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Network analysis indices reflect extreme hydrodynamic conditions in a shallow estuarine lake (Lake St Lucia), South Africa

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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.

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 and 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 and Ulanowicz, 1989; Heymans and Baird, 2000; Wolff et al., 2000; Rybarczyk and Elkaim, 2003; Patrício et al., 2004; Scharler and Baird, 2005; Leguerrier et al., 2007; Niquil et al., 2012) 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 and 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 and 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

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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 and Stretch (2011b) show that these conditions are unprecedented and are characteristic of dry conditions under the current mouth management strategy. As a consequence a substantial decline 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 and Turpie, 2012) and is an important nursery area for estuary-associated marine fish and prawn species (Benfield et al., 1989; Forbes and Demetriades, 2005; Mann and 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 exacerbating knock-on effects to nearshore environments and fisheries (Whitfield et al., 2006; Mann and Pradervand, 2007; Ayers et al., 2013).

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 and 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, 1993) and Starfield et al. (1989) 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 and 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 mouths is present but not manipulated). Scharler and 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.

2. Methods

2.1. The case study site

The St Lucia estuarine lake (between 27°42′–28°24′ S, and 32°21′–32°34′E) is situated on the sub-tropical east coast of South Africa (Fig. 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 and Pitman, 1977; Lawrie and Stretch, 2011a). Simulations by Lawrie and 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 10 years at a time. During this time water levels and salinities fluctuate depending on catchment inflows and hypersalinity and desiccation are a common occurrence.

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. Pillay and Perissinotto, 2008; Vivier et al., 2009; Jerling et al., 2010). 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 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 $mgC\,m^{-2}$ and flow measurements (i.e. productivity, consumption, respiration, egestion, imports and exports) are expressed in $mgC^{-2}\,day^{-1}$. 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–July) each year.

Each compartment of the network was mass balanced where energy obtained via consumption was used for respiration, egestion and production (Jørgensen and Bendoricchio, 2001). For primary