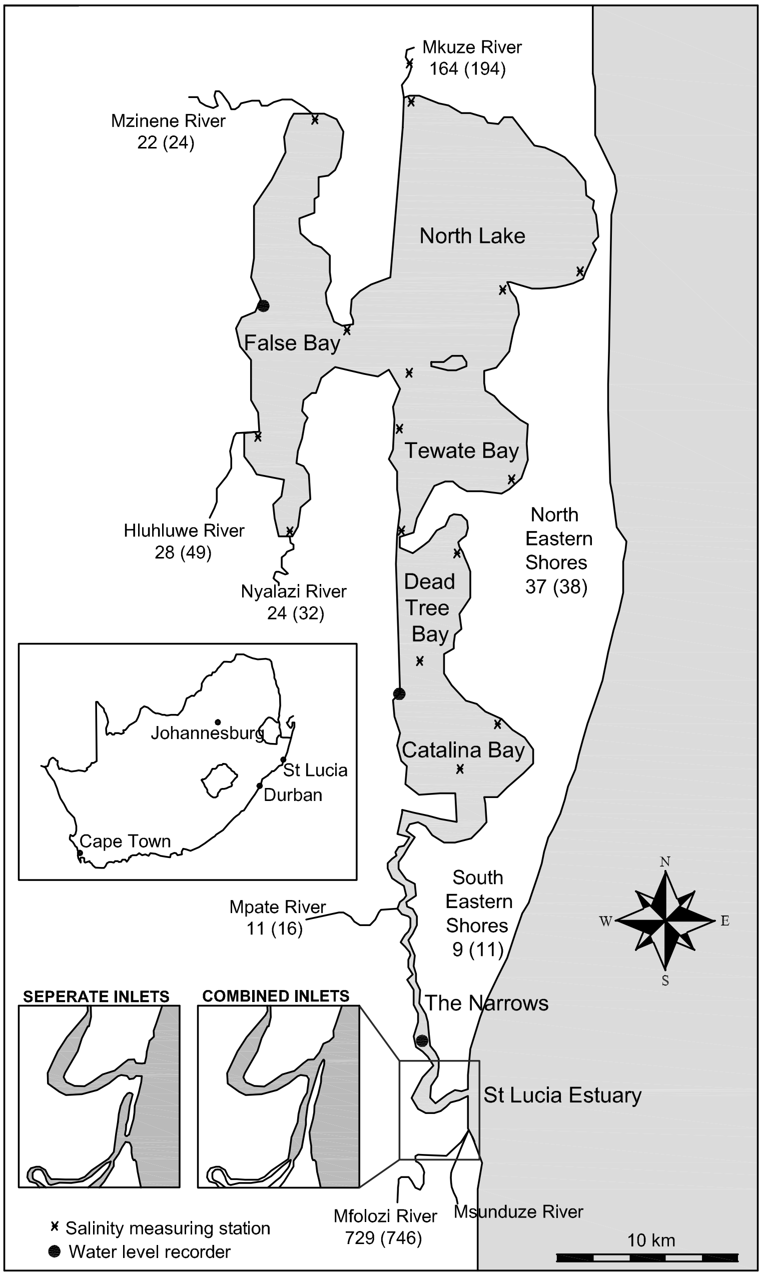

Figure 4.1: Location of St Lucia lake and estuary on the east coast of Africa. Approximate locations of water level and salinity measurements are shown. Annual inlow contributions (Mm^3) are indicated for the main catchments - bracketed values are for natural conditions (details in Table 4.1). The map inserts depict the two main mouth configurations investigated in this study.

respond to extreme events under different mouth management scenarios (3) How would importing additional fresh water into St Lucia change the functioning of the system?

The methods used for modeling the water and salt budgets are described in Section 4.2. Model validation and simulation results for different scenarios are presented in Section 4.3. The results are discussed in Section 4.4 and conclusions summarized in Section 4.5.

4.2 Methods

4.2.1 Overview

The approach used for the present study was to develop a model for the water and salt balance of the St Lucia system, and to apply the model to explore and evaluate how the functioning of the system has been affected by past human activities including management interventions. The model allows us to use simulations to explore "what if" questions with respect to historical outcomes and thereby evaluate the affect of alternative scenarios.

4.2.2 The case study site

The St Lucia lake/estuary system (located between $2742'$ – $2824'$ S, and $3221'$ – $3234'$ E) is situated on the sub-tropical east coast of South Africa (Fig. 4.1). The lake is fed directly by several freshwater sources including the Hluhluwe, Mpate, Mzinene, Mkuze and Nyalasi rivers, and groundwater seepage along its eastern shores. As previously noted, prior to 1952, the Mfolozi River also contributed to the water balance of St Lucia during drought periods.

A summary of physical and hydrological data for the St Lucia system, adapted from Hutchison and Pitman [1973] and Hutchison & Pitman [1977] is given in Table 4.1 (adapted from Hutchison and Pitman [1973]; Hutchison & Pitman [1977]). With an average surface area of 328 km^2 and average depth of only 1 m, the lake is sensitive to direct rainfall inputs and evaporative losses. The total mean annual runoff (MAR) from the lake's catchments is estimated to be 295 Mm^3 which is reduced from an original 364 Mm^3 by human activity. The breakdown of catchment inflows (including the Mfolozi) are included in Table 4.1. The Mfolozi catchment is about 30 % larger than the total catchment area directly feeding the lake and the MAR of the Mfolozi is more than double the combined inflows from all the lake catchments. The mean annual precipitation (MAP) over the lake is 890 mm while the mean annual (pan) evaporation (MAE) is 1470 mm.

Table 4.1: Summary of key elements contributing to the water balance of St Lucia lake and estuary. Values in parentheses are estimates that exclude human impacts such as irrigation abstractions. Data is adapted from Hutchison and Pitman [1973]; Hutchison & Pitman [1977].

Item	**Description**	**Values**
Lake basin	Average area	328 km^2
	Average volume	322 Mm^3
	Rainfall MAP	890 mm
	Evaporation MAE	1470 mm
Lake catchments	Total watershed area	7575 km^2
	Total MAR	295 (364) Mm^3
	Mkuzi MAR	164 (194) Mm^3
	Mzinene MAR	22 (24) Mm^3
	Hluhluwe MAR	28 (49) Mm^3
	Nyalasi MAR	24 (32) Mm^3
	Mpate MAR	11 (16) Mm^3
	NEastern shores MAR	37 (38) Mm^3
	SEastern shores MAR	9 (11) Mm^3
Mfolozi	Catchment Area	10 085 km^2
	Mfolozi MAR	729 (746) Mm^3

NOTES: MAP = mean annual precipitation; MAR = mean annual runoff; MAE = mean annual evaporation

4.2.3 Water budget

The water budget is based on a discrete time version of the continuity equation, namely

$$V_{n+1} = V_n + (I_n + R_n - E_n + Q_n)\ \Delta t \tag{4.1}$$

where V is the volume of water stored in the lake, I is the lumped inflow from all the lake's catchments, R and E are the direct rainfall and evaporation for the lake basin, Q is the exchange flow with the sea through the mouth (if open), and Δt. is the time step. The subscript n denotes values at the n^{th} time step. The implied sign convention for Q in Equation (4.1) is that outflows to the sea are negative while inflows are positive. The budget was formulated for a one month time step Δt. The main data requirements for the water budget are therefore monthly averaged rainfall R_n, evaporation E_n, river inflows I_n, and mouth discharges Q_n. The data in Table 4.1 give an overview of the main components of the water budget. The role of the Mfolozi in the water budget is discussed in §4.2.3.2.

Hutchison and Midgley [1978]; Hutchison & Pitman [1977] have previously reported a multi-cell model to simulate the water budget of St Lucia where each cell has its own inputs and outputs and provision is made for exchange flows between the cells. In the present study a single unified basin was used in order to reduce the number of uncertain parameters (e.g. those associated with the exchange flows) and to facilitate long-term simulations. This simplified formulation is limited to modeling salinities and water levels as averages over the whole lake basin. Spatial non-homogeneities tend to become significant during drought periods when average salinities are high and a reverse salinity gradient develops in the system. These spatial variations can be parameterized in terms of average conditions if necessary, but this refinement will not be discussed further here.

The water budget given by Equation (4.1) is formulated in terms of the volumes of inflows, outflows and storage. It does not use water levels directly. However, water level is used as an endogenous variable to determine the surface area of the lake at specific storage volumes, and for relating storage volumes to mouth discharges and breaching events. Water levels are given relative to a local datum that we refer to as the Estuary Mean Water Level (EMWL) which corresponds to the average water level when the mouth is open. The EMWL was previously used by Hutchison [1974]; Hutchison & Pitman [1977] and is 0.45 m above Geodetic Mean Sea Level (GMSL) which is the vertical land leveling datum used in South Africa. The actual mean sea level at this location is about +0.2 m GMSL. The relationships between water level, surface area, and volume for the lake basin were obtained from the bathymetric survey reported in Hutchison [1974].

4.2.3.1 Hydrological data - freshwater inflows

Flow gauges are not available for all rivers that feed St Lucia and where they exist they are located some distance away and provide only short duration or incomplete data. To overcome this problem, Hutchison and Pitman [1973] used a rainfall-runoff model [Pitman, 1973] to simulate the inflows from the contributing catchments for the period 1918 until 1971 (refer to Table 4.1). The Pitman model has been widely used in South Africa and has become the local *de facto* standard for simulating monthly averaged streamflows [Midgley *et al.*, 1994]. Hutchison and Pitman [1973] calibrated the simulations by comparing monthly flow duration curves with those derived from measured streamflow records where available. The simulated inflows from the eastern shores catchment of the lake (Fig. 4.1) are mainly in the form of subsurface flows. The total volume contributed from this source compared with the other river inflows is small but can be important during dry periods as they are more persistent than surface flows [Taylor, 2006].

For the present study the Hutchison and Pitman [1973] record of simulated flows was extended from 1971 to the present using the non-linear rainfall–flow mapping proposed by Smakhtin and Masse [2000]. Monthly area-averaged rainfall data from weather stations in the St Lucia catchments were filtered to get a current precipitation index from which exceedance probabilities were derived. Each value of the current precipitation index was then mapped to a flow with the same exceedance probability as determined from the original simulated inflows.

The average monthly evaporation data reported by Hutchison and Pitman [1973] were used for the water balance simulations since actual monthly data was not available for the whole period of interest.

Simulated inflows for both ”natural” and ”present” conditions were used. Natural conditions refer to those prior to significant anthropogenic influence, while present conditions incorporate losses due to abstractions, dams and afforestation. The losses amount to a reduction of approximately 20 % (about 60 Mm^3) in this case [Hutchison and Pitman, 1973]. This value was adopted until present time although losses are expected to be higher.

4.2.3.2 Mfolozi linkage and additional fresh water inputs

An important objective for the present modeling work was to clarify the role of the Mfolozi in the functioning of St Lucia. The model has therefore been formulated so that the degree of linkage between St Lucia and the Mfolozi can be varied. If St Lucia and the Mfolozi have a combined mouth, there are two main cases: (1) When the mouth is closed, the Mfolozi flow is assumed to be diverted into St Lucia [Taylor *et al.*, 2006; Whitfield & Taylor, 2009] ; (2) When the mouth is open, the Mfolozi flow is assumed to discharge out to the sea during ebb tides [Hutchison, 1976]. The Mfolozi has no direct contribution to the water budget for the latter case. Linkage to the Mfolozi also plays an important role in the mouth state model as discussed in §4.2.3.4.

The model formulation provides for a source of "imported" fresh water of specified volume to be included in the St Lucia water budget. This can be used to simulate the effects of a fresh water transfers into St Lucia from external sources. This issue was previously investigated by Hutchison & Pitman [1977] but without accounting for changes in mouth dynamics.

4.2.3.3 Estuary mouth inflows and outflows

The exchange flows between the lake and the sea when the estuary mouth is open are pivotal in modulating the salt and water balance. Hutchison [1976]; Hutchison and Midgley [1978] derived a relationship between lake water levels and mouth discharges based on field measurements and on results yielded by a one-dimensional hydrodynamic model. Their results indicated that there is a lake water level (and associated storage volume V_0) when net mouth discharges are zero. This corresponds to the average water level during open mouth conditions, denoted estuary mean water level (EMWL). When $V < V_0$ (water levels below EMWL) there is a net inflow from the sea into the lake and vice versa when

$V \geq V_0$.

For the present study an empirical relationship was used to relate the mouth inflow/outflows to lake volumes V as

$$\begin{aligned} Q/Q_M &= (V/V_0 - 1)^m \qquad \text{for } V \geq V_0 & (4.2) \\ &= \text{constant} \qquad \text{for } V < V_0. & (4.3) \end{aligned}$$

where Q_M is a characteristic magnitude for the mouth discharges. Values of $Q_M \simeq 95\text{m}^3\text{s}^{-1}$ and $m = 1.25$ were selected to match the mouth discharges predicted by the 1-D hydrodynamic model as reported by Hutchison and Midgley [1978]. The model suggested that when $V < V_0$ inflows are insensitive to lake water levels and are in the range 5 – 10 m^3s^{-1} depending on the frictional resistance of the 22 km channel linking the lake to the sea. More recent measurements of tidal flows by Chrystal and Stretch [unpubl.] have suggested that the net inflows at low lake water levels are in the range 500,000 to 1000,000 m^3 per day (depending on the tidal amplitude) which corresponds to an average flow in the range 6 – 12 m^3s^{-1} and corroborates the results of Hutchison and Midgley [1978].

4.2.3.4 Mouth state model

Estuary inlets that close intermittently are common in Australia, India and South Africa [Ranasinghe and Pattiaratchi, 2003; Roy *et al.*, 2001; Perissinotto *et al.*, 2010]. It is well known [e.g. Bruun, 1978] that large terrestrial flows and/or a large tidal prism can maintain an open inlet by overcoming the factors that drive inlet closure, namely wave and tide-driven sediment transport processes. In the case of the St Lucia inlet, tidal flows are strongly flood dominant during periods of low river flows with a tendency for the mouth to close at those times [Chrystal and Stretch, unpubl.]. It is therefore natural to assume that the St Lucia mouth state is mainly influenced by two key factors that are linked to mouth outflows, namely the lake water level and (if it shares a common inlet with St Lucia) the flow in the Mfolozi. Water levels also drive the breaching of the berm after the system has been closed. A rule-based model for the mouth state was therefore implemented based on these ideas. The rules for mouth state transitions are summarized in Table 4.2. The breaching level is indicated in Figures 4.3 to 4.7.

Table 4.2: St Lucia inlet rule-based model for mouth state transitions. The first set of rules (a) are applied when the St Lucia and Mfolozi inlets are separate, while the second set (b) are applied when the inlets are combined.

Transition	Rules(s)
(a) *Separate St Lucia inlet*	
open → open	Lake water level $\geq$ Threshold
open → closed	Lake water level $<$ Threshold
closed → open	Lake water level $\geq$ Breaching level
(b) *Combined St Lucia and Mfolozi inlets*	
open → open	Lake water level $\geq$ Threshold **OR** Mfolozi flow $\geq$ Threshold
open → closed	Lake water level $<$ Threshold **AND** Mfolozi flow $<$ Threshold
closed → open	Lake water level $\geq$ Breaching level

Some limited historical mouth state observations from 1918 to 1952 were compiled by Hutchison [1976, 1974]. The St Lucia/Mfolozi mouths were combined during that period. The historical record suggest that the mouth was open about 75 % of the time. The threshold values of lake water level and Mfolozi flow rates defined in Table 4.2 were selected so that predicted mouth states approximately matched the historical record. The threshold lake level was set at -0.07 mEMWL and the threshold Mfolozi flow was 4 Mm^3 per month. The simple rule-based model for the mouth state ignores the complexities of tidal and sediment dynamics that occur at the inlet (e.g. as discussed by Chrystal and Stretch [unpubl.]) but nevertheless adequately mimics the observed mouth state transitions.

4.2.4 Salt budget

Inflows and outflows through the mouth of the estuary govern the salt loading in the system. Salt loads increase when lake levels are low enough that there is a net inflow from the sea. Salt is flushed from the system when lake levels are high and there is a net outflow to the sea.

A simplified model for the salt budget was used that assumes a fully mixed state for the lake storage volume. The discrete-time salt budget follows as

$$\begin{aligned} S_{n+1}\,V_{n+1} &= \left(S_n\,V_n - S_n\,Q_n\,\Delta t\right) && \text{for } V \geq V_0 && (4.4)\\ &= \left(S_n\,V_n + \tfrac{35}{1000}\,Q_n\,\Delta t\right) && \text{for } V < V_0 && (4.5) \end{aligned}$$

where S_n and V_n are the lake salinity and volume at the n^{th} time step respectively, and Q_n is the mouth discharge (Equations 4.2 & 4.3) at the n^{th} time step.

4.2.5 Implementation and testing of the model

The water and salinity budget model described above has been implemented in a spreadsheet software environment that provides a numerical solution (using Eqs. 4.1 to 4.5) for monthly volumes, water levels, mouth states and salinities. The spreadsheet environment makes the model and its application easily accessible to managers.

Water level and salinity measurements have been made at St Lucia since 1958 and can be used to validate the water balance model. The location of the measurement stations are indicated in Fig. 4.1. In cases where several measurements are available, they have been spatially averaged to obtain representative values for comparison with the model predictions.

4.2.6 Simulation scenarios

The main objective of this study was to use long-term simulations to provide a broad perspective of the functioning of the lake system under different scenarios and thereby illustrate and evaluate the consequences of different management strategies. Water levels, salinities and mouth states were simulated for a 92-year period (1918 until present) for each of the following scenarios:

Scenario 1 : Separate Mfolozi and St Lucia inlets with mouth manipulation to keep St Lucia inlet open. Simulations for this scenario can be used to validate the model since this corresponds to the actual conditions that existed for the period 1955 – 2002 and for which salinity and water level measurements are available for comparison.

Scenario 2 : Separate Mfolozi and St Lucia inlets but no mouth manipulation i.e. a ”what if” study to investigate the long term functioning of the system with separate inlets but without management interventions to maintain an open St Lucia inlet. Since 2002 this has been the management strategy and there has been no direct manipulation of the St Lucia mouth. However, interventions to keep the Mfolozi separate have continued.

Scenario 3 : A combined Mfolozi/St Lucia inlet with no active manipulation i.e. a ”what if” study to predict the long term functioning of the system with minimal management interference in the functioning of the system.

In addition to these three scenarios, which are all linked to mouth management strategies, we also present results of simulations using both “natural” and “present” flows to show the impact of human activities such as water abstractions, dams etc. This was done previously for scenario 1 by Hutchison [1976]; Hutchison & Pitman [1977] - here we focus on scenarios 2 & 3.

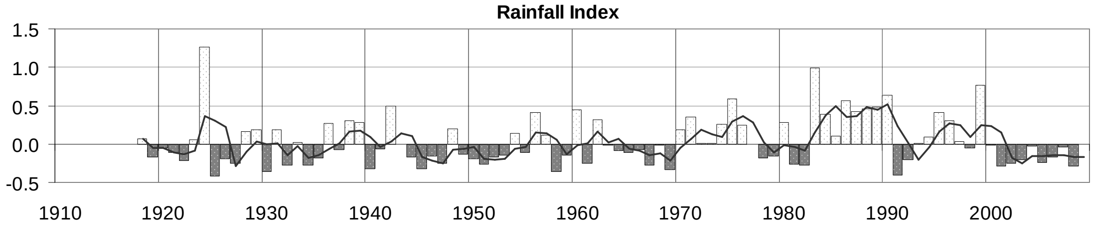

Figure 4.2: Time history of a normalized annual rainfall index and its 3-year moving average over the last century.

4.3 Results

4.3.1 Rainfall and evaporation

The lake water balance is sensitive to direct rainfall inputs and evaporative losses due to the large surface area to volume ratio. Direct rainfall contributes about

300 Mm^3 per year to the water balance which is similar to the lake's catchment inflows . Evaporative losses average about 450 Mm^3 per year.

An annual rainfall index, defined as the normalized deviation from the annual average is shown plotted in Figure 4.2. A positive rainfall index indicates a relatively wet year while relatively dry years have negative indices. Negative index values occur for 60 % of the time and about 25 % of these periods have a duration of three years or longer.

4.3.2 Long term simulations

Simulation results for each scenario are presented as time histories of monthly averaged water levels and salinities. Average annual water balance contributions for scenarios 2 and 3 are given in Table 4.3 and selected statistics in Table 4.4.

4.3.2.1 Scenario 1: Separate inlets with mouth manipulation to keep St Lucia open

Simulation results for scenario 1 are shown in Fig. 4.3. Water level and salinity measurements from the period 1958 – 2009 are also shown for comparison with the simulations. Except for the period after 2002 when the mouth was closed, the simulations agree well with the measurements and therefore validate the basic components of the water balance model. Note that there are no adjustable parameters for these simulations since the mouth state was assumed open i.e. the mouth state model was not used. Both simulated and measured salinities increase in the dry cycles and decrease during wet cycles on decadal timescales. With an open mouth these trends are caused by the increase in salt loading during dry periods when sea water flows into the system to replace losses due to evaporation. The occurrence of hypersaline conditions are therefore related to sustained periods with a negative rainfall index (refer Figs.4.2 and 4.3). In contrast, during wet periods freshwater inputs are sufficient to reduce salinities.

4.3.2.2 Scenario 2: Separate inlets, no mouth manipulation

Simulation results for Scenario 2 (Figure 4.4) indicate that without artificial interference in the mouth state, a separate St Lucia inlet would be predominantly

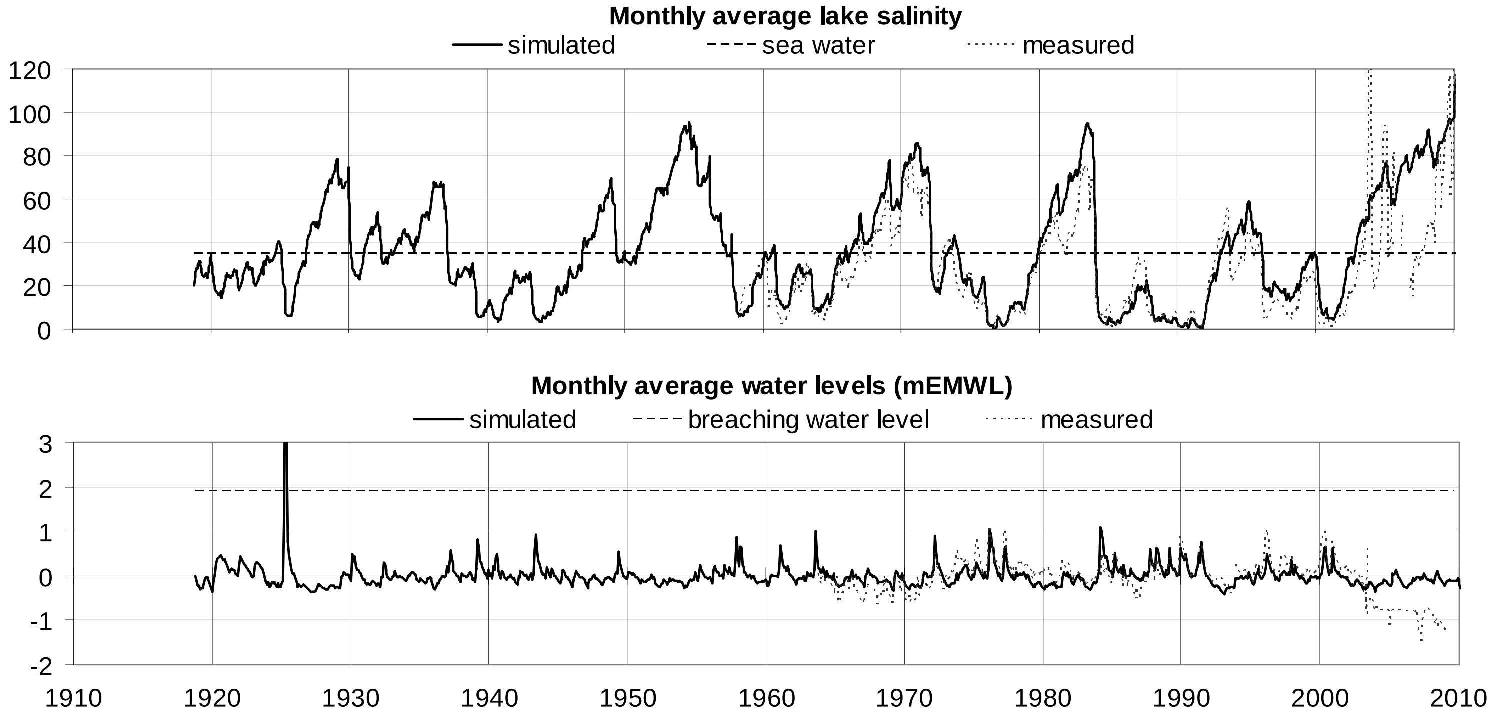

Figure 4.3: Scenario 1 simulation results showing average monthly lake salinities (top panel) and water levels (bottom panel). Also shown (as dotted lines) are measured average salinities and water levels for the period after 1960 for comparison with the simulation results. For the simulations the mouth was forced to be open continuously. Note that the actual mouth state has been closed since 2002.

closed (about 90% of the time). The mouth could remain closed for ten years or more before beaching. Analysis of the inflows during the closed mouth periods suggests that a ten-year return period flood event is typically required to breach the mouth in this scenario. The model predicts that the mouth generally remains open only for one to two years.

A key feature of this scenario is that water levels fluctuate over a wide range, and in particular reach very low levels during dry periods. Water levels below −0.25 m EMWL occur about 40 % of the time and those below −1.0 m EMWL for 16 % of the time (Table 4.4). During severe droughts large portions of the lake would be desiccated e.g. compared to average conditions the lake surface area is reduced by 50 % when water levels reach −1.0 m EMWL. The average recurrence interval of these events is about 12 years in this scenario. The volume distribution in the lake means that the northern sectors are more severely impacted by reduced water levels, while Catalina Bay in the south (see Fig. 4.1) is less impacted.

During closed conditions salinities rise exponentially as water levels reduce since the salt loading remains constant. Average salt loading in the lake for this scenario is however low due to the limited time that it is connected to the sea. The lake is thus predicted to be a predominantly fresh water system with salinities less than 4 nearly half the time (Table 4.4) but with episodic hypersaline conditions associated with low water levels during droughts.

Note that the simulations for scenario 2 predict mouth closure in 2002 which corresponds with what actually occurred. The model results for this scenario can therefore be compared with the measurements available for this period (see Fig. 4.3). It can be seen that the scenario 2 simulations shown in Fig. 4.4 predict low water levels and hypersaline conditions after the 2002 mouth closure which agrees well with the measurements.

4.3.2.3 Scenario 3: Combined inlets, no mouth manipulation

Simulations of scenario 3 (Fig. 4.5) indicate that without artificial interference in the mouth state, a combined St Lucia/Mfolozi inlet would be predominantly open (about 70% of the time) and would remain open for about 5 – 6 years at a time. The extended connection to the sea stabilizes lake water levels and gives

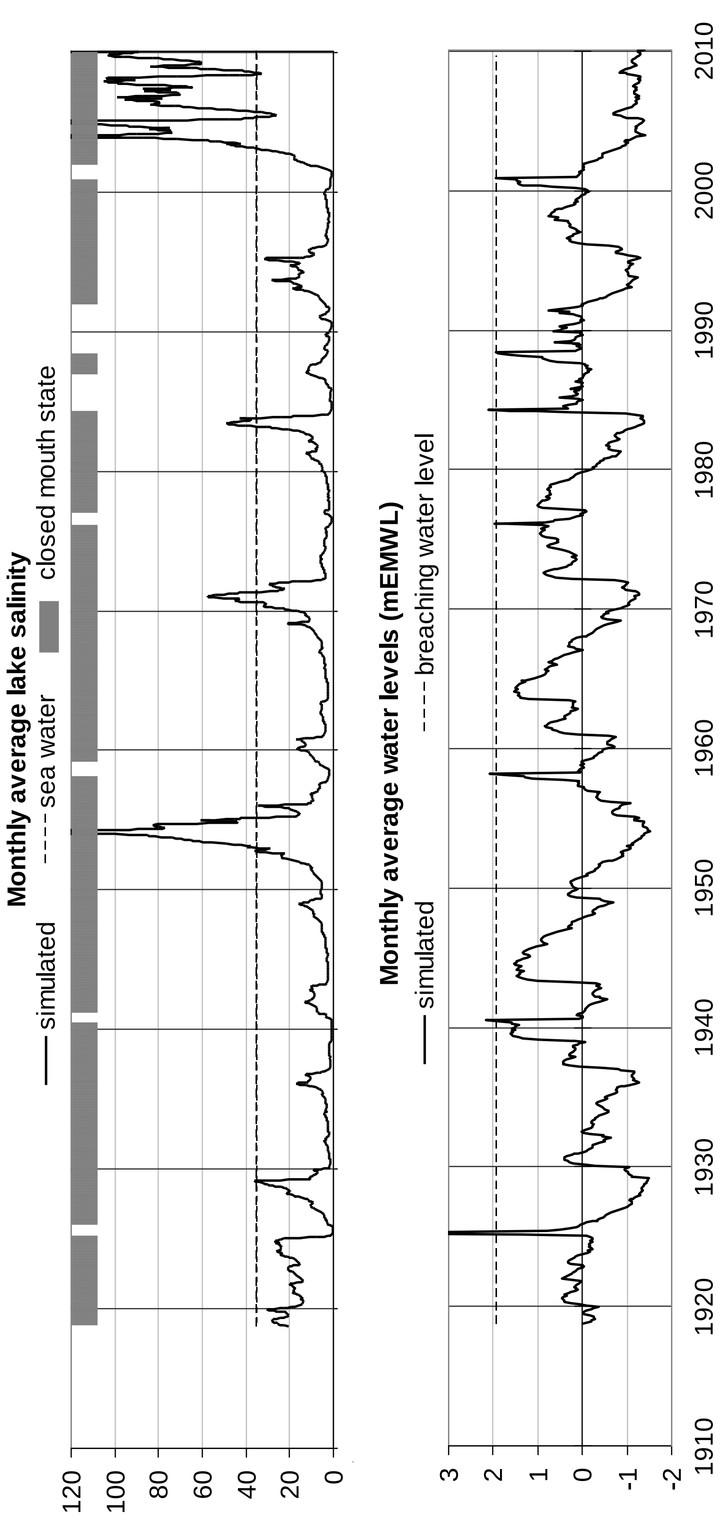

Figure 4.4: Scenario 2 simulation results showing monthly average lake salinities, water levels and mouth states.

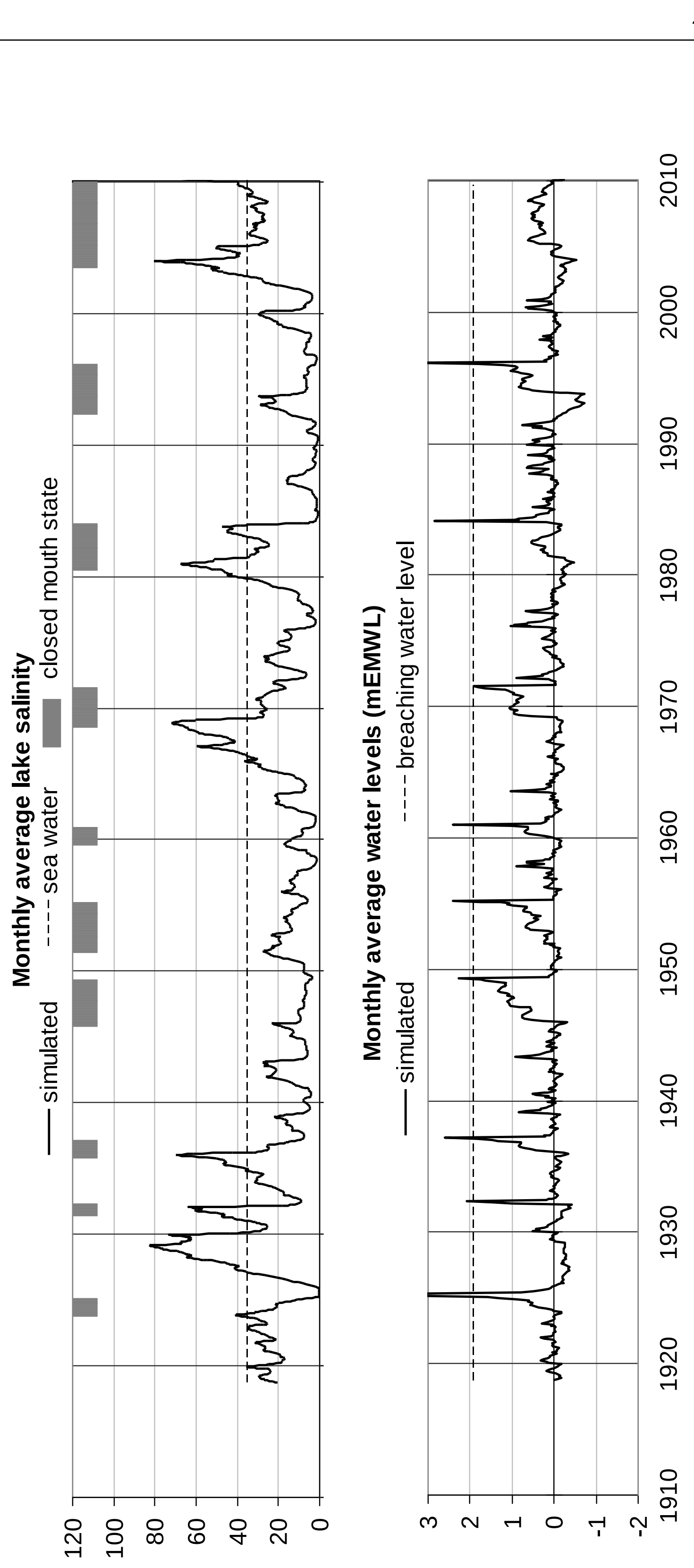

Figure 4.5: Scenario 3 simulation results showing monthly average lake salinities, water levels and mouth states.

rise to an average salt loading about 3 times higher than in scenario 2 (Table 4.4). Salinities vary significantly as a result of the influx of seawater, especially during dry periods.

At the onset of dry periods evaporation losses together with low freshwater inflows cause a gradual increase in lake salinities resulting in hypersaline conditions. Seawater inflows maintain water levels at about EMWL but increase the salt loading in the lake. Eventually a build-up of marine sediments can occur in the mouth region leading to closure of the inlet and diversion of the Mfolozi flows into the lake. This diverted fresh water can be vital during dry periods since it sustains (or increases) water levels and can prevent hypersaline conditions (see Fig. 4.5). Eventually water levels increase until the breaching level is reached.

The summary in Table 4.3 shows that on average the Mfolozi contributes about 20 % of the total freshwater supply of the lake during intermittent mouth closures. The mouth is estimated to remain closed for 2 to 3 years at a time (Table 4.4). The simulations suggest that a three year return period flood would usually be sufficient to cause breaching of the estuary mouth under these conditions.

4.3.2.4 The impact of water losses due to human activities

As noted in §4.2.3.1 anthropogenic activities have reduced the inflows into St Lucia by about 20% or 60Mm^3 per year. Results of simulations for scenarios 2 and 3 using "natural" flows are shown in Figures 4.6 and 4.7 and illustrate the impact of the inflow changes. Comparing these results with those shown in Figs. 4.4 and 4.5 respectively, it is evident that the higher inflows significantly reduce salinities during dry periods (see also Table 4.4). Other changes are slightly longer open mouth conditions and increased water levels for scenario 2 during droughts. While desiccation of the lake is a regular feature of scenario 2 simulations under the reduced inflow regime (Fig. 4.4) it is less likely to occur under "natural" inflow conditions. However, it is worth emphasizing that the model predicts that the mouth state in cenario 2 (i.e. with inlet separated from Mfolozi) remains predominantly closed even with the increased inflows that existed in the past.

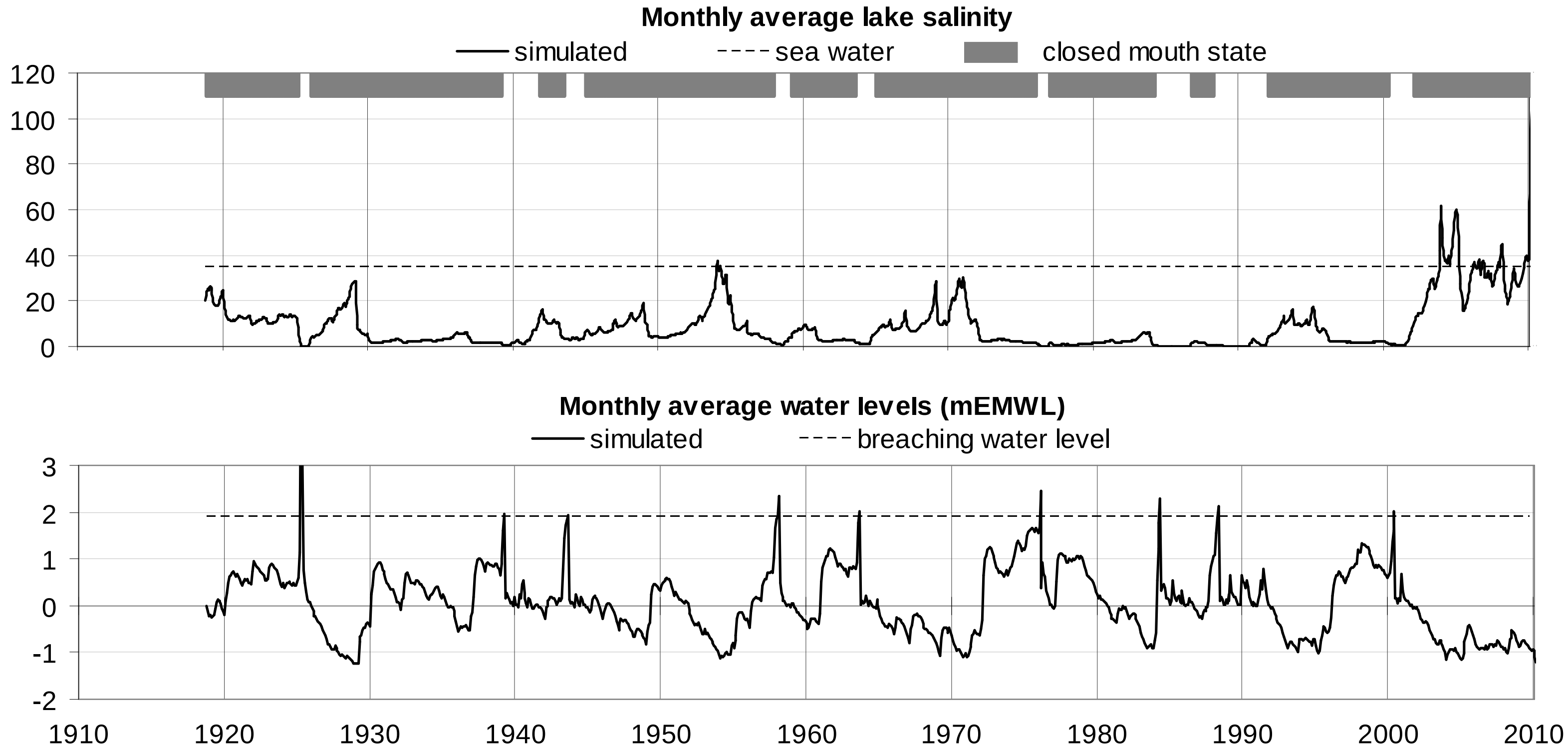

Figure 4.6: Simulated monthly average lake salinities and mouth states using “natural” flows (prior to any losses due to anthropogenic activities) for Scenario 2. These results should be compared with those shown in Figure 4.4.

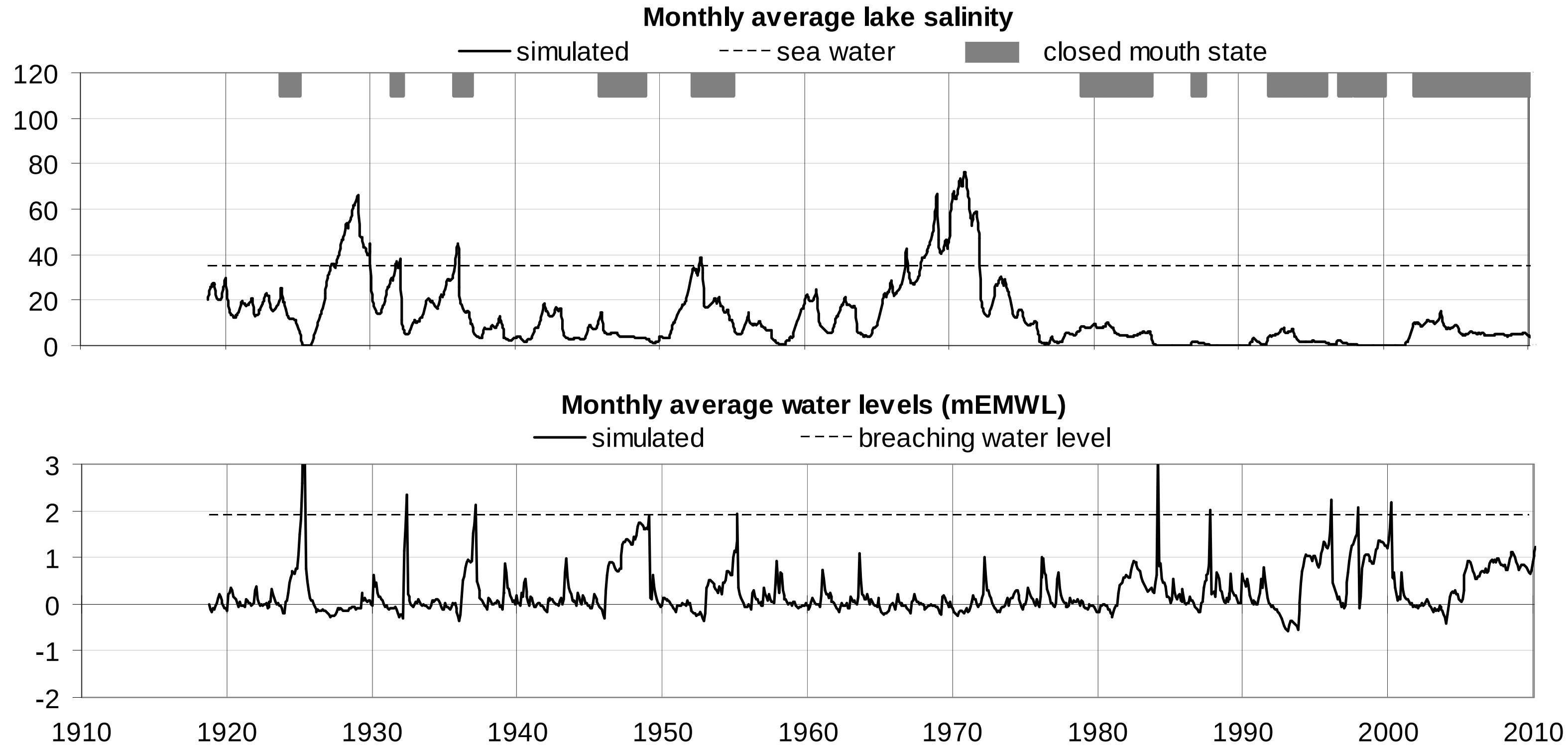

Figure 4.7: Simulated monthly average lake salinities and mouth states using "natural" flows (prior to any losses due to anthropogenic activities) for Scenario 3. These results should be compared with those shown in Figure 4.5.

Table 4.3: Summary of average annual lake water balance contributions for scenarios 2 and 3. Negative values are losses from the lake basin while positive values are gains. The values in brackets are estimates for "natural" conditions before human impacts.

Contributions (Mm^3)	**Scenario 2**	**Scenario 3**
Catchment inflows	279 (343)	279 (343)
Lake rainfall	248 (261)	288 (303)
Mouth inflow	5 (5)	55 (58)
Mfolozi (when mouth closed)	0 (0)	156 (110)
Mouth outflow	-130 (-187)	-312 (-322)
Evaporation	-402 (-422)	-467 (-491)

4.4 Discussion

4.4.1 Overview of modelling results

The simulations elucidate how the separation of the Mfolozi/St Lucia inlets has had a major impact on the natural functioning of the system. In particular, scenario 3 shows that prior to 1952 the system mostly remained connected to the sea via a combined inlet and only closed for short periods during droughts. Hypersaline conditions occurred during dry conditions and while the mouth remained open. When the mouth closed salinities were diluted by Mfolozi inflows.

In contrast, scenario 2 simulations suggests that the post-1952 inlet configuration, without any mouth manipulation, results in a predominantly closed system that is only connected to the sea for brief periods during wet conditions i.e. when there are high freshwater flows into the lake. Salt loadings are therefore low because of limited seawater influxes. However, in this scenario water levels are very variable and can fall to low levels during droughts with desiccation of large portions of the lake.

In terms of impacts on the water/salinity regime of the system, the simulations show that the change in mouth dynamics due to separation from the Mfolozi is much more significant than the reduced terrestrial inflows into the lake.

Table 4.4: Summary of key simulation statistics regarding the functioning of St Lucia for scenarios 2 and 3. The values in brackets are for "natural" conditions before human impacts.

Description	**Scenario 2**	**Scenario 3**
(a) *Mouth state statistics*		
Mouth open	12% (18%)	70% (80%)
Mouth closed	88% (82%)	30% (20%)
No of breaching events	8 (9)	11 (8)
Avg open duration (yrs)	1.2 (1.6)	5.2 (8.0)
Avg closed duration (yrs)	9.0 (7.6)	2.5 (2.2)
(b) *Salinity statistics*		
< 4	45% (50%)	19% (27%)
$5 \rightarrow 35$	43% (47%)	67% (60%)
$36 \rightarrow 65$	5% (3%)	12% (11%)
> 65	7% (0%)	2% (2%)
Median salinity	6 (4)	16 (13)
Avg salt loading (Mtons)	2 (2)	7 (6)
(c) *Water level statistics*		
< -1.0 m	16% (4%)	0% (0%)
$-1.00 \rightarrow -0.25$ m	26% (30%)	6% (2%)
$-0.25 \rightarrow +0.25$ m	30% (30%)	64% (72%)
$+0.25 \rightarrow +1.0$ m	20% (27%)	21% (15%)
$> +1.0$ m	8% (9%)	9% (10%)

The basic reason for the change in the mouth dynamics of St Lucia when separated from the Mfolozi is clear from the water balance results summarized in Table 4.3. Total terrestrial outflows through a combined inlet are on average about 6 times higher than those through a separate St Lucia inlet (about 900 Mm^3 per year versus 150 Mm^3). The increased outflows maintain the inlet in an open state for longer by flushing sediments that accumulate in the mouth during low flows.

The anthropogenic impacts highlighted here are similar to those for other major systems worldwide (see e.g. McLusky and Elliot [2004]; Wolanski [2007]). Two examples are the Coorong estuary in Australia [Webster, 2010] and the Chilika lagoon in India [Gosh *et al.*, 2006]. The Coorong is managed using a strategy analogous to that of scenario 1: the mouth is artificially maintained in an open state by dredging because terrestrial flows have been substantially reduced by agricultural abstractions. Like St Lucia, the system now develops reverse salinity gradients and hypersalinity during low flow conditions. On the other hand, the Chilika lagoon is similar to St Lucia under scenario 2: inflow changes due to abstractions and impoundments, together with mouth sedimentation and closures, have led to reduced salinities and lower water levels. In both examples the ecological implications have been significant and further interventions are planned to mitigate them [Gosh *et al.*, 2006; Webster, 2010].

4.4.2 The present state of St Lucia

The current state of Lake St Lucia is believed to be unprecedented [Cyrus *et al.*, 2010]. Although drought conditions are nothing new to the system, never before has the desiccation of most of the lake, as experienced in 2006, been historically recorded. Is this a rare but natural event or is it attributable to anthropogenic impacts on the system?

Lake St Lucia experiences wet and dry cycles on decadal time scales. The rainfall index shown in Fig. 4.2 suggests that the current drought is not substantially worse than those experienced in the past (e.g. the 1950s and 1960s). It therefore seems apparent that human impacts are responsible for the current state of the system. Indeed our scenario 2 simulation (Fig. 4.4) shows that the current situation is a direct consequence of the management decision to allow the mouth to close while artificially maintaining the separation of the Mfolozi from St Lucia and is typical of drought conditions in this scenario.

It is evident from the simulations that the system would have had different responses to the current drought for different management strategies. In the case of scenario 1, where the mouth is artificially kept open, Fig. 4.3 shows that hypersaline conditions would have occurred but water levels would have been maintained near EMWL.

In the case of Scenario 3, where the Mfolozi and St Lucia have a combined inlet and there is minimal management intervention, the simulations (Fig. 4.5 and Table 4.4) suggest that the mouth would have stayed open for longer after the onset of the drought, and that salinities would have increased during that period. However, the mouth would then have closed and salinities reduced due to dilution by Mfolozi inflows. Water levels would also not have reduced substantially below EMWL and may even have increased.

4.4.3 Biological responses for each scenario

The water and salt budgets are fundamental drivers of the biological functioning of the ecosystem. The simulations show that the physico-chemical environment associated with various scenarios are very different and may be expected to result in fundamental changes in biological structure. An indication of these biological responses can be found in recent observations by Govender *et al.* [2011]; Cyrus *et al.* [2010] and Perissinotto *et al.* [2010a, 2010b] who all reported significant changes at St Lucia during the current drought cycle that started in 2002. Salinity and water level are key drivers of these changes which include a severe loss of biodiversity and an inability to sustain a viable food web when water levels drop to low levels. It is therefore evident that when salinities exceed the tolerance levels of keystone species it can trigger major changes in biological structure.

The persistence or residence times associated with particular salinity/water level regimes is also important since the recruitment, growth and/or adaption of species requires some time to occur. Scenarios 2 and 3 also have quite different characteristics in this regard - the former has relatively more variable water levels (and thus depths) while the latter has more variable salinities (Table 4.4). Models that link biological changes to the results from the water/salinity balance model in a dynamic way are required to provide more detailed insights into ecological responses for the different scenarios.

4.4.4 Management implications

Management interventions in the functioning of St Lucia over the last 50 years have focussed on changes to the inlet configuration, manipulation of the mouth state through breaching and/or dredging, general sedimentation control through dredging, and development of schemes to increase freshwater inputs.

An important management question is whether to maintain an artificially open mouth state or to allow the mouth close naturally at the onset of drought conditions (Taylor, 2006). Simulations of scenarios 1 and 3 show that when the mouth is open during drought periods, salinities increase approximately linearly while water levels remain fairly constant due to the influx of sea water. Taylor [2006] noted that the combination of average water levels ($\sim$ EMWL) and high salinities in 1970 caused fringe vegetation to die with subsequent wave-driven erosion of the lake shoreline. However, the current management policy of allowing the mouth to close at the onset of droughts means that water levels may fall to low levels with widespread desiccation since the freshwater supply cannot fully compensate for evaporation losses under these conditions. The water balance model provides managers with a means to evaluate the outcomes of the different management options under various future rainfall scenarios - an example is given in Lawrie and Stretch [2010].

Management schemes to supplement the fresh water supply to the lake by transfers from nearby catchments have been considered in the past e.g. Hutchison [1976] identified and evaluated various options. Some were subsequently partially implemented but did not prove to be entirely successful nor sustainable [Whitfield & Taylor, 2009]. The results shown in Figures 4.6 and 4.7, indicate that additional freshwater inputs of 60 Mm^3 per year (which would effectively restore "natural' inflow volumes) would significantly decrease salinities and the risks of desiccation. However, the mouth dynamics would not be significantly impacted. A more detailed recent evaluation of this option is given by Lawrie and Stretch [2010].

A perceived threat of sedimentation due to the silt-laden Mfolozi is a fundamental driver for the strategy of artificially maintaining a separate Mfolozi inlet (e.g. Cyrus and Blaber [1988]; Grenfell and Ellery [2009]; Cyrus *et al.* [2010]; Taylor [2006]; Whitfield & Taylor [2009]. The issue is however poorly understood and there appears to be no scientific evidence linking sedimentation of the St Lucia lake basin to the Mfolozi. Given its historically important role in the management of St Lucia there is clearly a need for a sediment budget to clarify the origins and transport of sediments in the system. Of particular concern is the dynamics of fine suspended sediments in the clay/silt particle size range (1μm – 60μm) for which flocculation processes can be important.

The outflows created by mouth breaching events can have magnitudes similar to those of large floods [Parkinson and Stretch, 2007]. The implication is that these flows may result in substantial scouring of accumulated sediments from the mouth and narrows and thus play an important role in the sediment budget of the system. Artificial manipulation of the mouth state, including premature breaching at low water levels, may reduce the scour potential of these breaching events. Furthermore, the number of breaching events in scenario 2 is significantly less than for scenario 3 (Table 4.4) so that differences in the sediment dynamics may be expected. The water balance statistics also reflect significantly higher average outflows for scenario 3 which will also play a role in the sediment budget.

Climate change may significantly affect the long-term management requirements for St Lucia and other similar systems. An example is the prediction of an increase in the frequency of extreme events [Hewitson *et al.*, 2005; Mason *et al.*, 1999]. More frequent and/or severe droughts will have obvious effects in the context of the results presented here e.g. more severe episodic hypersaline events. Similarly, changes to the frequency and/or intensities of floods will also have significant impacts e.g. on breaching patterns and sediment loadings.

4.4.5 Uncertainties in the model

Are the results of the water balance simulations robust to changes in the underlying assumptions, parameters and data embedded in the formulation of the model?

Sources of uncertainties in the model include (1) the simulated hydrological input data; (2) the physical data for the lake basin (bathymetry and hypsometry); (3) the sub-model for the inlet hydraulics; (4) the sub-model for the mouth dynamics. The agreement between measured and simulated salinities and water levels shown in Figure 4.3 gives confidence in the basic hydrological and physical data and suggest that the results are robust with respect to those factors. With respect to the inlet hydraulics, simulations suggest that the salt balance can be sensitive to modeled inflows and outflows (see §4.2.3.3) in some scenarios e.g. in scenario 2 the salt loadings in the lake are sensitive to seawater inflows during the short open mouth periods, and salinities during subsequent closed mouth periods can change, but the patterns of variation remain the same. The overall model results can also be sensitive to the mouth dynamics. The morphodynamics of inlets on sandy coastlines with energetic wave climates involve complex processes while the current rule-based mouth state model is simple and pragmatic in the spirit of Occam's razor. Nevertheless mouth states predicted by the model mimic historical observations well and a more sophisticated model is therefore unlikely to change the basic conclusions regarding the difference in mouth states between scenarios 2 and 3. Overall we conclude that the simulation results are robust to reasonable uncertainties in the model formulation and data.

4.5 Conclusions

In this study we have used scenario simulations to investigate the impacts of inflow changes and management strategies (particularly those concerning mouth state manipulation) on the functioning of St Lucia. These issues are common to many important estuarine systems worldwide.

The main conclusion of our water balance simulations is that the separation of the Mfolozi and St Lucia mouths is by far the most significant anthropogenic intervention in terms of long-term impacts on the functioning of the St Lucia system. Aside from providing an important source of fresh water inflow to the system during dry conditions, the Mfolozi also plays a pivotal role in providing a more stable mouth state regime for the system. This is due to the large increase in mouth outflows that counteract the tide-driven sediment influxes and thus maintain an open mouth for most of the time. In other words it is not only the supply of water into the lake, but also the flow of water out of the mouth that are key to the "natural" functioning of the system. Therefore the restoration and sustainability of the system seems to depend on restoring a fully functional combined tidal inlet fed by both the lake and the Mfolozi.

Our simulation results suggest that an appropriate "minimum impact" management strategy should avoid persistent interference with the inlet configuration - as has occurred in the last 50 years - and instead focus on minimal intervention supplemented by monitoring and guided by predictive "what if" modeling. In particular this means re-establishing a combined Mfolozi/St Lucia inlet with minimal mouth manipulation. The monitoring program, together with ongoing research, should focus on the sedimentation issue and on a deeper understanding of the mouth dynamics. Furthermore, to fully understand the implications of the impacts discussed in this paper requires linking the water level/salinity dynamics to the biological responses of the ecosystem.

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Chapter 5

Occurrence and persistence of water level/salinity states and the ecological impacts for St Lucia estuarine lake, South Africa

This chapter is based on the paper: Lawrie, R.A. and Stretch, D.D, 2011. Occurrence and persistence of water level/salinity states and the ecological impacts for St Lucia estuarine lake, South Africa. Estuarine Coastal and Shelf Science 95, 67–76.

Abstract

The St Lucia estuarine lake in South Africa forms part of a World Heritage Site and is an important local source of biodiversity. Like many estuarine systems worldwide, St Lucia has experienced significant anthropogenic impacts over the past century. Abstractions have decreased fresh water inflows from the lake catchments by about 20 %. Furthermore the Mfolozi river, which previously shared a common inlet with St Lucia and contributed additional freshwater during droughts, was diverted from the system in 1952 because of its high silt loads. The separated St Lucia mouth was subsequently kept artificially open until the onset of a dry period in 2002 when the mouth was left to close naturally. These changes and the current drought have placed the system under severe stress with unprecedented hypersaline conditions coupled with desiccation of large portions of the lake. Long term simulations of the water and salt balance were used to estimate the occurrence and persistence of water levels and salinities for different management scenarios. The risks of desiccation and hypersalinity were assessed for each case. The results show that the configuration of the Mfolozi/St Lucia inlets plays a key role in the physico-chemical environment of the system. Without the Mfolozi link desiccation (of about 50 % of the lake area) would occur for 32 % of the time for an average duration of 15 months. Artificially maintaining an open mouth would decrease the chance of desiccation but salinities would exceed 65 about 17 % of the time. Restoring the Mfolozi link would reduce the occurrence of both desiccation and hypersaline conditions and a mostly open mouth state would occur naturally. Integrating these modeled scenarios with observed biological responses due to changes in salinity and water depth suggests that large long-term changes in the biological structure can be expected in the different management scenarios.

5.1 Introduction

The St Lucia estuarine lake on the east coast of South Africa has a surface area of about 300 km^2 and average depth of 1 m. It is the largest of its kind in Africa and along with a number of other important ecological attributes has been identified as an important juvenile fish nursery area on the south-east African coastline [Cyrus *et al.*, 2010; Vivier *et al.*, 2009]. The lake is part of the iSimangaliso World Heritage site.

Like many estuarine systems worldwide, fresh water reductions and other anthropogenic impacts have drastically altered the natural functioning of St Lucia over the past century [Kennish *et al.*, 2008; Lawrie and Stretch, 2011; Whitfield & Taylor, 2009; Hutchison & Pitman, 1977]. Appropriate management is required in order to prevent further degradation and sustain the important ecosystem services provided by systems like St Lucia.

Lawrie and Stretch [2011] investigated the anthropogenic impacts on the water and salt budgets of St Lucia. Their results indicate that before 1952 the Mfolozi was both an important source of freshwater to the lake during dry conditions and had a pivotal role in providing a more stable mouth state regime for the system. The Mfolozi river was artificially diverted to a separate inlet in 1952 because of concerns regarding the impact of increasing silt loads on the sedimentation of St Lucia. This management intervention has caused significant changes to the mouth dynamics and the salinity/water level characteristics of the system (see also Hutchison and Midgley [1978]; Hutchison & Pitman [1977]).

Lake water levels and salinities change continually depending on cyclic wet and dry seasons and on the mouth state. The occurrence and persistence of specific water level and salinity states are basic drivers for biological functioning. The St Lucia system has recently been subjected to severe drought conditions following closure of the mouth in 2002. Extremely low water levels, hypersaline conditions and desiccation of up to 90 % of the lake have occurred and caused major impacts on the system, most notably severely reduced biodiversity [e.g. Cyrus *et al.*, 2010; Whitfield & Taylor, 2009]. In the past the biological components have shown considerable resilience in recovering from less extreme conditions [Taylor, 2006], but questions remain concerning the long-term health and sustainability of the system. It is therefore important to understand the way that management interventions can influence the occurrence and persistence of specific physico-chemical states, as well as the biological responses that may be expected as a result of any changes [see e.g. Sutherland, 2006].

High salinities also occur at other important estuarine lakes when evaporative losses are higher than fresh water inputs. The Coorong in South Australia is a well known example where similar impacts have been reported [Webster, 2010]. Alternatively, at Lake Chilika in India reduced water levels and lower salinities have occurred due to constricted (or closed) mouth conditions, and have led to ecosystem changes such as loss of biodiversity and reduced fish catches [Ghosh *et al.*, 2006].

Building on the work of Lawrie and Stretch [2011] the objective of this study was to use simulations to investigate the occurrence and persistence of water levels and salinities at St Lucia during wet and dry cycles and under different management scenarios, and the broad implications for the biological functioning of the system. The key research questions for each management scenario include: (1) what are the dominant water level and salinity states of the system (i.e. the most probable and persistent states); (2) what are the risks of extreme adverse conditions i.e. very low water levels and/or very high salinities; (3) what are the likely biological responses to the physico-chemical conditions characteristics of each scenario.

5.2 Methods

5.2.1 The case study site

St Lucia is a sub-tropical estuarine lake (Figure 5.1) that experiences wet and dry periods on decadal time scales. The lake has a mean annual rainfall of about 300 Mm^3 and mean annual evaporation losses of 450 Mm^3. It therefore depends on catchment inflows which contribute an average of 300 Mm^3 annually. This has been reduced from an original 370 Mm^3 due to human activity (refer Lawrie and Stretch [2011] and references cited therein). Simulations indicate that when the Mfolozi and St Lucia had a combined inlet, as in the past, the Mfolozi contributed an average annual fresh water inflow of about 150 Mm^3 and maintained an open mouth state for about 70 % of the time. With the inlets separated (as they have been since 1952) St Lucia is predicted to remain closed for more than 80 % of the time without active mouth management. In either scenario the intermittent link to the sea and cyclic climatic patterns create a very variable physicochemical environment and a dynamic ecosystem [Taylor, 2006].

Lawrie and Stretch [2011] defined three key management scenarios for their investigation of the water and salt budgets of St Lucia, namely:

Scenario 1: Separate Mfolozi and St Lucia inlets with management interventions to keep the St Lucia mouth open and maintain inlet separation. This corresponds to the actual situation that prevailed between 1952 and 2002.

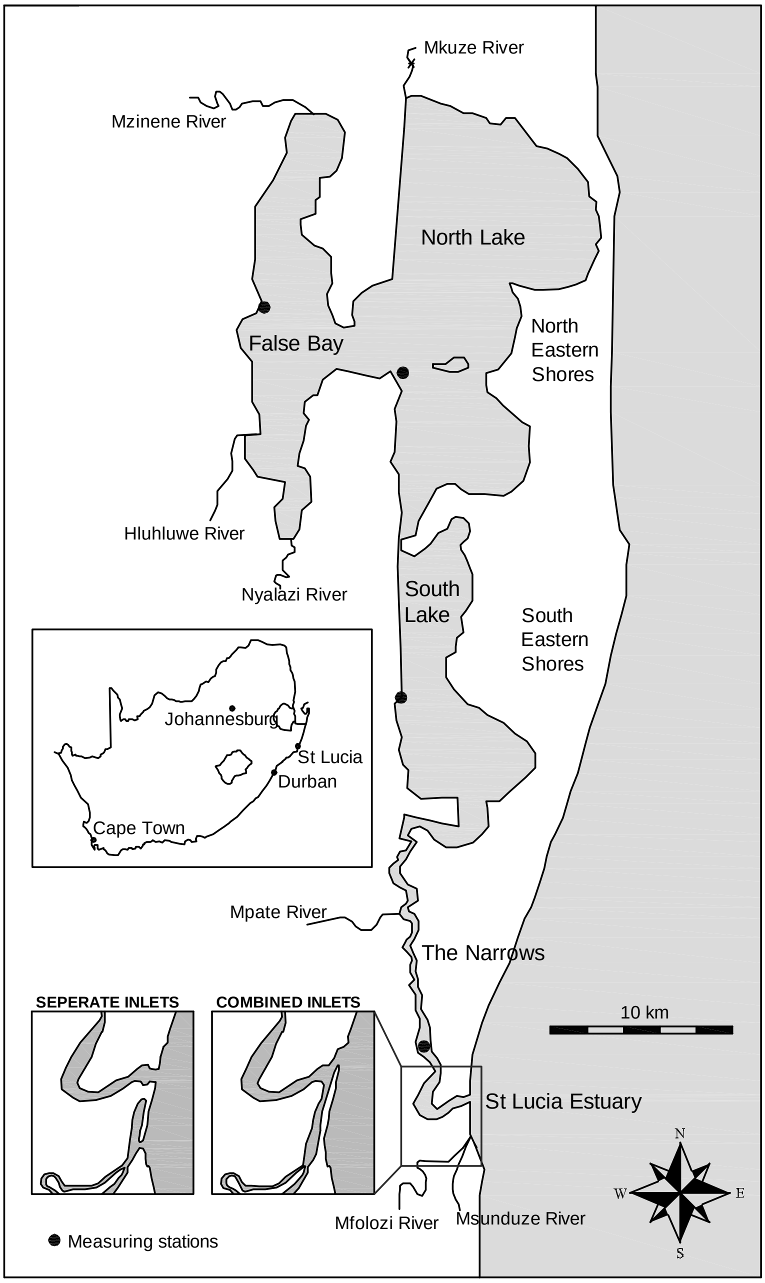


Figure 5.1: Location map for St Lucia on the east coast of South Africa. Also shown are the different mouth configurations i.e. with separate and combined Mfolozi/St Lucia inlets and also the positions of the salinity and water level measurement stations.

Scenario 2: Separated Mfolozi and St Lucia inlets but without any mouth manipulation to keep St Lucia open. This reflects the management strategy since 2002.

Scenario 3: A combined Mfolozi/St Lucia inlet with no active manipulation i.e. the "natural" state of the system.

5.2.2 Salinity and water levels

5.2.2.1 Measurements

Monthly average salinities (from 1958) and water levels (from 1963) have been measured at a number of stations around the lake by EKZN Wildlife and the Department of Water Affairs, respectively (refer Figure 5.1). These data provide an indication of the water level and salinity characteristics of the system with an artificially open mouth and separate Mfolozi and St Lucia inlets (as defined in scenario 1).

5.2.2.2 Simulations

Scenario 2 describes the management strategy since 2002 when the mouth was left to close. The system has experienced significant desiccation and hypersalinity since then and there are insufficient data available to establish long term trends for this scenario. Furthermore, since the Mfolozi was separated from St Lucia in 1952 there are also no detailed data available for a scenario where the two systems have a combined mouth. Therefore average water levels and salinities were simulated using the water and salt balance model. The general features of these simulations are discussed in Lawrie and Stretch [2011]. In this paper we focus in more detail on the occurrence and persistence of the water level/salinity states of the system and how they evolve.

5.2.2.3 Defining salinity and water level states

The monthly averaged salinities and water levels were classified into 6 different ranges as defined in Table 5.1. The selected salinity ranges are consistent with those used to delineate salinity-based ecological states by Taylor [2006]. Water level ranges were selected to provide a broad range of lake surface areas based on the hypsometric data reported by Hutchison [1974]. Lake levels are given relative to the Estuary Mean Water Level (EMWL) which is the average water level when the mouth is open. EMWL is 0.45 m above Geodetic Mean Sea Level (GMSL) which is the vertical land leveling datum used in South Africa. The actual mean sea level at this location is about +0.2 m GMSL. When water levels are −0.5 m EMWL the lake surface area is reduced by 25 % relative to that at EMWL and at −1.0 m EMWL the surface area is decreased by about 50 %.

Table 5.1: Definition of salinity and water levels states for the St Lucia estuarine-lake [salinity states adapted from Taylor, 2006].

States	**Ranges**
Salinity states	(psu)
1. Fresh	≤ 4
2. Brackish	5 – 12
3. Low estuarine	13 – 25
4. High estuarine	26 – 45
5. Hypersaline	46 – 65
6. Extreme hypersaline	> 65
Water level states	(m EMWL)
1. Very Low (> 50 % desiccated)	$\leq$ - 1.0
2. Low (25 – 50 % desiccated)	$-1.0 \rightarrow -0.5$
3. Med/low (< 25 % desiccated)	$-0.5 \rightarrow 0.0$
4. Med/high	$0.0 \rightarrow 0.5$
5. High	$0.5 \rightarrow 1.0$
6. Very high	> 1.0

5.2.2.4 Occurrence and persistence statistics

The occurrence probability of each water level/salinity state is a measure of that state's importance as a physico-chemical driver of the system. It was estimated from the long-term simulated data by accumulating all the time spent in each state as a proportion of the total duration of the simulation.

The average persistence time of a particular water level/salinity state is an indication of the time available for the system to adjust to that state. It was estimated from the simulated data by calculating the average duration for occurrences of that state.

While occurrence and persistence are useful statistical indicators of the water level/salinity regime for each scenario, it is also important to understand how conditions evolve and change in time. This can influence how biological systems adapt to the changes. For example there may be hysteresis effects associated with the temporal history of changes. Therefore time histories or "trajectories" through the water level/salinity state space were also extracted from the data and analyzed.

5.2.3 Biological responses

A detailed analysis of ecosystem responses for St Lucia is beyond the scope of this paper. However, some basic insights into the biological responses in different physico-chemical conditions can be obtained from published observations made by various researchers over the last 50 years.

During the period from 1952 to 2002 St Lucia was artificially separated from the Mfolozi and an open mouth was maintained (i.e. scenario 1). Publications that deal with the responses of various biological components under these conditions include: (a) *Birds* – Berruti [1983]; (b) *Fish* – Forbes & Cyrus [1993]; Whitfield [1982]; (c) *Macrobenthic fauna* – Boltt [1975]; Blaber *et al.* [1983]; Forbes & Cyrus [1993]; Weerts [1993]; (d) *Zooplankton* – Grindley [1982]; (e) *Microalgae* – Fielding *et al.* [1991]; Johnson [1976]; (f) *Macrophytes* – Taylor [1987, 2006, 1993]; Taylor *et al.* [2006]; Ward [1982].

After 2002 manipulation of the St Lucia mouth ceased, but separation from the Mfolozi was artificially maintained (i.e. scenario 2). The St Lucia mouth closed as a result of this change except for a brief 5-month interval from March to August 2007 after it was breached by high waves [Cyrus *et al.*, 2010; Lawrie and Stretch, 2011; Whitfield & Taylor, 2009]. The closed system has experienced low water levels (including desiccation of large areas), hypersaline conditions, and lack of recruitment from the ocean due to the closed mouth state. Publications that deal with the responses of various biological components under these conditions include: (a) *Birds* – Whitfield *et al.* [2006]; (b) *Fish* – Whitfield *et al.* [2006]; Vivier *et al.* [2009]; (c) *Macrobenthic fauna* – MacKay *et al.* [2010]; Pillay & Perissinotto [2008]; (d) *Zooplankton* – Carrasco *et al.* [2010]; Jerling *et al.* [2010]; (e) *Microalgae* – Perissinotto *et al.* [2010]; (f) *Macrophytes* – Taylor [2006]; Taylor *et al.* [2006].

Prior to 1952 the St Lucia/Mfolozi system functioned without significant management intervention but the available information on biological responses under those conditions is limited to the work of Day *et al.* [1954] who provided information on a range of biological components.

Analysis of the occurrence and persistence of water level/salinity states for the three key management scenarios was integrated with information from the abovementioned references to deduce likely biological responses for each management scenario and for various water level/salinity ranges. To simplify this process the salinity/water level states defined in Table 5.1 were further grouped into only 3 ranges each to represent high (H), medium (M) and low (L) values. For example low values are those that fall within the combined range of states 1 and 2, while medium values are in states 3 and 4, etc. The focus was on biodiversity (or number of species recorded) and abundance (or biomass) of key biological components, both of which were classified in relative terms as simply high, medium or low. This preliminary classification is essentially qualitative while future work may apply quantitative methods such as statistical cluster analysis to delineate characteristic ecosystem states – an example is the work of Lester & Fairweather [2009] on the Coorong estuary in South Australia.

The actual occurrence of particular ecosystem states will depend on the persistence of their associated salinity/water level states as well as the time history of changes. For example Whitfield *et al.* [2006] noted that macrophytes require about 6 months to get established after salinity conditions become favorable for them. Hysteresis effects may also occur in the biological responses – for example the response during times when salinities are increasing and water levels are decreasing could be different if/when the direction of the changes is reversed.

5.3 Results

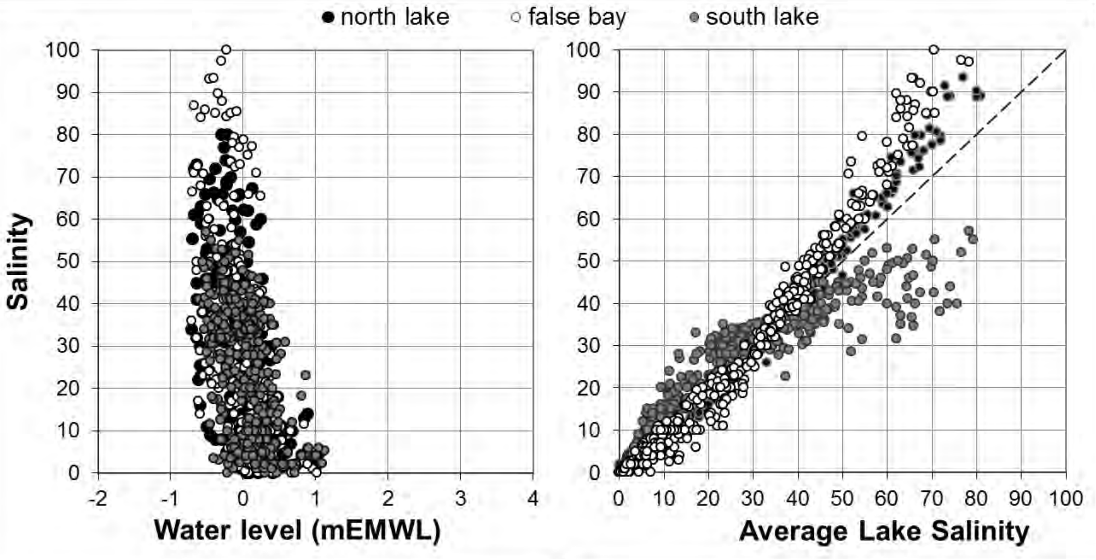
5.3.1 Overview of lake water levels and salinities

The prolonged connection to the sea in scenario 1 led to relatively stable water levels but salinities varied significantly with the changes in rainfall and freshwater inflows. Measured water levels and salinities for North Lake, False Bay and South Lake for the period 1963 – 2002 are shown in Figure 5.2a. Measured salinities were also plotted against the average lake salinity in Figure 5.2b to show the spatial divergence from the mean under different conditions. When average lake salinities are below 35 there is a normal salinity gradient i.e. low salinities in the northern reaches of the lake increasing towards that of sea water near the mouth. This occurs during wet periods when freshwater inflows are high. As average salinities increase above 35 a reverse salinity gradient develops as sea water flows into the lake to compensate for evaporative losses during dry conditions. Note that extreme hypersalinity (> 65) occurred 15 % of the time in North Lake and 7 % in South Lake from 1963 – 2002.

After the mouth closed in 2002 water levels dropped – low water levels and associated desiccation of exposed areas can only occur when the mouth is closed. The northern parts of the lake are more susceptible to these conditions because of the volume distribution and hypsometry of the lake basin.

Figure 5.3 shows scatter plots of simulated monthly averaged lake salinities and water levels for each management scenario. Spatial variations are not resolved by the model and the results shown are averages over the whole lake. Figure 5.2b can be used to infer spatial variations if required.

The water level – salinity combinations vary considerably for the different management scenarios. Results from scenario 1 simulations (Figure 5.3a) mimic those of the measurements shown in Figure 5.2 with small water level variations but highly variable salinities. For the scenario 2 simulations (Figure 5.3b) the mouth is predominantly closed due to the separation from the Mfolozi. In closed mouth conditions the water levels and salinities vary widely in response to rainfall and evaporation but the salt loading remains constant. Each of the salinity/water level trajectories visible in Figure 5.3b represents a separate closed mouth period



(a) (b)

Figure 5.2: (a) Measured water levels vs salinities from 1963 until 2002 (open mouth conditions) in North Lake, False Bay and South Lake and the (b) measured salinity of each station vs the average lake salinity.

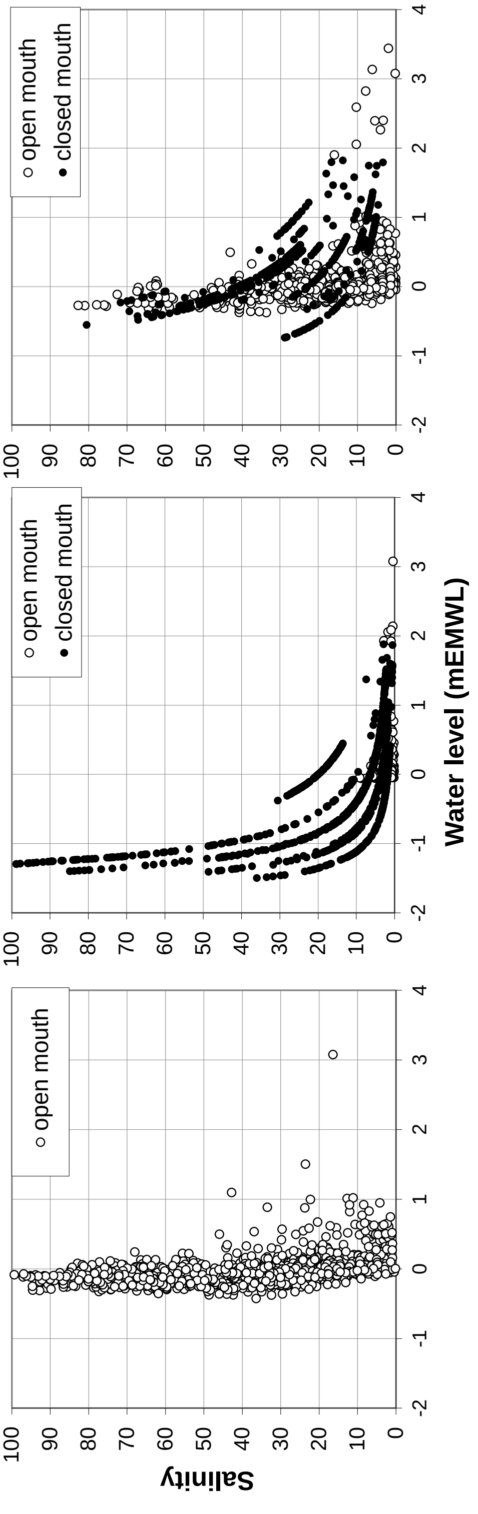
with a different salt load.

Scenario 3 with a combined Mfolozi/St Lucia inlet (Figure 5.3c) yields a mostly open mouth that only closes during extended dry periods. When the mouth closes fresh water from the Mfolozi enters the lake and reduces salinities and increases water levels. In this case the general trend is from high salinities and medium/low water levels to low salinities and high water levels until the mouth breaches. This is similar to scenario 2 during closed mouth conditions. The highest salinities in scenario 3 occur when the mouth is open during persistent dry conditions and where the trends are similar to those of scenario 1.

5.3.2 Trajectories through the salinity/water level state space

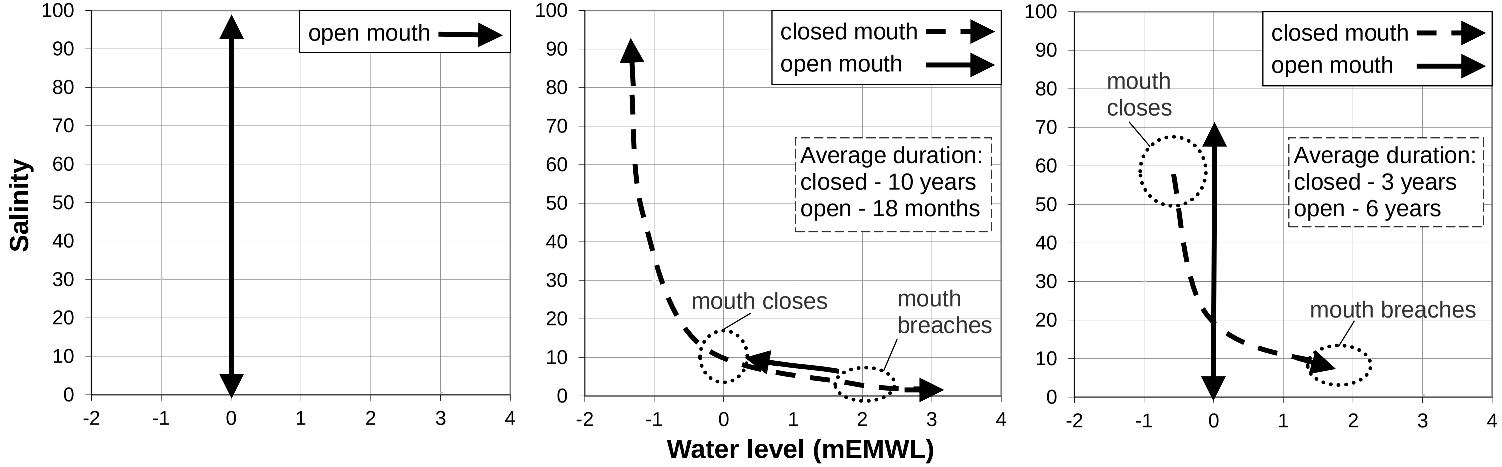
The main trajectories through the water level/salinity state space for each scenario are evident in Figure 5.3 and are summarized schematically in Figure 5.4.

There are two main trajectories that are associated with open and closed



(a) (b) (c)

Figure 5.3: Long term average lake water level vs salinity for (a) scenario 1, (b) scenario 2 and (c) scenario 3. Open symbols denote open mouth states while solid symbols denote closed mouth states



(a) (b) (c)

Figure 5.4: Schematic depiction of the main trajectories in the salinity - water level state space for (a) scenario 1, (b) scenario 2 and (c) scenario 3.

mouth states respectively. During open mouth conditions there is a 1-dimensional bi-directional pathway in the salinity/water level state space. This characterizes scenario 1 but also occurs in other scenarios when the mouth is open. Under closed mouth conditions the salinities and water levels follow characteristic curved trajectories. These pathways are bi-directional in scenario 2 and uni-directional in scenario 3 when the mouth closes (refer Figures 5.3b, c and 5.4b, c).

In scenario 2 the closed mouth trajectories extend to more extreme values than in scenario 3 (refer Figure 5.4b). In extreme conditions the system is prone to desiccation and hypersalinity in this scenario. The combination of low lake levels and high salinities is unique to scenario 2 and reflects the actual current situation in the lake. These extreme conditions are unprecedented in the recorded history of St Lucia and are a direct consequence of human intervention in the inlet configuration and mouth state i.e. the scenario 2 management strategy.

5.3.3 Occurrence and persistence of water level/salinity states

Marginal occurrence probabilities for the salinity and water level states and for the three management scenarios are summarized in Table 5.2.

High salinities occur in each scenario and are a feature of any estuarine system. Hypersaline conditions are however most common in scenario 1 (Table 5.2). Salinities exceed that of seawater about 45 % of the time of which extreme hypersalinity (≥ 65) occurs 17 % of the time. Fresh conditions are only expected to occur 6 % of the time (Table 5.2).

Salinities are more variable in scenario 3 but remain below 45 for 90 % of the time and extreme hypersalinity is rare. Water levels mostly remain above -0.5 mEMWL so that significant desiccation does not occur.

Scenario 2 is predominantly a fresh water system. There is a 41 % probability that salinities are below 4 (Table 5.2) and a 10 % chance that salinities exceed that of sea water. Hypersaline conditions then occur in combination with very low water levels and desiccation. Water levels are below -0.5 mEMWL for about 30 % of the time (> 25 % desiccation) and below -1.0 mEMWL for 18 % of the time (> 50 % desiccation).

Table 5.2: Marginal occurrence probabilities for each salinity and water level state and for the three management scenarios defined in Section 5.2.2.1.

STATES	**Scenario 1**	**Scenario 2**	**Scenario 3**
Average salinities			
1. Fresh (≤ 4)	6 %	41 %	14 %
2. Brackish (5 – 12)	13 %	28 %	26 %
3. Low estuarine (13 – 25)	21 %	16 %	27 %
4. High estuarine (26 – 45)	29 %	7 %	24 %
5. Hypersaline (46 – 65)	15 %	2 %	7 %
6. Extreme hypersaline (> 65)	17 %	6 %	2 %
Water level ranges (m)			
1. $\leq$ -1.0 (Note 1)	0 %	18 %	0 %
2. -1.0 → -0.5 (Note 2)	0 %	15 %	1 %
3. -0.5 → 0	60 %	22 %	41 %
4. 0 → +0.5	35 %	26 %	40 %
5. +0.5 → +1.0	3 %	11 %	13 %
6. $\geq$ +1.0	1 %	8 %	5 %

NOTE 1 : > 50 % OF THE AVERAGE LAKE AREA DESICCATED

NOTE 2 : 25 – 50 % OF THE AVERAGE LAKE AREA DESICCATED

Joint occurrence probabilities and persistence times for all water level/salinity states and for the three management scenarios are shown as bubble plots in Figures 5.5 and 5.6.

In Scenario 1 the system spends from 1 to 7 months in each state and changes states frequently. With a permanent connection to the sea, salinities > 45 occur for an average of 17 months at a time and hypersaline conditions persist for about 10 months at a time. Once water levels drop below -0.25 mEMWL they remain in that state for about 3 months before sea water inflow stabilizes levels again.

In scenario 2 extreme hypersalinity and desiccation persists for an average of 15 months at a time during dry periods. During wet periods high water levels and fresh conditions occur for about 10 months at a time. The highest persistence times (10 – 15 months) occur in extreme conditions when the mouth is closed or when the mouth is open, otherwise the system changes every 1 to 7 months.

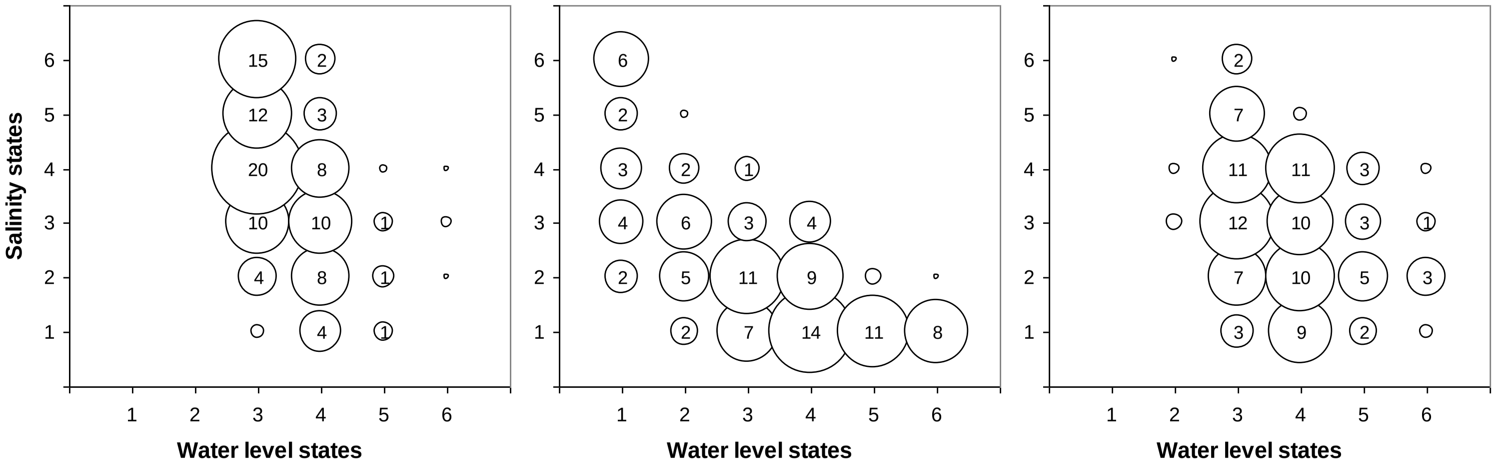
In scenario 3 persistence times are generally shorter than scenarios 1 and 2 and range from 1 to 5 months. The Mfolozi link provides a mostly open inlet and the resulting exchange flows stabilize water levels and salinities. During dry periods, salinities > 45 can occur for about 10 months at a time but Mfolozi inflows prevent extreme hypersaline conditions from persisting for more than about 4 months. The risks of low water levels and significant desiccation are negligible in this scenario.

5.3.4 Biological responses to physico-chemical changes

A consolidated qualitative overview of observed biological responses based on the references cited in section 5.2.3 is shown in Table 5.3. A key to the 9 water level/salinity states used for this assessment is provided below the table (refer Figure 5.7). Blank table entries indicate where there is insufficient information to make even a qualitative judgment or where no species have been found in the lake. Apparent contradictory entries such as ”HIGH/LOW” in the table indicate cases where hysteresis effects may be present i.e. the status is different depending on the direction of the trajectory through the salinity/water level state space. For example, in state L|H piscivorous birds are attracted by high concentrations of fish due to dropping water levels. However, as salinities increase and the fish die, they move away leaving flamingos as a dominant species. Note that the high abundance of macrophyte species in states M|L and M|M are species *Stuckenia pectinatus* and *Ruppia cirrhosa* and/or *Zostera capensis* respectively.

The biological responses for each salinity/water level state, as summarized in Table 5.3, should be viewed together with the occurrence and persistence of the associated states. For example low water levels (below -0.5 m) together with hypersalinity only occur in scenario 2. Furthermore, the establishment of a specific biological response takes some time and will therefore depend on the persistence of that state.

It is evident from the results shown in Table 5.3 that the biological structure of the system has been completely different depending on the predominant physico-chemical states and that these in turn depend on the management scenario.



(a) (b) (c)

Figure 5.5: Percentage of time spent in each salinity-water level state combination for (a) scenario 1, (b) scenario 2 and (c) scenario 3. The area of each bubble is proportional to the magnitude of its associated variable.

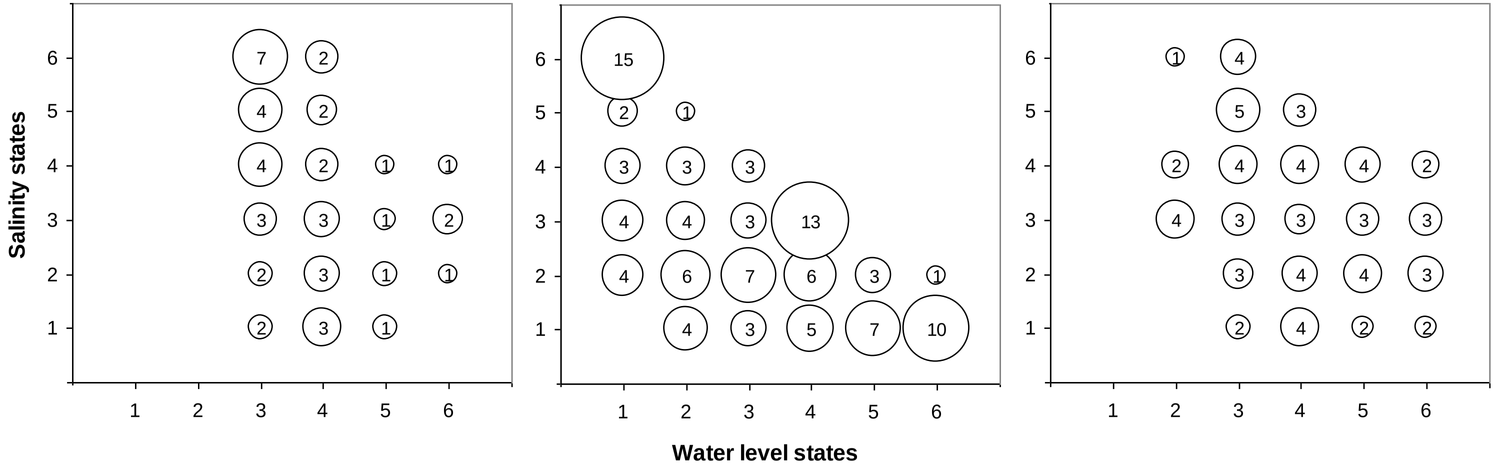


Figure 5.6: Average persistence time (in months) for each salinity-water level state combination for (a) scenario 1, (b) scenario 2 and (c) scenario 3. The area of each bubble is proportional to the magnitudes of its associated variable.

Table 5.3: Qualitative assessment of biological responses in terms of relative levels of biodiversity and abundance/biomass for various biological components. No entry implies insufficient data available or no recordings of that species in that state.References for the table are listed in the footnotes and discussed in Section 5.2.3.

Physicochemical Drivers & Biological Responses : Biodiversity & Key Species Biomass/Abundance											
Component		WaterLevel | Salinity States									
		L|L	L|M	L|H	—— M|L ——		—— M|M ——		M|H	H|L	H|M
Physicochemical Drivers											
Mouth state[1]		closed	closed	closed	closed	open	closed	open	open	closed (open)	closed (open)
Occurrence (%)	– scenario 1	0	0	0	0	17	0	48	32	0 (2)	0 (1)
	– scenario 2	10	14	9	31	10	8	0	0	18 (2)	0 (0)
	– scenario 3	0	1	0	0	29	13	29	9	7 (4)	7 (0)
Persistence (months)	– scenario 1	0	0	0	0	9	0	17	18	0 (2)	0 (2)
	– scenario 2	6	8	11	13	9	28	0	0	15 (2)	0 (0)
	– scenario 3	0	12	1	2	12	7	15	10	16 (2)	2 (1)
WL/Depth	– average	low	low	low	med	med	med	med	med	high	high
Salinity	– average	low	med	high	low	low	med	med	high	low	med
	– spatial gradient	low	med	high	low	low	low	med	high	med	low
Average rainfall/inflows		low	low	low	high	high	med	med	low	high	med
Biological – Primary Producers											
Macrophytes[2]	– abundance	-	med	low	-	high	-	high	low	-	-
Phytoplankton [3]	– biomass	-	med	low	-	-	-	-	high	-	-
Microphytobenthos[3]	– biomass	-	low	high	-	-	-	-	med	-	-
Biological – Consumers/Predators											
Zooplankton[4]	– diversity	-	low	low	med	high	med	high	low	-	-
	– abundance	-	med	low	high	high	high	high	low	-	-
Macrobenthos[5]	– diversity	-	-	low	med	med	med	high	med	-	-
	– abundance	-	-	low	med	high	high	med	low	-	-
Prawns (nekton)[6]	– diversity	-	-	-	low	high	low	high	low	-	-
	– abundance	-	-	-	low	med	med	high	low	-	-
Fishes[7]	– diversity	-	low	low	low	med	med	high	low	-	-
	– abundance	-	low	low	low	med	med	high	low	-	-
Birds[8]	– diversity	-	med	high/low	low	med	med	high	low	-	-
	– abundance	-	high	high/low	low	med	med	high	low	-	-

Notes:

[1] Lawrie & Stretch, 2011 [2] Ward, 1982; Taylor, 2006, Taylor *et al.*, 2006 [3] Fielding *et al.*, 1991; Perissinotto *et al.*, 2010 [4] Grindley, 1982; Cyrus *et al.*, 2009; Jerling *et al.*, 2010 [5] Boltt, 1975; Blaber *et al.*, 1983; Weerts, 1993; MacKay *et al.*, 2010 [6] Fielding *et al.*, 1990 [7] Whitfield, 1982; Cyrus & Vivier, 2006; Whitfield *et al.*, 2006; Vivier *et al.*, 2009 [8] Turpie, 1995; Taylor, 2006; Taylor *et al.*, 2006.

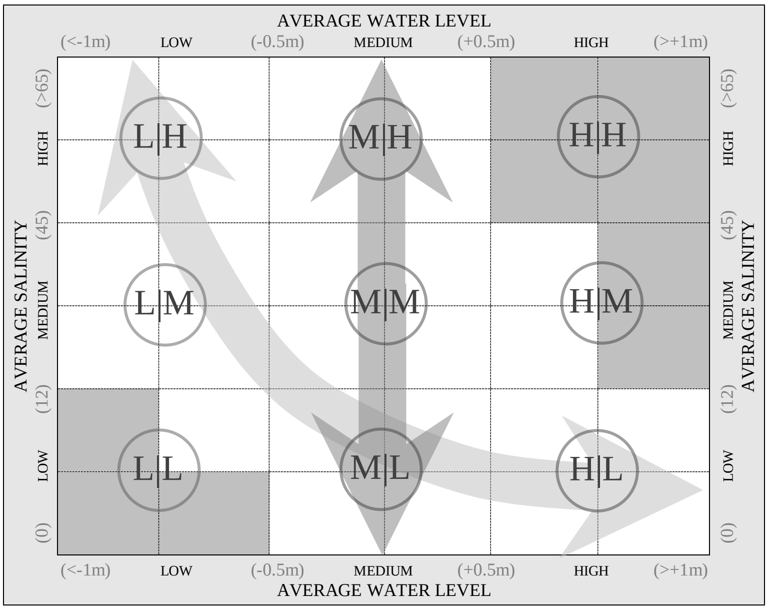


Figure 5.7: Schematic of the 9 water level/salinity states used for the assessment of biological responses (see Table 5.3). The arrows depict the trajectories for open (vertical arrow) and closed (curved arrow) mouth conditions respectively (refer Section 5.3.2). The shaded regions do not typically occur in the system.

5.4 Discussion

5.4.1 Persistence and occurrence of extreme dry conditions

The St Lucia estuarine lake system has recently experienced significant hypersaline conditions and desiccation. The occurrence of these severe conditions has been attributed to fresh water abstractions and the current dry period, but our long term simulations suggest that these extreme events would be driven by specific mouth management scenarios.

The permanent connection to the sea in scenario 1 maintains lake levels near EMWL thereby preventing desiccation although salinities vary widely. Scenario 3 follows the same linear bi-directional pathway during open mouth conditions but alternates to a curved 2-dimensional trajectory when the mouth closes. This curved trajectory is characteristic of scenario 2 where the mouth remains closed for periods of about 9 years at a time [Lawrie and Stretch, 2011]. Note that the curve is bi-directional in scenario 2 depending on wet/dry cycles.

Scenario 1 has the highest occurrence of hypersaline conditions and scenario 2 the highest occurrence of fresh conditions. Scenario 3 incorporates aspects of both scenario 1 and 2 (refer Figure 5.3) but without the concomitant risks of extreme hypersalinity and desiccation. Scenario 2 is the most stable of the three scenarios in terms of higher average persistence times, but the highest persistence times are generally in extreme conditions.

The current state of the Coorong in South Australia is similar to that of St Lucia under scenario 1. In the case of the Coorong extensive water abstractions and/or diversions have significantly reduced fresh water inflows. A dredging program was initiated to keep the mouth permanently open thus resulting in an inverse estuary [Webster, 2010]. As river inflows (or barrage flows in the case of the Coorong) decrease during dry periods, salinities rise. These conditions are exacerbated during very dry conditions. For example summertime salinities have exceeded 140 in the Coorong during droughts, while at St Lucia salinities reached 110 during the droughts of the 1970s and 1980s. These salinities can drive significant changes in the ecological functioning of the system.

Scenario 2 shares some of the same characteristics as the Chilika Lagoon in India where decreased fresh water inflows and closed mouth conditions have caused a gradual transformation towards a fresh water ecosystem (refer Table 5.2). Without a connection to the sea, the system relies on fresh water inflows to replace evaporative losses and avoid low water levels during dry periods. The average surface area of Chilika has decreased by about 35 % [Ghosh *et al.*, 2006]. In the case of St Lucia, drought periods in this scenario coincide with prolonged closed mouth conditions. As fresh water inputs reduce, the system becomes vulnerable to evaporative losses, desiccation and hypersalinity e.g. extensive desiccation of about 90 % of the lake occurred in 2006 [Whitfield & Taylor, 2009]. We emphasize that these conditions are unprecedented in the recorded history of the lake.

Spatial heterogeneities are another key aspect of extreme dry conditions. Before 2002 (i.e. scenario 1) salinity gradients of up to 50 were recorded during dry conditions. South Lake was found to provide a refuge for fauna that could not tolerate the extreme conditions in North Lake [Forbes & Cyrus, 1993]. After the mouth was left to close in 2002 (i.e. scenario 2), salinities of 60 were measured in South Lake while salinities of 200 occurred in North Lake. In addition as water levels dropped, the different parts of the lake began to separate out. The spatial heterogeneity created during dry conditions in both of these scenarios inevitably affect the biota of the system creating distinct biological responses in different parts of the lake [Taylor, 2006]. During prolonged droughts hyper-salinity and desiccation occur first in the northern parts of the lake before extending to the southern parts.

5.4.2 Biological responses

Over the last decade, conditions in the St Lucia estuarine lake have deteriorated. The diversity and abundance of species such as zooplankton, benthic invertebrates and fish have decreased due to extreme hypersalinities, very low water levels and prolonged closed mouth conditions [Cyrus *et al.*, 2011]. These conditions are typical of dry periods in scenario 2 (refer state L|H in Table 5.3) and are expected to occur 10 % of the time for periods of about a year at a time. Macroinvertebrates and zooplankton in particular do not tolerate extreme hypersaline conditions and microalgal biomass has been observed to increase as grazing pressures are reduced [Govender *et al.*, 2011; Perissinotto *et al.*, 2010; Pillay & Perissinotto, 2008].

Another outcome associated with scenario 2 is the predominantly closed mouth state. A closed mouth prevents the recruitment and passage of fish and other invertebrates into and out of the system (Carrasco *et al.* [2010]; Forbes & Cyrus [1993]). In 1979, Whitfield [1982] compiled a fish list of 108 fish species at St Lucia. This is substantially higher than the 30 species recorded in 2004 when the mouth was closed [Vivier *et al.*, 2009]. Although species numbers doubled in 2007 after the mouth breached, they are only expected to return to those measured in 1979 once drought conditions cease and the mouth opens for longer periods. A similar situation occurred in the Chilika Lagoon where the total fish diversity dropped from 217 to 69 species with the blockage of the mouth and the subsequent decrease in salinity [Ghosh *et al.*, 2006].

Prolonged closed mouth periods can also have a significant impact on marine stocks because the estuary cannot fulfill its nursery function, e.g. Mann &

Pradervand [2007] reported a significant decline in the estuarine-dependent fish *Rhabdosargus sarba* in the adjacent St Lucia Marine Reserve between 2001 and 2005.

Scenario 2 exhibits relatively high persistence times at extremes of either high or low salinity with corresponding low/high water levels (states L|H and H|L in Table 5.3). There are currently no available biological data for state H|L and the effect of the extreme conditions of state L|H on the recovery of the biological components of the system remains unclear.

Past studies (refer Section 5.2.3) suggest that the permanently open state of scenario 1 would generally be characterized by high biodiversity and abundance. However, extreme hypersaline conditions occur for about 30% of the time in this scenario and persist for about a year. These salinities have detrimental effects on biodiversity and the abundance of most species. High salinities and water levels near EMWL have been known to cause significant damage to shoreline vegetation [Whitfield & Taylor, 2009; Taylor *et al.*, 2006] and are expected to to have an average recurrence interval of about 18 years for this scenario.

Scenario 3 is generally characterised by high biodiversity and abundance (refer Table 5.3) and the occurrence and persistence of extreme dry conditions is lowest in this case.

5.4.3 Climate change effects

Climate change predictions suggest an increase in the frequency of extreme events [Hewitson *et al.*, 2005; Mason *et al.*, 1999]. More frequent and/or intense droughts and floods could increase the occurrence of episodic hypersaline events, desiccation, breaching events, high sediment loadings, etc. If extreme conditions occur more frequently there will also be less time available for the system to recover. This may lead to the degradation of the system over time as effects such as a loss in biodiversity become irreversible. Model simulations can be useful for investigating how different management strategies can mitigate these effects and perhaps reduce the occurrence of the extreme conditions that require the longest times for recovery. The results presented in this paper indicate that different management strategies, particularly those dealing with manipulation of the inlet configuration, can have significant effects. Taylor *et al.* [2006] has suggested that the impact of climate change on St Lucia in this century would be minor when compared to the anthropogenic impacts over the last century. This reflects the observation that the diversion of the Mfolozi river and the other fresh water abstractions have been shown to have significantly altered the natural functioning of the system [Lawrie and Stretch, 2011].

5.4.4 Sedimentation

The separation of St Lucia from the Mfolozi was implemented as a management strategy in 1952 to address the perceived threat of irreversible damage from sedimentation due the high silt loads carried by the Mfolozi. Historical narratives concerning this issue are given by Cyrus and Blaber [1988]; Grenfell and Ellery [2009]; Cyrus *et al.* [2010]; Taylor [2006]; Whitfield & Taylor [2009]. However, whether sediment accumulation from the Mfolozi in the lake basin has occurred remains unclear. While acknowledging the importance of the sedimentation concern, the results presented here suggest that maintaining the separation of the two systems whilst allowing the St Lucia mouth to close (as in scenario 2) has had major implications for the biodiversity and ecological structure of the system. The combination of extensive desiccation and hypersaline conditions are unique to this scenario. The sedimentation of the lake is still poorly understood and there is a need to evaluate the risks in comparison with those associated with maintaining the separation from the Mfolozi.

5.5 Conclusions

In this study we have used scenario simulations to investigate the occurrence and persistence of water level/salinity states in the St Lucia estuarine lake and the possible implications for the biological functioning of the system. The study highlights the exceptionally variable physicochemical characteristics of the system under different mouth management strategies.

In terms of occurrence and persistence, the risks of extreme adverse conditions, (i.e. very low water levels, very high salinities, or a combination of both) are highest in scenario 2 followed by scenarios 1 then scenario 3. In terms of the biological responses, biodiversity is expected to be highest in scenario 3 followed by scenario 1 then scenario 2. Significant changes in biological structure can be expected for the different management scenarios.

Overall the results reported here suggest that re-establishment of a combined Mfolozi/St Lucia inlet is important for the long term sustainability of the system as a source of biodiversity in the region. The risk of sedimentation is the primary motivation for artificially maintaining separated inlets. Given the new insights into the functioning of the system that have recently emerged, including those associated with the unprecedented extreme conditions of the current drought, a detailed re-evaluation of management options for dealing with the sedimentation issue is needed.

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Chapter 6

Ecosystem indices reflect extreme hydrodynamic conditions during an extended dry period

This chapter is based on the paper: Chrystal, R.A. & Scharler, U.M., (2013). Ecosystem indices reflect extreme hydrodynamic conditions during an extended dry period. Submitted to Ecological Indicators.

Abstract

Food web structure and function in ecosystems are a reflection of environmental conditions, this is especially apparent during extreme circumstances. The St Lucia estuarine-lake system in South Africa has recently experienced an unprecedented prolonged period of desiccation and hypersaline conditions caused by climatic variability and anthropogenic impacts. This has had a significant impact on species diversity, abundance and biomass. The system has received significant research attention over the past 70 years, however, little research has been conducted to understand how the system responds to changing environmental conditions as a whole. The aim of this study was to quantitatively assess the ecosystem response to different physico-chemical conditions and mouth states using ecological network analysis. The biomasses and trophic exchanges of various biotic species were estimated and used to establish ecological networks from which several ecosystem indices were calculated. Results indicate that the water level, salinity and mouth state have a significant impact on the total system biomass and productivity and the number and weight of energy flow pathways. These influence the biological structure and functioning of the St Lucia system. The substantial increase in the total living standing stock and species diversity during an intermittent open phase indicates that the system responds rapidly to such favourable conditions. This was reflected in the ecosystem indices calculated for before, during and after a breach which highlighted the importance of the short open mouth period after several years of mouth closure. Not only were biomass and productivity increased, but also the organisation of pathways to ensure more efficient energy transfer. At the same time adequate pathway redundancy was invigorated, resulting in a more robust and efficient functioning of the food web even after the re-closure of the inlet.

6.1 Introduction

Estuaries are highly dynamic systems and experience regular environmental variations brought on by seasonal and climatic changes. In many occasions human induced perturbations have exacerbated the effects of these changes and brought on a whole new range of environmental stresses. Naeem *et al.* [2012] state that ecology requires an understanding of the interactions between different species and an evaluation of their ability to explain observed trends and characteristics of an ecosystem. During recent decades, technologies and data have become available for biodiversity and ecosystem functioning research which has rapidly advanced [Hall & Raffaelli, 1991; Naeem *et al.*, 2012]. One of the few tools, ecological network analysis (ENA) has been increasingly used to analyse and characterise the food web structure and functioning of ecosystems (e.g. Baird & Ulanowicz [1989]; Heymans & Baird [2000]; Leguerrier *et al.* [2007]; Rybarczyk & Elkaim [2003]; Scharler & Baird [2005]; Wolff *et al.* [2000]; **?**]; **?**) and to provide an ecosystem-based approach for mitigation strategies (e.g. Chen *et al.* [2010]).

The St Lucia estuarine-lake system in South Africa was granted World Heritage Site Status in 1999 and is listed as a RAMSAR site of global importance. The system has however experienced numerous anthropogenic impacts over the past century including freshwater abstractions, catchment development and mouth manipulation (e.g. Whitfield & Taylor [2009]). The most significant alteration to the system was however the separation of the previously combined inlet of the Mfolozi River and the St Lucia system in 1952. Lawrie & Stretch [2011a] found that the Mfolozi was not only an essential source of freshwater to the system but more importantly it played a key role in providing a more stable mouth state regime ensuring a predominantly open mouth state and thus adequate exchange with the sea. Therefore, as a consequence there were numerous attempts to keep the St Lucia mouth open using hard engineering and continuous dredging operations. After fifty years the management authority decided to cease efforts to keep the mouth open and it was left to close in 2002. This was at the onset of a dry period. As a result of prolonged closed mouth conditions (2002-present, except for a brief period in 2007) and low freshwater inflows, hypersaline conditions (up to 200) and severe desiccation (up to 90% in 2006) occurred throughout the lake. Model simulations by Lawrie & Stretch [2011b] show that these conditions are unprecedented and are characteristic of dry conditions under the current mouth management strategy. As a consequence substantial declines in species diversity and abundance, such as zooplankton, macro-invertebrates and fish were recorded [Cyrus *et al.*, 2010, 2011]. In March 2007 equinox high tides and high ocean swell caused by Cyclone Gamede breached the St Lucia mouth. This allowed the recruitment of marine species into the system until the mouth closed again in August 2007 [Vivier *et al.*, 2009].

The St Lucia system is not only an example of the numerous shallow lakes and lagoons across the world, but is particularly important to South Africa as it constitutes about 50 % of the total surface area of all South African estuaries [Van Niekerk & Turpie, 2012] and is an important nursery area for estuary-associated marine fish and prawn species [Benfield *et al.*, 1989; Forbes & Demetriades, 2005; Mann & Pradervand, 2007; Vivier *et al.*, 2009]. Without careful management this system is at risk of further declines in diversity and abundance of these taxa as well as exacerbating knock-on effects to nearshore environments and fisheries [Ayers *et al.*, 2013; Whitfield *et al.*, 2006; Mann & Pradervand, 2007].

St Lucia has received considerable biological research attention over the past 70 years. Despite this, food web studies have largely been neglected and there has been little attempt to understand how the system responds to changing environmental conditions as a whole. The first and most comprehensive biological survey of the system was carried out in the late 1940s [Day *et al.*, 1954]. Subsequent data collection has generally focused on individual biological components and there have been few attempts to understand the trophic interaction between species. Whitfield & Blaber [1978a,b, 1979a] investigated the feeding ecology of piscivorous birds and Blaber [1979] investigated the food web dynamics of filter feeding fish. These studies highlighted several basic characteristics of the food web in St Lucia during the 1970s when the mouth was open and salinities were comparatively low. In the 1980s, Taylor [1987], Starfield *et al.* [1989] and Taylor [1993] established a rule-based ecological model for submerged macrophytes in St Lucia using qualitative or informal knowledge gained over previous years. This conceptual model was used to infer the dominant trophic pathways between broad groups based on the salinity regime. In 2006 Govender *et al.* [2011] investigated the food web structure of the system using carbon and nitrogen isotope analysis. Results showed that benthic carbon sources were predominantly utilised at sites with low water levels and high salinities while at sites with high water levels and lower salinities viable pelagic food webs were sustained. Lawrie & Stretch [2011b] defined nine different water level/salinity states for the system and compiled a qualitative overview of previously observed biological responses for most of these states. Findings suggest that the abundance and biodiversity would be low under the current mouth management strategy (separate Mfolozi/St Lucia mouths and no mouth manipulation) and high under conditions where a joint Mfolozi/St Lucia mouth is present but not manipulated. Scharler & MacKay [2013] reviewed the above and constructed qualitative food webs of the most historic data [Day *et al.*, 1954] and data available from the most recent drought period (2000s) to highlight the loss of functional groups and trophic pathways. The above studies provide valuable insights into the food web dynamics of the system, however, they do not provide both a holistic and quantitative analysis of the system.

The aim of this study was therefore to quantitatively assess the ecosystem response to different physico-chemical conditions and mouth states of the St.

Lucia estuarine-lake system. The main objective was to construct and analyse carbon flow models for St Lucia which depict trophic flows between biotic and abiotic components of the system during severe dry conditions (low water levels and high salinities) and the impact of the breaching event which occurred in March 2007.

6.2 Methods

6.2.1 The case study site

The St Lucia estuarine lake (between 2742′ – 2824′ S, and 3221′ – 3234′E) is situated on the sub-tropical east coast of South Africa (Fig. 6.1). The lake has an average surface area of 328 km^2 at an average depth of 1 m making it highly susceptible to evaporative losses. Average evaporative losses (450 Mm^3 per year) far outweigh water balance contributions from direct rainfall (300 Mm^3). The decrease in freshwater inflows from the surrounding catchments (from an estimated 364 to 295 Mm^3 per year) together with the diversion of the Mfolozi has therefore placed additional pressure on the already freshwater scarce system, especially during dry periods [Hutchison & Pitman, 1977; Lawrie & Stretch, 2011a]. Simulations by Lawrie & Stretch [2011a,b] show that under the current mouth management strategy (separated Mfolozi and St Lucia inlets and no mouth manipulation) the mouth is expected to remain closed for about ten years at a time. During this time water levels and salinities fluctuate depending on catchment inflows and hypersalinity and desiccation are a common occurrence.

6.2.2 Ecological network construction

A number of biological studies have been carried out over the last decade in order to assess the ecological status of the lake in relation to low lake levels and hypersalinity during the recent dry period (e.g. Jerling *et al.* [2010]; Pillay & Perissinotto [2008]; Vivier *et al.* [2009]). This comprehensive collection of data have provided a unique opportunity to construct detailed, weighted food webs and perform network analysis on the system. These datasets thus coincide with

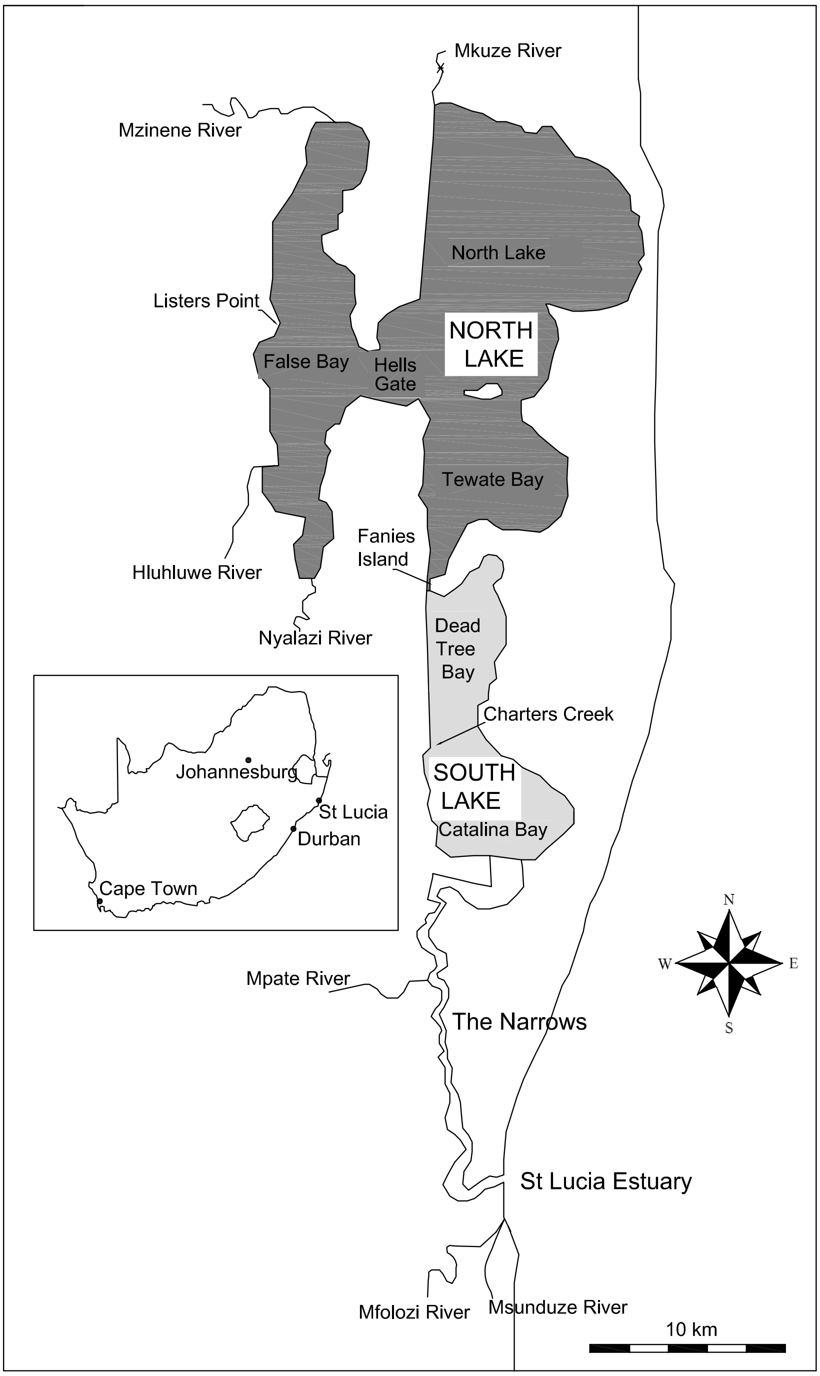

Figure 6.1: Location map for St Lucia on the east coast of South Africa.

conditions that have put this shallow lake ecosystem into its most extreme hydrological state (very low water levels, high salinities) documented to date. The breaching event in March 2007 provided an opportunity to compare open and closed mouth conditions and a partial recovery of the system. It is worth noting that the mouth was breached from the sea and is therefore not characteristic of a typical estuarine breaching event. Input data required for network analysis include the standing stocks of each compartment, the trophic flows between the various compartments as well as exchanges across the system boundary, such as imports and exports into and out of the ecosystem. Biological datasets were obtained from published and unpublished literature from 2006 until 2008 and used to construct trophic flow models based on guidelines in Fath *et al.* [2007]. Carbon was used as the flow currency where all biomass measurements are expressed as $mg.C.m^{-2}$ and flow measurements (i.e. productivity, consumption, respiration, egestion, imports and exports) are expressed in $mg.C.m^{-2}.day^{-1}$. Each dataset was assumed to represent steady-state conditions of the system for each time step. Datasets were compiled based on data gathered during winter (May to July) each year.

Each compartment of the network was mass balanced where energy obtained via consumption was used for respiration, egestion and production [Jørgensen & Bendoricchio, 2001]. For primary producers, the gross primary production was composed of net primary production and respiration [Krebs, 2009]. These data were incorporated into an adjacency (diet) matrix which was constructed using diet information from system and non-system specific literature. This matrix was used as input into ecological network analysis software [Allesina & Bondavalli, 2004; Ulanowicz & Kay, 1991].

For this study two areas of the lake were investigated, namely "North Lake" (inclusive of False Bay, North Lake and Tewate Bay) and "South Lake" (from the end of the Narrows to Fanies Island) (refer Figure 6.1). St Lucia has been described as a heterogeneous system temporally and spatially [MacKay *et al.*, 2010; Taylor, 2006] and although further divisions would have provided higher resolution, the available data did not allow for further apportionment as some groups were quantified per basin. The mean average surface area of North Lake and South Lake are 287 km^2 and 59 km^2 respectively at an average water depth of about 1 m [Hutchison, 1974]. These values were adjusted with changing water levels and biomass values of all pelagic biota were integrated over the water depth. Imports and exports were calculated using simulated river inflows and estuary mouth discharges [Lawrie & Stretch, 2011a] specifically for suspended POC.

The biological data were converted to carbon biomass and flows using conversion values and methods obtained from the literature. Chlorophyll-a [Perissinotto *et al.*, 2010] was converted to carbon using a ratio of 60 % [Cuff *et al.*, 1983; Shannon & Field, 1985]. Areal cover of submerged macrophytes [Adams *et al.*, 2013] were converted to carbon using average biomass and carbon values given in Adams & Bate [1999]. Zooplankton and macrobenthos abundances (e.g. Carrasco *et al.* [2013]; Pillay *et al.* [2013]) were converted to dry weight and then to carbon biomass using references in Scharler & Baird [2005] and measurements from the Mhlanga Estuary [Scharler, 2012]. Where no carbon measurements were available for the same or similar species, the carbon content was assumed equal to 40 % of the dry weight.

Fish abundance data were collected with seine and gill nets (data and gear described in Vivier *et al.* [2009]). Data on numbers caught and length were converted to mass using length-weight relationships given in Froese & Pauly [2010]. Dry weight was assumed to be 50 % of wet weight and the carbon conversion factors were taken from McLusky & Elliot [2004]. For the sample volume, it was assumed that gill nets sample an area equal to 4x(the length of the net)^2 and the volume sampled using a seine net was assumed equal to a quarter of a cylinder, where the length of the seine net is equal to half the circumference, and its width to the height of the cylinder. The biomass (mg/m^3) was then integrated over the water depth. The P/B, P/R and P/C ratios were obtained from references given in Scharler & Baird [2005]. Fish diets were obtained in Whitfield [1982]; Whitfield & Blaber [1978a,b, 1979a] and Heemstra & Heemstra [2004].

Biannual areal bird counts were provided by Fox (EKZN Wildlife) for 47 different species. The average weight and diet of each species was obtained from MacLean [1993]. Dry weight was assumed to be 50 % of the wet weight and the carbon conversion factors were taken from McLusky & Elliot [2004]. Consumption rates were taken from Bowker & Downs [2008]; Mock & Mock [1980]; Whitfield &

Blaber [1978a,b, 1979a] and Martin [1991]. About 70–90 % of the gross energy is assimilated [Marshall, 1961] and respiration equals about 97–99 % of the energy assimilated [Krebs, 2009]. The remainder is used for production.

Annual crocodile (*Crocodylus niloticus*) counts for each section of the lake were provided by Combrink (EKZN Wildlife). The data were divided into three groups: juveniles (average length < 1.5 m, average weight 9.1 kg), sub-adults (1.5–2.5 m, 24.4 kg) and adults (> 2.5 m, 124.8 kg). Carbon biomass was estimated by using a wet to dry weight ratio of 50 % and a dry weight to carbon ratio of 40 %. The respiration rate was estimated using the relationship provided by ECOTOX [Jørgensen *et al.*, 2000] for poikilothermic metazoan animals: $q = 16.54\ w^{0.75}$ where q is the daily metabolism in calories per animal per day and w is the wet weight (g). Consumption rates are given in Wallace [2006] and Whitfield & Blaber [1979b] and egestion was taken as 62 % of the consumption [Wallace, 2006].

Annual hippopotamus (*Hippopotamus amphibious*) counts for each section of the lake were provided by Taylor (EKZN Wildlife.). The average weight of a hippopotamus was assumed equal to 1000 kg [Coe *et al.*, 1976] and carbon biomass (mgC. m^{-2}) was estimated by using a wet: dry weight ratio of 50 % and a dry weight: carbon ratio of 40 % [Owen-Smith, 1988]. The respiration rate was estimated using the relationship established by ECOTOX [Jørgensen *et al.*, 2000] for large mammals $q = 422\ w^{0.75}$ where q is the daily metabolism in calories per animal per day and w is the wet weight (g).

For an estimate of the particulate organic carbon (POC) content, three replicate water column and sediment core samples (internal diameter of 2.2 mm, depth 10 mm) were collected at Charters Creek, Catalina Bay and Listers Point (refer Figure 6.1). The water column samples were filtered on GF/C 0.7 μm filters. Water column and core samples were dried and burnt at 460 $\deg C$ for 8 hours. The loss of organics was determined by weight and assumed to represent organic carbon content.

From the above data of production, consumption, respiration, egestion, imports and exports across the system boundary, a diet matrix was constructed for each database and the transfers between compartments were established using MATLOD procedures defined in Ulanowicz & Scharler [2008]. Here, an amount equivalent to 5 % of the residual flow was allocated to each specified trophic link, until either the demand by the recipient, or the resource was exhausted. Thereafter, the model was mass balanced and analysed using the software WAND [Allesina & Bondavalli, 2004]. Several ecosystem indices, which are described in more detail below, were used to compare the St Lucia ecosystem on a spatial (South and North Lake) and temporal scale (winter periods of 2006, 2007 and 2008). Note that there were insufficient biological data to represent each species component for North Lake in 2006 due to severe desiccation (about 90 % of the total surface area) and therefore a trophic network was not constructed for this period.

6.2.3 Analysis of networks

First, biomasses and compartmental throughputs were compared for the three different time steps (before breach, open phase, re-closure) in North and South Lake. Then, the flow distributions in the network (number and weight of links) were compared to elicit changes in ecosystem structure and functioning. From the diet matrix, the total dependency and contribution coefficients are estimated for each compartment in the network which indicates the extent to which a compartment is dependent for energy on any other compartments in the network or contributes to any other compartment in the network, via all direct and indirect pathways. [Szyrmer & Ulanowicz, 1987; Ulanowicz & Kay, 1991]. The combined dependencies and contributions from the benthic and pelagic domains were calculated in order to show the relative change in their dependencies and contributions over time and space.

Next, the overall trophic efficiencies of the different networks were calculated to track any changes in the efficiency of carbon transfers in response to the mouth breach. The Lindeman trophic analysis [Ulanowicz & Kemp, 1979; Ulanowicz & Kay, 1991] reduces the food web into integer trophic levels and quantifies the amount of energy transferred between the different levels. The trophic efficiency is the ratio of the output at one trophic level to the input of the next trophic level. The ratio of detritivory to herbivory elucidates the importance of primary producer and detrital food sources of the various states of the ecosystem. A high detritivory: herbivory ratio indicates a system mainly dependent on detritus as the primary food source [Scharler & Baird, 2005]. The St Lucia system experiences large physico-chemical fluctuations which have a significant effect on biomass concentrations of primary producers (e.g. Johnson [1977]), thereby influencing the ratio of detritivory to herbivory. Submerged macrophytes do not tolerate high salinities and can also be affected by high turbidities and light limitations at large depths while microalgal biomass is also dependent on water levels and the mouth state [Taylor, 2006; Johnson, 1977; Perissinotto *et al.*, 2010]. Together with a high Finn Cycling Index (FCI) that indicates the proportion of TST that is recycled in an ecosystem [Finn, 1980], the detritivory: herbivory ratio may indicate higher self-reliance of the system and lower dependence on new nutrient sources to sustain the food web. Several ecosystem indicators have been proposed to illustrate the trophic flow distribution within ecosystems and indicate robustness. These indices include information on the size, structure and development of the system. The Total System Throughput (TST) is defined as the sum of energy that flows in an ecosystem and across its boundaries and is used as a measure of the size and activity of the system [Ulanowicz, 1986].

The flow diversity (H) considers how much all trophic flows contribute to the complexity of the system and its value describes the abundance and evenness of flows [Ulanowicz, 1997]. A high H represents high uncertainty, complexity and flow diversity, whereas the value of H decreases as few flows dominate in a system [Scharler & Fath, 2012; Ulanowicz, 1986]. The average mutual information (AMI) describes the degree of flow specialisation of the overall network structure [Scharler & Fath, 2012; Ulanowicz, 2004]. It gives a measure of the average amount of constraint experienced by a quantum of energy as it moves from one compartment to another [Ulanowicz, 1997]. Constanza & Mageau [1999] described AMI as a comprehensive measure of system organisation because it measures both the number of nodes in an ecological network and how their trophic connections are organised. The AMI is expected to decrease with perturbations that decrease the efficiency of few flows to favour a more equal flow distribution.

The development capacity (DC) is defined as the product of TST and H and reflects the ecosystems potential to develop. Ascendency (A) is the product of the TST and AMI and describes both growth and development. An increase in ascendency indicates an increase in ecological succession, species richness, greater internalization of resources and finer trophic specialization. Ulanowicz [1997] stated that in theory, ascendency is higher when there is more specialization (fewer pathways) and when most of the material is transported by few pathways. In the absence of major perturbations, ecosystems develop and information replaces uncertainty i.e. AMI approaches H and A approaches DC [Constanza & Mageau, 1999]. However, empirical ecosystem networks seem to exist through a trade-off between flow specialization and a certain degree of flow redundancy [Goerner *et al.*, 2009].

The difference between A and DC is represented by the overheads. Overhead occurs due to uncertainty in import, export and dissipative flows (respirations) as well as redundant or parallel pathways. It is considered as insurance for the system since the alternate pathways and exchanges across the system boundary introduce degrees of resilience [Scharler & Baird, 2005; Ulanowicz & Kay, 1991].

6.3 Results

6.3.1 Biomass variability

The total estimated carbon biomass (mgC.m^{-2} and MgC.basin^{-1}) of each of the different species are given in Figure 6.2. Note that the surface area covered with water fluctuated significantly over the three years and was significantly lower than the average surface area of the lake (see Figure 6.2). In 2006 North Lake was 90 % desiccated, however, the biomass of certain species were included where data were available. The total biomass fluctuated significantly in South Lake, from 4.28 gC.m^{-2} in 2006, 37.05 gC.m^{-2} in 2007 and 15.66 gC.m^{-2} in 2008. The total biomass also decreased from 18.95 gC.m^{-2} in 2007 to 7.32 gC.m^{-2} in 2008 in North Lake. Note that the areal cover of submerged macrophytes was only recorded in 2008 and data for 2006 and 2007 were estimated using water levels and salinity tolerance levels of the various macrophyte species. The accuracy of the estimates for macrophytes for 2006 and 2007 is therefore lower compared to that of other groups in these models. The total biomass in South Lake excluding submerged macrophytes increased from 2.20 gC.m^{-2} in 2006 to 5.10 gC.m^{-2} in

2007 to 12.50 gC.m^{-2} in 2008 while the total biomass increased slightly from 5.31 gC.m^{-2} in 2007 to 6.23 gC.m^{-2} in 2008 in North Lake.

Over the three years, submerged macrophytes contributed the highest biomass (average of 58 % of the total biomass), followed by fish (23 %) and macrozoobenthos (6 %). However, in South Lake in 2008, fish biomass increased substantially, contributing nearly 60 % to the total biomass. This coincided with a decrease in submerged macrophyte biomass (with a 20 % contribution) and an increase in macrozoobenthos biomass (with a 17 % contribution). In South Lake (2006) hippos contributed almost 30 % to the total biomass.

6.3.2 Ecosystem indices

The Total System Throughput (TST) comprises all biotic and abiotic carbon flows in the system. It was highly variable in South Lake throughout the three years and reflects the biomass trends shown in Figure 6.2. In North Lake the TST halves in 2008 compared to 2007 although the total carbon biomass remains fairly stable (refer Figure 6.4a). The TST increased substantially in 2007 in both sections of the lake when the mouth was open. This can be expected as there was a net influx of seawater (0.5 to 1 Mm^3 per day, Chrystal & Stretch [unpubl.]) and recruitment of species from the sea into the system (e.g. Carrasco *et al.* [2010]; Vivier *et al.* [2009]) during that time. The TST was lowest (407 mgC.m^{-2} day^{-1}) in South Lake in 2006 during significant desiccation (about 90 % of the lake was exposed and dry, Whitfield & Taylor [2009]) and hypersaline conditions (see Table 6.1).

The low development capacity (DC) and ascendency (A) are indicative of the severe drought conditions experienced in 2006 (refer Table 6.1). These values were highest in both parts of the lake when the mouth was open. Ascendency was significantly higher than the overhead for each of the networks. Overhead has been considered as insurance (e.g. more path redundancies reflect a higher amount of parallel pathways [Ulanowicz, 1997]), therefore the system is more resilient at high values of overhead (high R/DC) than at high values of ascendency (high A/DC) when it is more prone to perturbations. Ascendency was highest when the mouth was open indicating both growth and development. Results

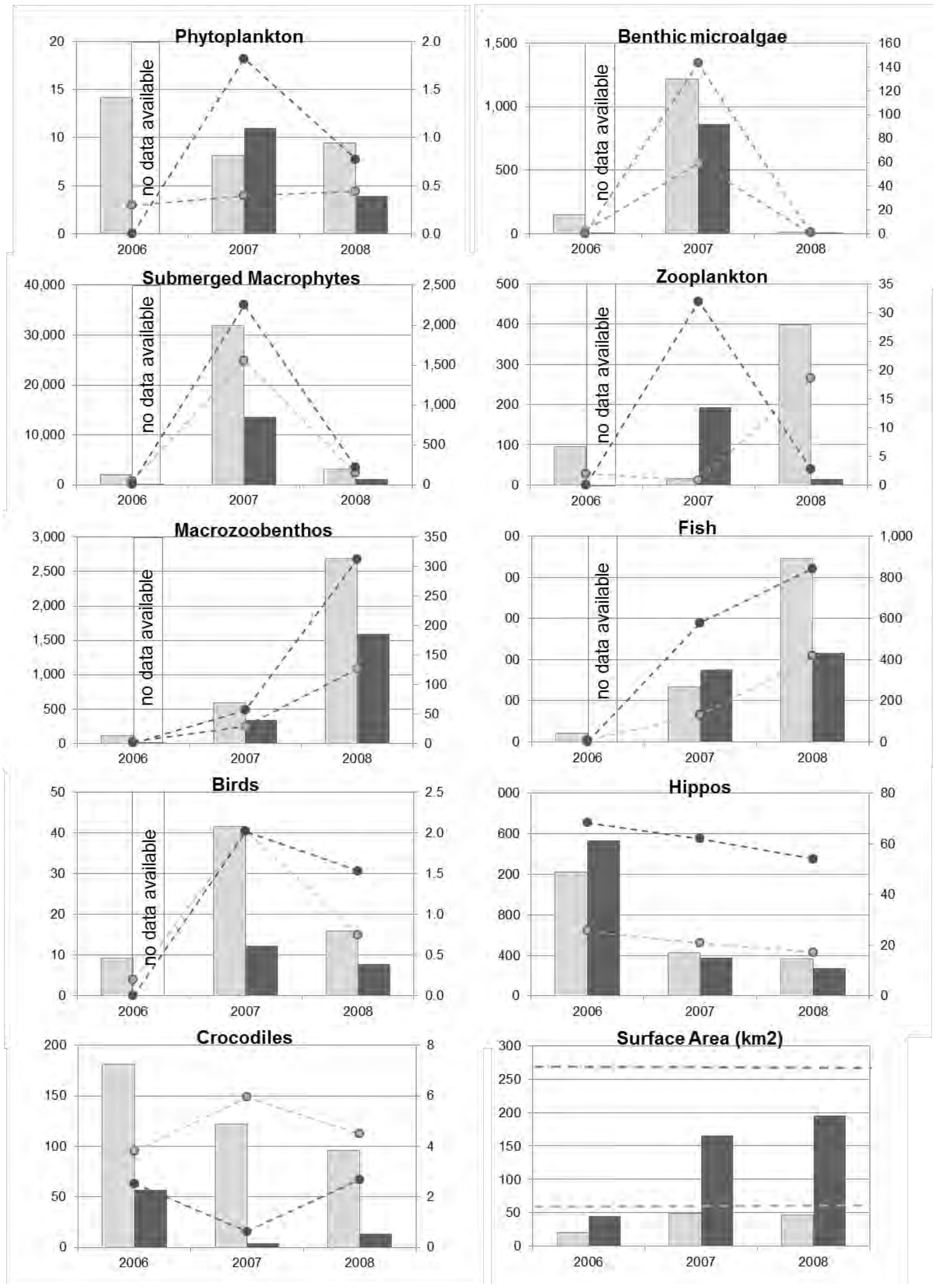

Figure 6.2: Total living carbon biomass, $mgC.m^{-2}$ (primary axis) and $MgC.basin^{-1}$ (secondary axis) sampled during winter 2006, 2007 and 2008 for each species group. The total surface area covered by water is also given. The dotted lines represent the average surface water for each basin.

Table 6.1: Ecosystem indices for the St Lucia estuarine-lake from 2006 until 2008 for North and South Lake.

Attribute	**South Lake**			**North Lake**	
	2006	**2007**	**2008**	**2007**	**2008**
Whole-System Indices					
Total system throughput *	407	217546	14786	81525	6994
Development capacity #	1693	421266	44690	164064	20860
Ascendency #	655	342020	29053	127484	11402
Relative ascendency (A/DC) (%)	39	81	65	78	55
Average mutual information (bits)	1.61	1.57	1.96	1.56	1.63
Flow diversity (bits)	4.16	1.94	3.02	2.01	2.98
Overhead on imports #	268	3617	1513	2031	605
Overhead on exports #	164	256	672	318	789
Overhead(imports+exports)/DC (%)	26	1	5	1	7
Dissipative overhead (#)	240	42739	3698	17888	3620
Redundancy #	366	32635	9755	16320	4443
Relative redundancy (R/DC) (%)	22	8	22	10	21
Pelagic compartmental throughput *	111	245	3163	230	271
Benthic compartmental throughput *	296	217301	11623	81295	11039
Pelagic contribution coefficients (%)	872	1148	2804	855	1978
Benthic contribution coefficients (%)	1882	1930	3501	1252	1710
Pelagic dependency coefficients (%)	1118	1005	4342	975	1876
Benthic dependency coefficients (%)	3413	4686	6892	3983	4812
Biogeochemical cycle analysis					
Average path length	1.60	1.72	1.97	1.62	2.29
Average residence time (days)	54.3	0.57	3.82	0.67	12.23
Finn Cycling Index (%)	5.99	0.04	21.5	0.10	6.54
Cycles count	69	202	763	234	534
Lindeman trophic analysis					
Trophic efficiency (%)	13.1	3.3	25.6	6.7	12.9
Detritivory:herbivory ratio	1.52	0.70	4.71	1.41	48.6

* mgC.m^{-2} day^{-1}

mgC.m^{-2} day^{-1} bits

indicate that overheads were highest in 2006 (South Lake) with overheads due to imports and exports making up about 40 % of the total. The contributions of dissipative overheads to respiration are roughly uniform throughout the three years and both sections of the lake.

The flow diversity (H=DC/TST) fluctuated more between open and closed mouth conditions compared to the average mutual information (AMI=A/TST). H was higher during closed mouth conditions in both sections of the lake indicating a higher diversity of trophic pathways. The increase from open to closed mouth conditions was similar for South and North Lake. AMI remained at about 1.6 for all networks except in South Lake in 2008 when it increased to about 2.0 (refer to Figure 6.4b). Overall it was slightly higher during closed mouth conditions which indicate that comparatively fewer links were carrying a higher proportion of the material. The relative ascendency (A/DC = AMI/H) increases substantially during open mouth conditions (2007) and corresponded with a substantial decrease in H. In South Lake in 2006 and 2008, the material flows were overall more equally distributed, whereas the flow constraints were only slightly higher compared to 2007 (i.e. substantially higher H and slightly higher AMI). In 2007, the flows were less constrained and specialised compared to 2006 and 2008 and about 2 % of the flows were responsible for carrying more than 90 % of the material i.e. lower H and AMI. These flows occurred between the submerged macrophytes and detritus.

The Finn Cycling Index, which refers to the amount of material/energy that is recycled in the ecosystem [Finn, 1980; Ulanowicz, 1986] was expected to be higher during the closed phase, when imports and exports are comparatively smaller than during the open phase. The FCI was lowest during the open phase at and below 1 %. During closed mouth conditions, the FCI was higher and increased to 21.5 % in South Lake and 6.5 % in North Lake. The detritivory: herbivory ratio was highest during closed mouth conditions, especially in North Lake in 2008. The higher detritivory corresponds to a higher degree of recycling (FCI) and to the decrease in the biomass of all the primary producers during the closed mouth phase. The trophic efficiency was higher during closed mouth conditions in South Lake. The trophic efficiency was highest at the third trophic level during closed mouth conditions and highest at the second trophic level during open mouth

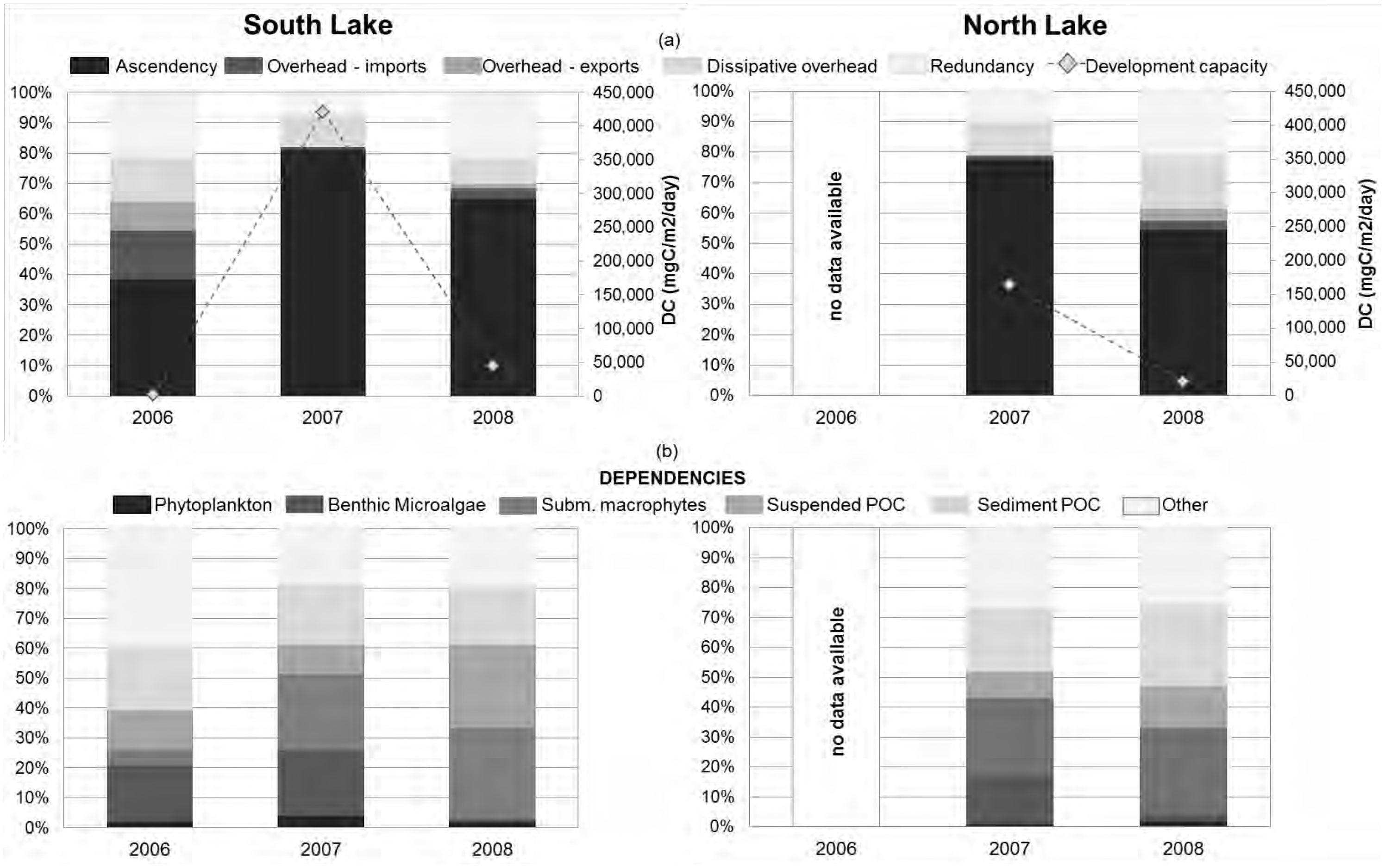

Figure 6.3: a) Development capacity, ascendency and overheads and b) dependency coefficients of the nodes indicated for south lake and north lake from 2006 until 2008.

conditions. The average residence time (ART) of a unit of carbon in the network was significantly higher in South Lake before the breach in 2006 (54 days) and lowest during open mouth conditions (less than 1 day). In both sections of the lake the ART and FCI are lowest during open mouth conditions.

The compartmental throughputs in all the networks were significantly higher via the pooled benthic compartments in comparison to the pooled pelagic compartments (see Table 6.1). The throughput ratio of pelagic and benthic compartments remained below 0.03 in North Lake but fluctuated from 0.37 to 0.01 to 0.27 in South Lake over the three years.

The contribution coefficients show that the benthic components generally contribute more carbon to the network than the pelagic compartments. There was however an increase in the contribution from the pelagic components over the three years in both parts of the lake. This corresponds to an increase in the surface area (and depth) of the lake (refer Figure 6.2). In South Lake benthic communities contributed from 54 % more in 2006 to 41 % more in 2007 to only 20 % more in 2008 than pelagic communities, whereas in North Lake benthic communities contributed from 32 % more in 2007 to 16 % less in 2008. In terms of compartmental input the system was about 65 % to 80 % more dependent on benthic communities rather than pelagic communities, except in South Lake in 2008 where it was 37 % more dependent on benthic communities.

The total dependency coefficients varied temporally rather than spatially and indicate to what extent (as a percentage) the system is dependent for energy on certain compartments (refer Figure 6.3). In 2007 the system was mainly dependent on benthic microalgae, submerged macrophytes and suspended and sediment POC whereas the dependency on benthic invertebrates was about 12 % and fish about 5 %. In 2008 the system was mainly dependent on submerged macrophytes followed by suspended and sediment POC. Note that the dependency on suspended POC was larger than on sediment POC. In 2006 the system was mainly dependent on benthic microalgae (19 %) and sediment POC (21 %), hippos (14 %) and fish (13 %). Note that hippos are important detritus producers and import material from their terrestrial feeding grounds. The results therefore suggest that St Lucia is mainly dependent on its primary producers and detritus (suspended and sediment POC), however, the proportions can vary significantly over time.

6.4 Discussion

The main aim of this study was to characterise the overall biological structure and functioning of the system using a set of normalised ecosystem indices and to investigate if in turn these indices reflect hydrodynamic conditions (i.e. salinity, water level and mouth state).

6.4.1 Population and community

During the current dry period Perissinotto *et al.* [2010] found that microalgal biomass is dependent on the mouth state and water depth and has been observed to increase as grazing pressures are reduced. Note the negative correlation between benthic microalgae and macrozoobenthos in Figure 6.2. The three main submerged macrophyte species found in St Lucia are *Stuckenia pectinatus*, *Ruppia cirrhosa* and *Zostera capensis* [Taylor *et al.*, 2006]. Taylor *et al.* [2006] noted that their growth may be affected by high turbidities and light limitations and while the tolerance range to salinity varies with each species all macrophytes tend to disappear when salinities exceed 50 [Ward, 1982]. Submerged macrophytes do not provide a direct primary food source but rather supplement the detrital pool Adams & Bate [1999].

Carrasco *et al.* [2010] found that zooplankton biomass was negatively correlated with salinity and positively correlated with water depth. In terms of the overall macrozoobenthic abundance and diversity MacKay *et al.* [2010]; Pillay & Perissinotto [2008] found no clear correlations with physico-chemical parameters although the drought conditions had a significant impact on the macrozoobenthic community. MacKay *et al.* [2010] suggested that these taxa have a self-recruiting strategy and therefore do not depend on the mouth state.

Fish make up an important component of the total biomass of heterotrophs at St Lucia. Whitfield *et al.* [2006] investigated the salinity tolerance levels of freshwater, estuarine and marine fish species in St Lucia. Marine fish species dominate when salinities range from 10 to 40 but can also be found in salinities up to 70.

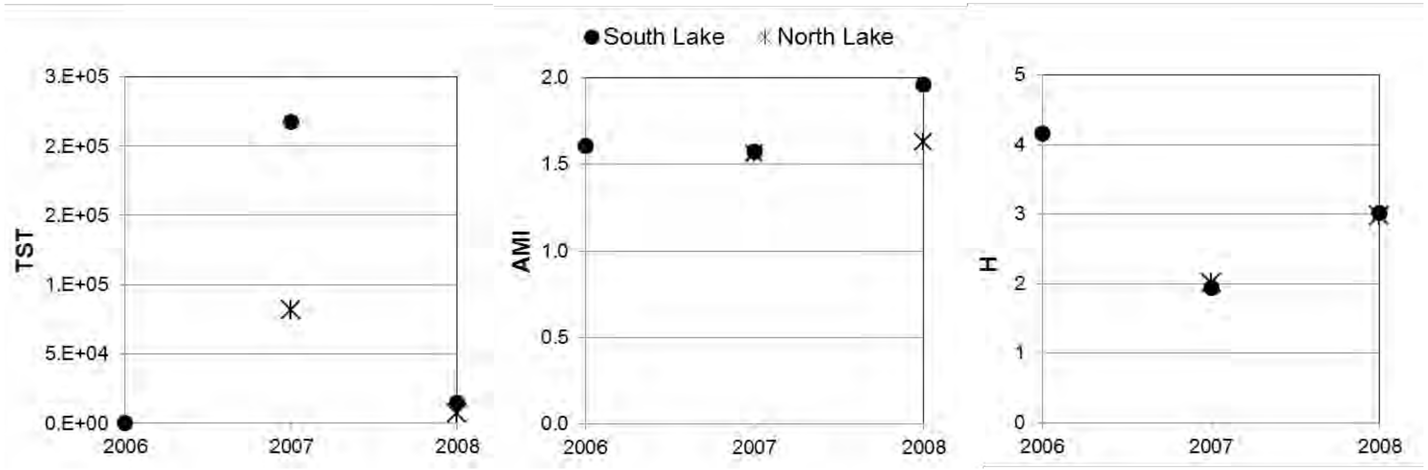

Figure 6.4: Ecosystem Indices (a) TST, (b) H and (c) AMI in south lake and north lake from 2006 until 2008.

Very few fish species are able to tolerate salinities above 70, however, *Oreochromis mossambicus* (classified as a freshwater fish) was able to survive for prolonged periods in salinities above 110 [Whitfield *et al.*, 2006; Vivier *et al.*, 2009]. Fish abundance may however decline before tolerance levels have been attained due to the loss of an important food resource. In 1979 Whitfield [1982] compiled a list of 108 fish species at St Lucia, this was significantly less than the 30 species recorded in 2004 when the mouth was closed [Vivier *et al.*, 2009]. Although salinities remained high over the current drought period, the number of fish species doubled and fish biomass increased significantly following the breaching of the mouth in 2007 (Figure 6.2). Salinity does however have an important impact of the structuring of estuarine fish assemblages (e.g. Whitfield *et al.* [2006]; Vivier *et al.* [2009]) as the majority of the fish biomass was made up of marine fish species.

Zooplankton species increased from 27 species recorded during closed mouth conditions to 69 species after the mouth opened [Carrasco *et al.*, 2010] and corresponded to an increase in zooplankton biomass (Figure 6.2). Although salinities have a significant impact on species diversity and abundance, an open mouth state is imperative for the recruitment and passage of marine species into and out of the system [Carrasco *et al.*, 2010; Forbes & Cyrus, 1993; Vivier *et al.*, 2009]. In addition a prolonged closed mouth state inhibits the ability of an estuary to perform its nursery function and can cause significant declines in estuarine-associated marine fish and invertebrate stocks locally and regionally [Whitfield *et al.*, 2006]. Mann & Pradervand [2007] measured a decline in the estuarine-dependent marine fish *Rhabdosargus sarba* in the St Lucia Marine Reserve between 2001 and 2005 and [Ayers *et al.*, 2013] modeled the effect of decreased prawn recruitment to the Thukela Banks ecosystem following the closure of St. Lucia, one of their main nursery areas.

The spatial distribution of different bird species is mainly determined by water depth whereas the bird community structure is determined by water depth and salinity [Turpie *et al.*, 2013]. Taylor [2013] found that the hippo population has increased steadily over the past forty years by 2 to 3 % each year. Over the current drought period freshwater for drinking and lie-up sites became scarce as water levels began to drop. Hippos resident in North Lake congregated in a small freshwater pool in Tewate Bay and about half of the hippo population sought refuge in the Narrows [Taylor, 2013]. Note that the decrease in hippo biomass indicated in Figure 6.2 in both North and South Lake was due to the movement of hippos to the Narrows. The spatial distribution of crocodiles is determined by a number of parameters including salinity, water levels and nutritional demands [Combrink *et al.*, 2013]. Combrink *et al.* [in prep.] found that crocodiles can tolerate a wide salinity range by moving to more favourable microhabitats once conditions become unfavourable. When low water levels inhibit the movement of crocodiles to more favourable sites crocodiles will seek refuge in freshwater seepage ponds.

6.4.2 Ecosystem responses to physical changes

In 2006 the significant decrease in lake water levels and the subsequent loss in habitat in combination with hypersaline conditions had a profound impact on species abundances. These conditions were reflected in the low total living standing stock and Total System Throughput (TST) of the system. Following the mouth opening in March 2007 there was a significant increase in the biomass of several biota due to the recruitment of fish and invertebrates into the system. After the mouth closed again, salinities increased and the TST decreased in both sections of the lake. A clear biomass pattern between the open and closed mouth state of the system is therefore present and is reflected in the TST in each of the networks. The increased TST, in combination with a lower H value is furthermore reflected in a significantly higher DC value (where DC = H x TST) during open mouth conditions. This indicates that during open mouth conditions there is more capacity for development.

The AMI is higher when there are fewer connections entering a compartment and/or the total inflow is unevenly distributed among these pathways. The AMI is lower when all nodes are fully connected and the material is more equally distributed among the different links [Scharler & Fath, 2012]. Results show overall higher flow diversity as well as a higher degree of flow constraints during closed mouth conditions relative to open mouth conditions, especially when H decreased dramatically. Scharler [2012] also found an increase in AMI at the Mdloti Estuary in South Africa during closed mouth conditions. Latham & Scully [2002] stated that in Shannon's theory information quantifies the degree of uncertainty about what message will be produced by a message source. There is more information and more uncertainty about the message (trophic flow, Tij) produced when less is known about the source (all flows leaving i, Ti.) resulting in a higher Kullback-Leibler divergence. The St Lucia system displayed overall higher growth and development (as A) and complexity (as DC) during open mouth conditions, but a distinctly lower diversity of flows (as H). This was unforeseen, as in 2006 species abundance and diversity was lowest before it increased in 2007 and 2008 for both basins. The lower diversity of flows during open mouth conditions were more than likely due to the increase in predominant flows of imports and exports causing an overall unequal distribution of flows in the system. The apparent high organization of the network flows during open mouth conditions (A/C, or AMI/H = 81

Ulanowicz [2000] stated that the ascendency of an ecosystem will tend to grow at the expense of its overhead when external perturbations are relatively small. The resilience of the St Lucia system was very low during open mouth conditions, however, the growth and development of the system at that stage was significantly high. The R/DC ratio did not vary spatially but was higher during the closed phase. This indicates that as the mouth closed and the growth and development of the system declined, the resilience of the system increased. The overheads due to imports and exports are expected to decrease during closed mouth conditions when external exchanges are restricted. The proportion of overheads (imports and exports) of DC were however significantly higher during 2006 when the dependency on hippos (detritus importers) was highest.

The A/DC ratio of other estuaries in South Africa (e.g. the Swartkops, Sundays, Kromme, Mdloti and Mhlanga estuaries [Scharler, 2012; Scharler & Baird, 2005]), the USA (e.g. Chesapeake, Narragansett and Delaware Bays [Monaco & Ulanowicz, 1997]) and Europe (e.g. Ems and Ythan estuaries [Baird & Ulanowicz, 1993]) generally range between 28 and 60 %. The A/DC ratios for the present study only fall within this range during closed mouth conditions which indicates that by comparison St Lucia exhibits similar degree of flow constraints even during severe drought conditions. The R/DC ratios of the above mentioned systems range between 27 and 42 %, and are therefore higher than all estimates for St Lucia thereby indicating its comparatively lower resilience to external perturbations.

St Lucia was dominated by benthic communities in terms of its compartmental throughput especially during the open phase. There was however a significant increase in the compartmental throughput of the collective pelagic communities in South Lake in 2008 compared to the pelagic community of the other networks. This corresponded to a substantial increase in the biomass of piscivorous fish following recruitment during the open phase and the subsequent build-up of biomass (refer Figure 6.2). The system relied more on benthic communities in terms of the total contribution and dependency coefficients; however, there was an increase in the contributions from pelagic communities over the study period in both parts of the lake as water levels increased. Although the system remains benthos dominated, the increase in water level has to some extent suppressed the dependence on and contributions from the benthic compartments. This is in agreement with Govender *et al.* [2011] who found that food sources were mainly benthic dominated in shallow regions. A comparison between three temperate South African estuaries by Scharler & Baird [2005] found that all three estuaries were also more dependent on the benthic components in terms of the system throughput as opposed to the pelagic components.

The detritivory: herbivory ratio was significantly lower during the open phase and is a good reflection of the availability of primary producers as a direct food source. In addition the system showed a higher (about 1.5 times higher) dependency coefficient on primary producers than detritus. van der Molen & Perissinotto [2011] found that the breaching event in March 2007 caused a significant increase (9 to 20 times higher) in the benthic productivity of the system. As the biomass of primary producers decreases during the closed phase the system relies more heavily on benthic biota and detritus. Note that although less than 2 % of the carbon produced by these primary producers is directly consumed by herbivores, the system is indirectly highly dependent on submerged macrophytes as detritus producers. Our results indicate that St Lucia is similar to other South African estuaries and substantiate the common key features summarised by Scharler & MacKay [2013], namely that detritus is an important food source

[Govender *et al.*, 2011; Heymans & Baird, 1995; Scharler & Baird, 2005], that benthic microalgae have a higher biomass compared to that of phytoplankton [Perissinotto *et al.*, 2002; van der Molen & Perissinotto, 2011] and that benthic invertebrates make up a significant proportion of the total living standing stock of estuaries and are an important food source [Heymans & Baird, 1995; Scharler & Baird, 2005].

The results discussed here show substantial temporal changes over the three year study period due to the breaching of the mouth and the subsequent recovery of the system, however, spatial changes are less pronounced. The TST, DC and ascendency of North Lake are less than half that of South Lake, but the A/DC and R/DC ratios are similar. This indicates that North Lake has a lower capacity for development and growth than South Lake. North Lake is also characterised by a higher detritivory: herbivory ratio and lower compartmental throughput of both pelagic and benthic compartments.

6.5 Conclusions and Recommendations for Future Research

It is evident from this investigation that water level, salinity and mouth state have a significant impact on species abundance and biodiversity, and in turn on the biological structure and functioning of the St Lucia system. The substantial increase in the total living standing stock and species diversity during the open phase indicates that the system responds rapidly during favourable conditions. This is further emphasized by the subsequent decrease after the mouth closed and salinities increased. The indices estimated in this study show that temporal changes experienced in the system during the current dry period far outweigh spatial changes between the northern and southern regions of the system. It is not yet clear whether this is a key feature of the system, or if the temporal changes due to the breaching event in 2007 and the subsequent recovery of the system overshadowed the spatial changes over this particular period of time.

The St Lucia estuarine-lake system has received significant research attention over the past 70 years; however food web studies are limited. The available datasets from the past 70 years are inconsistent in space and time with only a relatively small proportion of quantitative information. For example, submerged macrophytes contribute significantly to the total biomass of the system as well as the overall functioning, but the availability of aerial survey data are restricted to 1996 and 2008. In addition the available data have been collected by numerous sources often using different sampling techniques and temporal resolution. In order to analyse the St Lucia system more specifically at the ecosystem level, more deliberate data collection from the full array of species present in the system is required. Foodweb studies distinguish key species and therefore identify which species require research attention. The results from this study indicate that ecosystem studies would benefit from more frequent bird, crocodile, hippopotamus and submerged macrophyte surveys in order to establish seasonal trends. Bacteria and heterotrophic microplankton also require research attention.

Results show that the St Lucia estuarine-lake system shares common traits with other, smaller, South African estuaries. Although the present study provides insight into the ecosystem functioning during severe drought conditions and the initial response of the system to a breaching event, ecosystem responses during other conditions (e.g. wet period, open mouth, low salinity) remain unknown. Future foodweb studies under other conditions (e.g. low salinities, high water levels) can provide further valuable insight into how physico-chemical changes influence ecosystem functioning. It is expected that the reestablishment of the Mfolozi/St Lucia combined mouth will provide a more stable physico-chemical regime and therefore the opportunity to investigate the system during water level/salinity states different to extreme conditions.

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Chapter 7

Biophysical responses for Lake St Lucia

7.1 Introduction

The National Biodiversity Assessment [Van Niekerk & Turpie, 2012] was undertaken to assess the state of South Africa's estuarine biodiversity and intended to enable systematic planning for the conservation of these systems. The results of the assessment indicated that although many estuaries in South Africa were regarded as being in good condition, there was a general decline in the health of the larger important estuaries. The health of these estuaries was evaluated by using an Estuarine Health Index [Cooper *et al.*, 1994] to assess the extent to which current conditions differ from reference conditions. One of the priority actions for estuarine biodiversity management and conservation noted in the report was the restoration of the St Lucia system. The St Lucia estuarine-lake system represents more than 55 % of the total estuarine area of South Africa yet it is classified as being in very poor condition. In order to conserve this important system it is therefore imperative to understand the different components of the system as well as how the system functions as a whole.

Simulating and/or predicting the consequence of a given change is a vital tool in the sustainability and restoration of these ecosystems. Ecosystem response modelling is used to predict the impacts of management actions on a natural environment and is a simple tool that can be used to discern possible mitigation measures [Marsh & Cuddy, 2010]. Selecting an appropriate model or combination of models to represent an ecosystem depends on the desired outcomes of the modelling exercise. Stakeholders may have varying requirements of the model i.e. a manager is more likely to be concerned about the ability of the model to predict different scenarios while a scientist would be more interested in processes. Therefore an important outcome of ecosystem modelling is to provide an understanding of how the system behaves as a whole. This is imperative for making informed management decisions [Jakeman *et al.*, 2006] and highlights where research efforts need to be aimed.

Anthropogenic changes can impact both the biological (e.g. abundance and biomass) and physico-chemical (e.g. freshwater inflows, salinity) components of an ecosystem [Whitfield & Elliot, 2002]. The integration of these aspects into biophysical models is however complex and rare and available studies are generally focussed on a specific aspect of a system's functioning (e.g. Banas *et al.* [2009]; Beletsky *et al.* [2007]). In terms of St Lucia, Taylor [1987] developed a simple conceptual rule-based model for the system to determine the biological responses to changing physical conditions i.e. salinity and water level. The rules were however based on qualitative data and there has been little attempt to validate simulated results since then.

7.2 Towards a biophysical model

St Lucia is the most researched estuary in South Africa [Whitfield & Taylor, 2009], however, biological data remains patchy in space and time and there has been little overlap in sampling methodologies and locations. In addition certain species have received more research attention than others and have been the subject of ongoing research (e.g. fish), while other species have had little consideration (e.g. submerged macrophytes). In this case it would not be appropriate to use complicated modelling techniques but rather simple tools that are easily understood and have the ability to be easily improved as more data becomes available. Therefore, to predict the biophysical responses of different management actions for the St Lucia system requires a flexible approach. Lester & Fairweather [2009] had similar difficulties in modelling the Coorong in Australia and developed an ecosystem response model based on ecosystem states and a state-and-transition framework model.

7.2.1 Biophysical responses

Nine different water level/salinity states were established for the St Lucia system in Chapter 5. Results show that the system follows two main trajectories through the water level/salinity state space that are associated with open and closed mouth states respectively (refer Figure 7.1). Open mouth conditions are characterised by a 1-dimensional bi-directional pathway while closed mouth conditions are represented by characteristic curved trajectories. These curved trajectories are typically uni-directional (i.e. in scenario 3), however, the trajectory follows a bi-directional curve during prolonged closed mouth conditions i.e. in scenario 2. In addition these closed mouth trajectories extend to more extreme values.

Understanding how the system functions under different management scenarios provides a platform for predicting changes that may occur with regards to the biology. A consolidated qualitative assessment of the biological responses (i.e. expected levels of biodiversity and abundance/biomass) of the different biological components was performed for the nine different water level/salinity states and is summarised in Table 5.1. A summary of the responses of the different biological components for the different states is given in Figure 7.1 and are to be viewed together with the occurrence and persistence of the associated states. Note that based on the analysis done in Chapter 5 for different mouth management scenarios conditions within the shaded areas do not typically occur in the system.

7.2.2 Indicator species

Monitoring of ecosystems is often time consuming, costly, logistically problematic and requires specialist knowledge. It is therefore not always possible to measure all that is of potential interest in an ecosystem. Resource managers often select indicator species to assess the state of water resources and to evaluate manage-

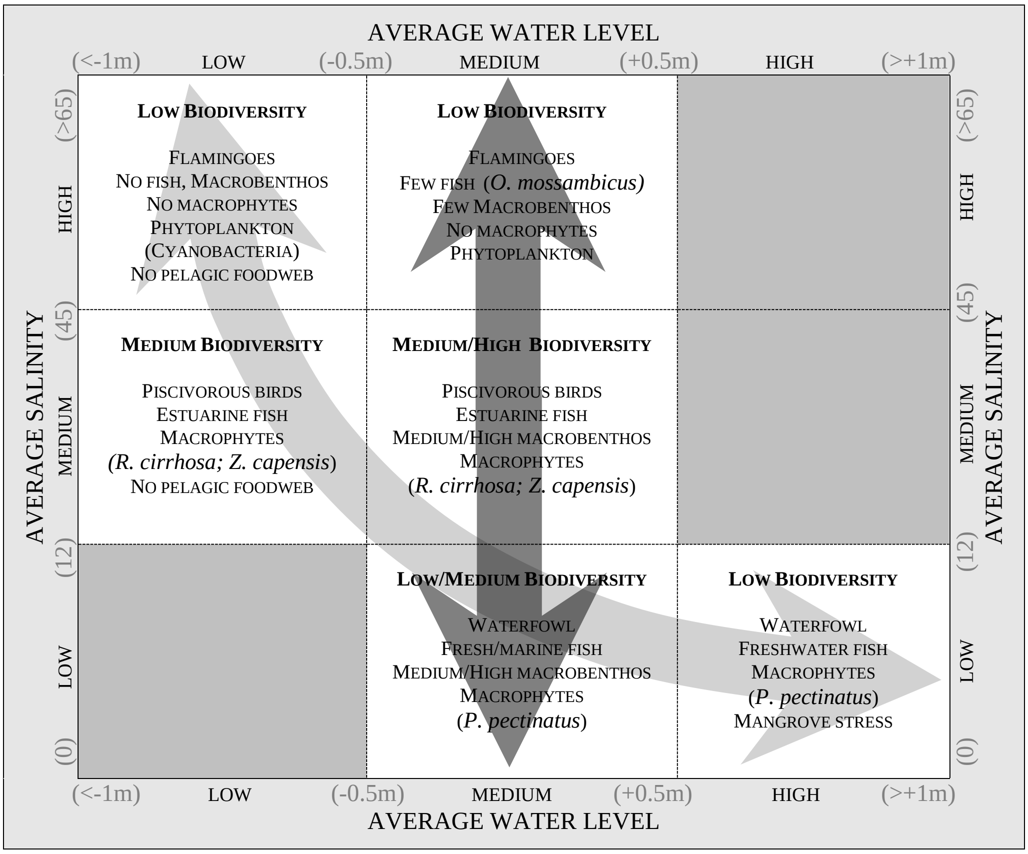

Figure 7.1: Schematic of the possible water level/salinity states at St Lucia. The arrows depict the possible trajectories for open (vertical arrow) and closed (curved arrow) mouth conditions. Included are some of the biological responses for each of the water level/salinity states.

ment actions (refer to Section 2.2.1), however, selecting the appropriate species is not necessarily a straightforward exercise [Carignan & Villard, 2002]. The main challenge is to determine which components characterise the entire system but are simple enough to be easily measured and modelled [Dale & Beyeler, 2001; Tulloch *et al.*, 2011]. While there are no standard indicator groups, scientists generally focus on fishes, macroinvertebrates, birds and plants [Turpie, 2005; Whitfield & Elliot, 2002]. Whitfield & Elliot [2002] describe the advantages and disadvantages of using fishes as indicators of environmental and ecological change in estuaries and state the importance of performing fish studies in conjunction with chemical, hydrographical and other biological components.

As stated before, in an attempt to simulate biological responses to hydrological changes at St Lucia, Taylor [1987] and Starfield *et al.* [1989] developed simple rule based ecological models after insufficient quantitative knowledge prevented the development of equation-based models. Taylor [1987] and Taylor [2006] noted that the main ecosystem components change with salinity. At low salinities they comprise mainly water plants and herbivorous birds. With salinity near to that of sea water, the main components include benthic fauna, fishes and piscivorous birds and at higher salinities benthic fauna die off and zooplankton become dominant and are fed upon by flamingos. The model was based on the assumption that the dominance of the fauna in these ecosystem states is influenced by the distribution of primary producers which in turn is driven by water level and salinity changes [Gordon *et al.*, 2008; Starfield *et al.*, 1989; Taylor, 2006]. The development of these ecosystem states also depends on the length of time that the system remains within specific salinity/water level ranges (i.e. their residence times).

There have been numerous studies documenting the salinity tolerances of certain species at St Lucia (e.g. Carrasco *et al.* [2010]; Johnson & Breen [1982]; Miranda *et al.* [2010]; Nel *et al.* [2011]; Owen & Forbes [2002]; Whitfield *et al.* [2006]. Although some of these studies were performed under laboratory conditions, St Lucia is an ideal environment to test the salinity tolerance ranges of species because changes occur over extended periods exposing biota to extreme salinities for longer. In 1979, Whitfield [1982] compiled a fish list of 108 fish species at St Lucia of which Whitfield *et al.* [2006] documented the recorded salinity ranges of 50 of them. Figure 7.2 shows the salinity tolerance ranges of the 50 freshwater, estuarine and marine fish species. Included are the known salinity ranges of other species (e.g. submerged macrophytes, prawns and the alien invasive species *Tarebia granifera*). The number of fish species present within each salinity range was estimated. Considering the salinity ranges (i.e. low, medium and high) low salinities are characterised by all the 50 species, medium salinities by 47 species and high salinities by 18 species.

Note that in terms of fish and macroinvertebrates, the recruitment and passage into and out of the system is imperative and therefore the mouth state also needs

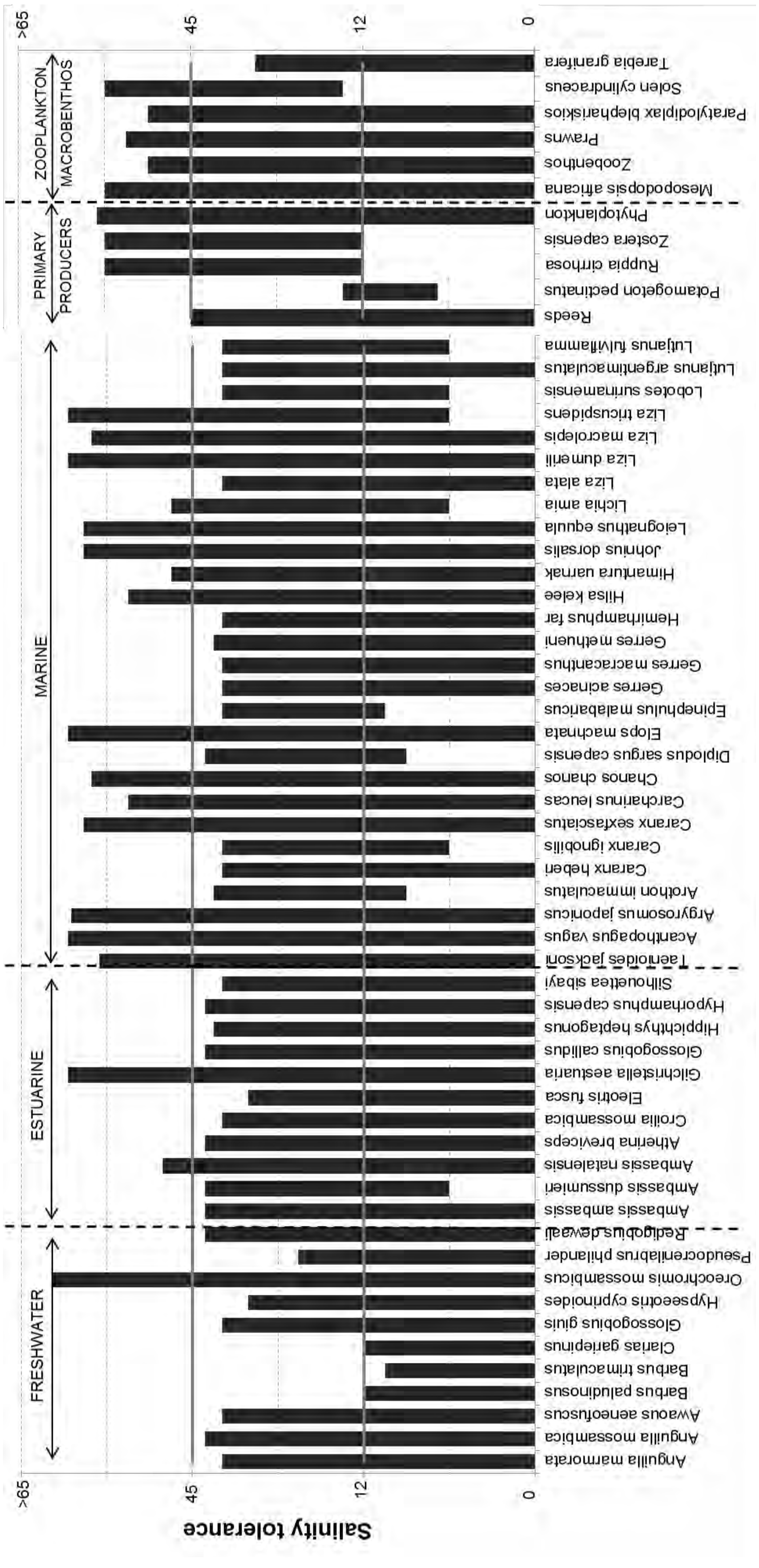

Figure 7.2: The salinity tolerance range of fifty fish species of St Lucia, including freshwater, estuarine and marine species (after Whitfield *et al.* [2006]).

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to be considered in addition to the salinity tolerance.

7.2.3 Ecosystem Indices

A number of ecosystem indices were determined for the current dry period. Although there were insufficient data to perform an ecosystem network analysis for each water level/salinity state, the ecosystem indices estimated in Chapter 6 represent the system under one of these states, i.e. low water levels/high salinities (L|H). Figure 7.3 shows the locations in the water level/salinity state space that have been represented by a suite of ecosystem indices. The arrows depict the typical trajectories for open (vertical arrow) and closed (curved arrow) mouth conditions as in Figure 7.1. The water level/salinity combinations during closed mouth conditions both before (2002-2007) and after (2007-2013) the breaching event in March 2007 were also included. Note that the breaching event that occurred in 2007 was due to a combination of unusual climatic events and therefore the indices representative of conditions in 2007 (open mouth state) and 2008 (closed mouth state) may not be a typical representation of the conditions experienced in that water level/salinity state. These indices do however illustrate the rapid recovery of the system following a breaching event and the significant capacity for development of the system under open mouth conditions.

The AMI/H (or A/DC) was significantly higher during open mouth conditions and illustrates the exponential increase in the total biomass and biodiversity of the system at that time. It has already been stated that an open mouth state is imperative for the recruitment and passage of fish and other macroinvertebrates into and out of the system as it has a substantial impact on the total biomass of the system.

7.2.3.1 System health

Constanza & Mageau [1999] described a healthy ecosystem as being sustainable and having three ecosystem attributes, namely organisation, vigour and resilience. The organisation of a system is described by the diversity and magnitude of the interactions between the system components and may be measured by the Average Mutual Information (AMI) index. The vigour of a system is simply a measure

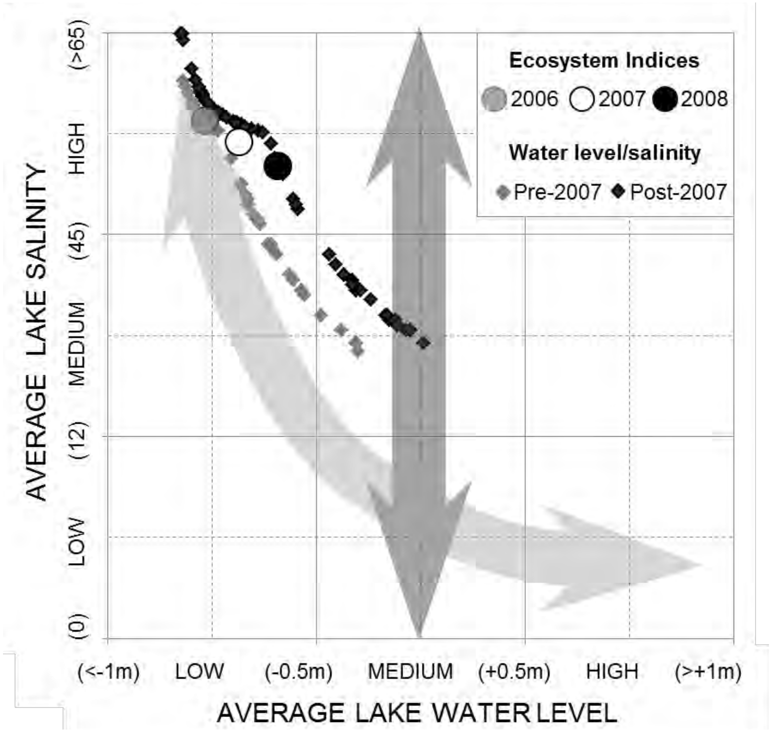

Figure 7.3: Schematic of the possible water level/salinity states at St Lucia illustrating where in the water level/salinity state space the available ecosystem indices occur.

of activity, metabolism or primary production and can be measured directly, e.g. by the Total System Throughput (TST). The system resilience describes the ability of a system to maintain its structure and functioning whilst under stress and can be measured as the difference between the flow diversity (H) and the AMI. Ascendency (A) describes both vigour and organisation (A=TSTxAMI) and resilience can be defined as overhead and is estimated by TSTx(H-AMI). Plotting ascendancy versus the overhead gives a quantitative assessment of the health of an ecosystem [Constanza & Mageau, 1999; Mageau *et al.*, 1995]. Constanza & Mageau [1999] state that a healthy system is one that has the ability to develop to capacity in the absence of severe perturbations while having the resilience to insure against stress and the vigour to recover from minor perturbations. This implies that a healthy ecosystem will have a balance between organisation and resilience within a given range of system vigour (see Figure 7.4). Note that the healthy region is system specific [Constanza & Mageau, 1999].

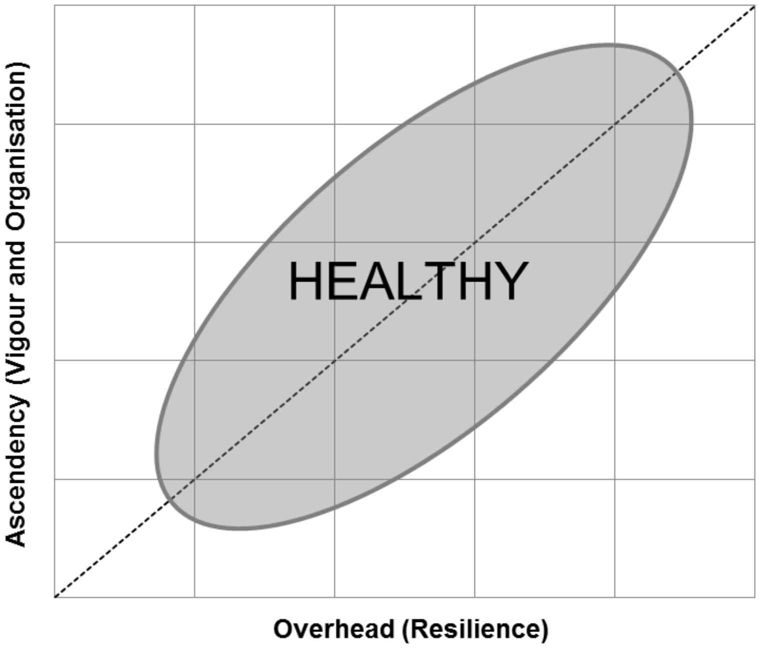

Figure 7.4: A conceptual diagram of the network analysis-based quantitative index of ecosystem health. Note that the healthy region is indicated by the shaded area (after Constanza & Mageau [1999]).

The "health" of the St Lucia system was plotted using the given indices derived in Chapter 6 (see Figure 7.5). Note that although there was a significant drop in species diversity and abundance in 2006 there was a balance between the system ascendancy and resilience. When the mouth was open in 2007 the development capacity of the system increased substantially and the system moved to an area of high ascendency and low resilience. This was due to the subsequent increase in species abundance and diversity (i.e. the TST) as a result of more favourable physico-chemical conditions and the recruitment of species into the system. The increase in vigour and organisation occurred at the expense of the system's resilience. At the time when the indices were calculated, the system had only been open for three to four months. Given a prolonged open mouth state the system may have moved towards having a higher resilience. Note that the healthy region has not yet been defined for the St Lucia system.

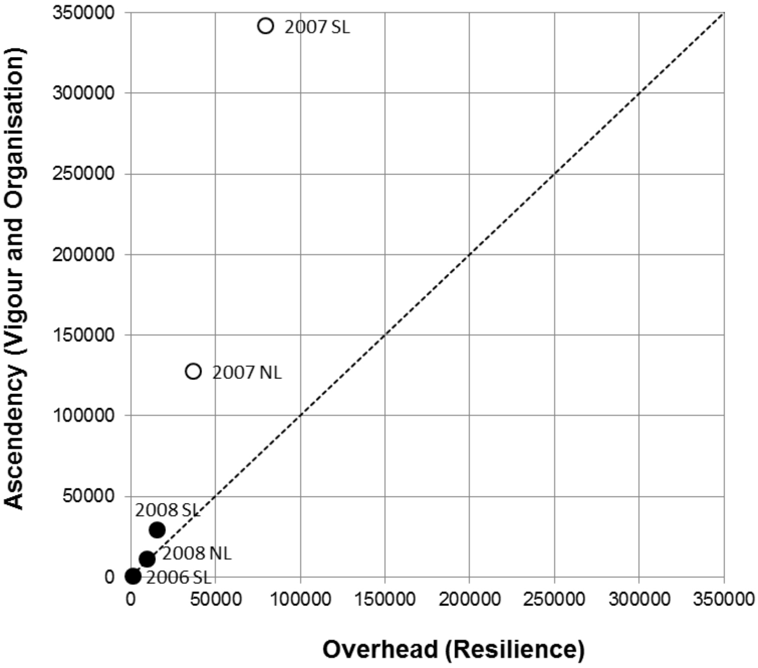

Figure 7.5: A comparison of the relative positions of the ecosystem networks for Lake St Lucia (from 2006 until 2008) using Constanza & Mageau [1999] network-analysis assessment of ecosystem health.

7.3 Biophysical responses of the different water level/salinity states

The St Lucia/Mfolozi mouth has been manipulated for over half a century, however, there has been little contribution to understanding the overall functioning of the system let alone the effects of diverting the Mfolozi River in 1952. The previous chapters of this thesis show that the system functions fundamentally differently under different management scenarios both physico-chemically and biologically. The construction of a complex biophysical model was unattainable due to the inconsistency of available biological data in both space and time. The results, deductions and assumptions derived from a combination of all methods described above were encapsulated in Figure 7.6 to provide an abridged overview of the biophysical functioning of the St Lucia system.

The vertical and curved trajectories depict open and closed mouth conditions respectively and the arrows have been shaded to indicate the level of biodiversity and abundance of species (i.e. the dark regions depict high biodiversity and abundance and the light regions low biodiversity and abundance). The occurrence of the average lake salinity has been included for each scenario. Note that scenario 1 is depicted by the vertical arrow (open mouth conditions), scenario 2 by the curved arrow (i.e. predominantly closed mouth conditions) and scenario 3 by a combination of the two. The expected AMI/H (A/DC) ratio was also included for each scenario using the indices calculated in Chapter 6 under different mouth states and salinity as a reference.

The water and salt budget model was used to determine the occurrence and persistence of average lake water levels and salinities and therefore the presence of these ”indicator species”. It is important to note that the average lake salinity does not take into account the salinity gradient and that biota move into more ideal environments when conditions become unfavourable (e.g. Forbes & Cyrus [1993]; MacKay *et al.* [2010]). Therefore saying that a species is not present during a particular average lake salinity would be false. However, by inferring the salinity in south and north lake using the relationship between the average lake salinity and the salinity of South Lake, North Lake and False Bay (Figure 5.2(b)) it is possible to deduce a more accurate salinity for each basin.

The results from the ecosystem network analysis (refer Chapter 6) suggest that an open mouth state is a determining factor of the biodiversity and abundance of species in the system.

7.4 The rejoining of the Mfolozi and St Lucia systems

In a bid to restore the system functioning to its natural state measures have been made to rejoin the Mfolozi and St Lucia systems. The proposed changes to the mouth management strategy is expected to have a significant impact on the occurrence and persistence of water level/salinity states and in turn the biological functioning. This scenario would be mainly represented by the trajectory for open mouth conditions (vertical arrow, Figures 7.1 and 7.6) and although hypersaline

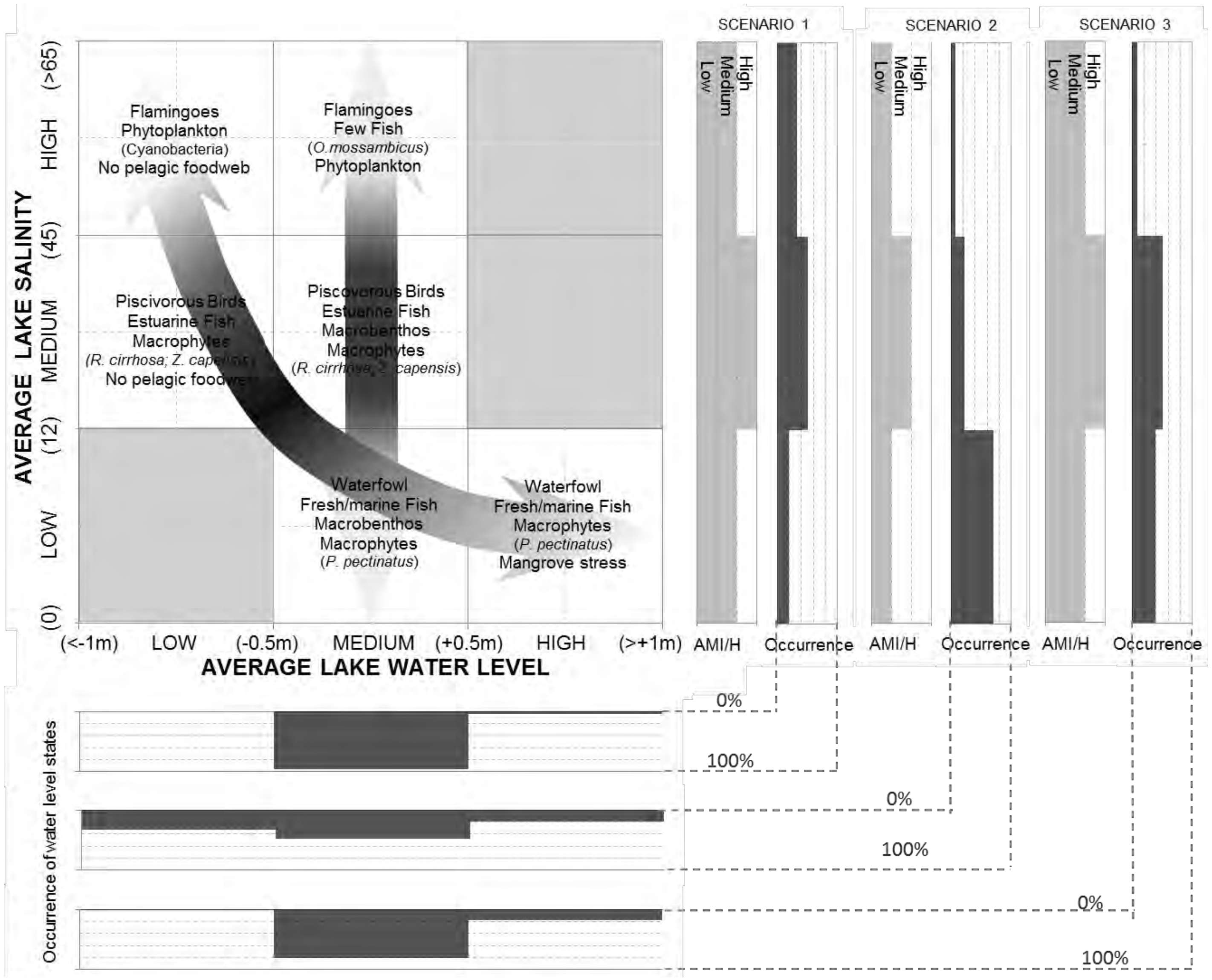

Figure 7.6: Schematic of the possible water level/salinity states at St Lucia. Open and closed mouth conditions are depicted by the vertical and curved trajectories respectively. The arrows have been shaded to illustrate the areas of high (dark) and low (light) biodiversity. The occurrence of water level states and salinity states has been included for each scenario. The expected AMI/H is also given for each salinity state.

conditions may still occur, they are unlikely to coincide with low water levels or persist for more than about 4 months at a time. In addition the open mouth state will stabilise water levels and enable the recruitment of fish and other macroinvertebrates into the system. There was a substantial increase in the biomass and TST of the system during the brief open phase in 2007 which gives an indication of the ability of the system to recover following severe adverse conditions such as desiccation and hypersaline conditions. While the system would function predominately in the salinity/water levels states M|H or M|L, the system is expected to accommodate a high abundance and biodiversity of most species and therefore a large total biomass and total system throughput. This will provide a unique opportunity to monitor the system during the recovery process and will provide a closer look into how the system functioned in a more natural state.

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Chapter 8

Conclusion

8.1 Introduction

The St Lucia estuarine-lake has experienced considerable anthropogenic impacts over the past century, however, little has been done to understand how these impacts have effected the biophysical functioning of the system. This chapter provides a synthesis of the findings of this study including the advancements made towards understanding the physico-chemical dynamics of the system and its effect on the biology. The conclusions are presented by answering the research questions and recommendations for future research are made.

8.2 Research answers

The main aim of this thesis is to improve the understanding of the biophysical interactions in the St Lucia estuarine-lake complex and to provide new knowledge to underpin the development of improved models for predicting the response of the system to changing climatic conditions.

The research questions presented in Chapter 1 are provided below together with a brief summary of their answers.

In order to understand the biophysical interactions of the St Lucia system, it was necessary to analyse it holistically in terms of the physical processes and their interaction with the biological system. Therefore the research questions below are divided into two main components :

Water and salt budget

What was the effect of separating the St Lucia and Mfolozi systems on the water/salt budgets and mouth dynamics?

A water and salinity budget model of the St Lucia estuarine-lake was constructed and used to simulate various management scenarios (refer Chapter 4). The simulations show that the separation of the Mfolozi and St Lucia mouths had the most significant impact on the functioning of the St Lucia system. In addition to contributing an important source of fresh water to the system during dry conditions, the Mfolozi also plays a pivotal role in providing a more stable mouth state regime for the system. The Mfolozi causes a substantial increase in mouth outflows which counteracts the flood dominance of the tidal hydro/sediment dynamics and therefore tends to maintain a predominantly open mouth state regime. Without the Mfolozi link, the mouth tends to remain closed for periods of about 10 years at a time and therefore requires ongoing dredging efforts to keep it open (as occurred since 1952).

How does the system respond to extreme events under different mouth management scenarios?

This question is addressed in Chapters 4 and 5. The St Lucia system experiences quasi-cyclic wet/dry periods on a decadal time-scale during which there can be significant shifts in the physico-chemical characteristics of the system. Long-term simulations of the water and salt balance were used to estimate the occurrence and persistence of water levels and salinities for different mouth management scenarios and the risks of hypersalinity and desiccation were assessed. Results show that the mouth state and therefore the configuration of the St Lucia/Mfolozi mouths play a pivotal role in the physico-chemical functioning of the system.

The combined Mfolozi/St Lucia mouth maintains an open mouth state for most of the time, however, during dry conditions salinities increase linearly before the mouth closes. During closed mouth conditions, water levels rise while salinities decrease due to the addition of fresh water from the Mfolozi. The rising water levels would eventually cause the mouth to breach. The risks of dessication and hypersaline conditions in the closed state are very low. The separation of the Mfolozi mouth results in a predominantly closed, fresh water system with highly variable water levels. During dry conditions salinities increase exponentially while water levels drop and there is a high risk of hypersalinity and desiccation (as occurred during the recent dry period). The system breaches on average every 10 years in this scenario. The risk of desiccation is reduced if the mouth is kept open under this scenario however hypersaline conditions would be a common occurrence.

How would importing additional fresh water into St Lucia change the functioning of the system?

The option of importing additional fresh water from the Mfolozi River into St Lucia was addressed in Chapter 4. Anthropogenic activities have reduced catchment inflows by about 20 % or 60 Mm^3 per year. Results indicate that higher fresh water inflows would significantly dampen the effect of drought conditions, however, it is important to note that it would have little impact on the mouth state regime of the system.

Biological responses

Can the overall biological structure and functioning of the system be characterized using a set of normalized ecosystem indices?

This question was addressed in Chapter 6. The ecosystem indices characterise the low species abundance and total biomass of the system during 2006 as well as depict the recovery of the system during open mouth conditions in 2007. The significant increase in the total biomass, the TST and A/DC illustrate the impressive potential of the system to rapidly recover from severe adverse conditions. These indices charaterise the significant decline in species abundance and biodiversity measured by other researchers during 2006 and the subsequent increase following the mouth opening in 2007 (Section 6.4.1).

Applying the idea of ecosystem health (discussed in Chapter 7) shows that although the biodiversity and total biomass of the system was low in 2006, there was a balance between the resilience and organisation of the system. When the mouth opened in 2007 the development capacity of the system increased exponentially and the system shifted towards having a higher vigour and organisation at the expense of system resilience. The resilience of the system would be expected to increase if the system had more time to recover.