

**Diversity of bivalve molluscs within the St Lucia
estuarine system, with emphasis on the
ecophysiology of *Solen cylindraceus* and
*Brachidontes virgiliae***

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Submitted in fulfilment of the academic requirement for the degree of
Doctor of Philosophy in the School of Life Sciences, University of
KwaZulu-Natal, Westville

March 2014

As the candidate's Supervisor, I have approved this thesis for submission.

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Abstract

The St Lucia estuarine system, Africa's largest estuarine lake, is characterised by cyclic changes from hypersaline to oligo/mesohaline conditions in response to alternations between drought and wetter than average years. In addition, St Lucia also experiences stochastic disturbances, such as flooding events that rapidly decrease salinity levels. Due to their sessile and slow moving nature, bivalves are particularly vulnerable to rapid or prolonged changes in the physico-chemical environment. The recent freshwater deprivation crisis that prevailed for the last decade resulted in a significant loss in bivalve species richness within the system. An annotated and illustrated bivalve census revealed the occurrence of twenty-four species within St Lucia between the years 1925 and 2011. However, only six species were recorded during the most recent survey in March 2011. The infaunal razor clam, *Solen cylindraceus*, and the epifaunal brackwater mussel, *Brachidontes virgiliae*, are currently the dominant bivalve species within St Lucia. This study, therefore, aimed to record the species richness of bivalves found in Lake St Lucia and to investigate key biological aspects of the two dominant bivalve taxa within the system, under different salinity regimes. Experiments revealed that *S. cylindraceus* can tolerate salinities between 15 and 65, while *B. virgiliae* prefers salinity levels ranging from freshwater to 20. The varying tolerance limits, therefore, dictate the distribution of these species during different climatic conditions within the estuarine lake. During wet periods, *S. cylindraceus* is restricted to the northern reaches, unable to tolerate the oligohaline conditions present in the rest of the system. Conversely, *B. virgiliae*, often restricted to the Narrows, becomes ubiquitous throughout the system under such conditions. *Solen cylindraceus* can reach a maximum length of 95 mm. However, in the St Lucia estuarine system, specimens seldom exceed a length of 55 mm, probably because prevailing/re-occurring harsh conditions prevent them from reaching maximum size. *In situ* measurements of this species also revealed less growth during the first year of life than for the same species in different systems. While *B. virgiliae* is substantially smaller than *S. cylindraceus*, the high densities that this species is able to attain makes it an important grazer with the potential to have significant feeding impacts on the local phytoplankton biomass. Results showed that in localised areas, *B. virgiliae* populations may consume up to eight times the available phytoplankton biomass. These key bivalve species are strongly influenced by the fluctuation in climatic conditions from wet to dry phases. Thus, understanding the effects that climatic shifts have on key estuarine species is essential, as flood and drought events are predicted to increase in frequency, intensity and duration as a result of global climate change.

Preface

The experimental work described in this PhD thesis was carried out in the School of Life Sciences, University of KwaZulu-Natal, Westville, from January 2011 to November 2013, under the supervision of Professor Renzo Perissinotto and co-supervision of Dr Ricky Taylor.

These studies represent original work by the author and have not otherwise been submitted in any form for any degree or examination at any other university. Where use has been made of the work of others it is duly acknowledged in the text.

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DETAILS OF CONTRIBUTION TO PUBLICATIONS that form part and/or include research presented in this thesis are as follows:

Publication 1: Nel HA, Perissinotto R, Taylor RH (2012) Diversity of bivalve molluscs in the St Lucia Estuary, with an annotated and illustrated checklist. *African Invertebrates* 53: 503–525.

Author contributions: Conception and design: H.A.N, R.P and R.H.T. Performed experiments and analysed data: H.A.N. Wrote the draft paper: H.A.N.

Publication 2: Nel HA, Perissinotto R, Taylor RH, Carrasco NK (2011) Salinity tolerance of the bivalve *Solen cylindraceus* (Hanley, 1843) (Mollusca: Euheterodonta: Solenidae) in the St Lucia Estuary. *African Invertebrates* 52: 575–586.

Author contributions: Conception and design: H.A.N, R.P, R.H.T and N.K.C. Performed experiments and analysed data: H.A.N. Wrote the draft paper: H.A.N.

Publication 3: Nel HA, Perissinotto R, Taylor RH (In review) The effect of salinity on the survival of the Brackwater mussel, *Brachidontes virgiliae*, in the St Lucia estuarine system, South Africa. *Water SA*.

Author contributions: Conception and design: H.A.N, R.P and R.H.T. Performed experiments and analysed data: H.A.N. Wrote the draft paper: H.A.N.

Publication 4: Nel HA, Perissinotto R, Taylor RH (2013) *In situ* growth rate of *Solen cylindraceus* (Mollusca: Euheterodonta: Solenidae) in the St Lucia estuarine lake, South Africa. *African Zoology* 48: 266–273.

Author contributions: Conception and design: H.A.N, R.P and R.H.T. Performed experiments and analysed data: H.A.N. Wrote the draft paper: H.A.N.

Publication 5: Nel HA, Perissinotto R, Carrasco RH (In review) Ingestion rates and grazing impact of the Brackwater mussel, *Brachidontes virgiliae*, in Lake St Lucia, iSimangaliso Wetland Park, South Africa. *Marine and Freshwater Research*.

Author contributions: Conception and design: H.A.N, R.P and N.K.C. Performed experiments and analysed data: H.A.N. Wrote the draft paper: H.A.N.

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Acknowledgments

My supervisor, Professor Renzo Perissinotto has provided me with an invaluable opportunity to pursue my career in marine and estuarine ecology, for this I owe an enormous debt of gratitude. He also provided his guidance, constructive criticisms and expertise, which have been fundamental in my progress over the years. I would also like to sincerely thank my co-supervisor, Dr Ricky Taylor for his enormous contribution to my PhD it has been monumental. Dr Nicola Carrasco: thank you for assisting in all aspects of my PhD. You have been a friend throughout this process and I am grateful for everything you have taught me.

Without the funding provided by the National Research Foundation (NRF, Pretoria) through the program Knowledge Fields Development - Society, Ecosystems and Change (SEACHANGE), as well as the South African Netherlands Research Programme on Alternatives in Development (SANPAD, Durban) and the University of KwaZulu-Natal (UKZN, Durban) these studies would not have been possible and for this I am grateful to the above institutions.

To the staff and managers at Ezemvelo KZN Wildlife and the iSimangaliso Wetland Park Authority, thank you for supporting this project with logistical and field assistance. My thesis involved the use of a number of experiments, which would not have been possible without the technical support from fellow colleagues that have assisted me in the field and laboratory. A particular mention needs to be made to Dick Kilburn, Dai Herbert, Richard Willan and Markus Huber for their help with species identification and for providing data on specimens deposited in museums. I would like to thank Stuart McLean who, with his intense interest in natural history, collected many of the specimens in the 1982/83 survey, and Chantal Dickson who, walked most of the shoreline of St Lucia in 2005, collecting bivalves used in this study.

Lastly, but by no means least, I would like to thank my family and friends who have all supported and encouraged me to continue studying. To my mom: without your encouragement and strength none of this would have happened. You have always known just what to say even if I was not prepared to hear it.

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General Introduction

Potter *et al.* (2010) revised the definition of an estuary as “*a partially enclosed coastal body of water that is either permanently or periodically open to the sea and which receives at least periodic discharge from a river(s), and thus, while its salinity is typically less than that of natural sea water and varies temporally and along its length, it can become hypersaline in regions when evaporative water loss is high and freshwater and tidal inputs are negligible.*” This definition was adapted from both Pritchard (1967) and Day (1980; 1981), in order to incorporate the numerous estuaries, located in south-western Australia, southern Africa and to a lesser extent in the northern hemisphere, which experience hypersalinity (Potter *et al.* 2010). Hypersalinity occurs worldwide in systems such as the Wellstead Estuary (Young & Potter 2002) and Coorong in Australia (Webster 2010); Mar Menor lagoon in Spain (Lloret *et al.* 2005); Laguna Madre in Mexico (Quammen & Onuf 1993; Raz-Guzman & Huidobro 2002) and the St Lucia estuarine system in South Africa (Whitfield & Taylor 2009; Carrasco *et al.* 2010).

Estuaries are now recognised as being highly important both economically and ecologically, however they are subjected to severe anthropogenic modifications (Henninger & Froneman 2011). St Lucia, situated on the eastern seaboard of South Africa, is Africa’s largest estuarine lake. Declared a RAMSAR Wetland of International Importance in 1986, St Lucia covers approximately 80% of the estuarine area of KwaZulu-Natal (Begg 1978). It is a core feature of the iSimangaliso (previously referred to as Greater St Lucia) Wetland Park, which became South Africa’s first UNESCO World Heritage Site in 1999 (Begg 1978; Whitfield & Taylor 2009). Prior to 1952, the St Lucia estuarine system and the adjacent Mfolozi River shared a common mouth. However, due to the development of sugarcane farming in the Mfolozi floodplain, the Mfolozi River was artificially diverted away from Lake St Lucia in an attempt to avoid excessive siltation. As a result, Lake St Lucia was deprived of its most important freshwater source (Begg 1978; Ngqulana *et al.* 2010).

St Lucia also exhibits wide cyclic changes in climatic conditions, from wet to dry phases, with each phase lasting between four to ten years (Begg 1978; Cyrus & Vivier 2006). Without the freshwater input from the Mfolozi, St Lucia is unable to maintain lake levels during dry periods and as a result, hypersaline conditions and low water levels persist. During the most recent freshwater deprivation crisis (2002–2011), a reversed salinity gradient existed, with salinity levels in excess of 200 at times recorded in the northern regions. In addition, during the peak of the drought (2005), more than 50% of the lake bed was dry (Whitfield & Taylor 2009; Carrasco *et al.* 2010). At the opposite end of the scale, St Lucia is also exposed to both flooding events (e.g. Cyclone Domoina and Imboa in 1984) and a series of wetter than average years (Cyrus 1988; Forbes & Cyrus 1992; Pillay & Perissinotto

2008). During these conditions, the lake system is usually dominated by oligohaline to limnetic conditions (salinity < 5, Perissinotto *et al.* 2013). In July 2012, in an attempt to initiate system restoration, the decision was made to reconnect the Mfolozi River with the St Lucia Estuary by means of a beach spillway (Whitfield *et al.* 2013). This reconnection coincided with the commencement of a new wet phase, as the area began receiving higher than average rainfall since December 2011. This has resulted in a shift from unprecedented hypersaline extremes to a wet period dominated by oligohaline to polyhaline (< 25) conditions. This shift between wet and dry phases is an important mechanism structuring the local macrofaunal communities (Pillay & Perissinotto 2008; 2013; Pillay *et al.* 2013). During hypersalinity, the northern reaches may become barren, with a loss of stenohaline species throughout the lake (Bolt 1975). Additionally, large portions of the lake dry out and become uninhabitable for macrofaunal species (Pillay & Perissinotto 2008). In contrast, species that are unable to tolerate low salinity are eliminated during freshwater conditions (Pillay *et al.* 2013). Pillay & Perissinotto (2013) suggest that species found in a variable system, such as St Lucia, have evolved physiological mechanisms resulting in the tolerance of wide salinity fluctuations. It is thus essential to understand the effects that these climatic shifts have on key estuarine species, as flood and drought events are predicted to increase in frequency, intensity and duration as a result of global climate change (Lumsden *et al.* 2009; Mather *et al.* 2013). In this context, there is a need to identify species that are able to survive dramatic fluctuations in salinity regimes.

Particularly vulnerable to extreme changes in the estuarine environment are the sessile and slow moving benthic organisms that are unable to relocate at the onset of unfavourable conditions (Hill 1981; Ysebaert *et al.* 2002). Bivalves (i.e. mussels, clams and oysters) are often numerically dominant within an estuary and are, therefore, important both economically and ecologically (Dame *et al.* 1991; Gerritsen *et al.* 1994; Pilditch & Grant 1999). They perform vital functional roles within estuarine ecosystems. Bivalves serve as a link between primary producers and higher trophic consumers (Kamermans 1994), they are involved in benthic/pelagic coupling (Fanslow *et al.* 1995; Pilditch & Grant 1999; Inoue & Yamamuro 2000), and they are also capable of adjusting the water clarity by filtering particulate organic matter (Gerritsen *et al.* 1994). In addition, bivalves may also provide a multi-dimensional environment for other invertebrates to settle (Vaughn & Hakenkamp 2001). Pillay *et al.* (2013) stated that it is essential to provide updated studies on the biology and taxonomy of benthic invertebrates in St Lucia as the majority of the published literature is severely outdated. The central aim of this study was, therefore, to record the species richness of bivalves found in Lake St Lucia and to investigate key biological aspects of the two species that currently dominate the bivalve community within the system, under different salinity regimes.

Although bivalve species present within Lake St Lucia have been recorded in the published literature (Day *et al.* 1954; Millard & Broekhuysen 1970; Bolt 1975; Blaber *et al.* 1983; Owen & Forbes 1997;

Pillay & Perissinotto 2008; MacKay *et al.* 2010), there has been no attempt to compile a taxonomically updated and comprehensive list to reduce erroneous identifications in future research. Thus, the aim of the first chapter was to provide an annotated and illustrated checklist of all bivalves within St Lucia, clarifying any misidentifications and providing synonyms. Additionally, emphasising changes associated with variable climatic conditions (i.e. drought-induced stress and flooding events) and highlighting potentially new species found in this unique estuarine system. This long-term data set will contribute to global estuarine management, highlighting extensive loss of bivalve species richness under extreme events, thus emphasising the need for mitigation strategies.

It is also fundamental to understand the biology and ecophysiology of key species within an estuary, in order to establish a greater understanding of how an estuarine ecosystem functions under different climatic conditions (de Villiers 1989). The taxonomic census (Chapter 1) highlighted the dominance of two bivalve species, *Solen cylindraceus* (Hanley, 1843) and *Brachidontes virgiliae* (Barnard, 1964), both varying temporally and spatially according to salinity. Salinity is an important factor influencing all estuarine organisms (McLachlan & Erasmus 1974; Perissinotto *et al.* 2013). The predicted increase in drought due to climate change may result in prolonged hypersaline conditions, as well as flooding events that would drastically increase the frequency of hyposaline conditions (Mather *et al.* 2013). While the infaunal bivalve *S. cylindraceus* is usually numerically dominant within St Lucia during periods of marine to hypersaline conditions, *B. virgiliae* prefers oligohaline to limnetic conditions. A salinity tolerance between 10 and 70 was suggested for *S. cylindraceus* by MacKay *et al.* (2010), however, this was based on observations of live individuals in the field within this salinity range. *Brachidontes virgiliae*, on the other hand, has a suggested salinity tolerance from 0 to 34 in the Kowie Estuary, Eastern Cape, South Africa, but this is also based on anecdotal evidence (Davies 1980). The experimentally determined salinity tolerance of estuarine invertebrates in southern Africa, such as the invasive gastropod *Tarebia granifera* (Miranda *et al.* 2010), the mysid *Mesopodopsis africana* (Carrasco & Perissinotto 2011) and the decapods *Callinassa kraussi* and *Chromantes eulimene* (Thwala *et al.* 2011), were derived by exposing individuals to either rapid or gradual salinity changes, simulating possible effects caused by flood or drought events. Similarly, Matthews and Fairweather (2004) exposed the bivalve *Soletellina alba* to lowered salinity in an attempt to mimic the annual flooding events in the Hopkins River Estuary, Australia. Thus the primary aim of Chapters 2 and 3 were to experimentally determine the salinity tolerance of *S. cylindraceus* and *B. virgiliae*, respectively using both shock and acclimation techniques. Although, *S. cylindraceus* is predicted to have a wide salinity tolerance, able to withstand high salinity levels, it is susceptible to low and rapidly changing salinity (Pillay & Perissinotto 2008). Thus, it is vulnerable during flood events. In contrast, *B. virgiliae* is predicted to have an affinity for low salinity levels, increasing in dominance during the wet phase. This information is also key to predicting shifts in distribution and dominance

of these two bivalve taxa, which will have a substantial effect on the ecosystem structure and function.

Solen cylindraceus is a major contributor to the diet of birds such as the greater flamingo and fish, such as grunter and tilapia (Hodgson & de Villiers 1986; Forbes & Cyrus 1992; Weerts *et al.* 1997; Dyer *et al.* 2013). This fast growing species has a life span of approximately 5 years, with a reported maximum size of 95 mm (McLachlan 1974; Kilburn & Rippey 1982). St Lucia exhibits periods of hypersalinity (salinity > 100) alternating with periods of oligohaline conditions (salinity < 5), which cause mass mortality of bivalves, including *S. cylindraceus* as this is outside its tolerance range (Chapter 2; Nel *et al.* 2011), and preventing individuals from reaching their maximum potential size. McLachlan (1974) investigated the growth rate of *S. cylindraceus* in the Swartkops Estuary, Eastern Cape, South Africa. However, this estuary exhibited a stable physico-chemical environment. Thus, a direct method of monitoring *S. cylindraceus* shell length *in situ* was used in the fourth chapter, to determine basic growth rate data in an unstable subtropical estuary. This information may be used to investigate the recovery of *S. cylindraceus* populations after a mass mortality event and whether a population will reach sexual maturity before the onset of additional fluctuations.

Since the commencement of the new wet phase, *S. cylindraceus* has disappeared from South Lake and is at present only recorded in the northern reaches of Lake St Lucia (i.e. False Bay) where the salinity still falls within its range of tolerance. The new salinity regime has, however, been advantageous for *B. virgiliae*, which has now become very abundant and widespread throughout St Lucia. Nel *et al.* (2012) recorded the average benthic density of *B. virgiliae* at 51 ind.m⁻², however, this does not take into account the extremely dense aggregations currently observed on macrophytes, such as *Stukenia pectinata*, on boat hulls, rocks and dead shells (H.A. Nel, pers. obs.). Given their extremely high localised densities, there was a need to establish the effect this mussel could have on the available phytoplankton community. Grazing by invertebrates is regarded as the main top-down factor affecting microalgal biomass in estuaries and other aquatic ecosystems (Gerritsen *et al.* 1994; Inoue & Yamamuro 2000), as they form an important link between primary producers and the higher trophic consumers (Kamermans 1994). The final chapter, thus, investigated the trophic role of *B. virgiliae* by estimating the ingestion rates and grazing impact, using a specially adapted *in situ* gut fluorescence technique.

In summary, the main objectives of the study were as follows:

1. To compile an updated list of bivalve taxa for Lake St Lucia, highlighting the conditions under which the taxa occur and investigating which species are no longer recorded in the system.

2. To determine the upper and lower lethal salinity limits for the infaunal bivalve *Solen cylindraceus*, using both shock and acclimation techniques.
3. To determine the upper and lower lethal salinity limits of *B. virgiliae* exposed to both sudden and gradual changes in salinity, using animals collected from localities experiencing substantially different salinity regimes.
4. To investigate the growth of *S. cylindraceus* spat, and provide preliminary morphometric estimates for this species.
5. To investigate the ingestion rates of *B. virgiliae* and determine the potential grazing impact of this species within Lake St Lucia.

References

- Begg GW (1978) The estuaries of Natal. (Part II). Natal Town and Regional planning Commission Report. 41: 1–657.
- Blaber SJM, Kure NF, Jackson S, Cyrus DP (1983) The benthos of South Lake, St Lucia following a period of stable salinities. South African Journal of Zoology 18: 311–319.
- Bolt RE (1975) The benthos of some Southern African Lakes Part V: The recovery of the benthic fauna of St Lucia Lake following a period of excessively high salinity. Transactions of the Royal Society of South Africa 41: 295–323.
- Carrasco NK, Perissinotto R, Pillay D (2010) Zooplankton of the St. Lucia Estuary during the current drought cycle: a comparison between open- and closed-mouth conditions. Marine Ecology Progress Series 399: 157–171.
- Carrasco NK, Perissinotto R (2011) Temperature and salinity tolerance of *Mesopodopsis africana* O. Tattersall in the freshwater-deprived St. Lucia Estuary, South Africa. Journal of Experimental Marine Biology and Ecology 399: 93–100.
- Cyrus DP (1988) Episodic events and estuaries: Effects of cyclonic flushing on the benthic fauna and diet of *Solea bleekeri* (Teleostei) in Lake St Lucia on the southeastern coast of Africa. Journal of Fish Biology 33: 1–7.
- Cyrus D, Vivier L (2006) Status of the estuarine fish fauna in the St Lucia estuarine system, South Africa, after 30 months of mouth closure. African Journal of Aquatic Science 31: 71–81.

- Dame R, Dankers N, Prins T, Jongsma H, Smaal A (1991) The influence of mussel beds on nutrients in the Western Wadden Sea and Eastern Scheldt estuaries. *Estuaries* 14: 130–138.
- Davies BR (1980) The identification of the mytilids *Musculus virgiliae* Barnard, *Arcuatula capensis* (Krauss) and *Brachidontes variabilis* Krauss, with corrections to the literature and a note on their distribution. *Transactions of the Royal Society of South Africa* 44: 225–235.
- Day JH, Millard NAH, Broekhuysen GJ (1954) The ecology of South African estuaries. Part IV: the St Lucia system. *Transactions of the Royal Society of South Africa* 34: 129–156.
- Day JH (1980) What is an estuary? *South African Journal of Science* 76: 198.
- Day JH (1981) The nature, origin and classification of estuaries. Pp. 1–6 In: Day JH (ed.), *Estuarine Ecology: With Particular Reference to Southern Africa*. Balkema, Rotterdam.
- de Villiers CJ (1989) Aspects of the biology of the infaunal bivalve mollusc *Solen cylindraceus* (Hanley) in the Kariega Estuary. PhD thesis. Grahamstown, Rhodes University. Pp. 226
- Dyer DC, Perissinotto R, Carrasco NK (2013) Post-flood dietary variation in the Mozambique tilapia *Oreochromis mossambicus* in the St Lucia Estuary, South Africa. *Marine Ecology Progress Series* 476: 199–214.
- Fanslow DL, Nalepa TF, Lang GA (1995) Filtration rates of the zebra mussel (*Dreissena polymorpha*) on natural seston from Saginaw Bay, Lake Huron. *Journal of Great Lakes Research* 21: 489–500.
- Forbes AT, Cyrus DP (1992) Impact of a major cyclone on a southeast African estuarine lake system. *Netherlands Journal of Sea Research* 30: 265–272.
- Gerritsen J, Holland AF, Irvine DE (1994) Suspension-feeding bivalves and the fate of primary production: an estuarine model applied to Chesapeake Bay. *Estuaries* 17: 403–416.
- Henninger TO, Froneman PW (2011) Macrofaunal community structure in the littoral zone of a freshwater- deprived, permanently open Eastern Cape estuary. *African Zoology* 46: 263–279.

- Hill BJ (1981) Adaptations to temperature and salinity stress in southern African estuaries. Pp. 187–196 In: Day JH (ed.), *Estuarine Ecology*. Cape Town: A.A. Balkema.
- Inoue T, Yamamuro M (2000) Respiration and ingestion rates of the filter-feeding bivalve *Musculista senhousia*: implications for water-quality control. *Journal of Marine Systems* 26: 183–192.
- Kamermans P (1994) Similarity in food source and timing of feeding in deposit-feeding and suspension-feeding bivalves. *Marine Ecology Progress Series* 104: 63–75.
- Kilburn R, Rippey E (1982) *Sea shells of southern Africa*. Johannesburg: Macmillan South Africa. Pp. 249
- Lloret J, Marin A, Marin-Guirao L, Velasco J (2005) Changes in macrophytes distribution in a hypersaline coastal lagoon associated with the development of intensively irrigated agriculture. *Ocean Coastal Manage* 48: 828–842.
- Lumsden TG, Schulze RE, Hewitson BC (2009) Evaluation of potential changes in hydrologically relevant statistics of rainfall in Southern Africa under conditions of climate change. *Water SA* 35: 649–656.
- MacKay F, Cyrus D, Russell KL (2010) Macrobenthic invertebrate responses to prolonged drought in South Africa's largest estuarine lake complex. *Estuarine, Coastal and Shelf Science* 86: 553–567.
- Mather AA, Stretch DD, Maro AZ (2013) Climate change impacts. Pp. 397–412 In: Perissinotto R, Stretch DD, Taylor RH (eds.), *Ecology and Conservation of Estuarine Ecosystems: Lake St Lucia as a Global Model*. New York: Cambridge University Press.
- Matthews TG, Fairweather PG (2004) Effect of lowered salinity on the survival, condition and reburial of *Soletellina alba* (Lamarck, 1818) (Bivalvia: Psammobiidae). *Austral Ecology* 29: 250–257.
- McLachlan A (1974) Notes on the biology of some estuarine bivalves. *Zoologica Africana* 9: 15–34.

- McLachlan A, Erasmus T (1974) Temperature tolerances and osmoregulation in some estuarine bivalves. *Zoologica Africana* 9: 1–13.
- Millard NAH, Broekhuysen GJ (1970) The ecology of South African estuaries. Part X: St Lucia: a second report. *Zoologica Africana* 5: 277–307.
- Miranda NAF, Perissinotto R, Appleton CC (2010) Salinity and temperature tolerance of the invasive freshwater gastropod *Tarebia granifera*. *South African Journal of Science* 106: 55–61.
- Nel HA, Perissinotto R, Taylor RH, Carrasco NK (2011) Salinity tolerance of the bivalve *Solen cylindraceus* (Hanley, 1843) (Mollusca: Euheterodonta: Solenidae) in the St Lucia Estuary. *African Invertebrates* 52: 575–586.
- Nel HA, Perissinotto R, Taylor RH (2012) Diversity of bivalve molluscs in the St Lucia Estuary, with an annotated and illustrated checklist. *African Invertebrates* 53: 503–525.
- Ngqulana SG, Owen RK, Vivier L, Cyrus DP (2010) Benthic faunal distribution and abundance in the Mfolozi-Msunduzi estuarine system, KwaZulu-Natal, South Africa. *African Journal of Aquatic Science* 35: 123–133.
- Owen RK, Forbes AT (1997) Salinity, floods and the infaunal macrobenthic community of the St Lucia Estuary, KwaZulu-Natal, South Africa. *African Journal of Aquatic Science* 23: 14–30.
- Perissinotto R, Carrasco NK, Taylor RH (2013) Physico-chemical environment. Pp. 168–185 In: Perissinotto R, Stretch DD, Taylor RH (eds.), *Ecology and Conservation of Estuarine Ecosystems: Lake St Lucia as a Global Model*. New York: Cambridge University Press.
- Pilditch CA, Grant J (1999) Effect of variations in flow velocity and phytoplankton concentration on sea scallop (*Placopecten magellanicus*) grazing rates. *Journal of Experimental Marine Biology and Ecology* 240: 111–136.

- Pillay D, Bownes SJ, Nel HA (2013) Benthic Invertebrates. Pp. 226–245 In: Perissinotto R, Stretch DD, Taylor RH (eds.), Ecology and Conservation of Estuarine Ecosystems: Lake St Lucia as a Global Model. New York: Cambridge University Press.
- Pillay D, Perissinotto R (2008) The benthic macrofauna of the St Lucia Estuary during the 2005 drought year. *Estuarine, Coastal and Shelf Science* 77: 35–46.
- Pillay D, Perissinotto R (2013) Benthic macrofauna of an estuarine lake during a drought: spatio-temporal drivers under different hydrological states. *Marine Ecology Progress Series* 492: 111–123.
- Potter IC, Chuwen BM, Hoeksema SD, Elliott M (2010) The concept of an estuary: A definition that incorporates systems which can become closed to the ocean and hypersaline. *Estuarine Coastal and Shelf Science* 87: 497–500.
- Pritchard RW (1967) What is an estuary? Physical viewpoint. Pp. 3–5 In: Lauff, G.H. (ed.), *Estuaries*. American Association for the Advancement of Science, Washington D.C.
- Quammen ML, Onue CP (1993) Laguna Madre – Seagrass changes continue decades after salinity reduction. *Estuaries* 16: 302–310.
- Raz-Guzman A, Huidobro L (2002) Fish communities in two environmentally different estuarine systems of Mexico. *Journal of Fish Biology* 61: 182–195.
- Thwala M, Newman BK, Cyrus DP (2011) Influence of salinity and cadmium on the survival and osmoregulation of *Callinassa kraussi* and *Chiromantes eulimene* (Crustacea: Decapoda). *African Journal of Aquatic Science* 36: 181–189.
- Vaughn CC, Hakenkamp CC (2001) The functional role of burrowing bivalves in freshwater ecosystems. *Freshwater Biology* 46: 1431–1446.
- Webster IT (2010) The hydrodynamics and salinity regime of a coastal lagoon – The Coorong, Australia – Seasonal to multi-decadal timescales. *Estuarine, Coastal and Shelf Science* 90: 264–274.
- Weerts SP, Cyrus DP, Forbes AT (1997) The diet of juvenile *Sillago sihama* (Forsskål, 1775) from three estuarine systems in KwaZulu Natal. *Water SA* 23: 95–100.

- Whitfield AK, Taylor RH (2009) A review of the importance of freshwater inflow to the future conservation of Lake St Lucia. *Aquatic Conservation: Marine and Freshwater Ecosystems* 19: 838–848.
- Whitfield AK, Bate GC, Forbes T, Taylor RH (2013) Relinkage of the Mfolozi River to the St Lucia estuarine system urgent - imperative for the long-term management of a RAMSAR and World Heritage Site. *Aquatic Ecosystem Health & Management* 16: 104–110.
- Young GC, Potter IC (2002) Influence of exceptionally high salinities, marked variations in freshwater discharge and opening of estuary mouth on the characteristics of the ichthyofauna of a normally-closed estuary. *Estuarine, Coastal and Shelf Science* 56: 223–246.
- Ysebaert T, Meire P, Herman PMJ, Verbeek H (2002) Macrobenthic species response surfaces along estuarine gradients: prediction by logistic progression. *Marine Ecology Progress Series* 225: 79–95.

Diversity of bivalve molluscs in the St Lucia Estuary, with an annotated and illustrated checklist

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ABSTRACT

Bivalves play a vital role in estuarine ecosystems, but are vulnerable to rapid or prolonged changes in the physico-chemical environment. The St Lucia estuarine lake exhibits sub-decadal changes from wet to dry periods, resulting in fluctuating physico-chemical conditions. This paper represents a census of the diversity of bivalve molluscs in this estuary, emphasising changes associated with climate-induced hydrological states. Twenty-four bivalve species were recorded within St Lucia between 1925 and 2011. Twelve that had not been reported previously from St Lucia in the literature were encountered during the present study. These are *Anadara natalensis*, *Anomia achaeus*, *Arcuatula capensis*, *Chambardia wahlbergi*, *Corbicula fluminalis*, *Dendostrea sandvichensis*, *Fulvia fragilis*, *Macra cuneata*, *Martesia striata*, *Meretrix meretrix*, *Saccostrea forskahlii* and *Tellina s.l. bertini*. Single shells of another two previously unrecorded species, *Anodontia edentula* and *Timoclea lavrani*, were also found, although these may have been introduced dead from the ocean through tidal exchange. *Meretrix meretrix*, an unexpected yet abundant species, represents a new record for South African waters, but the timing and mode of its introduction into the estuary remain unresolved. Extremely large numbers (>100 ind.m⁻²) of dead specimens of *Barnea manilensis* were observed in 2011 along the western shoreline of the estuarine lake, which indicates that the species was a major role-player in the settling of suspended silt within the system. Currently, this function appears to be fulfilled only by *Solen cylindraceus*. Apart from this species, *Brachidontes virgiliae*, *Dosinia hepatica*, *Macomopsis moluccensis*, *Salmacoma litoralis* and an undescribed *Tellina* sp. (reported here as *T. cf. rousi*) are the only bivalves that were found alive in St Lucia during the latest survey, in March 2011.

KEY WORDS: Bivalvia, molluscs, South Africa, St Lucia, taxonomy, biogeography, estuarine variability, checklist.

INTRODUCTION

Estuaries are characterised by large spatial and temporal variations in the physico-chemical environment. The St Lucia estuarine lake exhibits changes in climatic conditions from wet to dry periods, with a duration of four to ten years (Begg 1978). During dry periods, the system is subjected to high evaporation, low rainfall input and low river inflow (Cyrus & Vivier 2006; Pillay & Perissinotto 2008). St Lucia was artificially separated from the Mfolozi River in 1952, which deprived it of its most essential freshwater source during drought periods (Begg 1978; Ngqulana *et al.* 2010). As a result, during dry periods the northern reaches of the estuarine system become hypersaline (Cyrus & Vivier 2006; Vivier & Cyrus 2009), with salinity levels of >200‰ recorded on several occasions. The estuary is also exposed to stochastic disturbances, such as floods (Forbes & Cyrus 1992), which may very rapidly decrease the salinity within the system (Cyrus 1988; Hanekom 1989; Forbes & Cyrus 1993). Forbes and Cyrus (1992) recorded a decrease in salinity from 45‰ to <10‰ in approximately two weeks, in large parts of its South Lake during the flood caused by cyclone Domoina in 1984. These changes between hypersaline and low salinity conditions may cause drastic alterations in estuarine structure and function (Cyrus 1988).

The range of conditions that occur between the extremes of floods and severe droughts shapes the estuarine biotic communities (McLusky & Elliott 2004). Specifically, hyper-

saline conditions and hyposaline events may cause large reductions in species numbers and changes to species composition (Cyrus 1988; Hanekom 1989; Forbes & Cyrus 1992; Pillay & Perissinotto 2008). Flood events can cause mass mortality (Matthews & Fairweather 2004; Nel *et al.* 2011) and redistribution of benthic bivalve species in estuaries (Forbes & Cyrus 1992). Hill (1981) stated that sessile and slow-moving benthic organisms in St Lucia are particularly susceptible to mass mortality events during periods of escalated salinity levels. This is partially due to their inability to move to areas with lower salinity and a more favourable physico-chemical environment (Hill 1981; Ysebaert *et al.* 2002). During the most extreme of droughts, more than 50% of the St Lucia estuarine lake may dry out and, along with hypersaline conditions, this may drastically alter the distribution of macrofaunal communities (Pillay & Perissinotto 2008). Bolt (1975) suggested that even when a bivalve species is eliminated from a particular area due to unfavourable physico-chemical conditions, it may have the ability to recolonise these areas once favourable conditions return. It is clear that the distribution of benthic macrofauna in an estuary is not static but changes according to the physico-chemical conditions that prevail at any given time.

Benthic macrofauna play an important role in estuarine ecology by acting as intermediate links in food webs and contributing to bioturbation (Hempel *et al.* 2009; Cyrus *et al.* 2010; MacKay *et al.* 2010). Bivalves, in particular, fulfil a vital function in estuaries as they collect and settle a significant amount of sediment while filter-feeding, and may alter phytoplankton biomass and composition in the water-column (Gerritsen *et al.* 1994; Vaughn & Hakenkamp 2001). The filtering of phytoplankton and suspended solids from the water-column may also affect the water clarity of an estuary (Gerritsen *et al.* 1994). Bivalve shells provide a settlement medium for algae and other invertebrates, creating a multi-dimensional environment (Vaughn & Hakenkamp 2001). A shift in climatic conditions can alter species numbers and composition, as well as cause the loss of important functional roles played by the bivalves.

Despite the physico-chemical variability observed in the St Lucia estuarine lake, the system has a rich biological diversity (Pillay & Perissinotto 2008; MacKay *et al.* 2010). It is for this reason that the estuary has attracted a number of investigations concerning its benthic community, under varying physico-chemical conditions (Owen & Forbes 1997). Past work on the benthic community was done during hypersaline (Day *et al.* 1954; Bolt 1975), marine (Blaber *et al.* 1983; Weerts 1993), and low salinity conditions (Millard & Broekhuysen 1970; Cyrus 1988; Weerts 1993). Studies on the benthic community found in the Narrows have been fewer, but focused on a longer time frame, from 1983 to 1994 (Owen & Forbes 1997). Although all these surveys mention bivalve taxa, to date no attempt has been made to compile a comprehensive list of the species that occur in the different areas of the St Lucia Estuary and to assess how they respond to the climatic shifts that characterise the system.

The purpose of the present paper is to provide a census of the bivalve species that have been recorded from the St Lucia estuarine system. Included is an overview of taxa that have been recorded in the past, and under what conditions, as well as what is currently found or no longer found in the system. Literature and museum collections relating to ecological surveys conducted in St Lucia since the 1920s were reviewed and references to bivalve species recorded. The updated taxonomic status of each species and synonyms are provided and attention is drawn to misidentifications. An annotated

and illustrated checklist of all bivalve molluscs conclusively identified during this study is given in the Appendix. The checklist will provide scientists, managers and visitors with means to identify the bivalves of the St Lucia Estuary. This will reduce the risk of erroneous identifications and hopefully stimulate further research interest in these important organisms.

MATERIAL AND METHODS

Study area

The St Lucia estuarine lake is a core feature of the iSimangaliso Wetland Park, which was awarded UNESCO World Heritage Site status in 1999 (Whitfield & Taylor 2009). It is the largest estuarine lake in Africa, covering 80% of the estuarine area of KwaZulu-Natal (KZN), South Africa (Begg 1978). The estuary is located between 27°52'S to 28°24'S and 32°21'E to 32°34'E (Fig. 1), and is subdivided into False Bay, North Lake, South Lake, the Narrows and a Mouth region (currently disconnected from the ocean by a sand berm). It has a total surface area of 300 to 350 km² during a non-drought period (Hutchison & Midgley 1978).

Museum specimens

The KwaZulu-Natal Museum (NMSA, Pietermaritzburg) and Iziko South African Museum (SAMC, Cape Town) have the most comprehensive bivalve collections in Africa. Housed in the two collections are numerous specimens from St Lucia, dating back to 1925. These specimens provided a record of collections on various dates in localities within St Lucia.

Historical surveys

Further historical data were obtained from the Natal Parks Board survey of 1982–1983 (R.H. Taylor) and the Ezemvelo KZN Wildlife survey of 2005 (R.H. Taylor). In all cases, no specialised equipment was used and specimens were collected by hand at the surface or within the sediment by using spades and/or mechanical grabs. Both the 1982/83 and 2005 surveys were carried out during the onset of drought conditions when salinity concentrations were rising and parts of St Lucia were being exposed as the water level dropped. These conditions killed bivalves, leaving them exposed or causing them to be washed up along the shorelines of St Lucia. The Natal Parks Board surveyed the banks of St Lucia from December 1982 to April 1983. Freshly dead bivalves were collected along the shores from False Bay, North Lake, South Lake and the Narrows (Fig. 1), and identified to species level. Ezemvelo KZN Wildlife surveyed the St Lucia banks in 2005 by taking samples at various points. Shells of freshly dead bivalves were retrieved from both South and North lakes (Fig. 1).

The 2011 survey

During 2011, bivalves were picked up by hand along the entire accessible shoreline of the estuarine lake. A dedicated survey was carried out from 18–21 March, during which both quantitative and qualitative benthic samples were taken. Quantitative samples were collected using a Zabalocki-type Ekman grab (sampling area 0.0236 m²; depth 15 cm). A single sample comprised three grabs and three replicate samples were taken at each site. Water was added to each sample, which was stirred vigorously, thereby suspending the benthic invertebrates. The supernatant was then washed through a 500 µm sieve.

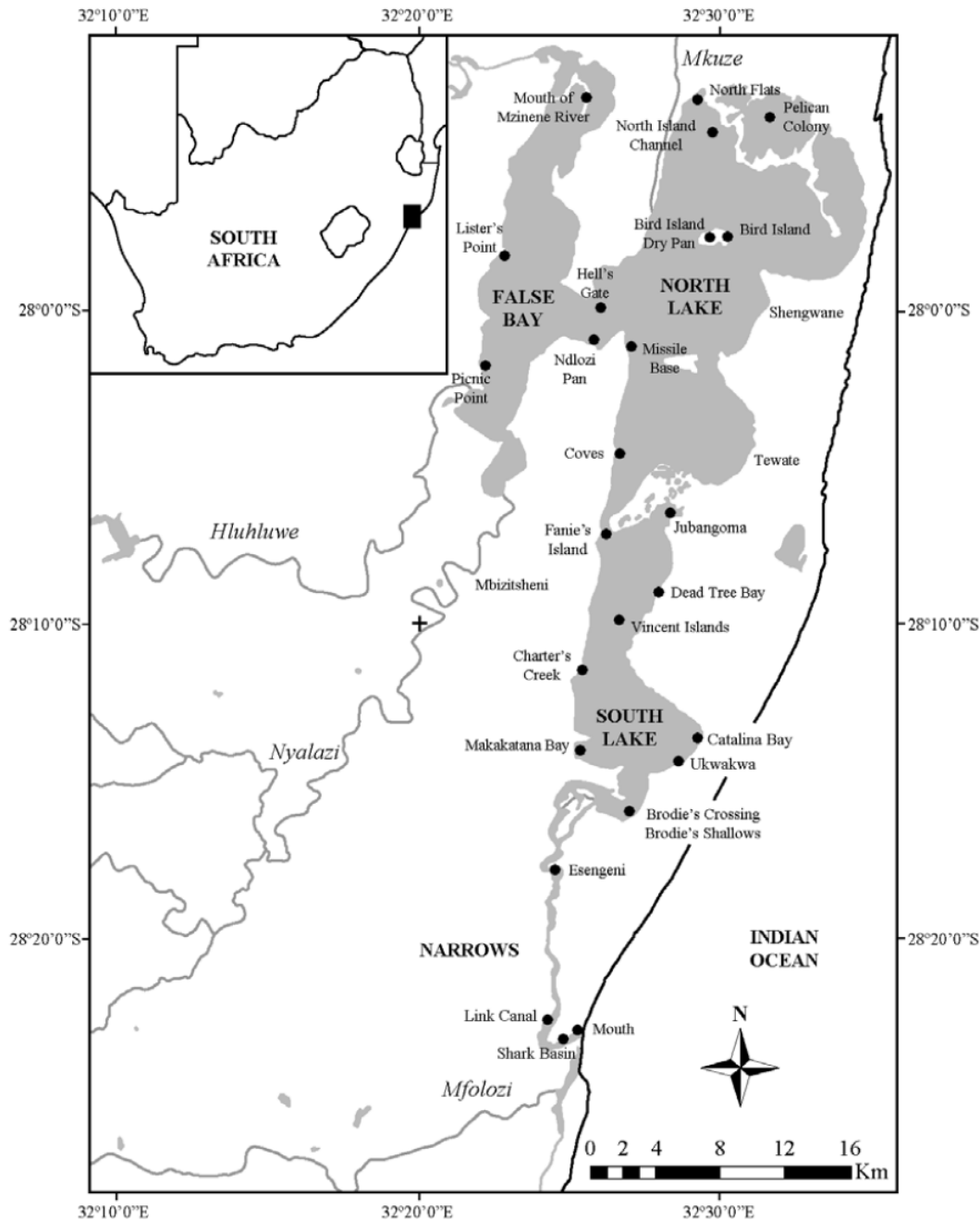


Fig. 1. Map of the St Lucia Estuary, showing the sampling sites where bivalves were collected from 1925 to 2011; and its geographical position relative to South Africa (adapted from Carrasco *et al.* 2010).

This process of adding water, stirring and sieving was repeated five times, and any material retained on the sieve was finally emptied into a plastic jar. This procedure has been shown to extract more than 95% of the macrofauna in a sample (Cyrus & Martin 1988). The remaining sediment was washed through a 2000 μm sieve in order to recover larger macrofauna such as bivalves, gastropods and crustaceans (Cyrus & Martin 1988). However, the Zabalocki-type Ekman grab may undersample larger bivalves found deeper within the sediment (MacKay *et al.* 2010). All macrofauna samples were preserved in 10% formaldehyde solution and stained with Phloxin-B. In the laboratory, bivalves were removed and identified to species level using voucher specimens deposited at the NMSA or the identification guidelines provided in Kilburn and Rippey (1982), Willan (1993),

Appleton (1996), Branch *et al.* (2010) and Huber (2010). Qualitative samples were obtained using a stainless-steel D-net (33 cm diameter) with a raking front edge, pushed by hand along 10–20 m transects and penetrating about 5–10 cm into the sediment. Samples collected in this way were preserved and analysed as explained above. Bivalves removed from samples were preserved in 70% ethanol solution. This survey differed from the two previous surveys in that live bivalves were collected. It also took place during a period of constant drought conditions when only those species that were able to withstand the extreme conditions were surviving, while the others had disappeared.

Some specimens from this and previous surveys are kept at the University of KwaZulu-Natal, Durban (UKZD).

Physico-chemical parameters

During the survey of March 2011, physico-chemical data were measured *in situ* at each site, using a portable YSI® 6920 data-logging multiprobe. Parameters included were salinity, temperature, turbidity, pH and dissolved oxygen content. Measurements were made at the sediment–water interface at all nine sites. On the other occasions, including the historical surveys, only salinity and temperature data were obtained at selected sites.

RESULTS

A total of 24 bivalve species were recorded in St Lucia between 1925 and 2011. Of these, only 12 have been reported in published literature, viz. *Barnea manilensis*, *Brachidontes virgiliae*, *Dosinia hepatica*, *Eumarcia paupercula*, *Irus irus*, *Macomopsis moluccensis*, *Salmacoma litoralis*, *Siliqua cf. polita*, *Solen cylindraceus*, *Soletellina lunulata*, *Tellina cf. rousi* and *Theora lata* (Table 1). Ten species, identified during the survey of 1982/83 (Table 2), had not appeared in published literature for St Lucia. Only nine of these were considered true inhabitants of the estuary, while *Timoclea lavrani* was excluded because only a single valve had been found. The clam *Meretrix meretrix* was first found in St Lucia in 2000 (NMSA) and subsequently recorded in huge numbers during the survey of 2005. This was the only additional bivalve species found in the 2005 survey (Table 3) that had not previously been mentioned for St Lucia. Another two species, not included in the literature, are in the NMSA. These are *Macra cuneata* and *Martesia striata* (Tables 4a, 4b). During the survey of 1982/83, 22 bivalve species were found, as empty shells, on the shorelines and islands of the St Lucia estuarine system (Table 2). Only 11 species were recorded during the survey of 2005 (Table 3). A total of 18 and seven species, respectively, from the St Lucia estuarine system are currently in the NMSA and the SAMC (Tables 4a, 4b, 5). As the majority of the bivalves were collected as empty shells, there is some uncertainty regarding the exact time at which the bivalves were alive and growing in the system.

Siliqua cf. polita has only been collected from Picnic Point, Lister's Point and Bird Island in 1982/83 (Table 2), and in False Bay in April 1987 (Table 4b). This appears to be an undescribed species (R.N. Kilburn pers. comm.), which has not been seen again in subsequent surveys. The first record of the mytilid *Brachidontes virgiliae* at St Lucia dates from July 1948, when it was found at the estuary mouth (Table 5). In December 1962, it was found at Charter's Creek in beds of the submerged macrophyte *Zostera capensis* (Table 4a). Empty *B. virgiliae* shells were found as far north as Lister's Point and

Bird Island (Table 2) as well as from Charter's Creek to Fanie's Island during 1982/83 and 2005, respectively (Table 3). In 2011, live *B. virgiliae* were found in numbers at Fanie's Island, Catalina Bay and Charter's Creek. Live *B. virgiliae* were also present in the *Stuckenia pectinata* beds along the Narrows. In the quantitative samples, a maximum density of 51 ind.m⁻² was recorded at Fanie's Island in 2011 (Table 6).

Barnea manilensis specimens were first collected at False Bay in July 1948 (Table 5). In the 1982/83 and 2005 surveys, this species was detected throughout the western lake shoreline, at False Bay, and at North and South lakes (Tables 2, 3). Dead *B. manilensis* were recorded *in situ* in large numbers (often >100 m⁻²) in 2011 throughout the western shores, wherever cretaceous sandstone was available for burrowing (Fig. 2).

Soletellina lunulata occurred throughout the St Lucia lake complex at the time of the 1982/83 and 2005 surveys, and is well represented in the NMSA collection (Tables 2, 3, 4a).

The semelid species *Theora lata* was collected in False Bay, South Lake and the Narrows and deposited at the NMSA in 1981 and 1987 (Table 4b). It was also found in False Bay in 1964 and deposited in the SAMC (Table 5). In 1982/83, it was recorded as being abundant throughout North Lake and False Bay, whereas in 2011, only a few empty shells were encountered, on the western shoreline.

Solen cylindraceus has been reported in a number of studies (Table 1), and has been an abundant feature in all three lakes since 1948 (Tables 2, 3, 4b, 5). It was occasionally present in the Narrows (Table 2). In March 2011, it was found alive at Charter's Creek and Catalina Bay at densities ranging from 14 to 494 ind.m⁻² (Table 6), and was recorded at Fanie's Island and Lister's Point in the qualitative samples.



Fig. 2. *Barnea manilensis*, a large concentration of dead shells at False Bay, Lake St Lucia, in April 2011. (Photo: Lynette Perissinotto)

TABLE 1

Bivalve species reported in the literature from the St Lucia Estuary. Species marked with the asterisk have been identified in the estuary during the present study.

Identification		Publication
Currently used	Previously used	
Mytilidae		
<i>Brachidontes semistriatus</i>	<i>Brachidontes variabilis</i>	Day <i>et al.</i> 1954; Millard & Broekhuysen 1970; Weerts 1993
<i>Brachidontes virgiliae</i> *	<i>Brachidontes virgiliae</i>	Blaber <i>et al.</i> 1983; MacKay <i>et al.</i> 2010
<i>Brachidontes virgiliae</i> *	<i>Modiola capensis</i>	Day <i>et al.</i> 1954
<i>Brachidontes virgiliae</i> *	<i>Musculus virgiliae</i>	Millard & Broekhuysen 1970
Ostreidae		
<i>Saccostrea cucullata</i>	<i>Crassostrea cucullata</i>	Millard & Broekhuysen 1970
<i>Saccostrea cucullata</i>	<i>Gryphaea cucullata</i>	Day <i>et al.</i> 1954
Solenidae		
<i>Solen capensis</i>	<i>Solen capensis</i>	Day <i>et al.</i> 1954
<i>Solen cylindraceus</i> *	<i>Solen corneus</i>	Millard & Broekhuysen 1970; Bolt 1975
<i>Solen cylindraceus</i> *	<i>Solen cylindraceus</i>	Blaber <i>et al.</i> 1983; Weerts 1993; Owen & Forbes 1997; Pillay & Perissinotto 2008; MacKay <i>et al.</i> 2010
Pharidae		
<i>Siliqua cf. polita</i> *	<i>Siliqua</i> sp.	Blaber <i>et al.</i> 1983
Tellinidae		
<i>Tellina cf. rousi</i> *	<i>Tellina</i> sp.	Day <i>et al.</i> 1954
<i>Tellina triliatera</i>	<i>Tellina triangularis</i>	Day <i>et al.</i> 1954; Pillay & Perissinotto 2008
<i>Salmacoma litoralis</i> *	<i>Macoma litoralis</i>	Millard & Broekhuysen 1970; MacKay <i>et al.</i> 2010
<i>Macomopsis moluccensis</i> *	<i>Macoma retrorsa</i>	Millard & Broekhuysen 1970; Kilburn & Rippey 1982; Blaber <i>et al.</i> 1983; Owen & Forbes 1997
Psammobiidae		
<i>Soletellina humulata</i> *	Psammobiidae sp. 1	MacKay <i>et al.</i> 2010
Semelidae		
<i>Theora lata</i> *	<i>Theora lata</i>	Millard & Broekhuysen 1970; Bolt 1975; Blaber <i>et al.</i> 1983; Weerts 1993; MacKay <i>et al.</i> 2010
Veneridae		
<i>Dosinia hepatica</i> *	<i>Dosinia hepatica</i>	Millard & Broekhuysen 1970; Bolt 1975; Blaber <i>et al.</i> 1983; Weerts 1993; Owen & Forbes 1997
<i>Tivela compressa</i>	<i>Tivela cf. compressa</i>	MacKay <i>et al.</i> 2010
<i>Tivela natalensis</i>	<i>Tivela natalensis</i>	MacKay <i>et al.</i> 2010
<i>Pitar abbreviatus</i>	<i>Pitar abbreviatus</i>	MacKay <i>et al.</i> 2010
<i>Irus irus</i> *	<i>Venerupis macrophylla</i>	Millard & Broekhuysen 1970
<i>Irus irus</i> *	<i>Irus irus</i>	Kilburn & Rippey 1982
<i>Eumarcia paupercula</i> *	<i>Eumarcia paupercula</i>	Blaber <i>et al.</i> 1983; Owen & Forbes 1997
<i>Eumarcia paupercula</i> *	<i>Pitaria kochii</i>	Millard & Broekhuysen 1970
Hiatellidae		
<i>Hiatella arctica</i>	<i>Saxicava</i> sp.	Day <i>et al.</i> 1954
Pholadidae		
<i>Barnea manilensis</i> *	<i>Barnea manilensis</i>	Millard & Broekhuysen 1970

TABLE 3

Bivalve species recorded as freshly-dead or alive along the shores of the St Lucia Estuary during the Ezemvelo KZN Wildlife survey of 2005. Abbreviations: Aa – *Anomia achaeus*, Bm – *Barnea manilensis*, Bv – *Brachidontes virgiliae*, Dh – *Dosinia hepatica*, Ep – *Eumarcia paupercula*, Ff – *Fulvia fragilis*, Ii – *Irus irus*, Mm – *Meretrix meretrix*, Sc – *Solen cylindraceus*, Sl – *Soletellina lumulata*, Tr – *Tellina cf. rousi*. The underlined species represents a new record for the St Lucia estuary.

	Site	Aa	Bm	Bv	Dh	Ep	Ff	Ii	Mm	Sc	Sl	Tr
North Lake	Hell's Gate to Fanie's	-	-	-	-	-	X	-	-	-	-	-
	Tewate to Shengwane	-	-	-	X	X	-	X	X	X	X	-
	Jubangoma to Tewate	-	X	-	X	X	-	-	X	X	X	-
South Lake	Fanie's Island to Charter's Creek	X	X	X	X	X	-	X	X	X	X	X
	Catalina Bay to the Narrows	-	-	-	X	X	-	-	X	X	X	-
	Jubangoma to Vincent Island	-	-	-	X	X	-	-	X	X	X	-
	Charter's Creek to Makakatana	-	X	-	X	X	-	X	X	X	X	X
	Catalina Bay northwards	-	-	-	X	X	-	-	X	X	X	-

Three tellinid species, *Macomopsis moluccensis*, *Salmacoma litoralis* and *Tellina cf. rousi*, have been reported from St Lucia. *Macomopsis moluccensis* and *S. litoralis* were collected at False Bay, North Lake, South Lake and the Narrows, from 1925 to 2005 (Tables 2, 4b). Both were found alive in 2011 at Charter's Creek, while *S. litoralis* was also found at Makakatana (Table 6). *Tellina cf. rousi* was present during 1982/83 from the Narrows to False Bay (Table 2), in the South Lake during 2005 (Table 3), and was collected at Shark Basin in 1987 (Table 4b). It also occurred, as shells, at False Bay in 2011. It now appears that it may represent an undescribed species (M. Huber pers. comm.). The highest densities for the three tellinid species *M. moluccensis*, *S. litoralis* and *T. cf. rousi*, were 65, 37 and 80 ind.m⁻² respectively, in 2011 (Table 6).

Three venerid species, *Dosinia hepatica*, *Eumarcia paupercula* and *Irus irus*, also featured prominently in this estuary. *Dosinia hepatica* was first recorded at Fanie's Island in November 1971 (Table 4a) and was common throughout the surveys done in 1982/83 and 2005 (Tables 2, 3). In 2011, this species was found alive only at Charter's Creek, at a density of 4 ind.m⁻² (Table 6). Specimens of *E. paupercula* deposited at the NMSA were collected from 1927 to 1981 (Table 4a). During the 1982/83 and 2005 surveys, it was found in abundance throughout the entire estuary, except at False Bay (Tables 2, 3). It was also found in July 1948 and deposited in the SAMC (Table 5). *Irus irus* was collected from 1949 to 1987 (NMSA and SAMC) and was abundant but dead *in situ* during all three surveys.

Twelve bivalve species have not been documented previously in any literature on St Lucia. These are *Anadara natalensis*, *Anomia achaeus*, *Arcuatula capensis*, *Chambardia wahlbergi*, *Corbicula fluminalis*, *Dendostrea sandvichensis*, *Fulvia fragilis*, *Mactra cuneata*, *Martesia striata*, *Meretrix meretrix*, *Saccostrea forskahlii* and *Tellina s.l. bertini*.

A single shell of *A. natalensis* was collected at the dredge spoils during 1983, but several dead shells (*ca* 10) were found at Charter's Creek in April 2011.

The freshwater bivalve *C. fluminalis* was only found at the Hluhluwe River mouth in 1983 (Table 2). *Chambardia wahlbergi*, a freshwater mussel, was collected in 1982 at the Hluhluwe River mouth and in the Mkuzi swamps (Table 2).

TABLE 4a

Bivalve species collected from St Lucia and held at the NMSA. Abbreviations: Ac – *Arcuatula capensis*, Bm – *Barnea manilensis*, Bv – *Brachidontes virgiliae*, Dh – *Dosinia hepatica*, Ep – *Eumarcia paupercula*, Ff – *Fulvia fragilis*, Ii – *Irus irus*, Sl – *Soletellina lumulata*, Tb – *Tellina s.l. bertini*.

	Site	Ac	Bm	Bv	Dh	Ep	Ff	Ii	Sl	Tb
False Bay	False Bay	-	-	-	-	-	6/1987	4/1987	6/1987	-
	Near mouth of Mzinene River	-	11/1966	-	-	-	-	-	-	-
South Lake	West bank opposite Fanie's Island	-	-	-	11/1971	11/1971	-	11/1971	-	-
	Northern end of Dead Tree Bay	-	-	-	-	9/1980	-	-	-	-
	Charter's Creek	-	-	12/1962	-	-	-	4/1963	7/1981	-
	Catalina Bay (Old Jetty)	12/1981	-	-	-	-	-	11/1982	-	-
	0.5 km N of Makakatana Point	-	-	-	-	-	-	-	-	-
Narrows	Brodie's Crossing	-	-	-	-	-	-	-	4/1987	-
	Esengeni	-	-	-	-	7/1981	-	-	-	X
Estuary Mouth	Shark Basin	-	-	-	-	-	-	-	1987	-
	St Lucia Lake	-	-	-	-	1/1927	-	6/1962	X	-

TABLE 4b

Bivalve species collected from St Lucia and held at the NMSA. Abbreviations: Mc – *Mactra cuneata*, Ml – *Salmacoma litoralis*, Mm – *Meretrix meretrix*, Mr – *Macomopsis moluccensis*, Ms – *Martesia striata*, Sc – *Solen cylindraceus*, Sp – *Siliqua cf. polita*, Tl – *Theora lata*, Tr – *Tellina cf. rousi*. Species underlined represent new records for the St Lucia Estuary.

	Site	Mc	Ml	Mm	Mr	Ms	Sc	Sp	Tl	Tr
False Bay	False Bay	-	-	-	-	-	4/1987	4/1987	4/1987	-
South Lake	West bank opposite Fanie's Island	-	11/1971	-	2/1971	-	2/1971	-	-	-
	Catalina Bay	-	-	-	-	-	12/2005	-	-	-
	Catalina Bay (Old Jetty)	-	-	12/2005	12/1982	-	-	-	12/1981	-
	Charter's Creek	-	4/1963; 7/1981	7/2000	3/1969	-	-	-	-	-
	Northern end of Dead Tree Bay	-	-	-	9/1980	-	9/1980	-	-	-
	0.5 km North of Makakatana Point	X	-	-	-	4/1987	-	-	-	-
Narrows	Brodie's Crossing	-	4/1987	-	-	-	-	-	-	-
	Esengeni	-	-	-	-	-	-	-	X	-
Estuary Mouth	Shark Basin	-	-	-	-	-	-	-	-	6/1987; 8/1987
	St Lucia Lake	-	-	9/2003	7/1925	-	6/1962	-	-	-

TABLE 5

Bivalve species (in alphabetical order) collected from St Lucia and held at the SAMC. Abbreviations: Bm – *Barnea manilensis*, Bv – *Brachidontes virgiliae*, Ep – *Eumarcia paupercula*, Ii – *Irus irus*, Sc – *Solen cylindraceus*, Sf – *Saccostrea forskahlii*, Tl – *Theora lata*.

	Site	Bm	Bv	Ep	Ii	Sc	Sf	Tl
False Bay	False Bay	7/1948	-	-	7/1949	7/1948; 7/1964	-	7/1964
North Lake	Hell's Gate	-	-	-	7/1949		-	-
South Lake	Charter's Creek	7/1948	-	7/1948		7/1948; 7/1964	-	-
Estuary Mouth	Mouth	-	7/1948	-	-	-	7/1948	-
	In the middle of the bay	-	7/1948	-	-	-	-	-

Tellina s.l. *bertini* was only found in October 1982 at Esengeni (Narrows) (Tables 2, 4a), while *A. capensis* was collected in numbers in 1981, at Catalina Bay (Table 4a), and was present in both the North Lake and False Bay in 1982/83 (Table 2).

Three oyster species were reported from St Lucia. *Anomia achaeus* was collected in the North Lake during the Natal Parks Board survey (Table 2) and in the South Lake during the Ezemvelo KZN Wildlife survey (Table 3). *Dendostrea sandwichensis* occurred throughout the St Lucia system (Table 2). In 2011, it was often seen attached, but only dead, to rocks on the banks of the lake. *Saccostrea forskahlii* was collected during July 1948 at the estuary mouth. It was also recorded in 1982/83 throughout North Lake (Table 2); and in April 1987, it was collected at False Bay (Table 4b).

Fulvia fragilis was reported as common during 1983/83 and 2005 in the North Lake and False Bay (Tables 2, 3, 4a). It was also present in the South Lake (Table 2), but in 2011, only a few empty shells were found at Charter's Creek. *Macra cuneata* was only collected at Makakatana, in July 1987 (Table 4b), while *M. striata* was sampled in numbers from decaying wood at Makakatana in April 1987 (Table 4b). *Meretrix meretrix* was recorded for the first time in July 2000, at Charter's Creek (Table 4b). It was also found in abundance in 2005 and 2011, but only dead (Table 3).

For two bivalve species, there are only single records. These are *Anodontia edentula* and *Timoclea lavrani*. The latter was recorded as a single valve at the Link Canal in 1982/83 (Table 2), while *A. edentula* was found as an empty shell at Charter's Creek in April 2011.

DISCUSSION

Twenty-four bivalve species were identified with high confidence by comparing them with museum specimens and in consultation with leading world experts. Identification was based on specimens obtained in the St Lucia estuarine system during surveys undertaken from December 1982 to April 2011, and on specimens deposited at the NMSA and SAMC. This is fewer than the number of 26 reported for St Lucia previously (Forbes & Cyrus 1993), but equal to it if the two species for which only a single valve was retrieved are included. The bivalve taxa *Tivela natalensis*, *Pitar abbreviatus* and a third species similar to *Tivela compressa* were reported by MacKay *et al.* (2010) from a survey of St Lucia that spanned 2004 to 2008. The three species were not recorded in

any of the major surveys done by the Natal Parks Board and Ezemvelo KZN Wildlife (Tables 2, 3). There is also no St Lucia-associated specimen of any of them in the museum collections (Tables 4a, 4b, 5). The records may be fortuitous or represent erroneous identifications of *Meretrix meretrix*, which is extremely variable in colouration and has more than ten synonyms in the literature (Boshoff 1965; Branch *et al.* 2010). Alternatively, these three taxa might have been situated near the mouth, when it was open in March–August 2007, and could have been carried into the estuary by inflowing water, because all three species are typically found in the surf zone of sandy beaches (Kilburn & Rippey 1982). *Hiatella arctica* was recorded at Fanie’s Island and in the North Lake during the first benthic survey of St Lucia, between 1948 and 1951 (Day *et al.* 1954; as *Saxicava* sp.). This species is not found in estuaries and it has a very similar appearance to *Irus irus*, which is common in St Lucia, often being present in great abundance (Kilburn & Rippey 1982). It is, therefore, almost certainly a misidentification of *I. irus* (Tables 2, 3). Large numbers of empty *I. irus* shells, embedded in cretaceous sandstone, were also encountered during 2011 from Charter’s Creek to Lister’s Point. Live individuals were found in False Bay between July 1964 and January 1965 (Millard & Broekhuysen 1970) and the species is considered to be uncommon in South Africa, except at St Lucia (Kilburn & Rippey 1982). Day *et al.* (1954) and Pillay and Perissinotto (2008) reported *Tellina trilatera* (= *triangularis*) as present in areas of the estuarine lake. However, this species is distributed from the Orange River to the former western Transkei (Kilburn & Rippey 1982) and considering that St Lucia does not fall within its distribution range, this suggests that *T. trilatera* might have been confused with *Tellina* cf. *rousi* (confirmed for the specimens of Pillay & Perissinotto 2008), which is distributed from Mozambique to Stillbaai (Kilburn & Rippey 1982). Indeed, *T. cf. rousi* was recorded in abundance during the surveys done in 1982/83 (Table 2) and 2005 (Table 3). The species was also collected in 1987 at Shark Basin (Table 4b) and many empty shells were observed in 2011, from Charter’s Creek to False Bay. In March 2011, *T. cf. rousi* was found alive in numbers at Charter’s Creek and Fanie’s Island (Table 6) and is regarded as an undescribed species (M. Huber pers. comm.).

Day *et al.* (1954) stated that *Brachidontes semistriatus* was considered locally common around the “Point” area. Millard and Broekhuysen (1970) also wrote that *B. semistriatus* was found in St Lucia, on damp stones along the shore of the estuarine basin. Davies (1980) showed that there have been many misidentifications between the three mytilid species, *B. virgiliae*, *B. semistriatus* and *Arcuatula capensis*. He suggested that the reported *B. semistriatus* from St Lucia may have been *B. virgiliae*. *Brachidontes semistriatus* is commonly found on exposed marine rocky shores, while *B. virgiliae* is a true estuarine species (Davies 1980). Both Millard and Broekhuysen (1970) and Day *et al.* (1954) mentioned *Saccostrea cucullata* as being the main oyster species recorded from St Lucia. However, this species is normally replaced by *S. forskahlii* in estuaries (R.N. Kilburn pers. comm.) and in view of the fact that no specimens of *S. cucullata* were obtained in the surveys described in this study, it seems likely that these old identifications were erroneous.

Only a single record for each of the two bivalves, *Anodontia edentula* and *Timoclea lavrani* was obtained at St Lucia. *Anodontia edentula* is distributed from the tropical Indo-Pacific to as far south as Knysna (Kilburn & Rippey 1982; Branch *et al.* 2010). Kilburn and Rippey (1982) stated that this species was on a trajectory to extinction in

TABLE 6

Abundance (ind.m⁻²) of bivalve species reportedly found alive at the St Lucia Estuary during the survey of March 2011. Abbreviations: Bv – *Brachidontes virgiliae*, Dh – *Dosinia hepatica*, Ml – *Salmacoma litoralis*, Mr – *Maccomopsis moluccensis*, Sc – *Solen cylindraceus*, Tr – *Tellina cf. rousi*.

Site	Bv	Dh	Ml	Mr	Sc	Tr
Lister's Point	-	-	-	-	-	-
Hell's Gate	-	-	-	-	-	-
Fanie's Island (Shore)	51	-	-	-	-	-
Fanie's Island (Boat)	-	-	-	-	-	-
Catalina Bay	-	-	-	-	127	-
Charter's Creek 1	-	4	37	65	494	4
Charter's Creek 2	-	-	9	4	14	80
Makakatana	-	-	4	-	-	-
Mouth	-	-	-	-	-	-

southern Africa. A single valve of *A. edentula* was found at Charter's Creek in April 2011, suggesting that the species may have lived inside St Lucia in the past. However, since it was not present in any of the historical or current bivalve collections from this estuary (Tables 2, 3, 4a, 4b), it is possible that the valve may have been accidentally introduced into the system. Similarly, *T. lavrani* was recovered as a single valve in the Link Canal during the 1982/83 survey. The taxon is considered an offshore species with a distribution from northern Mozambique to the South Coast of KwaZulu-Natal (Kilburn & Rippey 1982). Given the small size of the valve concerned, it is considered likely that this was advected into the estuary from the ocean by tidal inflow.

All surveys undertaken by specialists in past and recent years have failed to produce evidence of the existence in the estuary of small species such as nuculids, nuculanids, philobryids, micro-tellinids and micro-venerids. Furthermore, no previous literature on St Lucia has mentioned the families Cardiidae, Carditidae, Chamidae, Corbulidae, Donacidae, Glycymerididae, Limidae, Mesodesmatidae, Myidae, Pectinidae, Pinnidae, Pteriidae and Spondylidae, which usually dominate shallow marine ecosystems elsewhere.

One of the twelve bivalve species not previously reported in the literature for St Lucia is *Meretrix meretrix*. It has a general Indo-Pacific distribution, reaching as far south as Maputo Bay along the East African coast (Scarlet 2005; Branch *et al.* 2010). The Maputo Bay population is thought to have been introduced for food from further north in East Africa (Scarlet 2005; R.N. Kilburn pers. comm.). Boshoff (1965) commented that *M. meretrix* was common in Inhaca Island, Mozambique. Kilburn and Rippey (1982) stated that this species does not live south of Mozambique. Steyn and Lussi (1998) report a South African distribution range for this species from Kosi Bay to around Port Alfred. However, as their atlas is based on the occurrence of "beached specimens", it is likely that no live individuals/populations were involved in this work. The first record of *M. meretrix* in St Lucia is from July 2000 at Charter's Creek (Table 4b) (details of the specimen are at the NMSA). In 2005 and 2011, freshly dead *M. meretrix* were found in great abundance in both the South and North lakes (Table 3). This is a highly visible species because of its thick and robust shell. Specimens ranged in size from 0.5 to 7 cm, suggesting that a viable population was at some stage thriving within the estuary.

Notwithstanding the equivocal report of Steyn and Lussi (1998), this represents the first confirmed record for this species in South African waters. However, the timing and mode of its introduction into the St Lucia Estuary remain unresolved. Two possible scenarios are that: (1) it might have been introduced as veligers, transported from Maputo Bay via the Agulhas Current; or (2) it was artificially introduced into St Lucia (R.N. Kilburn pers. comm.). Additionally, the ability to live further south may be due to warming of the oceans globally (R. Willan pers. comm.). The absence of live *M. meretrix* in the bivalve survey of 2011 and the huge numbers of dead *M. meretrix* observed then, most of them still with the periostracum intact, suggest that the species may have died out in the system only recently.

Millard and Broekhuysen (1970) reported the occurrence of dead *Barnea manilensis* shells in St Lucia. This species was also recorded at St Lucia by Barnard (1964). It was commonly found from South Lake to False Bay (Tables 2, 3, 4a), but only dead in 2011, embedded in the cretaceous sandstone exposed by the drought along the western banks of the estuarine lake. This is in agreement with Kilburn and Rippey (1982), who described the bivalve as boring into hard clay and soft sandstone. The extremely large numbers (>100 ind.m²) of dead specimens observed lately along the entire western shoreline of the estuarine lake indicate that until recently, the species was a major filter-feeder and thus a role-player in the settling of suspended silt within the system. Although *Irus irus* is found in the same localities as *B. manilensis*, it nestles in pre-existing crevices or boreholes already dug by other bivalves and isopods (R. Willan pers. comm.).

Currently, most of the filtering action within the lake appears to be fulfilled only by *Solen cylindraceus*, which despite the adverse conditions prevailing at present, can still be found in concentrations exceeding 200 ind.m⁻². It is likely that this light-shelled species is able to disperse easily and grow rapidly. Moreover, it has a fairly wide salinity tolerance range of 15 to 65 ‰ (Nel *et al.* 2011). Day *et al.* (1954) mentioned that *S. capensis* was found in the Narrows, Fanie's Island and North Lake between 1948 and 1951. However, as the distribution range of *S. capensis* is from the Olifants River to the Eastern Cape (Kilburn & Rippey 1982; Branch *et al.* 2010), a misidentification of *S. cylindraceus* was almost certainly involved. During the 1964/65 assessment of the entire St Lucia estuarine system (Millard & Broekhuysen 1970), *S. cylindraceus* was found alive and in abundance at Hell's Gate, Makakatana Bay and Brodie's Crossing (Millard & Broekhuysen 1970). In January 1972, *S. cylindraceus* was only found in the South Lake, while the system was experiencing hypersaline conditions (Bolt 1970). In July 1972, as salinity dropped below 35 ‰, *S. cylindraceus* penetrated North Lake and in January 1973 it moved even further up into the North Lake (Bolt 1970). From 1981 to 1982, the South Lake exhibited stable salinities of 35 ‰ and *S. cylindraceus* was found alive at all sampling sites (Blaber *et al.* 1983). It was rare in the Narrows in 1983; thereafter, it became common as a result of a flood flushing juveniles from the South Lake into the channel, yet this population did not persist (Owen & Forbes 1997). The mouth of the estuary closed in 1992, resulting in hypersaline conditions and the reappearance of *S. cylindraceus* in the Narrows (Owen & Forbes 1997). Pillay and Perissinotto (2008) investigated the benthic community of St Lucia during the 2005 drought year. A total of 14 sites were sampled from the Mouth to False Bay and salinities ranged from 0–125.6 ‰ within the system (Pillay & Perissinotto 2008). On that occasion, live *S. cylindraceus* occurred at six of the fourteen sites, i.e. Fanie's Island, Charter's

Creek, Makakatana, Catalina Bay, Bridge and Mouth (Pillay & Perissinotto 2008). *Solen cylindraceus* was also found alive in St Lucia from 2004 to 2008 (MacKay *et al.* 2010). In 2010, St Lucia exhibited hypersaline conditions, with living *S. cylindraceus* found only at Catalina Bay and Charter's Creek (Nel *et al.* 2011). In January 2011, salinities had reduced dramatically due to heavy rainfall, which resulted in a new cohort of *S. cylindraceus* (size range: 0.5–1.5 cm) being found alive and in large numbers at Charter's Creek, Catalina Bay, Fanie's Island and even reaching Lister's Point (Table 6). Apart from this species, *Brachidontes virgiliae*, *Dosinia hepatica*, *Macomopsis moluccensis*, *Salmacoma litoralis* and *Tellina cf. rousi* were the only bivalves found alive in the estuarine lake during the latest survey, in March 2011.

In conclusion, 12 species from St Lucia have been conclusively reported in this study for the first time. The species *Brachidontes semistriatus*, *Saccostrea cucullata*, *Pitar abbreviatus*, *Hiatella arctica*, *Solen capensis*, *Tellina triliatera*, *Tivela compressa* and *T. natalensis*, despite having been mentioned previously in the literature for St Lucia, are not considered to be part of the bivalve fauna of the estuarine lake. *Meretrix meretrix* is a new record for South Africa, but the mode of its introduction into St Lucia is still unresolved. The large numbers of empty *Barnea manilensis* shells observed along the entire western shoreline suggest that this species has played a major role in settling suspended silt within the system. This role is now fulfilled only by *Solen cylindraceus*. Apart from this species, *B. virgiliae*, *D. hepatica*, *M. moluccensis*, *S. litoralis* and *T. cf. rousi* are the only bivalves that were found alive in the estuarine lake in 2011.

ACKNOWLEDGEMENTS

We are very grateful to Dick Kilburn, Dai Herbert, Richard Willan and Markus Huber for their help with specimen identification and for providing data on specimens deposited in museums. We thank Stuart McLean who, with his intense interest in natural history, collected many of the specimens in the 1982/83 survey, and Chantal Dickson who, with great endurance, walked most of the shoreline of St Lucia in 2005, collecting bivalves. Siphepile Khanyile, Nasreen Peer, Schalk du Plooy, David Dyer, Nicola Carrasco, Nelson Miranda and Sarah Bownes are gratefully acknowledged for their help in the field and in the laboratory. Funding for this project was provided by the National Research Foundation of South Africa through the programme Knowledge Fields Development – Society, Ecosystems and Change (SEACHANGE); as well as by the South African – Netherlands Research Programme on Alternatives in Development (SANPAD, Durban).

REFERENCES

Note: The number in square brackets at the end of the reference corresponds to the in-text citations used in the annotated checklist (Appendix).

- APPLETON, C.C. 1996. *Freshwater molluscs of southern Africa*. Pietermaritzburg: University of Natal Press. [1]
- BARNARD, K.H. 1964. Contributions to the knowledge of South African marine Mollusca. Part V. Lamelli-branchiata. *Annals of the South African Museum* **47**: 361–593.
- BEGG, G.W. 1978. The estuaries of Natal. (Part II). *Natal Town and Regional Planning Commission Report* **41**: 1–657.
- BLABER, S.J.M., KURE, N.F., JACKSON, S. & CYRUS, D.P. 1983. The benthos of South Lake, St Lucia following a period of stable salinities. *South African Journal of Zoology* **18**: 311–319. [2]
- BOLTT, R.E. 1975. The benthos of some southern African lakes. Part V. The recovery of the benthic fauna of St Lucia Lake following a period of excessively high salinity. *Transactions of the Royal Society of South Africa* **41**: 295–323.
- BOSHOFF, P.H. 1965. Pelecypoda of Inhaca Island, Moçambique. *Memórias do Instituto de Investigação Científica de Moçambique* **7**: 65–206.
- BRANCH, G.M., GRIFFITHS, C.L., BRANCH, M.L. & BECKLEY, L.E. 2010. *Two oceans: a guide to the marine life of southern Africa*. Cape Town: Struik Nature. [3]
- CARRASCO, N.K., PERISSINOTTO, R. & PILLAY, D. 2010. Zooplankton of the St Lucia estuary during the current drought cycle: a comparison between open- and closed-mouth conditions. *Marine Ecology Progress Series* **399**: 157–171.

- CIESM (The Mediterranean Science Commission). 2002. *Atlas of exotic species in the Mediterranean*. (<http://www.ciesm.org/online/atlas/index.htm>; accessed 17/10/2012) [4]
- CYRUS, D.P. 1988. Episodic events and estuaries: effects of cyclonic flushing on the benthic fauna and diet of *Solea bleekeri* (Teleostei) in Lake St Lucia on the south-eastern coast of Africa. *Journal of Fish Biology* **33** (Suppl. sA): 1–7.
- CYRUS, D.P. & MARTIN, T.J. 1988. Distribution and abundance of the benthos in the sediments of Lake Cubhu: a freshwater coastal lake in Zululand, South Africa. *Journal of the Limnological Society of Southern Africa* **14**: 93–101.
- CYRUS, D. & VIVIER, L. 2006. Status of the estuarine fish fauna in the St Lucia estuarine system, South Africa, after 30 months of mouth closure. *African Journal of Aquatic Science* **31**: 71–81.
- CYRUS, D.P., VIVIER, L. & JERLING, H.L. 2010. Effect of hypersaline and low lake conditions on ecological functioning of St Lucia estuarine system, South Africa: an overview 2002–2008. *Estuarine, Coastal and Shelf Science* **86**: 535–542.
- DAVIES, B.R. 1980. The identification of the mytilids *Musculus virgiliae* Barnard, *Arcuatula capensis* (Krauss) and *Brachidontes variabilis* Krauss, with corrections to the literature and a note on their distribution. *Transactions of the Royal Society of South Africa* **44**: 225–236.
- DAY, J.H., MILLARD, N.A.H. & BROEKHUYSEN, G.J. 1954. The ecology of South African estuaries. Part IV: the St Lucia system. *Transactions of the Royal Society of South Africa* **34**: 129–156. [5]
- FORBES, A.T. & CYRUS, D.P. 1992. Impact of a major cyclone on a southeast African estuarine lake system. *Netherlands Journal of Sea Research* **30**: 265–272.
- 1993. Biological effects of salinity gradient reversals in a southeast African estuarine lake. *Netherlands Journal of Aquatic Ecology* **27**: 485–488.
- GERRITSEN, J., HOLLAND, A.F. & IRVINE, D.E. 1994. Suspension-feeding bivalves and the fate of primary production: an estuarine model applied to Chesapeake Bay. *Estuaries* **17**: 403–416.
- GLOBAL BIODIVERSITY INFORMATION FACILITY. 2011. <http://data.gbif.org/welcome.htm>. (accessed 17/10/2012) [6]
- HAMPEL, H., ELLIOTT, M. & CATTRISSE, A. 2009. Macrofaunal communities in the habitats of intertidal marshes along the salinity gradient of the Schelde estuary. *Estuarine, Coastal and Shelf Science* **84**: 45–53.
- HANEKOM, N. 1989. A note on the effects of a flood of medium intensity on macrobenthos of soft substrata in the Swartkops estuary, South Africa. *South African Journal of Marine Science* **8**: 349–355.
- HILL, B.J. 1981. Adaptations to temperature and salinity stress in southern African estuaries. In: Day, J.H., ed., *Estuarine Ecology*. Cape Town: A.A. Balkema, pp. 187–196.
- HUBER, M. 2010. *Compendium of bivalves*. Hackenheim: ConchBooks. [7]
- HUTCHISON, I.P.G. & MIDGLEY, D.C. 1978. Modelling the water and salt balance in a shallow lake. *Ecological Modelling* **4**: 211–235.
- KILBURN, R. & RIPPEY, E. 1982. *Sea shells of southern Africa*. Johannesburg: Macmillan South Africa. [8]
- MACKAY, F., CYRUS, D. & RUSSELL, K.-L. 2010. Macrobenthic invertebrate responses to prolonged drought in South Africa's largest estuarine lake complex. *Estuarine, Coastal and Shelf Science* **86**: 553–567. [9]
- MATTHEWS, T.G. & FAIRWEATHER, P.G. 2004. Effect of lowered salinity on the survival, condition and reburial of *Soletellina alba* (Lamarck, 1818) (Bivalvia: Psammobiidae). *Austral Ecology* **29**: 250–257.
- McLUSKY, D.S. & ELLIOTT, M. 2004. *The estuarine ecosystem: ecology, threats and management*. 3rd ed. Oxford: Oxford University Press.
- MILLARD, N.A.H. & BROEKHUYSEN, G.J. 1970. The ecology of South African estuaries. Part X: St Lucia: a second report. *Zoologica Africana* **5**: 277–307. [10]
- MUSSELP. 2012. <http://mussel-project.uwsp.edu>. (accessed 17/10/2012) [11]
- NEL, H.A., PERISSINOTTO, R., TAYLOR, R.H. & CARRASCO, N.K. 2011. Salinity tolerance of the bivalve *Solen cylindraceus* (Hanley, 1843) (Mollusca: Euheterodonta: Solenidae) in the St Lucia Estuary. *African Invertebrates* **52**: 575–586.
- NGQULANA, S.G., OWEN, R.K., VIVIER, L. & CYRUS, D.P. 2010. Benthic faunal distribution and abundance in the Mfolozi-Msunduzi estuarine system, KwaZulu-Natal, South Africa. *African Journal of Aquatic Science* **35**: 123–133.
- OBIS (The Academy of Natural Sciences). 2006. *Indo-Pacific Molluscan Database*. (http://clade.ansp.org/obis/find_mollusk.html; accessed 17/10/2012) [12]
- OLIVER, P.G. 1992. *Bivalved seashells of the Red Sea*. Wiesbaden: Christa Hemmen & Cardiff: National Museum of Wales. [13]
- OWEN, R.K. & FORBES, A.T. 1997. Salinity, floods and the infaunal macrobenthic community of the St Lucia estuary, KwaZulu-Natal, South Africa. *African Journal of Aquatic Science* **23**: 14–30. [14]
- PALOMARES, M.L.D. & PAULY, D., eds. 2012. *SeaLifeBase*. Version (08/2012). (<http://www.sealifebase.org>; accessed 17/10/2012) [16]

- PILLAY, D. & PERISSINOTTO, R. 2008. The benthic macrofauna of the St Lucia Estuary during the 2005 drought year. *Estuarine, Coastal and Shelf Science* **77**: 35–46. [15]
- SCARLET, M.P.J. 2005. *Clams as a resource in Maputo Bay – Mozambique*. MSc Thesis. Gothenburg, Sweden: University of Gothenburg.
- STEYN, G.D. & LUSSI, M. 1998. *Marine shells of South Africa*. Hartebeespoort: Ekogilde Publishers. [17]
- VAUGHN, C.C. & HAKENKAMP, C.C. 2001. The functional role of burrowing bivalves in freshwater ecosystems. *Freshwater Biology* **46**: 1431–1446.
- VIVIER, L. & CYRUS, D.P. 2009. Alternative nursery habitat for estuarine associated marine fish during prolonged closure of the St Lucia estuary, South Africa. *Estuarine, Coastal and Shelf Science* **85**: 118–125.
- WEERTS, K.A. 1993. *Salinity, sediments and the macrobenthic communities of Lake St Lucia*. MSc Thesis. Durban: University of Natal.
- WHITFIELD, A.K. & TAYLOR, R.H. 2009. A review of the importance of freshwater inflow to the future conservation of Lake St Lucia. *Aquatic Conservation: Marine and Freshwater Ecosystems* **19**: 838–848.
- WILLAN, R.C. 1993. Taxonomic revision of the family Psammobiidae (Bivalvia: Tellinoidea) in the Australian and New Zealand region. *Records of the Australian Museum, Supplement* **18**: 1–132. [18]
- YSEBAERT, T., MEIRE, P., HERMAN, P.M.J. & VERBEEK, H. 2002. Macrobenthic species response surfaces along estuarine gradients: prediction by logistic progression. *Marine Ecology Progress Series* **225**: 79–95.

APPENDIX

An annotated checklist of bivalve molluscs conclusively identified from St Lucia Estuary during this study. (Photographs are courtesy of Lynette Perissinotto and Nicola Carrasco.)

Family Arcidae Lamarek, 1809

Anadara natalensis (Krauss, 1848)^(7,12) (Fig. 3)

Synonyms: *Arca natalensis* Krauss, 1848;

Scapharca natalensis (Krauss, 1848).

Common name: Natal Ark.

Size: Maximum length 68 mm.⁽⁸⁾

Distribution: Red Sea to East London⁽⁸⁾; introduced into the Mediterranean (first recorded in Palestine in 1935) through the Suez Canal.⁽¹³⁾

St Lucia records: Not previously reported from St Lucia; single record in dredge spoil of 1983, but several empty shells (*ca* 10) found at Charter's Creek in April 2011.



Family Mytilidae Rafinesque, 1815

Brachidontes virgiliae (Barnard, 1964)⁽⁸⁾ (Fig. 4)

Synonyms: *Mytilus emarginatus* (non Benson in Reeve, 1858); *Musculus virgiliae* Barnard, 1964.

Common name: Brackwater Mussel.⁽³⁾

Size: Maximum length 25 mm.⁽³⁾

Distribution: Mozambique to Great Brak River.⁽⁸⁾

St Lucia records: Recorded during most past surveys^(2,5,9,10) and as far North as Lister's Point and Bird Island in 1982; alive and abundant from Fanie's Island to Charter's Creek during 2005 and recently (March–April 2011) in the Narrows, at Makakatana, Charter's Creek and Fanie's Island.



Arcuatula capensis (Krauss, 1848)⁽⁸⁾ (Fig. 5)

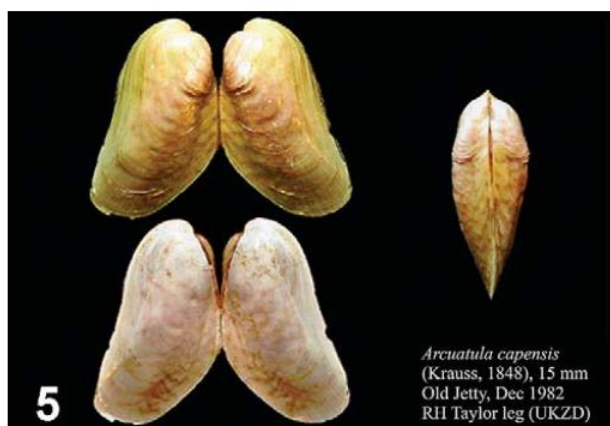
Synonyms: *Lamya capensis* auct.; *Modiola elegans* (non Philippi in Sowerby, 1889); *M. capensis* Krauss, 1848; *M. tenerrima* Smith, 1904.

Common name: Estuarine Mussel.⁽³⁾

Size: Maximum length 76 mm.⁽³⁾

Distribution: Mozambique to Cape False Bay.⁽³⁾

St Lucia records: No published records from St Lucia; collected in numbers in 1981 at Catalina Bay (NMSA), as well as on the western shores of North Lake (Missile Base and Coves) and False Bay in 1982/83.



Family Ostreidae Rafinesque, 1815

Saccostrea forskahlii (Gmelin, 1791)⁽¹²⁾ (Fig. 6)

Synonyms: *Ostrea forskahlii* Gmelin, 1791.

Common name: Forsskål's Oyster

Size: Maximum length 76.5 mm.⁽⁶⁾

Distribution: Mozambique to Durban.⁽⁶⁾

St Lucia records: Recorded previously as abundant at St Lucia^(4,10); collected alive or freshly dead in 1982/83 throughout North Lake and False Bay, but only as empty and old shells in 2011.



***Dendostrea sandvichensis* (Sowerby in Reeve, 1871)⁽¹²⁾ (Fig. 7)**

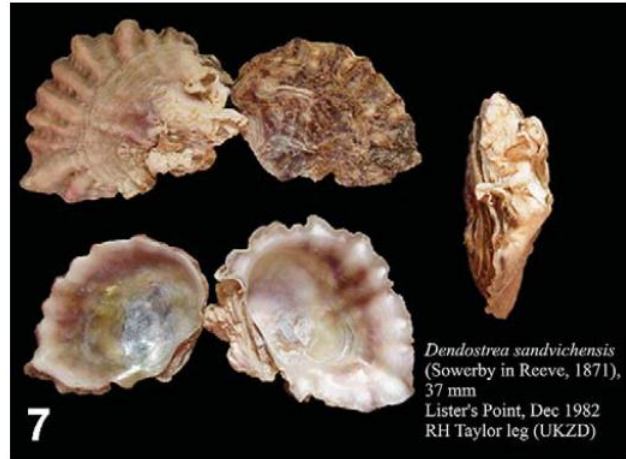
Synonyms: *Ostrea kapua* Dall, Bartsch & Rehder, 1938; *O. nomades* Iredale, 1939; *O. crenulifera* Saville-Kent, 1981.

Common name: Sandwich Islands Oyster.

Size: Up to 65 mm.

Distribution: Indo-Pacific to Port Alfred.

St Lucia records: Not reported previously from St Lucia; found in abundance throughout the estuary during the 1982/83 survey, mainly on rocky surfaces of the western shores of False Bay and North Lake; many, but all dead shells either attached to rocks or loose on the shore were seen in 2005 and 2011.



Dendostrea sandvichensis
(Sowerby in Reeve, 1871),
37 mm
Lister's Point, Dec 1982
RH Taylor leg (UKZD)

Family Anomiidae Rafinesque, 1815

***Anomia achaeus* Gray, 1850⁽⁸⁾ (Fig. 8)**

Synonyms: None.

Common name: Saddle Oyster.⁽³⁾

Size: Maximum length 70 mm.⁽⁸⁾

Distribution: Tropical Indian Ocean to Algoa Bay.⁽⁸⁾

St Lucia records: Not reported previously from St Lucia; recorded on the western shores of North Lake (Coves and Hell's Gate) during the 1982/83 survey and retrieved dead in numbers, particularly at Charter's Creek, during 2005 and 2011.



Anomia achaeus
Gray, 1850, 62 mm
Amatikulu Est, Aug 1977
H Champion leg (NMSA)

Family Cardiidae Lamarck, 1809

***Fulvia fragilis* (Forsskål in Niebuhr, 1775)⁽¹²⁾ (Fig. 9)**

Synonyms: *Cardium fragile* Niebuhr, 1775.

Common name: Fragile Cockle.⁽³⁾

Size: Up to 75 mm.⁽⁴⁾

Distribution: From Arabian Peninsula and Red Sea to southern KZN⁽¹²⁾; introduced into Mediterranean through Suez canal in 1955.⁽⁴⁾

St Lucia records: Not reported previously; recorded at northern end of North Lake and at False Bay during 1982/83; collected in June 1987 at False Bay (NMSA); several freshly-dead specimens found at Hell's Gate in 2005, but only few empty shells in 2011 at Lister's Point and Charter's Creek.



Fulvia fragilis
(Forsskål in Niebuhr, 1775),
38 mm
Hell's Gate, 2005
C Dickson leg (UKZD)

Family Mactridae Lamarck, 1809

***Mactra cuneata* (Gmelin, 1791)⁽¹²⁾ (Fig. 10)**

Synonyms: *Mactra delicatula* Preston, 1904; *Colorimactra florens* Iredale, 1929.

Common name: Wedge Trough Shell.⁽¹²⁾

Size: Up to 40 mm.⁽¹⁶⁾

Distribution: Indo-Pacific to Durban.⁽¹⁶⁾

St Lucia records: Not reported previously from St Lucia; collected in the upper reaches of the Narrows and at Makakatana in December 1982; not seen during any of the more recent surveys.



Mactra cuneata
(Gmelin, 1791), 19 mm
Makakatana, Dec 1982
S McLean leg (NMSA)

Family Solenidae Lamarck, 1809

***Solen cylindraceus* (Hanley, 1843)⁽¹²⁾** (Fig. 11)

Synonyms: *Solen corneus* auct.; *S. aspersus* auct.

Common name: Eastern Pencil-Bait or Stick-Bait.

Size: Maximum length 95 mm.⁽⁸⁾

Distribution: Indo-Pacific to Algoa Bay.⁽⁸⁾

St Lucia records: Consistently recorded in each study as dominant species in the estuary^(2,9,10,14,15); abundant at times in the Narrows at salinities >15‰⁽¹⁴⁾; recorded in 1982/83 throughout the three lakes, in 2005 in the North and South lakes, but in 2011 found alive only in the South Lake and as far north as Fanie's island.



Family Pharidae H. Adams & A. Adams, 1858

***Siliqua cf. polita* (non Wood, 1828)⁽¹⁷⁾** (Fig. 12)

Synonyms: None.

Common name: Wedge Shell.

Size: Maximum length 33 mm.

Distribution: Maputo Bay to northern KZN.

St Lucia records: Reported only once, from the western shores of South Lake (Gilly's Point)⁽²⁾; collected in relatively large numbers at Bird Island (middle of North Lake) and on western shores of False Bay during 1982/83 and in April 1987 (NMSA); not recorded in 2005 and only empty, old shells found in 2011.



Family Tellinidae Blainville, 1814

***Tellina cf. rousi* (Sowerby, 1892)⁽⁸⁾** (Fig. 13)

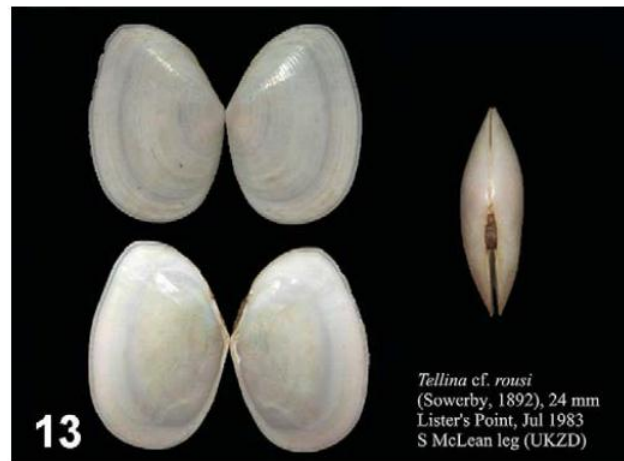
Synonyms: *Tellinides rousi* Sowerby, 1892.

Common name: Rous's Tellin.

Size: Maximum length 38 mm.⁽⁸⁾

Distribution: Mozambique to Stillbaai.⁽⁸⁾

St Lucia records: Erroneously identified as *T. trilatera* (= *triangularis*) in previous studies^(4,15); present during 1982/83 at False Bay, South Lake and Narrows; collected in June/August 1987 at Shark Basin (NMSA); many empty shells recorded on the western shores of False Bay and North Lake during 2005 and 2011; found alive in numbers at Charter's Creek and Fanie's Island in March–April 2011.



***Tellina s.l. bertini* (Jousseume, 1895)** (Fig. 14)

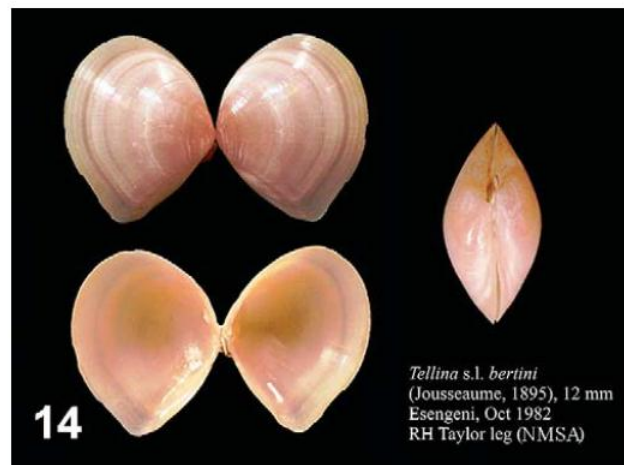
Synonyms: *Tellina (Angulus) yemenensis* Melvill, 1898; *T. siebenrocki* Sturany, 1901; *T. bertini* Lamy, 1918.

Common name: Bertin's Tellin.

Size: Up to 18 mm long and 13 mm high.⁽¹⁷⁾

Distribution: Red Sea (Aden) to Durban.⁽¹⁷⁾

St Lucia records: Known only from a small collection made in October 1982 at Esengeni (mid-Narrows) by R.H. Taylor and currently deposited at the NMSA; not recorded, even as empty shells, during the 2005 and 2011 surveys.



***Macomopsis moluccensis* (von Martens, 1865)**

(Fig. 15)

Synonyms: *Tellina retrorsa* Sowerby, 1867.

Common name: Back-leaning Tellin.

Size: Maximum length 22 mm.⁽⁸⁾Distribution: Indo-Pacific to Port Alfred.⁽⁸⁾

St Lucia records: Reported widely in the past^(2,8,10,14); specimens at NMSA collected on several occasions since July 1925; common at the southern end of South Lake but scarce at False Bay during 1982/83; found alive and in moderate numbers at Charter's Creek and Fanie's Island during 2011.

***Salmacoma litoralis* (Krauss, 1848)⁽³⁾** (Fig. 16)Synonyms: *Tellina litoralis* Krauss, 1848.Common name: Littoral Tellin.⁽³⁾Size: Maximum length 37 mm.⁽⁸⁾Distribution: Mozambique to Stillbaai.⁽⁸⁾

St Lucia records: Recorded previously from the estuary^(9,10); present but in low numbers during 1982/83, at False Bay and the North Lake; several specimens collected on four occasions from 1963 to 1987 are in the NMSA; recorded alive at Makakatana, Charter's Creek and Fanie's Island in 2011.



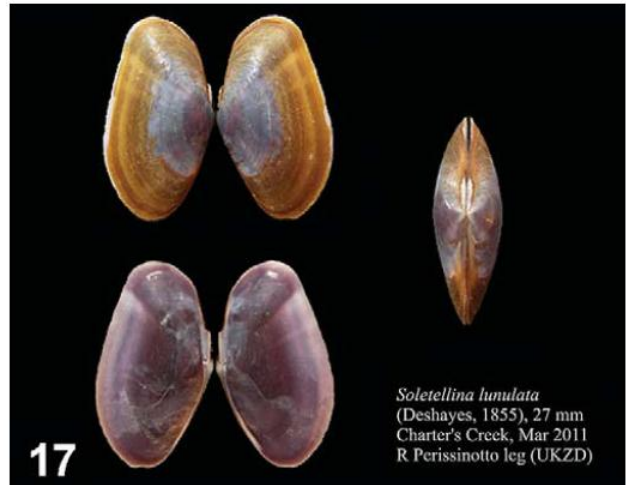
Family Psammobiidae Fleming, 1828

***Soletellina lunulata* (Deshayes, 1855)^(3,7,18)**

(Fig. 17)

Synonyms: *Capsa* (*Capsella*) *lunulata* Deshayes, 1855.Common name: Sunset Clam.⁽³⁾Size: Maximum length 37 mm.⁽⁸⁾Distribution: Indo-Pacific to the Xora River in the Eastern Cape Province.⁽⁸⁾

St Lucia records: Not reported explicitly from the St Lucia previously, but probably so under the record "Psammobiidae sp. 1"⁽⁹⁾; collected throughout the western shores of the three lakes in 1982/83; empty shells recorded in numbers from Charter's Creek to Lister's Point in 2005 and 2011.



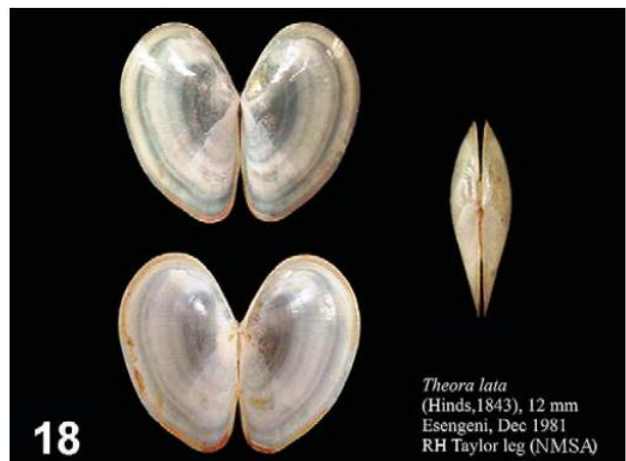
Family Semelidae Stoliczka, 1870

***Theora lata* (Hinds, 1843)⁽⁸⁾** (Fig. 18)Synonyms: *Neaera lata* Hinds, 1843.

Common name: Fragile Mud Clam.

Size: Maximum length 20 mm.⁽⁸⁾Distribution: Indo-Pacific to Durban Bay.⁽⁸⁾

St Lucia records: Reported from the estuary in most previous studies^(2,9,10,15); collected in numbers at Esengeni (Narrows) during December 1981 (NMSA) and at False Bay during July 1964 (SAMC); recorded often as abundant throughout North Lake and False Bay in 1982/83; rare and only as empty shells in 2011, on the western shores.



Family Veneridae Rafinesque, 1815

***Dosinia hepatica* (Lamarck, 1818)⁽³⁾** (Fig. 19)

Synonyms: *Artemis hepatica* auct.; *Cytherea hepatica* Lamarck, 1818; *C. hepatica* var. *subquadrata* Krauss, 1848.

Common name: Lesser Heart Clam.⁽³⁾

Size: Maximum length 32 mm⁽⁸⁾, seldom >25 mm.⁽³⁾

Distribution: Red Sea to Stillbaai.⁽⁸⁾

St Lucia records: Reported from St Lucia on several occasions^(2,10,14,17); collected at Fanie's Island in November 1971 (NMSA); common in 1982/83 and 2005 in the lakes and Narrows; alive but rare in 2011 at Charter's Creek.



***Irus irus* (Linnaeus, 1758)⁽¹²⁾** (Fig. 20)

Synonyms: *Rupellaria macrophylla* auct.; *Notirus macrophyllus* auct.; *Donax irus* Linnaeus, 1758; *Venerupis macrophylla* Deshayes, 1853; *V. pulcherrima* Deshayes, 1854; *V. attenuata* Reeve, 1874; *Irus macrophyllus* Deshayes, 1853; *Rupellaria semipurpurea* Dunker, 1882.

Common name: Rock Venus.⁽¹⁶⁾

Size: Maximum length 28 mm.⁽⁸⁾

Distribution: Tropical Indo-Pacific to Port Alfred and Europe.⁽⁸⁾

St Lucia records: Reported previously. Nestles in pre-existing crevices or boreholes already dug by other bivalves and isopods^(8,10); collected from 1962 to 1987 (NMSA); abundant but dead during the three surveys.



***Eumarcia paupercula* (Holten, 1802)⁽³⁾** (Fig. 21)

Synonyms: *Chione paupercula* auct.; *Venus paupercula* Chemnitz, 1795; *V. kochii* Philippi, 1843; *Chione ambigua* Deshayes, 1853; *Anomalocardia alfredensis* Bartsch, 1915.

Common name: Beaked Clam.⁽³⁾

Size: Maximum length 42 mm.⁽⁸⁾

Distribution: Northern Indian Ocean to Stillbaai.⁽⁸⁾

St Lucia records: Reported previously from South Lake and Narrows^(2,10,14); collected from 1927 to 1981 (NMSA and SAMC); scarce during 1982/83 and 2005 in the whole estuary, except False Bay; only old shells found in 2011.



***Meretrix meretrix* (Linnaeus, 1758)** (Fig. 22)

Synonyms: *Venus meretrix* Linnaeus, 1758; *V. lusoria* Röding, 1798; *Meretrix labiosa* Lamarck, 1801; *Cytherea ponderosa* Schumacher, 1817; *C. zonaria* Lamarck, 1818; *C. morphina* Lamarck, 1818; *C. graphica* Lamarck, 1818; *C. catanea* Lamarck, 1818; *C. impudica* Lamarck, 1818; *C. formosa* Sowerby, 1851; *Meretrix fusca* Deshayes, 1853.

Common name: Thick-shelled Clam.⁽³⁾

Size: Maximum length 70 mm.⁽¹⁶⁾

Distribution: Indo-Pacific to Maputo Bay.⁽³⁾

St Lucia records: Recorded for the first time in July 2000, at Charter's Creek (NMSA); freshly-dead clams very abundant during 2005 and 2011.



Family Iridinidae Swainson, 1840

***Chambardia wahlbergi* (Krauss, 1848)⁽¹¹⁾** (Fig. 23)

Synonyms: *Iridina wahlbergi* Krauss, 1848; *Platiris wahlbergi* (Krauss, 1848); *Spatha wahlbergi* (Krauss, 1848); *Spathella wahlbergi* (Krauss, 1848); *Mutela wahlbergi* (Krauss, 1848); *Aspatharia wahlbergi* (Krauss, 1848); *Spathopsis wahlbergi* (Krauss, 1848).

Common name: Giant Freshwater Mussel.

Size: Up to 122×54 mm.⁽¹⁾

Distribution: Africa except Congo basin; southern Africa from the Kunene River to northern KZN.⁽¹⁾

St Lucia records: Not previously recorded from the estuary; collected in 1982 at the Hluhluwe River mouth and in the Mkuzi swamps.



Chambardia wahlbergi
(Krauss, 1848), 90 mm
Mkuzi Swamps, Dec 1982
RH Taylor leg (UKZD)

Family Cyrenidae Gray, 1847

***Corbicula fluminalis* (Müller, 1774)⁽¹¹⁾** (Fig. 24)

Synonyms: *Cyrena africana* Krauss, 1848; *C. gauritziana* Prime, 1860; *Corbicula radiata* Smith, 1877; *C. kirkii* Prime, 1864; *C. natalensis* Clessin, 1879; *C. oliphantensis* Craven, 1880; *C. nyassana* Bourguignat, 1889; *C. astartina* Haas, 1936; *C. quinzii* Connolly, 1939; *C. africana* (Krauss, 1848).

Common name: African Freshwater Clam.

Size: Up to 23×18 mm.⁽¹⁾

Distribution: Throughout Africa; in southern Africa, absent from arid western parts.⁽¹⁾

St Lucia records: Not previously recorded from the estuary; collected in 1983 at the Hluhluwe mouth.



Corbicula fluminalis
(Müller, 1774), 17 mm
Hluhluwe Mouth, Jul 1983
S McLean leg (UKZD)

Family Pholadidae Lamarck, 1809

***Barnea manilensis* (Philippi, 1847)⁽¹²⁾** (Fig. 25)

Synonyms: *Barnea durbanensis* van Hoepen, 1941; *Barnia* (sic) *erythraea* Gray, 1851; *Barnea inornata* Pilsbry, 1901.

Common name: Manila Rock Piddock.⁽¹⁶⁾

Size: Maximum length 78 mm.⁽⁸⁾

Distribution: Tropical Indo-Pacific to Durban Bay.⁽⁸⁾

St Lucia records: Previously recorded in the estuary only once, as empty shells⁽¹⁰⁾; specimens were collected at False Bay in July 1948 (SAMC); recorded in large numbers (often >100 ind.m²) but not alive during three surveys of 1983/83, 2005 and 2011. Found throughout western shores, wherever cretaceous sandstone is available for burrowing.



Barnea manilensis
(Philippi, 1847), 78 mm
Lister's Point, Apr 2011
R Perissinotto leg (UKZD)

***Martesia striata* (Linnaeus, 1758)⁽¹²⁾** (Fig. 26)

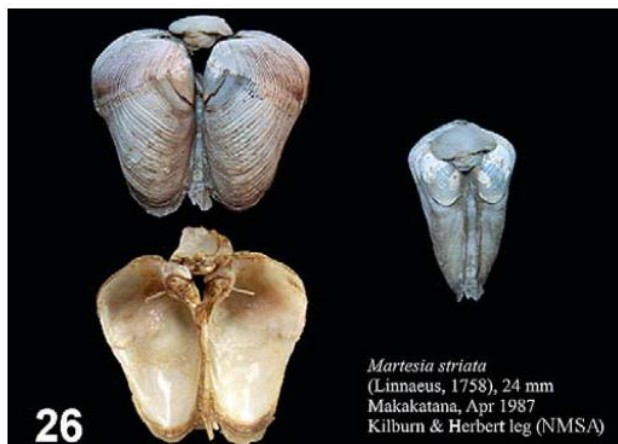
Synonyms: *Pholas striatus* Linnaeus, 1758.

Common name: Timber Piddock.

Size: Maximum length 35 mm.⁽⁸⁾

Distribution: Indo-Pacific to Cape False Bay and western Atlantic.⁽⁸⁾

St Lucia records: Not previously reported from St Lucia; collected in numbers from decaying wood at Makakatana in April 1987 (NMSA).



Martesia striata
(Linnaeus, 1758), 24 mm
Makakatana, Apr 1987
Kilburn & Herbert leg (NMSA)

Salinity tolerance of the bivalve *Solen cylindraceus* (Hanley, 1843) (Mollusca: Euheterodonta: Solenidae) in the St Lucia Estuary

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ABSTRACT

Solen cylindraceus (Hanley, 1843) is an infaunal bivalve that in the St Lucia Estuary is currently restricted to the southern part of its South Lake, having disappeared from the northern reaches due to persisting hypersaline conditions (>70‰) and air exposure at low water levels. The system experiences marked fluctuations in salinity due to quasi-decadal changes from wet to dry periods. In this study, the salinity tolerance of *S. cylindraceus* is determined using both shock and gradual change tests. Animals were collected at Catalina Bay (eastern shores of South Lake) and acclimated under laboratory conditions to naturally occurring salinities of 50‰ and 45‰ for the shock and gradual test, respectively. Mortalities were recorded for animals exposed to a sudden change in salinity, using eight different treatments ranging from 0 to 80‰. The second test involved exposing bivalves to a gradual change in salinity, using eight different treatments from 0 to 85‰. In the shock test, the lower salinity tolerance limit for *S. cylindraceus* was 30‰ and the upper 60‰, while in the gradual test, these limits were 15 and 65‰, respectively. The time it took for 50% of animals to die increased from the shock to the gradual test for 10, 20 and 70‰, and decreased for 0 and 80‰. This knowledge may be useful towards predicting major crises in the *S. cylindraceus* populations, as drought and flood events alternate in the region. Major losses will be expected when salinities exceed 65‰ during dry phases or drop below 15‰ during flood events.

KEY WORDS: Mollusca, *Solen cylindraceus*, pencil bait, salinity tolerance, hypersaline conditions, flood events, iSimangaliso Wetland Park, St Lucia Estuary.

INTRODUCTION

Macrofauna in estuarine systems are exposed to marked fluctuations in the physico-chemical environment (Pillay & Perissinotto 2008; Hampel *et al.* 2009; MacKay *et al.* 2010). Salinity fluctuations are among the most important, as they have major effects on the osmotic physiology of organisms (McLachlan & Erasmus 1974). Specifically, hypersaline conditions and flood events may cause large reductions in species numbers and changes to species composition (Cyrus 1988; Hanekom 1989; Forbes & Cyrus 1992; Pillay & Perissinotto 2008). Mass mortality (Matthews & Fairweather 2004) and redistribution of benthic bivalve species have been recorded during flood events (Forbes & Cyrus 1992). Hill (1981) stated that mass mortality was particularly evident in sessile and slow moving benthic organisms in the St Lucia estuarine system, during periods of elevated salinities. This was partially due to their inability to move to areas with lower salinity and a more favourable physico-chemical environment (Hill 1981; Ysebaert *et al.* 2002).

The St Lucia Estuary exhibits wide cyclic changes in climatic conditions, from wet to dry periods (Begg 1978; Cyrus & Vivier 2006). During dry periods the system is subjected to high evaporation, low rainfall input and low river inflow (Cyrus & Vivier 2006; Pillay & Perissinotto 2008). Traditionally, St Lucia shared a common mouth with the adjacent Mfolozi River, but in 1927 canalisation of the Mfolozi floodplains for sugarcane farming occurred (Ngqulana *et al.* 2010). This resulted in an increased silt load entering St Lucia and in an attempt to prevent this, the two systems were

artificially separated in 1952, thus St Lucia is currently deprived of its most essential freshwater source (Whitfield & Taylor 2009; Ngqulana *et al.* 2010). As a result, during dry periods the northern reaches of the estuarine system become hypersaline, with salinity levels of $>200\text{‰}$ having been recorded on several occasions (Cyrus & Vivier 2006; Vivier & Cyrus 2009; Cyrus *et al.* 2011). St Lucia also experiences episodic flooding events, which may rapidly decrease the salinity within the system (Cyrus 1988; Hanekom 1989; Forbes & Cyrus 1993). Forbes and Cyrus (1992) recorded a decrease in salinity, from 45‰ to $<10\text{‰}$ in approximately two weeks, in large parts of its South Lake during the flood caused by Cyclone Domoina in 1984. This rapid change in salinity may cause an alteration in the estuarine structure and function (Cyrus 1988). *Solen cylindraceus* has previously been recorded in the North Lake of St Lucia (Boltz 1975), but it has been absent from this area after December 2004 (Cyrus *et al.* 2011).

Solen cylindraceus is an infaunal bivalve endemic to southern African estuaries, where it inhabits muddy and sandy sediments (Hodgson & de Villiers 1986; de Villiers *et al.* 1989a; MacKay *et al.* 2010). In the St Lucia Estuary it is considered a key species, as it is a major food source to fish and birds (including the greater flamingo), which feed on its fleshy body and siphon (Hodgson & de Villiers 1986; Forbes & Cyrus 1992; Weerts *et al.* 1997), as well as being an important filter-feeder (Hodgson & de Villiers 1986). Benthic macrofauna such as *S. cylindraceus* play an important role in sediment dynamics, catching and settling a significant amount of sediment (Hampel *et al.* 2009; Cyrus *et al.* 2010; MacKay *et al.* 2010). *S. cylindraceus* is abundant in the South Lake of St Lucia in densities of up to 1200 ind.m^{-2} (Blaber *et al.* 1983; MacKay *et al.* 2010) and even $>3000 \text{ ind.m}^{-2}$ (Pillay & Perissinotto 2008). The species is an euryhaline osmoconformer (McLachlan & Erasmus 1974) and MacKay *et al.* (2010) suggested that it may tolerate salinities ranging from 10 to 70‰ , having been recorded previously at St Lucia in areas within this salinity range. Pillay and Perissinotto (2008) stated that *S. cylindraceus* is less dense at low and rapidly changing salinity values. They suggested that the optimal salinity range may be from 25 to 50‰ , as this is the range within which the highest densities of *S. cylindraceus* were found (Pillay & Perissinotto 2008).

Model predictions show that climate change in north-eastern KwaZulu-Natal will probably cause an increase in the occurrence of extreme weather conditions, such as floods and droughts (Schulze 2006). It is important to predict how *S. cylindraceus* may respond to a greater frequency of extreme weather conditions. For example, prolonged droughts may result in prolonged periods of hypersaline conditions, while an increase in the occurrence of floods may result in increased hyposaline conditions. These changes may restrict the distribution of *S. cylindraceus* within St Lucia. There is, therefore, a need to determine directly and experimentally the salinity tolerance of *S. cylindraceus* at St Lucia, and in particular the time scales of tolerance to exposure to critical salinity levels, such as those experienced during droughts or floods. It is important to monitor changes in key macrofaunal species such as *S. cylindraceus*, as they can provide early warning signs of change that can be used to support the sustainable management of this unique and extremely variable estuary (Perissinotto *et al.* 2010). The primary aim of this study was to determine the salinity tolerance of *S. cylindraceus*. The objectives were to determine its upper and lower lethal salinity limits under shock and gradual change tests. A secondary aim was to verify whether

natural *S. cylindraceus* populations in South Lake are found in an environment which coincides with their salinity tolerance found in the experiments.

MATERIAL AND METHODS

Study area

The St Lucia estuarine system is the largest estuarine lake in Africa, covering 80% of the estuarine area of KwaZulu-Natal (Begg 1974; Cyrus & Vivier 2006; Pillay & Perissinotto 2008; Vivier & Cyrus 2009). It is of high importance to KwaZulu-Natal and the adjacent ocean region (Cyrus & Vivier 2006), due to its high biodiversity (Begg 1974), its importance as a nursery area for fish (Cyrus & Vivier 2006) and its invertebrate assemblages (Pillay & Perissinotto 2008). Positioned in the iSimangaliso

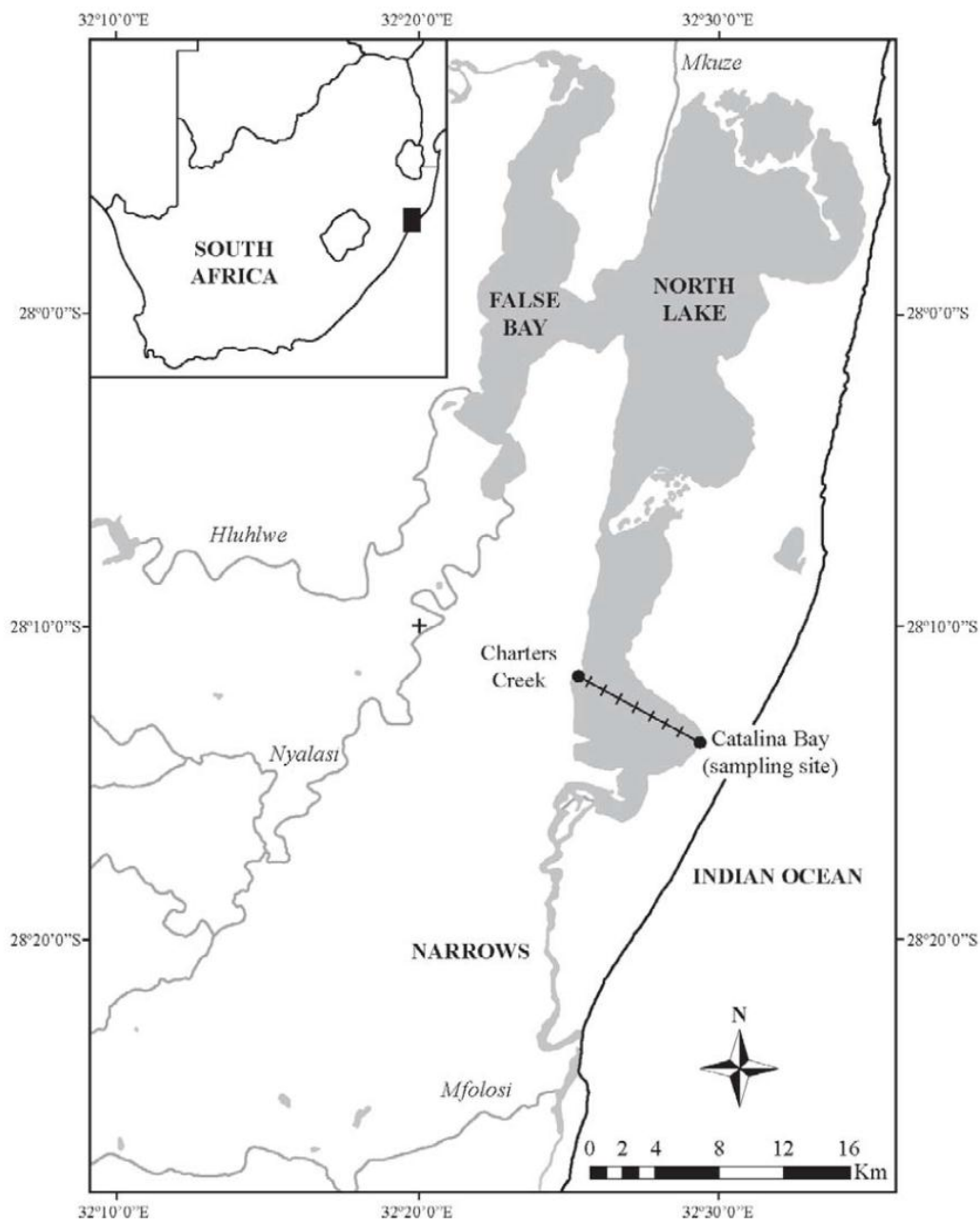


Fig. 1. Geographic position of the St Lucia Estuary showing the sampling site, Catalina Bay, and the abundance transect occupied in June 2010 (adapted from Carrasco *et al.* 2010).

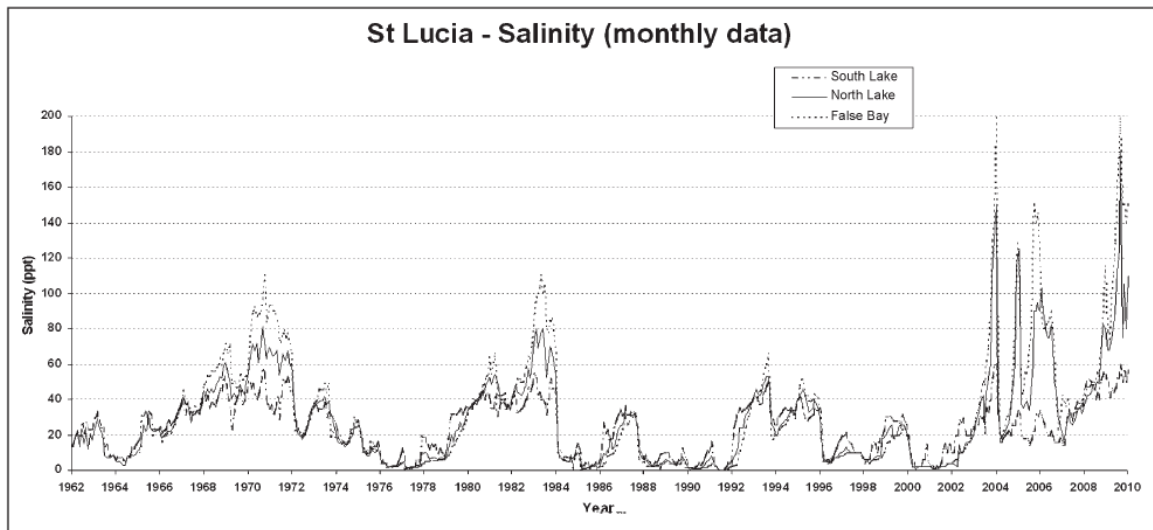


Fig. 2. Changes in salinity (ppt) recorded in False Bay and the South and North lakes of the St Lucia Estuary during the period 1960–2010.

Wetland Park, St Lucia was awarded UNESCO World Heritage Site status in 1999 due to its importance and magnitude (Pillay & Perissinotto 2008; Vivier & Cyrus 2009; Whitfield & Taylor 2009). The estuary is located between 27°52'S to 28°24'S and 32°21'E to 32°34'E and is subdivided into False Bay, North Lake, South Lake and the Narrows (Fig. 1). It has a total surface area of approximately 300 to 350 km² (Begg 1978). The focus of the present study was on South Lake, in particular Catalina Bay (Fig. 1). Historically the estuarine lake has experienced large scale water level and salinity fluctuations, with quasi-decadal ranges in salinity from virtual freshwater to extreme hypersaline conditions (>200‰) (Fig. 2).

Sampling procedure

Large *S. cylindraceus* individuals ranging from 4 to 5.5 cm shell length were collected from the sampling site (Catalina Bay). This was done by shovelling sediment from a water depth of 0.5 m, onto the lake banks. The sediment was carefully separated to remove individual bivalves without damaging them. Undamaged animals with an active foot were placed at a density of 15 individuals per 10 litre bucket. The buckets contained clean sediment from the bank (10–15 cm depth) and estuarine water. The buckets were left standing in the estuary to allow animals to burrow under near-natural temperature conditions. After approximately one hour, each bucket was checked for animals which had not burrowed. These were removed and replaced, as it was previously observed that animals that do not burrow promptly are unhealthy and will die (H. Nel, pers. observ.). Buckets were transferred to laboratory conditions and aerated within 3–4 hours after collection. Animals were acclimated in natural estuarine water at salinities of 50‰ for the shock test and 45‰ for the gradual test, at ambient temperature. The animals were fed a concentrated suspension of naturally occurring benthic microalgae every two days, while they acclimated and for the duration of the experiment. Animals were subjected to a 12:12 hr light:dark regime, using artificial light during both the acclimation and experimental periods. Shock and gradual experiments were conducted in May and July 2010, respectively. A fresh batch of individuals was collected 12 days prior to the start of each experiment.

Shock change test

Prior to the experiment, animals were acclimated in the lab for 11 days and any dead or dying animals were removed to avoid contamination of water. Following acclimation, five animals were transferred to 2.5 l buckets containing pre-made, aerated saline solutions ranging from 0 to 80‰, and clean sediment from their natural habitat, which had been washed with fresh/distilled water. “Instant Marine” artificial seawater salt was used to prepare the pre-made saline solutions. A 10 cm layer of sediment in each 2.5 l bucket enabled animals to burrow completely. Three replicates were used for each salinity treatment (0, 10, 20, 35, 50, 60, 70 and 80‰), containing five animals per replicate. After the initial time was recorded, mortality was determined at pre-determined intervals (1, 2, 4, 8, 16, 24, 48, 72, 96, 120, 144 and 168 hrs) for seven days. Salinity was checked each day using a refractometer and a stable salinity maintained (± 1 ‰). The condition of each animal, at each time interval, was determined by its response to mechanical stimulation of the foot, siphon or body surface.

Gradual change test

The same experimental set up of the shock test was used, except that animals were acclimated for two days under laboratory conditions. Four replicates for each salinity level and five animals per replicate were prepared. The salinity treatments were 0, 5, 10, 20, 45, 70, 80 and 85‰, gradually reached by daily adjusting the 45‰ acclimated salinities by between 2.5 and 5‰ over 10 days.

S. cylindraceus abundance

Macrofauna samples were collected in June 2010, along a transect of seven stations from Charters Creek across to Catalina Bay (Fig. 1). The initial site, Station 0, was 20 m from the lake margin at Charters Creek; thereafter samples were taken at 1 km intervals. A Zabalocki-type Ekman grab (sampling area 0.0236 m², depth 15 cm) was used to collect samples. A single sample containing three grabs was taken at each station, placed into a 20 l bucket containing estuarine water and stirred vigorously, to suspend the benthic invertebrates. The supernatant was then sieved through a 500 µm sieve. This process of suspending and removing benthic invertebrates was repeated five times. Material caught on the sieve was stored in a plastic jar. Sediment remaining in the bucket was washed through a 2000 µm sieve, in order to collect larger macrofauna left behind, and added to the same plastic jar. All macrofauna samples were preserved in 4% formaldehyde solution and stained with Phloxin-B. Physico-chemical data were recorded *in situ* at each station, using a portable YSI® 6920 data-logging multiprobe. In the laboratory, samples were processed and individual *S. cylindraceus* (juveniles and adults) were counted. A dissecting microscope (Kyowa SDZ) was used to identify and count the smaller juvenile individuals. The total number of individuals per square metre (ind.m⁻²) was determined by dividing the number of individuals found in each sample by the total area sampled by the grab.

Analysis of data

The STATISTICA package version 6.1 was used to generate the graphs for both shock and gradual tests (Statsoft 2004). A repeated-measures ANOVA was used to analyse the effect of exposure time and salinity, as well as their interaction on animal survival. In both the shock and gradual test, the fixed independent variable (Time)

was the within-subject factor and the fixed independent variable (Salinity) was the between-subject factor. Measure name was Survival, in both analyses. In the shock test there were 13 levels, while in the gradual test there were 14 levels. The original degrees of freedom and mean square values for the shock test were $df = 12$ and $ms = 40.532$, while for the gradual test these were $df = 13$ and $ms = 23.046$. Sphericity was tested using the Mauchly's Test of Sphericity. To test the null hypothesis, that the error variance of the dependent variable is equal across groups, a Levene's Test of Equality of Error Variance was applied. The assumptions were not met and, therefore, the Greenhouse-Geisser Epsilon value was used instead. SPSS 15.0 for Windows was used for all statistical analyses (SPSS 2006). LT_{50} , which is the time at which 50% of the animals exposed to a lethal salinity level die, was calculated for both gradual and shock tests.

RESULTS

Shock test responses

Animals exposed to a series of shock salinity changes had a salinity tolerance range of 30 to 60‰ (Fig. 3). Animals kept at salinities within the range of 30 to 60‰ had a 60 to 80% survival at the end of the experiment. A 40% survival was found for salinities ranging from 20 to 30‰ and from 60 to 70‰. At the end of the experiment, a low survival of 20% or less was found for animals kept at salinities below 20‰ and above 70‰ (Fig. 3).

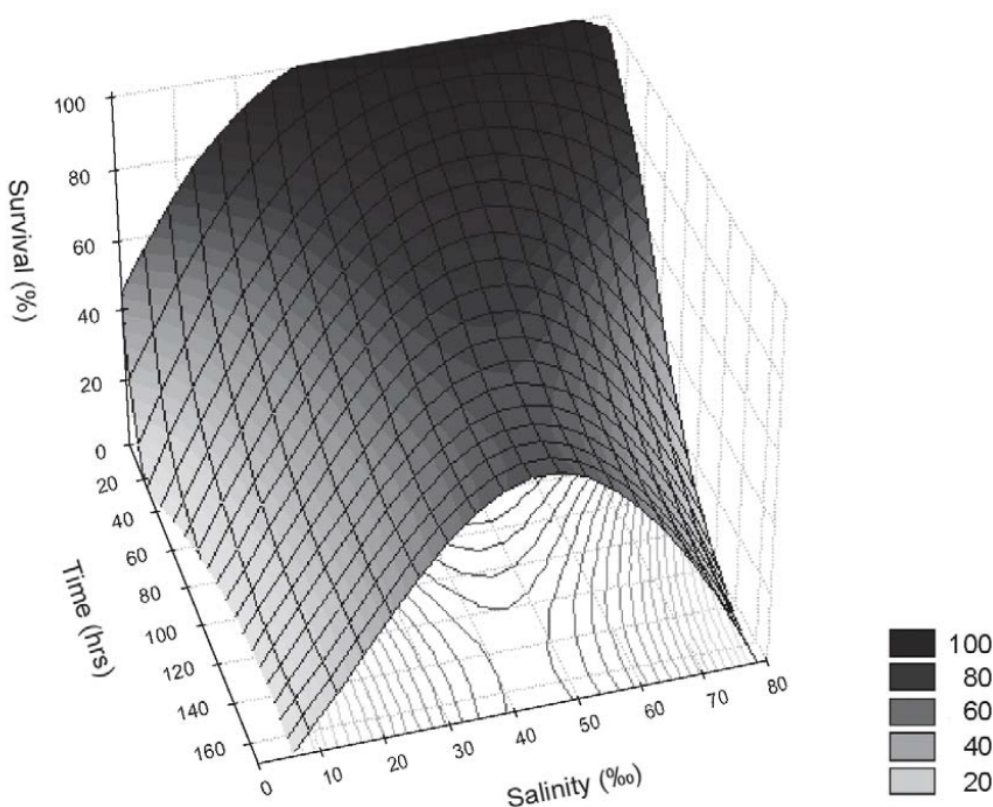


Fig. 3. Percent survival of *Solen cylindraceus* exposed to varying salinities between 0 and 80‰ over time (hrs), after being acclimated to 50‰ (shock change test).

TABLE 1

Repeated-measures ANOVA comparing the effects of salinity, exposure time and the interaction between salinity and exposure time on the % survival of *Solen cylindraceus* over a period of seven days.

Experiment	Treatment	df	<i>F</i>	<i>GG</i>
Shock	Exposure Time	2.78	83.3	< 0.001
Shock	Salinity	7.00	24.4	< 0.001
Shock	Exposure Time X Salinity	19.5	7.53	< 0.001
Gradual	Exposure Time	3.162	45.1	< 0.001
Gradual	Salinity	7.00	28.3	< 0.001
Gradual	Exposure Time X Salinity	22.1	6.17	< 0.001

All animals maintained at 0‰ died within the first two hours of the experiment and exhibited a flaccid and extended foot and siphon and bloated body. Animals at 10‰ survived for only 8 hrs after the start of the experiment. The majority of animals at 20‰ died between 24 and 120 hours. At salinities of 35, 50 and 60‰ animals died sporadically, with the majority surviving the entire experimental period of 168 hrs (7 days). At 70‰ the majority survived for 120 hrs, with very few animals surviving the full extent of the experiment. The majority of animals at 80‰ survived for 48 hrs only and all died before 72 hrs. Salinity, exposure time and the interaction of exposure time with salinity had a significant effect on the survival of *S. cylindraceus* (Table 1).

Gradual test responses

Exposure to a gradual salinity change resulted in the wider salinity tolerance of between 15 and 65‰ (Fig. 4). Animals kept within this salinity range had a 60 to 100% survival at the end of the experiment. Animals placed in water with a gradually declining salinity that ended between 5 to 15‰ and 65 to 75‰ exhibited a 40% survival. The upper and lower extremes, with salinities above 75‰ and below 5‰ respectively, had 20% or less survival of animals (Fig. 4).

Once the 0‰ salinity was reached, all animals died within the first hour of the experiment. At 5‰ the majority of individuals died within the first 4 hrs, with the exception of 2 individuals which survived for 96 hrs. A few animals exposed to 10‰ survived the entire experiment, with the majority of individuals dying within 96 hrs. Very few individuals died at 20‰ and none died at 45‰ (control). At 70‰ the majority survived for 120 hrs, with very few surviving the full extent of the experiment. All individuals exposed to 80‰ were dead within 72 hrs, with the majority of these dying within 24 hrs. Only five out of 20 individuals survived the acclimation period to reach the target salinity of 85‰. Thus, after the 11 days of acclimation, only 5 individuals remained to undergo the experiment and all died after 8 hrs. Again, a significant effect was found for salinity, exposure time and the interaction of exposure time with salinity on the survival of *S. cylindraceus* (Table 1).

While in the shock test the LT_{50} for 10‰ was reached after 4 hrs, this was increased to 45 hrs in the gradual test. At a salinity of 20‰, LT_{50} was reached after 50 hrs in the shock test. However, in the gradual test only 13% mortality was found at the end of the experiment, thus LT_{50} was not reached. The LT_{50} at 70‰ in the shock test was reached after 105 hrs and increased to 125 hrs in the gradual test. At 0‰ all animals died after 2 hrs in the shock test, while total mortality decreased to 1 hr in the gradual test. A

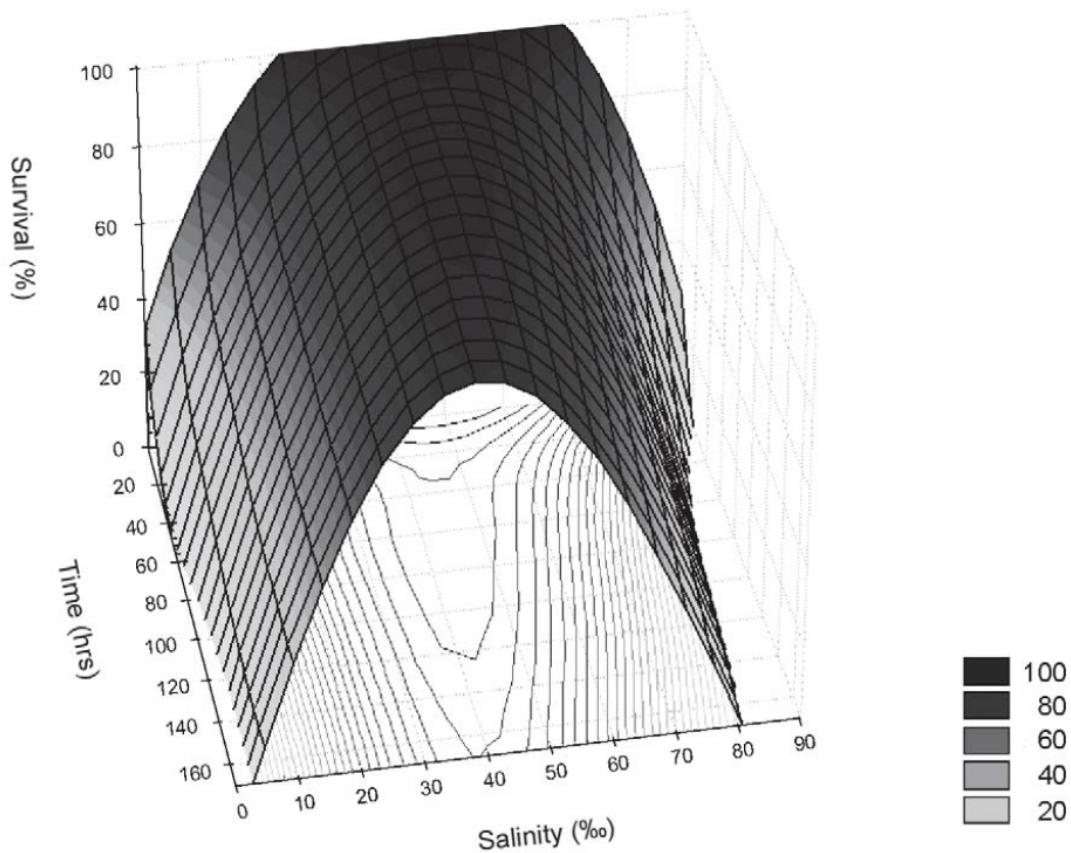


Fig. 4. Percent survival of *Solen cylindraceus* for varying salinities between 0 and 80‰ over time (hrs), after acclimation to varying salinities (gradual change test).

decrease between the shock and gradual test was observed in the LT_{50} at 80‰, which was achieved after 52 hrs and 24 hrs, respectively.

S. cylindraceus abundance

S. cylindraceus was found in every sample collected along the transect from Charters Creek across to Catalina Bay (Table 2). Abundances ranged from 14.1 to 3319 ind.m⁻², with the lowest recorded value at site 0 and the highest at site 1. Salinity along the transect ranged from 45.6 to 48.6‰, with Charters Creek exhibiting slightly higher values than all other stations at the time of the survey (Table 2).

DISCUSSION

The cyclic changes in climate, from wet to dry periods, observed historically in the St Lucia Estuary show that *S. cylindraceus* is exposed to periodic floods and droughts (Begg 1978; Cyrus & Vivier 2006). In the shock test, *S. cylindraceus* had a salinity tolerance of between 30 and 60‰. A wider salinity tolerance of between 15 and 65‰ was observed during the gradual change test. An optimal salinity tolerance, defined as the salinity at which 100% survival is recorded at the end of the experiment, was identified at a salinity of 45‰ in the gradual test. Salinity variations may occur either as sudden changes (such as a flood causing a rapid drop in salinity) or as slow rises

TABLE 2

Solen cylindraceus density and physico-chemical data for the eight sites sampled along a transect from Charters Creek (0) across to Catalina Bay (7) during June 2010.

Station no.	0	1	2	3	4	5	6	7
<i>S. cylindraceus</i> (ind.m ⁻²)	14.1	3319	84.8	890	1031	42.4	1102	3206
Temperature (°C)	19.8	14.2	15.0	14.9	15.3	15.8	16.2	13.6
Salinity (‰)	48.6	46.7	46.3	47.1	46.6	46.6	46.7	45.6
Dissolved Oxygen (mg/L)	8.5	8.7	9.1	9.8	9.7	11.6	9.5	8.9
Depth (m)	0.2	0.3	0.9	0.9	0.9	0.9	1	0.3
pH	9.0	9.2	9	9.1	9.0	9.1	9	8.9
Turbidity (NTU)	235	20.3	28.5	15	59.4	41.2	46.8	8.5

or falls in salinity over periods of months. This study looked at both the shock and gradual change in salinity. There was an increase in time it took for 50% of animals to die from the shock test to the gradual test for the 10, 20 and 70‰ treatments. *S. cylindraceus* is not tolerant of rapidly changing salinity levels, but if salinity levels are changed gradually then it may exhibit increased salinity tolerance (Pillay & Perissinotto 2008). De Villiers *et al.* (1989b) stated that salinity has an effect on the ctenidial ciliary activity of bivalves, but that gill tissues show an acclimatory response when salinity is changed gradually. The opposite occurred for the extreme salinities of 0 and 80‰, where a decrease in salinity tolerance was observed. The reason for this may have been a cumulative effect, as the animals were already exposed to sub-lethal stress and entered the experiment in poor health, compared to the animals used in the shock test. However, *S. cylindraceus* is reportedly rare when salinities are high, above 65‰ (Forbes & Cyrus 1993).

Until now, there has been no experimentally-proven salinity tolerance for *S. cylindraceus*, but salinity preferences have been suggested in the past (McLachlan & Erasmus 1974; Hodgson & de Villiers 1986; de Villiers & Allanson 1989). The results obtained from the current study are in agreement with the findings of Pillay and Perissinotto (2008), who reported the highest abundances of *S. cylindraceus* in St Lucia at relatively stable salinity levels in the range of 25–50‰, with abundances decreasing at low (<10‰) and rapidly changing salinity. An increase in *S. cylindraceus* abundance was seen in the South Lake during stable marine salinities of about 30 to 45‰ (Blaber *et al.* 1983; Forbes & Cyrus 1993). In the study of MacKay *et al.* (2010), the highest density of 1200 ind.m⁻² was found at 45‰. This is consistent with the results obtained in the current study, where the highest percent survival in laboratory experiments was found at 45‰. The highest densities (>3000 ind.m⁻²) along the transect from Charters Creek to Catalina Bay occurred at salinities of 45.6 and 46.7‰, while the lowest were observed at a salinity >48‰ (Table 2).

S. cylindraceus has limited horizontal mobility and thus employs behavioural strategies to cope with exposure to unfavourable environmental parameters. MacKay *et al.* (2010) found *S. cylindraceus* in the field at salinities from 10 to 70‰. Burrowing, as a survival strategy, may be the reason why *S. cylindraceus* in the field is found at salinities which it is unable to tolerate in the laboratory. In the field, animals may burrow deep (approximately 40 cm), thereby achieving the protection of a stable environment for a short period, despite the variations in salinity experienced in the over-

lying water column (de Villiers & Allanson 1989; Matthews & Fairweather 2004). However, this buffering action, provided by the surrounding sediment, may not have a substantial effect on animals which have to filter water constantly from the overlying water-column in order to acquire food and oxygen (Matthews & Fairweather 2004). *Dosinia hepatica*, a bivalve found in St Lucia, can remain tightly shut when there is a rapid change in salinity, thus can tolerate larger salinity fluctuations (McLachlan & Erasmus 1974; Hanekom 1989; Ngqulana *et al.* 2002). *S. cylindraceus*, even when completely shut, is exposed at its anterior and posterior ends, which may result in a lower tolerance to rapidly changing salinities (McLachlan & Erasmus 1974; Ngqulana *et al.* 2002; Matthews & Fairweather 2004). Another possible option is that animals may be present at the upper and lower salinity extremes, but their health at these levels may have already been compromised. Thus the population may be declining and the animals found there may be the last remaining individuals, probably on their way out.

St Lucia is currently experiencing a reversed salinity gradient, with hypersaline conditions recorded in the upper reaches (Pillay & Perissinotto 2008; Vivier *et al.* 2010). For example, at False Bay salinity has repeatedly reached 200‰ during the past 5 years (Pillay & Perissinotto 2008; Vivier *et al.* 2010). High abundances of *S. cylindraceus* were observed in the North Lake and False Bay in the earlier stages of this drought, when salinity values were still within its tolerance limits (R. Taylor, pers. observ.). This high abundance of *S. cylindraceus* may have been due to the severe reduction in numbers of its main fish predators at this salinity (R. Taylor, pers. observ.). High salinities have been suggested to cause poor faunal assemblages as well as mass mortality of bivalves in the False Bay area (Boltt 1975). Mortality of bivalves in this area may also have been compounded by desiccation and the drying up of habitable sediment. The development of basin compartmentalisation may have resulted in bivalves being unable to recolonise parts of the lake. The salinity tolerance range of *S. cylindraceus* may also be one of the factors causing its absence in the river-dominated Mfolozi-Msunduzi estuarine system (Ngqulana *et al.* 2010).

The implication of a salinity tolerance ranging from 30 to 60‰ under shock treatment is that, under flood conditions, a decrease in salinity below 30‰ may cause mass mortality in the population of *S. cylindraceus*. Floods in the Kariega Estuary have in the past caused a large percentage of *S. cylindraceus* to die, because of rapid salinity decreases (Hodgson & de Villiers 1986). Similarly, 93% of the *S. cylindraceus* population died in the Swartkops Estuary following a flood event (Hanekom 1989). At St Lucia, *S. cylindraceus* previously recorded in the South Lake, was redistributed into the Narrows after Cyclone Domoina (Forbes & Cyrus 1992). Cyrus (1988) described the effect of flooding on *S. cylindraceus* as causing a sharp decrease in its abundance and the failure to re-establish itself in all areas previously occupied. The implication of a salinity tolerance ranging from 15 to 65‰ under gradual change treatment is that, if the current drought persists, an increase in salinity above 65‰ may cause the demise of an already reduced population of *S. cylindraceus* at St Lucia, and may possibly lead to its virtual disappearance from the system. The bivalve has already disappeared from the upper reaches of the estuarine lake (False Bay and North Lake) (Cyrus *et al.* 2011). Persisting drought conditions have already caused a sharp decrease in the available habitable substrate, by drying out over half of the available lake surface (Pillay & Perissinotto 2008).

Benthic fauna sustain the communities of benthic-feeding fish in the St Lucia Estuary (Blaber *et al.* 1983; Cyrus *et al.* 2010). Loss in invertebrate biomass can cause a decrease in available food sources for fish (Forbes & Cyrus 1993). Hodgson and de Villiers (1986) and MacKay *et al.* (2010) described *S. cylindraceus* as an important source of food for fish and bird populations. For instance, during conditions of stable salinities, *S. cylindraceus* provided 80% of the diet for *Solea bleekeri*, the blackhand sole (Cyrus 1988; Forbes & Cyrus 1992). After a flood event, however, the diet of the sole was predominately the amphipod *Grandidierella lignorum*, with only 19% provided by *S. cylindraceus* siphons and 6% whole *S. cylindraceus* (Cyrus 1988; Forbes & Cyrus 1992). *S. cylindraceus* is considered a key species in the St Lucia Estuary, thus future studies should investigate thoroughly the dynamics of this species within its food webs.

In conclusion, St Lucia is characterised by an alteration of wet and dry periods, which have been documented since the early 1900s (Perissinotto *et al.* 2010). With climate change threatening to escalate the intensity and occurrence of extreme events within the next 50 to 100 years, it is imperative to determine the effects of these conditions on the key macrofaunal species that support the ecological functioning of this estuary (Schulze 2006). In this study, the salinity tolerance of *S. cylindraceus* was determined using shock and gradual tests. Results show a significant effect of salinity, exposure time and the interaction of salinity and exposure time on the survival of these animals. Informed management decisions may now be made, in order to mitigate the effects of floods or persisting droughts on the *S. cylindraceus* populations of the St Lucia and other similar ecosystems. Mitigating the effects of floods may be done by excluding further inflow of freshwater into the system, while the effects of persisting drought may be alleviated by increasing flow via the tributaries.

ACKNOWLEDGEMENTS

We are grateful to the iSimangaliso Park Authority and Ezemvelo KZN Wildlife for supporting this project. Funding was provided by the National Research Foundation and the University of KwaZulu-Natal. Thanks to D. Muir, U. Scharler, N. Miranda, D. Dyer, S. Bownes, S. Stevens and J. Godlonton for assisting with the collection of animals at St Lucia and with the execution of the experiments in the laboratory.

REFERENCES

- BEGG, G.W. 1978. The estuaries of Natal. (Part II). *Natal Town and Regional Planning Commission Report* **41**: 1–657.
- BLABER, S.J.M., KURE, N.F., JACKSON, S. & CYRUS, D.P. 1983. The benthos of South Lake, St Lucia following a period of stable salinities. *South African Journal of Zoology* **18**: 311–319.
- BOLTT, R.E. 1975. The benthos of some Southern African Lakes Part V: The recovery of the benthic fauna of St Lucia Lake following a period of excessively high salinity. *Transactions of the Royal Society of South Africa* **41**: 295–323.
- CARRASCO, N.K., PERISSINOTTO, R. & PILLAY, D. 2010. Zooplankton of the St Lucia Estuary during the current drought cycle: a comparison between open- and closed-mouth conditions. *Marine Ecology Progress Series* **399**: 157–171.
- CYRUS, D.P. 1988. Episodic events and estuaries: Effects of cyclonic flushing on the benthic fauna and diet of *Solea bleekeri* (Teleostei) in Lake St Lucia on the southeastern coast of Africa. *Journal of Fish Biology* **33**: 1–7.
- CYRUS, D.P., JERLING, H., MACKAY, F. & VIVIER, L. 2011. Lake St Lucia, Africa's largest estuarine lake in crisis: Combined effects of mouth closure, low levels and hypersalinity. *South African Journal of Science* **107** (3/4): 59–71. (doi: 10.4102/sajs.v107i3/4.291)
- CYRUS, D. & VIVIER, L. 2006. Status of the estuarine fish fauna in the St Lucia Estuarine System, South Africa, after 30 months of mouth closure. *African Journal of Aquatic Science* **31**: 71–81.

- CYRUS, D.P., VIVIER, L. & JERLING, H.L. 2010. Effect of hypersaline and low lake conditions on ecological functioning of St Lucia estuarine system, South Africa: An overview 2002–2008. *Estuarine, Coastal and Shelf Science* **86**: 535–542.
- DE VILLIERS, C.J. & ALLANSON, B.R. 1989. Osmotic properties of an infaunal estuarine bivalve *Solen cylindraceus* (Hanley). *Journal of Molluscan Studies* **55**: 45–51.
- DE VILLIERS, C.J., ALLANSON, B.R. & HODGSON, A.N. 1989a. The effect of temperature on the filtration rate of *Solen cylindraceus* (Hanley) (Mollusca: Bivalvia). *South African Journal of Zoology* **24**: 11–17.
- DE VILLIERS, C.J., HODGSON, A.N. & ALLANSON, B.R. 1989b. Effect of salinity and temperature on the filtration rate and distribution of *Solen cylindraceus* (Hanley). In: Ryland, J.S. & Tyler, P.A., eds, *Reproduction, genetics and distributions of marine organisms*. Fredensborg: Olsen and Olsen, pp. 459–465.
- FORBES, A.T. & CYRUS, D.P. 1992. Impact of a major cyclone on a southeast African estuarine lake system. *Netherlands Journal of Sea Research* **30**: 265–272.
- 1993. Biological effects of salinity gradient reversal in a southeast African estuarine lake. *Netherlands Journal of Aquatic Ecology* **27**: 485–488.
- HAMPEL, H., ELLIOT, M. & CATTRIJSE, A. 2009. Macrofaunal communities in the habitats of intertidal marshes along the salinity gradient of the Schelde Estuary. *Estuarine, Coastal and Shelf Science* **84**: 45–53.
- HANEKOM, N. 1989. A note on the effect of a flood of medium intensity on macrobenthos of soft substrata in Swartskops Estuary, South Africa. *South African Journal of Marine Science* **8**: 349–355.
- HILL, B.J. 1981. Adaptations to temperature and salinity stress in southern African estuaries. In: Day, J.H., ed., *Estuarine Ecology*. Cape Town: A.A. Balkema, pp. 187–196.
- HODGSON, A.N. & DE VILLIERS, C.J. 1986. Notes on the biology of ‘pencil-bait’ (*Solen capensis* and *Solen cylindraceus*). *The Naturalist* **30**: 16–19.
- MACKAY, F., CYRUS, D. & RUSSELL, K.L. 2010. Macrobenthic invertebrate response to prolonged drought in South Africa’s largest estuarine lake complex. *Estuarine, Coastal and Shelf Science* **86**: 553–567.
- MATTHEWS, T.G. & FAIRWEATHER, P.G. 2004. Effect of lowered salinity on the survival, condition and reburial of *Soletellina alba* (Lamarck, 1818) (Bivalvia: Psammobiidae). *Austral Ecology* **29**: 250–257.
- MCLACHLAN, A. & ERASMUS, T. 1974. Temperature tolerances and osmoregulation in some estuarine bivalves. *Zoologica Africana* **9**: 1–13.
- NGQULANA, S.G., OWEN, R.K., VIVIER, L. & CYRUS, D.P. 2010. Benthic faunal distribution and abundance in the Mfolozi-Msunduzi estuarine system, KwaZulu-Natal, South Africa. *African Journal of Aquatic Science* **35**: 123–133.
- PERISSINOTTO, R., PILLAY, D. & BATE, G. 2010. Microalgal biomass in the St Lucia Estuary during the 2004 to 2007 drought period. *Marine Ecology Progress Series* **405**: 147–161.
- PILLAY, D. & PERISSINOTTO, R. 2008. The benthic macrofauna of the St Lucia Estuary during the 2005 drought year. *Estuarine, Coastal and Shelf Science* **77**: 35–46.
- SCHULZE, R.E. 2006. *Climate change and water resources in southern Africa*. Report No. 1430/1/05. Pretoria: Water Research Commission.
- SPSS, INC. 2006. *IBM SPSS Statistics*. Version 15.0. (<http://www.spss.com>; accessed 22/08/2011)
- STATSOFT, INC. 2004. *STATISTICA (data analysis software system)*. Version 6. (<http://www.statsoft.com>; accessed 22/08/2011).
- VIVIER, L. & CYRUS, D.P. 2009. Alternative nursery habitat for estuarine associated marine fish during prolonged closure of the St Lucia estuary, South Africa. *Estuarine, Coastal and Shelf Science* **85**: 1–8.
- VIVIER, L., CYRUS, D.P. & JERLING, H.L. 2010. Fish community structure of the St Lucia estuarine system under prolonged drought conditions and its potential for recovery after mouth breaching. *Estuarine, Coastal and Shelf Science* **86**: 568–579.
- WEERTS, S.P., CYRUS, D.P. & FORBES, A.T. 1997. The diet of juvenile *Sillago sihama* (Forsskal, 1725) from three estuarine systems in KwaZulu Natal. *Water SA* **23**: 95–100.
- WHITFIELD, A.K. & TAYLOR, R.H. 2009. A review of the importance of freshwater inflow to the future conservation of Lake St Lucia. *Aquatic Conservation: Marine and Freshwater Ecosystems* **19**: 838–848.
- YSEBAERT, T., MEIRE, P., HERMAN, P.M.J. & VERBEEK, H. 2002. Macrobenthic species response surfaces along estuarine gradients: prediction by logistic progression. *Marine Ecology Progress Series* **225**: 79–95.

Water SA: Manuscript in review

**The effect of salinity on the survival of the Brackwater mussel,
Brachidontes virgiliae, in the St Lucia estuarine system, South Africa**

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ABSTRACT

During drought periods, the razor clam *Solen cylindraceus*, is the dominant bivalve species present in the St Lucia estuarine system, although restricted to its South Lake region. However, with the recent onset of a wet phase, the mussel *Brachidontes virgiliae* has become widespread throughout the system and overwhelmingly dominant. In this study, the salinity tolerance of *B. virgiliae* is determined using both rapid and gradual changes in salinity. Mussels were collected at Esengeni in the Narrows (salinity ≈ 0) and Lister's Point in False Bay (salinity ≈ 20). Mortalities were recorded for animals exposed to a sudden change in salinity using 8 different treatments ranging from 0 to 70. Additionally, animals were also exposed to a gradual change in salinity, using treatments that exceeded what the mussels were previously able to tolerate. In all four experiments, animals were able to tolerate salinity levels up to 20. However, a wider salinity tolerance was seen in animals collected from Lister's Point and those gradually acclimated to test conditions. These mussels were able to tolerate salinity levels up to 50. Mobility severely decreased in the higher salinity treatments and attachment to the sides of bottles was only seen in the low salinity treatments. With an increase in flood events predicted for this region, it is imperative to understand how key species may be affected. During wet phases *B. virgiliae* becomes ubiquitous throughout the system and it is unlikely that the species will disappear from the system even if floods escalate in the future, as it has an ability to withstand near freshwater salinity levels. Although dramatic decreases in salinity caused by flood events may not affect this mussel, silt loading during these events may have more of a negative impact on its survival. During dry periods, however, the mussel will be concentrated in the Narrows (oligohaline to limnetic conditions), especially if an inverse salinity gradient with hypersaline conditions prevails within the system.

KEY WORDS: *Brachidontes virgiliae*, salinity tolerance, wet and dry periods, hypersaline conditions, flood events, iSimangaliso Wetland Park, St Lucia estuarine system.

INTRODUCTION

Salinity is an important factor structuring estuarine ecosystems (McLeod & Wing, 2008). This is manifested as spatial and temporal variations in salinity modify species composition and distribution within an estuary (Boltt, 1975; Cyrus, 1988; Owen & Forbes, 1997; Pillay & Perissinotto, 2008). The salinity regimes of many estuaries have been severely altered by anthropogenic modifications within their catchments (e.g. Coorong System in Australia and St Lucia Estuary in South Africa). As a result of low freshwater inflow into the Coorong, a reverse salinity gradient and hypersaline conditions have developed, causing benthic invertebrates to become restricted to the lower reaches (Rolston & Dittmann, 2009). Similarly, an impoverished benthic community due to extreme hypersaline conditions is often present in the northern reaches of St Lucia (Day et al., 1954; Millard & Broekhuysen, 1970; Boltt, 1975; Pillay & Perissinotto, 2008).

Although St Lucia is naturally variable, exhibiting large-scale temporal changes from wet to dry periods, the dry periods have been exacerbated by the artificial historical divergence of the adjacent Mfolozi River into the sea (Begg, 1978; Forbes & Cyrus, 1993; Whitfield & Taylor, 2009). This has deprived St Lucia of its most essential freshwater source (Forbes & Cyrus, 1993), which is fundamental to maintaining lake levels during dry periods and mitigating the occurrence of hypersaline events (Whitfield & Taylor, 2009). As a result, the system has experienced crises for extended periods, the last from 2002 to 2011. A reverse salinity gradient develops during dry periods, with salinities as high as 200 in the northern reaches recorded on numerous occasions (Forbes & Cyrus, 1993; Cyrus et al., 2010). A unique halotolerant community can be established in the northern reaches of the estuarine system, as few species are able to tolerate such salinity extremes (Carrasco & Perissinotto, 2012).

In addition, St Lucia also experiences stochastic disturbances, such as flooding events and wetter than normal years (Cyrus, 1988; Forbes & Cyrus, 1992; Pillay & Perissinotto, 2008), both causing a dramatic decrease in salinity. Cyclones Domonia and Imboa in 1984 resulted in a large scale decline in salinity that caused the disappearance and re-distribution of most benthic species (Cyrus, 1988; Forbes & Cyrus, 1992; Owen & Forbes, 1997). Similarly, Matthews and Fairweather (2004) suggested that mass mortality of the bivalve *Soletellina alba* in the Hopkins River Estuary was a result of winter flooding. In November/December 2010, St Lucia received high rainfall, resulting in a drastic salinity reduction within the system (Nel et al., 2013). Additionally, the management decision to no longer keep the Mfolozi separated from St Lucia (Whitfield et al., 2013) allowed the re-linkage

of the two systems in July 2012. Therefore, St Lucia shifted into a wet period resulting in the system becoming dominated by an oligohaline environment (salinity < 5). This caused the disappearance of the infaunal bivalve *Solen cylindraceus* from the South Lake and the successful re-establishment of this species in False Bay, where the salinity fell within the species tolerance range (Nel et al., 2011; Nel et al., 2013).

During drought conditions, *S. cylindraceus* is considered to be the dominant bivalve species in St Lucia (Nel et al., 2011; Nel et al., 2013). Although restricted to the South Lake, it occurs at high densities ranging from 14 to 3000 ind.m⁻² (Nel et al., 2011). During the last hypersaline phase, *S. cylindraceus* was a key species for the system. Having a salinity tolerance between 15 and 65, it was able to withstand high salinities outside the tolerance range of other bivalve species (Nel et al., 2011). Currently, however, the mussel *Brachidontes virgiliae* has become so abundant and widespread throughout St Lucia that it has replaced *S. cylindraceus* as the dominant bivalve occurring in the system. Anecdotal evidence suggests that this ubiquitous mussel is able to withstand very low salinity levels and can rapidly invade denuded areas. Therefore, this study set out to investigate the experimental salinity tolerance of *B. virgiliae* populations currently occurring in the St Lucia estuarine system.

Brachidontes virgiliae is distributed from Mozambique to the Great Brak River (Kilburn & Rippey, 1982). With a habitat preference for the upper reaches of estuaries, this mussel is associated with low salinity levels (Davies, 1980). By contrast, in St Lucia this species is found in the lower reaches, the Narrows, due to the persistent reversed salinity gradient that prevails here. Tolerant of large salinity fluctuations, this species may remain shut avoiding unfavourable salinity fluctuations (Davies, 1980).

A species may have two types of controls on its tolerance ranges, genetic and phenotypic (Segnini de Bravo et al., 1998). The former is defined as the genetically imposed capability to withstand an external factor, while the latter is the ability to alter its tolerance in response to previously experienced conditions (Segnini de Bravo et al., 1998). Thus, an extreme or moderate change in salinity may yield varying adaptive potentials for a species (Berger & Kharazova, 1997). Castagna and Chanley (1973) and Nel et al. (2011) showed that a gradual change in salinity may allow a species to extend its environmental threshold. It is well established that a slow increase in salinity enables organisms to widen their tolerance range. However, there is less evidence to show that a species found in two habitats, with different salinity regimes, may exhibit different salinity tolerance ranges. Thus, the objectives of this study were to determine the salinity tolerances of *B. virgiliae* exposed to both sudden and gradual changes. Animals were collected from localities experiencing substantially different salinity regimes, Esengeni (salinity ≈ 0) and Lister's Point (salinity ≈ 20).

MATERIALS AND METHODS

Sample collection and maintenance

Mussels with a mean shell length of 9.76 ± 1.06 (SD) mm were collected from two sites within the St Lucia estuarine system during March 2013. At the time, St Lucia exhibited salinity levels ranging from freshwater to approximately 20. Therefore the two sites, Esengeni and Lister's Point (Fig. 1), were representative of the minimum and maximum salinity levels. At both sites, *Brachidontes virgiliae* were found attached to submerged macrophytes, which were subsequently removed. They were then placed in buckets containing naturally occurring estuarine water and transported back to laboratory conditions. Animals were aerated within 3 to 4 hours after collection and acclimated to laboratory conditions for 3 days prior to their exposure to experimental conditions. During acclimation, animals were maintained at salinity levels similar to those found at the collection site. This was measured using a portable refractometer (Atago S/Mill-E). At ambient temperature (24°C), mussels were exposed to a 12:12 hr light:dark regime using artificial light. Dead mussels were removed daily, to avoid contamination of the sample stock and animals were selected randomly from the holding buckets at the start of each experiment. All experiments took place between March and August 2013.

Shock change test

Animals collected at Esengeni and Lister's Point were exposed to a rapid change in salinity. Five animals were transferred into each replicate, with five replicates per salinity for the Lister's Point experiment and three for Esengeni. This was due to the availability and accessibility of animals at the time. Mussels were placed into 300 mL plastic bottles containing pre-made, aerated saline solutions that were prepared using "Instant Marine" artificial seawater salt and fresh/distilled water. The salinity treatments ranged from 0 to 70, increasing by increments of 10. Mortality was checked at 1, 2, 4, 8, 16 and 24 hours for the first day, thereafter they were checked daily for the next 30 days. Measured using a portable refractometer, salinity was maintained at a constant level (± 1) and mussels were fed a suspension of naturally occurring benthic microalgae, renewed once a week. Mussels that remained gaping and did not respond to physical stimulation were deemed to be dead. In addition, visible movement/activity was observed, but not quantified, as foot and siphon extension into the water column.

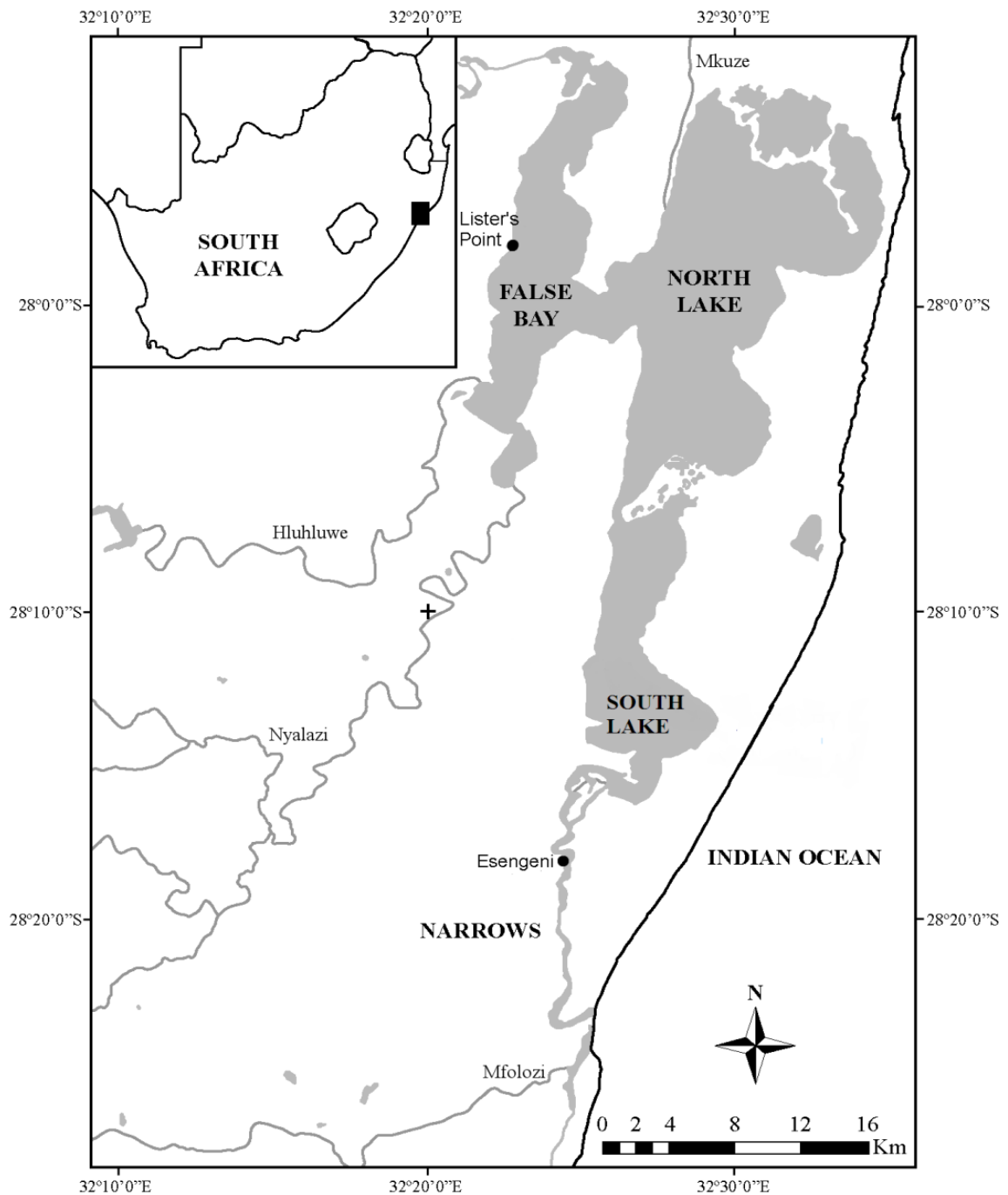


Fig. 1: Map of the St Lucia estuarine system, highlighting the two collection sites, Esengeni and Lister's Point, used for the salinity tolerance experiments carried out from March to August 2013 (adapted from Carrasco & Perissinotto, 2012).

Gradual change test

Fresh animals were collected from Esengeni and Lister's Point for the acclimation experiments. These mussels were gradually exposed to an increase in salinity over a period of 30 days. However, the treatments used were restricted to those salinity levels that did not show 100% survival after 30 days in the previous shock tests. Lister's Point animals were exposed to a change in salinity of 5 units

every 7.5, 5, 4 and 3 days for treatment 40, 50, 60 and 70, respectively. Treatments 30, 40, 50, 60 and 70 for the Esengeni experiment, were exposed to a change in salinity of 5 units every 5, 4, 3, 2.5 and 2 days, respectively. Mortality was checked daily and salinities were maintained at a constant level (± 1), measured using a portable refractometer. Thereafter, the same experimental set up used for the shock tests was employed.

Analysis of data

SigmaPlot version 11.0 was used to generate the graphs for all four experiments. A repeated-measures ANOVA was used to determine whether salinity, exposure time and the combination of the two variables had a significant effect on animal survival. In all experiments, the fixed independent variable (Time) was the within-subject factor and the fixed independent variable (Salinity) was the between-subject factor. Measure name was “Survival” in all analyses. In all experiments there were 36 levels (groups). The Mauchly’s Test of Sphericity was used to test the assumption that the variance was equal between the differences in all combinations of related groups (levels). The assumptions were not met and, therefore, the Greenhouse-Geisser Epsilon value was used instead. SPSS 21.0 for Windows was used for all statistical analyses.

RESULTS

During this study, *Brachidontes virgiliae* was recorded throughout St Lucia at salinities ranging from near freshwater to ~ 20 . The salinity maximum was recorded at Lister’s Point in the northern reaches, while the minimum was found at Esengeni in the Narrows (Fig. 1). Esengeni mussels exposed to a rapid change in salinity exhibited a narrow tolerance range. Visible movement was seen in the salinity treatments ranging from 0 to 20, with 100% survival at the end of the experiment (Fig. 2A). Unable to survive salinities above 20, animals exposed to levels above this threshold remained tightly shut. Animals exposed to salinities of 30, 40 and 50 had a faster mortality rate than those at 60 and 70 (Fig. 2A). However, within 5 days there was 100% mortality in all treatments above 20 (Fig. 2A).

A wider salinity tolerance was recorded when Esengeni mussels were gradually exposed to a rise in salinity. Animals increased their tolerance to include salinity levels from 30 to 50 (Fig. 2B). Previously those exposed to 30, 40 and 50 experienced 100% mortality within four days, yet with a gradual acclimation animals were able to survive these salinities indefinitely. However, the long-term survival of animals at 50 is unknown, as they had a 73% survival at the end of the experiment (after 30 days). Animals in these three treatments showed movement and were attached to the sides of the experimental bottles. Mussels were still unable to survive extreme salinities, 60 and 70, regardless of the slow acclimation to test conditions (Fig. 2B). The slowly acclimated mussels were unable to survive until the start of the experiment for the salinity treatment of 70. Additionally, only six

individuals survived till the start of the experiment in the 60 treatment, with 100% mortality reached within 3 days. This was less than the five days they were able to survive in the shock experiment (Fig. 2A).

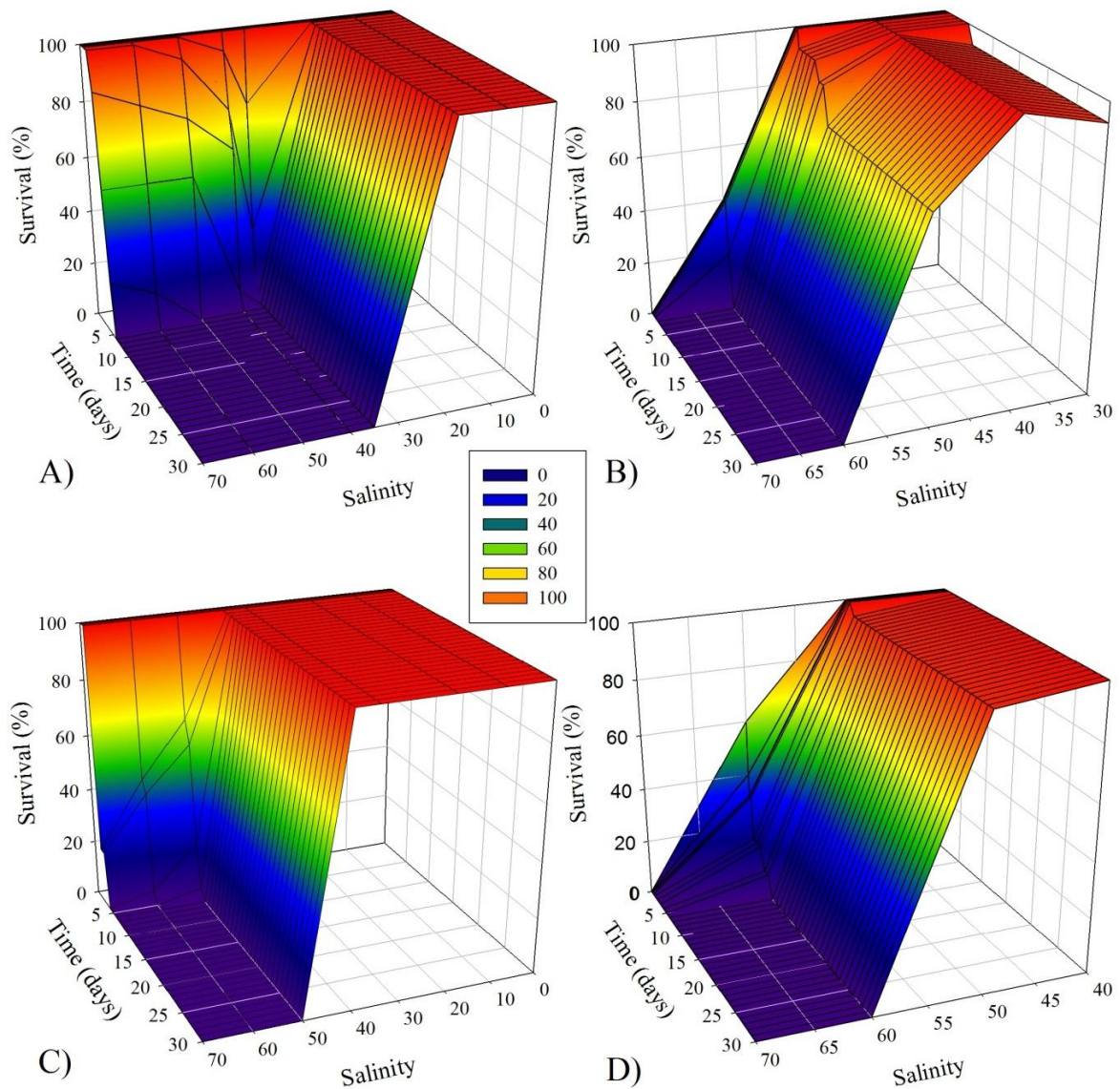


Fig. 2: Percent survival of *Brachidontes virgiliae* exposed to varying salinity treatments ranging between 0 and 70 for a 30 day period. Mussels were: A) collected at Esengeni (freshwater conditions) and exposed to a rapid change in salinity; B) collected at Esengeni (freshwater conditions) and gradually brought to test conditions; C) collected at Lister's Point (salinity \approx 20) and exposed to a rapid change in salinity; D) collected at Lister's Point (salinity \approx 20) and gradually brought to test conditions.

Animals collected from Lister's Point and exposed to a rapid change in salinity showed a similar trend to the Esengeni mussels acclimated to test conditions. They were able to tolerate lower salinities, from 0 to 40 (Fig. 2C). Mortality was seen in the 60 and 70 treatments, similar to that observed in both Esengeni shock and gradually acclimated animals (Fig. 2A, B and C). Activity was recorded in all treatments below 50, however above this treatment mussels were tightly shut. In the salinity treatment of 50, mussels experienced 100% mortality within five days, while complete mortality was reached faster in the 60 and 70

treatments, after four and three days respectively. Again, mussels exposed to a gradual increase towards test conditions showed a higher tolerance range than animals exposed to a rapid change in salinity. However, the treatments of 60 and 70 were still lethal for *B. virgiliae*, regardless of the site of collection or exposure method. Additionally, these animals were unable to survive the full acclimation period and did not reach the onset of the experiment. This was similar to the pattern observed with the gradually acclimated Esengeni mussels. Mussels were able to tolerate the salinity treatment of 50 (Fig. 2D), while 100% mortality occurred within five days in the Lister's Point shock experiment. Although the 60 treatment was still lethal for mussels, animals were capable of withstanding it for six days, as opposed to the four days previously recorded in the shock test. Similarly, not all animals survived until the end of the acclimation process and the majority of animals were dead within 24 hours in the 60 treatment (Fig. 2D).

Overall, *B. virgiliae* appeared to have a preferred tolerance ranging from 0 to 20, regardless of where they were collected from. An increase in tolerance was seen in those collected from sites with a higher salinity (i.e. Lister's Point). In addition, an increase in tolerance was also seen when animals were slowly exposed to an increase in salinity over a period of a month for both Esengeni and Lister's Point mussels. Salinity, exposure time and the combination of the two had a significant effect on the survival of *B. virgiliae* in all four experiments (Table 1).

Table 1: Repeated-measures ANOVA comparing the effects of salinity, exposure time and the interaction between salinity and exposure time on the % survival of *Brachidontes virgiliae* collected at Esengeni and Lister's Point over a 30 day period.

Site	Experiment	Variable	df	Adjusted df	F	GG
Esengeni	Shock	Exposure Time	35	2.27	393	< 0.001
		Salinity	7	7.00	56.9	< 0.001
		Exposure Time x Salinity	245	15.9	4585	< 0.001
		Salinity				
	Acclimation	Exposure Time	35	1.86	11.2	< 0.001
		Salinity	4	4.00	141	< 0.001
		Exposure Time x Salinity	140	7.45	4.09	< 0.001
		Salinity				
Lister's Point	Shock	Exposure Time	35	1.85	744	< 0.001
		Salinity	7	7.00	11130	< 0.001
		Exposure Time x Salinity	245	13.0	103	< 0.001
		Salinity				
	Acclimation	Exposure Time	35	2.16	18.0	< 0.001
		Salinity	3	3.00	783	< 0.001
		Exposure Time x Salinity	105	6.49	16.5	< 0.001
		Salinity				

DISCUSSION

Estuaries are characterised by large temporal and spatial fluctuations in physico-chemical parameters due to dynamic hydrological cycles. Thus, in order to successfully manage an estuary, it is essential to understand how the ecosystem will be affected by different climatic scenarios (Lester & Fairweather, 2009). Seasonal rainfall is highly variable in many parts of the world, including southern Africa and Australia, resulting in estuaries experiencing drought induced stress as well as periodic flooding events (Matthews, 2006; Davis, 2011). The Hopkins River Estuary in Australia experienced annual flooding prior to 1997, however floods were greatly reduced due to drought conditions occurring in the area until 2010 (Matthews, 2006). The Coorong in Australia has undergone severe salinity increases as a result of decreasing water levels over the last decade (Lester & Fairweather, 2009). The

St Lucia estuarine system in South Africa experiences cyclic alterations between dry and wet periods extending 4 to 10 years (Begg, 1978).

In St Lucia, salinity fluctuations are fundamental in determining the distribution and abundance of estuarine fauna and flora (Forbes & Cyrus, 1993). This is evident in the shift in bivalve dominance from *Solen cylindraceus* (dry period) to *Brachidontes virgiliae* (wet period). In addition, there has been a recent change in their distribution range, with *S. cylindraceus* previously widespread in the South Lake but currently established only in the northern reaches (salinity \approx 20). *Brachidontes virgiliae*, previously abundant in the Narrows, has now become ubiquitous throughout the system. Nel et al. (2011) determined an experimental salinity tolerance of between 15 and 65 for *S. cylindraceus*. Adjustment to a gradual decrease in salinity allows this bivalve to survive salinities as low as 10, although long term survival under such conditions is unknown (Nel et al., 2013). St Lucia is currently in a wet phase, resulting in *S. cylindraceus* unable to tolerate the predominantly oligohaline environment dominating the system. This has allowed the Brackwater mussel, *B. virgiliae*, to become dominant throughout St Lucia. Weerts (1993) described a similar situation during periods of low salinity, when *B. virgiliae* was considered the most abundant bivalve while *S. cylindraceus* was rare. According to results obtained with the current *in vitro* study, *B. virgiliae* has a salinity tolerance skewed towards the lower levels, able to tolerate virtually freshwater conditions. This mussel thrives in St Lucia during the wet period, as it has a preferred tolerance range from freshwater to 20. A similar dynamic may be seen in the Hopkins River Estuary, Australia, whereby winter flooding results in mass mortalities of the infaunal bivalve *Soletellina alba* but not *Arthritica helmsi* (Matthews & Constable, 2004). This is due to the ability of *A. helmsi* to tightly shut under unfavourable conditions, while *S. alba* is exposed at its anterior and posterior ends (Matthews & Constable, 2004). The estuarine mussel *Xenostrobus securis* is also able to tightly shut to avoid physiological stress, additionally it is able to tolerate a sudden decrease in salinity and low salinities similar to *B. virgiliae* (Wilson, 1968).

Brachidontes virgiliae is a minute, epifaunal mussel regularly underestimated in macrofaunal surveys, with only anecdotal evidence available on its salinity tolerance. At St Lucia, Day et al. (1954) found *B. virgiliae* at salinity levels ranging from 26.0 to 34.1. This is similar to the results obtained by Blaber et al. (1983), showing the presence of this mussel in South Lake under stable marine salinities. It has been described as a euryhaline species, commonly found in the salinity range of 34.4 – 36.0 (Millard & Broekhuysen, 1970). Absent or rare during periods of hypersalinity, the species has a preference for low salinities (Boltt, 1975). Davies (1980) suggested a tolerance range from 0 to 34 for mussels found in the Kowie Estuary, Eastern Cape, South Africa, although there has been no attempt to experimentally determine their salinity tolerance. This range is consistent with the results obtained

in the present study using mussels collected from Lister's Point and exposed to a rapid change in salinity (salinity tolerance: 0 to 40; Fig. 2C). In addition, mussels collected from both Esengeni and Lister's Point and gradually exposed to an increase in salinity showed a slightly wider salinity range, which included the 50 treatment (Fig. 2B and D). In Florida, the invasive mussel *Mytella charruana* had a similar salinity tolerance ranging from 2 to 40, surviving best at salinities between 2 and 23 (Yuan et al., 2010). The mussel *B. striatulus*, which occurs naturally in India, has a narrow salinity tolerance range of 7 to 11 and has successfully established in Singapore (Barber et al., 2005). Sarà et al. (2008) suggested a wider salinity tolerance range of 15 – 60 for the invasive *B. pharaonis* in the Mediterranean Sea. Although there is no evidence of *B. virgiliae* establishing outside of its natural distribution range, it is a potential biofouling threat given its wide salinity tolerance and ability to attach to boats hulls.

Tolerance limits have been extended in numerous bivalve species by acclimation (Castagna & Chanley, 1973; Nel et al., 2011). Berger and Kharazova (1997) stated that sensitivity to environmental fluctuations may be shifted by previous acclimation to low/high salinity. Bivalves exposed to long-term changes in environmental salinity may lose or gain osmolytes, which assist in maintaining cell volume (Neufeld & Wright, 1996 and references within). In this study a wider salinity tolerance range was seen in mussels collected from the site exhibiting the higher saline environment. In addition, an increase in tolerance was seen when animals were slowly exposed to an increase in salinity over a monthly period. A wider salinity tolerance was also seen for *S. cylindraceus* when gradually increased/decreased to test conditions (Nel et al., 2011). Numerous studies have illustrated an increase in the salinity tolerance of bivalve species, when slowly adjusted to test salinities (Yuan et al., 2010). This knowledge may be used to understand how species distribution may change as flood and drought-induced stress increases due to global warming. Additionally, mitigation of mass mortality events may be achieved by flow management, i.e. gradual versus sudden releases of water.

This mussel is often found attached to submerged macrophytes (Nel et al., 2012). In St Lucia, the three main macrophyte species are *Stukenia pectinata*, *Ruppia cirrhosa* and *Zostera capensis* (Adams & Bate, 1994). Floods may dislodge these submerged macrophytes and this will have an indirect effect on the mussel population. An increase or dramatic decrease in salinity may also affect *B. virgiliae* indirectly, by eliminating these macrophytes. *Stukenia pectinata* is excluded above salinity levels of 20, *Z. capensis* can tolerate salinity levels between 10 and 45, while *R. cirrhosa* is able to tolerate salinities as high as 50 (Adams & Bate, 1994; Adams et al., 2013). Although it is convenient to use simple experimental systems in studies of environmental tolerance, it is important to appreciate that the environment is a multivariate system (Perkins, 1974). Thus, apart from interactions between various abiotic factors, the interaction that biotic factors play on structuring a bivalve population must also be taken into account.

Salinity may affect an organism directly through its physiology and indirectly by altering the food, predator and habitat availability (Finney, 1979; Jassby et al., 1995; Montagna et al., 2002). The metabolic rates of an organism are affected with escalation to its activity level (Berger & Kharazova, 1997; Segnini de Bravo et al., 1998). In mussels, the formation of byssus threads can be affected by changes in the saline environment (Sundaram & Syed Shafee, 1989). Although these factors were not directly measured in this study, a reduction in activity was observed under unfavourable salinity levels. Additionally, mussels in the higher treatments did not attach to the sides of the incubation vessel, as opposed to their counterparts exposed to lower salinities. There is a need for future research to focus on sub-lethal effects of salinity on attachment, filtration and respiration as these factors will affect population dynamics.

Sessile and relatively sedentary species are unable to move away from unfavourable environmental conditions (Perkins, 1974). They, thus, employ behavioural strategies to cope with exposure to salinity levels outside of their tolerance range. Mussels may close their shells when exposed to abnormal salinities, this isolation reflex first occurring in the more sensitive individuals and later in all (Berger & Kharazova, 1997). Individuals are able to withstand prolonged asphyxia and accumulation of acidic products produced during anaerobic metabolism, while the mussel remains closed (Berger & Kharazova, 1997). However, this is a temporary mechanism and long-term survival under such conditions is unlikely. Zebra mussels are extremely starvation tolerant and this may be a mechanism used to withstand periods of closure (McMahon, 1996). In the current study, *B. virgiliae* displayed an ability to withstand unfavourable conditions for a few (4 to 7) days by tightly closing their shells. Although, long-term survival at these salinity levels is unlikely, this mussel may be able to tolerate short spikes in the saline environment.

St Lucia is characterised by floods, wetter than average years and periods of extreme drought conditions. Floods such as those caused by Cyclone Domoina in January/February 1984 reduced the salinity within St Lucia from ~ 40 to near freshwater conditions, in a matter of days (Cyrus, 1988; Forbes & Cyrus, 1993; Nel et al., 2011). This cyclonic activity and heavy rains caused a reduction in the macrofaunal density by ~ 40% (Cyrus, 1988). Owen and Forbes (1997) found that macrofaunal biomass declined following cyclonic activity. Prolonged periods of rainfall will also cause a decline in salinity, thus eliminating species unable to withstand oligohaline to limnetic conditions (Owen & Forbes, 1997). There is often a moderate to large decrease in abundance (e.g. 28 to 100%) of certain species, especially bivalves when exposed to a drastic decrease in salinity (McLachlan & Erasmus, 1974; Hakenom, 1989; Kanandjembo et al., 2001). Although, St Lucia has historically been subjected to cyclonic activity (Cyrus, 1988; Owen & Forbes, 1997), an increase in the frequency of occurrence and intensity of extreme events is expected in response to climate change (Schulze, 2006).

Brachidontes virgiliae may be positively affected by the dramatic decrease in salinity, however an associated high silt load entering the system may have detrimental effects on filter-feeding mussels (Adam, 1986; Thrush et al., 2004). Although preliminary observations show that *B. virgiliae* may withstand periods of about 30 days of exposure to high silt concentration, up to 1500 NTU (H.A. Nel, unpubl. data), this aspect needs to be investigated further.

St Lucia has recently experienced a severe drought period that has resulted in the development of a reverse salinity gradient and caused hypersaline events in its northern reaches. High salinities prevailing in False Bay and North Lake have resulted in a scarcity of benthic fauna and flora (Day et al., 1954). Similarly in the late 60s, Millard and Broekhuysen (1970) attributed the observed decrease in faunal richness in the northern reaches to extreme conditions. In addition, Bolt (1975) reported that an impoverished benthic community was seen when there were high salinities, between 45 and 80. Pillay and Perissinotto (2008) suggested that the reduction in macrofaunal abundance, species richness and diversity in the northern parts of the system were due to hypersaline conditions and low water levels. Thus localised elimination due to hypersaline conditions is well documented, whereby species that are unable to tolerate high salinities are temporarily eliminated from the system. *Brachidontes virgiliae* is able to withstand salinity levels up to 50, if slowly acclimated or found in habitats with higher salinities. Above 50, this species remains tightly shut and suffers mass mortality within a week. Mass mortalities of bivalves are also recorded during winter flooding in the Hopkins River Estuary (Matthews & Fairweather, 2006) and in St Lucia (Nel et al., 2011; Nel et al., 2012), but mass mortality events do not appear to be widely documented in the literature.

Similar to *S. cylindraceus* in St Lucia, higher salinity levels during the study done by Matthews (2006) appeared beneficial to *S. alba*, increasing its survivorship, although salinities never exceeded 35 in this study. The Swan-Canning Estuary in Australia is dominated by the bivalve *Arthritica semen* due to its ability to withstand the wide range of salinity experienced by the system (Kanandjembo et al., 2001). Both *S. cylindraceus* and *B. virgiliae* have a wide salinity tolerance that has enabled them to persist, while numerous other bivalves have previously been eliminated from this system due to unfavourable conditions (Nel et al., 2011; Nel et al., 2012).

Overall, this study has highlighted the extent of mass mortality in bivalves which is dependent on the extent and rate of change in salinity, i.e rapid versus gradual decrease during flood events. This has consequences for managing flows within the system. Subsequently, this species is unlikely to disappear from St Lucia, as it becomes widespread during wet periods, able to withstand the low salinities. During dry periods it remains abundant in the Narrows and is restricted to areas with salinity levels below 50. During the most extreme drought periods, when salinities may reach 200 in the northern reaches, the Narrows, with oligohaline to limnetic conditions, would act as a refuge area

for this mussel. This is in contrast to *S. cylindraceus* which uses South Lake as its reservoir during hypersaline conditions and the northern reaches during oligohaline conditions. Lancaster and Belyea (1997) described a refuge as an area that provides a species with protection from the negative effects of the surrounding environment. These areas are important during natural disturbances (i.e. drought and flood events), as they allow species to persist in a highly variable ecosystem (Magoulick & Kobza, 2003; Taylor et al., 2006). Posey *et al.* (2005) described how the blue crab, *Callinectes sapidus* used low salinity regions as refuge areas vital for maintaining estuarine populations. Madon (2008) also mentioned thermal refuges used by estuarine fish species. *Solen cylindraceus* and other estuarine bivalves in St Lucia rely on populations surviving within the system for recolonisation (Taylor *et al.*, 2006). It is, thus, important to identify and protect these refuge areas as they support the resilience of the estuary (Taylor *et al.*, 2006). Future studies should investigate the rate at which these areas act as nuclei from which recolonisation of the remaining lake can occur once favourable conditions have returned.

ACKNOWLEDGEMENTS

We are grateful to the iSimangaliso Park Authority and Ezemvelo KZN Wildlife for supporting this project. Funding for this project was provided by the National Research Foundation (NRF, Pretoria) through the program Knowledge Fields Development - Society, Ecosystems and Change (SEACHANGE), as well as the South African Netherlands Research Programme on Alternatives in Development (SANPAD, Durban) and the University of KwaZulu-Natal (UKZN, Durban). Thanks to Nicola Carrasco and David Dyer for assisting with the collection of animals at St Lucia and John Swart for assisting with the execution of the experiments in the laboratory.

REFERENCES

- Adam, M.E. 1986. The Nile bivalves – How do they avoid silting during the flood? *Journal of Molluscan Studies* 52:248-252.
- Adams, J.B. & Bate, G.C. 1994. The ecological implications of tolerance to salinity by *Ruppia-cirrhosa* (Petagna) Grande and *Zostera-capensis* Setchell. *Botanica Marina* 37:449-456.
- Adams, J.B., Nondoda, S. & Taylor, R.H. 2013. Macrophytes. Pp. 207-225 In: Perissinotto, R., Stretch, D.D., Taylor, R.H. (eds.), *Ecology and Conservation of Estuarine Ecosystems: Lake St Lucia as a Global Model*. New York: Cambridge University Press.

- Barber, B.J., Fajans, J.S., Baker, S.M. & Baker, P. 2005. Gametogenesis in the non-native green mussel, *Perna viridis*, and the native scorched mussel, *Brachidontes exustus*, in Tampa Bay, Florida. *Journal of Shellfish Research* 24:1087-1095.
- Begg, G.W. 1978. The estuaries of Natal. (Part II). Natal Town and Regional planning Commission Report.41:1-657.
- Berger, V.J. & Kharazova, A.D. 1997. Mechanisms of salinity adaptations in marine molluscs. *Hydrobiologia* 355:115-126.
- Blaber, S.J.M., Kure, N.F., Jackson, S. & Cyrus, D.P. 1983. The benthos of South Lake, St Lucia following a period of stable salinities. *South African Journal of Zoology* 18:311-319.
- Boltt, R.E. 1975. The benthos of some Southern African Lakes Part V: The recovery of the benthic fauna of St Lucia Lake following a period of excessively high salinity. *Transactions of the Royal Society of South Africa* 41:295-323.
- Carrasco, N.K. & Perissinotto, R. 2012. Development of a Halotolerant Community in the St. Lucia Estuary (South Africa) during a Hypersaline Phase. *Plos One* 7:1-14.
- Castagna, M. & Chanley, P. 1973. Salinity tolerance of some marine bivalves from inshore and estuarine environments in Virginia waters on the western mid-Atlantic coast. *Malacologia* 12:47-96.
- Cyrus, D.P. 1988. Episodic events and estuaries: Effects of cyclonic flushing on the benthic fauna and diet of *Solea bleekeri* (Teleostei) in Lake St Lucia on the southeastern coast of Africa. *Journal of Fish Biology* 33:1-7.
- Cyrus, D.P., Vivier, L. & Jerling, H.L. 2010. Effect of hypersaline and low lake conditions on ecological functioning of St Lucia estuarine system, South Africa: An overview 2002 - 2008. *Estuarine, Coastal and Shelf Science* 86:535-542.
- Davies, B.R. 1980. The identification of the mytilids *Musculus virgiliae* Barnard, *Arcuatula capensis* (Krauss) and *Brachidontes variabilis* Krauss, with corrections to the literature and a note on their distribution. *Transactions of the Royal Society of South Africa* 44:225-235.

- Davis, C.L. 2011. *Climate Risk and Vulnerability: A Handbook for Southern Africa*. Council for Scientific and Industrial Research, Pretoria, South Africa, pp. 92.
- Day, J.H., Millard, N.A.H. & Broekhuysen, G.J. 1954. The ecology of South African estuaries part IV: the St Lucia system. *Transactions of the Royal Society of South Africa* 34:129-156.
- Finney, C.M. 1979. Salinity stress in harpacticoid copepods. *Estuaries* 2:132-135.
- Forbes, A.T. & Cyrus, D.P. 1992. Impact of a major cyclone on a southeast African estuarine lake system. *Netherlands Journal of Sea Research* 30:265- 272.
- Forbes, A.T. & Cyrus, D.P. 1993. Biological effects of salinity gradient reversal in a southeast African estuarine lake. *Netherlands Journal of Aquatic Ecology* 27:485-488.
- Hakenom, N. 1989. A note on the effects of a flood of medium intensity on macrobenthos of soft substrata in the Swartkops Estuary, South Africa. *South African Journal of Marine Science* 8:349-355.
- Jassby, A.D., Kimmerer, W.J., Monismith, S.G., Armor, C., Cloern, J.E., Powell, T.M., Schubel, J.R. & Vendlinski, T.J. 1995. Isohaline positions as a habitat indicator for estuarine populations. *Ecological Applications* 5:272-289.
- Kanandjembo, A.N., Platell, M.E. & Potter, I.C. 2001. The benthic macroinvertebrate community of the upper reaches of an Australian estuary that undergoes marked seasonal changes in hydrology. *Hydrological Processes* 15:2481-2501.
- Kilburn R, Rippey E 1982 *Sea shells of southern Africa*. Johannesburg: Macmillan South Africa.
- Lancaster, J. & Belyea, L.R. 1997. Nested hierarchies and scale-dependence of mechanisms of flow refugium use. *Journal of the North American Benthological Society* 16:221-238.
- Lester, R.E. & Fairweather, P.G. 2009. Modelling future conditions in the degraded semi-arid estuary of Australia's largest river using ecosystem states. *Estuarine, Coastal and Shelf Science* 85:1-11.

- Madon, S.P. 2008. Fish community responses to ecosystem stressors in coastal estuarine wetlands: a functional basis for wetlands management and restoration. *Wetlands Ecology and Management* 16:219-236.
- Magoulick, D. D. & Kobza, R. M. 2003. The role of refugia for fishes during drought: a review and synthesis. *Freshwater Biology* 48:1186-1198.
- Matthews, T.G. & Constable, A.J. 2004. Effect of flooding on estuarine bivalve populations near the mouth of the Hopkins River, Victoria, Australia. *Journal of the Marine Biological Association of the United Kingdom* 84:633-639.
- Matthews, T.G. & Fairweather, P.G. 2004. Effect of lowered salinity on the survival, condition and reburial of *Soletellina alba* (Lamarck, 1818) (Bivalvia: Psammobiidae). *Austral Ecology* 29:250-257.
- Matthews, T.G. 2006. Spatial and temporal changes in abundance of the infaunal bivalve *Soletellina alba* (Lamarck, 1818) during a time of drought in the seasonally-closed Hopkins River Estuary, Victoria, Australia. *Estuarine, Coastal and Shelf Science* 66:13-20.
- McLachlan, A. & Erasmus, T. 1974. Temperature tolerances and osmoregulation in some estuarine bivalves. *Zoologica Africana* 9:1-13.
- McLeod, R. & Wing, S. 2008. Influence of an altered salinity regime on the population structure of two infaunal bivalve species. *Estuarine, Coastal and Shelf Science* 78:529-540
- McMahon, R.F. 1996. The physiological ecology of the zebra mussel, *Dreissena polymorpha*, in North America and Europe. *American Zoologist* 36:339-363.
- Millard, N.A.H. & Broekhuysen, G.J. 1970. The ecology of South African estuaries Part X: St Lucia: a second Report. *Zoologica Africana* 5:277-307.
- Montagna, P.A., Kalke, R.D. & Ritter, C. 2002. Effect of restored freshwater inflow on macrofauna and meiofauna in upper Rincon Bayou, Texas, USA. *Estuaries* 25:1436-1447.
- Nel, H.A., Perissinotto, R., Taylor, R.H. & Carrasco, N.K. 2011. Salinity tolerance of the bivalve *Solen cylindraceus* (Hanley, 1843) (Mollusca: Euheterodonta: Solenidae) in the St Lucia Estuary. *African Invertebrates* 52:575-586.

- Nel, H.A., Perissinotto, R. & Taylor, R.H. 2012. Diversity of bivalve molluscs in the St Lucia Estuary, with an annotated and illustrated checklist. *African Invertebrates* 53:503-525.
- Nel, H.A., Perissinotto, R. & Taylor, R.H. 2013. *In situ* growth rate of *Solen cylindraceus* (Mollusca: Euheterodonta: Solenidae) in the St Lucia estuarine lake, South Africa. *African Zoology*. 48:266-273.
- Neufeld, D.S. & Wright, S.H. 1996. Response of cell volume in *Mytilus* gill to acute salinity change. *The Journal of Experimental Biology* 199: 473-484.
- Owen, R.K. & Forbes, A.T. 1997. Salinity, floods and the infaunal macrobenthic community of the St Lucia Estuary, KwaZulu-Natal, South Africa. *African Journal of Aquatic Science* 23:14-30.
- Perkins, E.J. 1974. *The Biology of Estuaries and Coastal Waters*. London & New York: Academic Press, Pp. 678.
- Pillay, D. & Perissinotto, R. 2008. The benthic macrofauna of the St Lucia Estuary during the 2005 drought year. *Estuarine, Coastal and Shelf Science* 77:35-46.
- Posey, M.H., Alphin TD, Harwell H, Allen B: Importance of low salinity areas for juvenile blue crabs, *Callinectes sapidus* Rathbun, in river-dominated estuaries of southeastern United States. *Journal of Experimental Marine Biology and Ecology* 319:81-100.
- Rolston, A. & Dittmann, S. 2009. *The Distribution and Abundance of Macrobenthic Invertebrates in the Murray Mouth and Coorong Lagoons 2006 to 2008*. CSIRO: Water for a Healthy Country National Research Flagship, Canberra.
- Sarà, G., Romano, C., Widdows, J. & Staff, F.J. 2008. Effect of salinity and temperature on feeding physiology and scope for growth of an invasive species (*Brachidontes pharaonis* - MOLLUSCA: BIVALVIA) within the Mediterranean sea. *Journal of Experimental Marine Biology and Ecology* 363:130-136.
- Schulze, R.E. 2006. *Climate change and water resources in southern Africa*. Report No. 1430/1/05, Water Research Commission, Pretoria.

- Segnini de Bravo, M.I.S., Chung, K.S. & Perez, J.E. 1998. Salinity and temperature tolerances of the green and brown mussels, *Perna viridis* and *Perna perna* (Bivalvia: Mytilidae). *Revista De Biologia Tropical* 46:121-125.
- Sundaram, K.S. & Syed Shafee, M. 1989. Salinity tolerance of some bivalves of Ennore estuary. *Journal of the Marine Biological Association of India* 31:299-302.
- Taylor, R., Kelbe, B., Haldorsen, S., Botha, G.A., Wejden, B., Vaeret, L. & Simonsen, M.B. 2006. Groundwater-dependent ecology of the shoreline of the subtropical Lake St Lucia estuary. *Environmental Geology* 49:586-600.
- Thrush, S.F., Hewitt, J.E., Cummings, V., Ellis, J.I., Hatton, C., Lohrer, A. & Norkko, A. 2004. Muddy waters: elevating sediment input to coastal and estuarine habitats. *Frontiers in Ecology and the Environment* 2:299-306.
- Weerts, K.A. 1993. Salinity, sediments and the macrobenthic communities of Lake St Lucia. MSc Thesis, University of Natal, Durban.
- Whitfield, A.K. & Taylor, R.H. 2009. A review of the importance of freshwater inflow to the future conservation of Lake St Lucia. *Aquatic Conservation: Marine and Freshwater Ecosystems* 19:838-848.
- Whitfield, A.K., Bate, G.C., Forbes, T. & Taylor, R.H. 2013. Relinkage of the Mfolozi River to the St. Lucia estuarine system - urgent imperative for the long-term management of a RAMSAR and World Heritage Site. *Aquatic Ecosystem Health & Management* 16:104-110.
- Wilson, B.R. 1968 Survival and reproduction of mussel *Xenostrobus securis* (Lam.) (Mollusca–Bivalvia–Mytilidae) in a western Australian estuary. Part I. Salinity tolerance. *Journal of Natural History* 2:307–328.
- Yuan, W., Walters, L.J., Schneider, K.R. & Hoffman, E.A. 2010. Exploring the survival threshold: A study of salinity tolerance of the non-native mussel *Mytella charruana*. *Journal of Shellfish Research* 29:415-422.

***In situ* growth rate of *Solen cylindraceus* (Mollusca: Euheterodonta: Solenidae) in the St Lucia estuarine lake, South Africa**

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Received 7 May 2013. Accepted 1 August 2013

Solen cylindraceus, an infaunal bivalve, can reach a maximum length of 95 mm. However, in the St Lucia estuarine system specimens are seldom larger than 55 mm. Thus, the primary aim of this study was to investigate the growth rate and morphometrics of *S. cylindraceus* in St Lucia. Growth lines of this species are too indistinct and irregular to be of any use. This study, therefore, adopted a more direct method of monitoring the shell length of individuals, by caging them *in situ*. Shell measurements were taken from the individuals in cages and the surrounding environment at monthly intervals for one year. Thereafter, salinities decreased below their tolerance range and the experiment was terminated. Caged and uncaged animals had a shell length of 31.0 ± 4.5 and 31.7 ± 2.3 mm after a year of growth, respectively. An overall growth rate of 0.049 ± 0.059 mm/d was derived for the caged animals. In conclusion, first year growth rates appeared lower than previously recorded for *S. cylindraceus*. Additionally, it appears that animals are unable to survive in the prevailing harsh environment of St Lucia to reach maximum size.

Key words: iSimangaliso Wetland Park, Bivalvia, eastern pencil-bait, von Bertalanffy growth curve.

INTRODUCTION

Bivalve molluscs of the family Solenidae, generally known as razor shells, are important worldwide because of their large local/periodical abundance (Huber 2010). Ecologically, they play a critical role as infaunal filter-feeders in shallow estuarine and coastal waters, where they also act as a food source for a large variety of bottom predators (Hodgson & de Villiers 1986; Huber 2010). Most of the approximately 70 species currently described are edible and some have high commercial value in international markets (da Costa & Martínez-Patiño 2009; Saeedi *et al.* 2009).

Solen cylindraceus (Hanley, 1843) is one of the two Solenidae species currently known from South Africa and has a western Indian Ocean distribution, from the Arabian Peninsula to Algoa Bay (Kilburn & Rippey 1982; de Villiers *et al.* 1989; Branch *et al.* 2010; Huber 2010). Commonly named eastern pencil-bait or stick-bait (Kilburn & Rippey 1982; Branch *et al.* 2010), this species has been mentioned repeatedly in the literature as being found throughout the St Lucia estuarine lake (Day *et al.*

1954; Millard & Broekhuysen 1970; Bolt 1975; Blaber *et al.* 1983; Owen & Forbes 1997; Pillay & Perissinotto 2008; MacKay *et al.* 2010; Nel *et al.* 2011, 2012). This key species is also a major contributor to the diet of birds, such as the greater flamingo, and fish such as grunter.

Occurring at densities of up to 1200 ind/m² and exceptionally even >3000 ind/m², *S. cylindraceus* is considered a key species within Lake St Lucia (Fig. 1) (Blaber *et al.* 1983; Pillay & Perissinotto 2008; MacKay *et al.* 2010). During June 2010, Nel *et al.* (2011) recorded *S. cylindraceus* densities ranging from 14.1 to 3206 ind/m² in South Lake. A bivalve survey carried out in March/April 2011 found densities of >400 ind/m² at Charter's Creek and >100 ind/m² at Catalina Bay (Nel *et al.* 2012). In this survey only six bivalve species were recorded within the system, with *S. cylindraceus* exhibiting the highest densities among the infaunal bivalves (Nel *et al.* 2012).

The bivalve community in St Lucia experiences large fluctuations in its physico-chemical environment, due to the alternating phases of wet and dry periods typically experienced in the system (Begg

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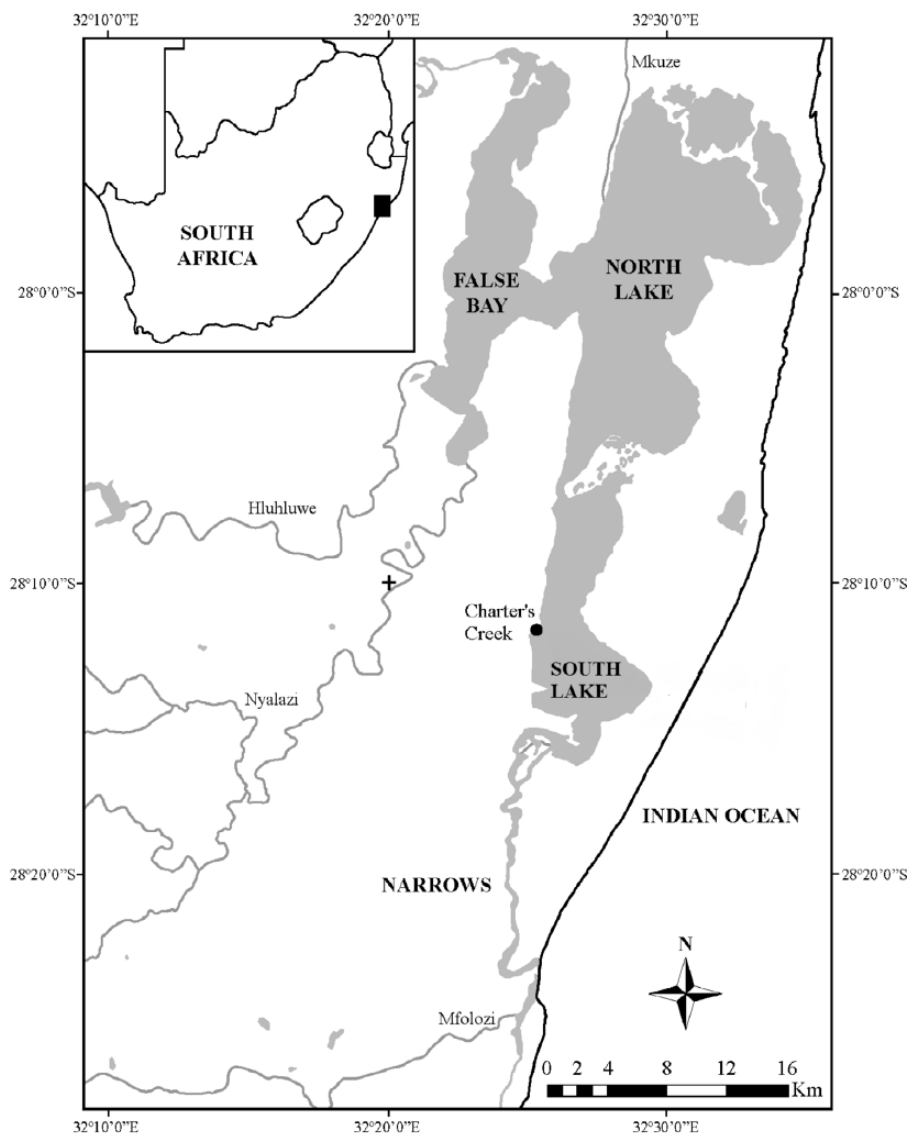


Fig. 1. Map of the St Lucia estuarine lake, showing the main basins and the sampling site (Charter's Creek). (Adapted from Carrasco & Perissinotto 2011a.)*

1978; Cyrus & Vivier 2006). In St Lucia, *S. cylindraceus* is often exposed to temperature and salinity levels outside its tolerance range, which results in mass mortality. McLachlan & Erasmus (1974) and de Villiers *et al.* (1989) suggested a lethal temperature for *S. cylindraceus* of 44–44.5°C and regarded this higher than any temperature this species is likely to be exposed to in its natural habitat. St Lucia, however, does experience similar and even higher temperatures in shallow waters (Carrasco & Perissinotto 2011a). St Lucia also exhibits periods of hypersalinity (salinity >100) alternating with periods of oligohaline conditions (salinity <5),

*We have been given permission by the authors to use and adjust the map.

which cause mass mortality of bivalves, including *S. cylindraceus* (Nel *et al.* 2011). In addition, large areas of the lake bed can be exposed and dried by lowering water levels. Although *S. cylindraceus* is considered a fast-growing species, with a lifespan of approximately five years (McLachlan 1974), it seldom reaches this potential age, due to the onset of environmental factors outside its tolerance range (Nel *et al.* 2011).

Branch *et al.* (2010) reported the maximum length of *S. cylindraceus* as 50 mm, but this shell length is often exceeded in the Swartkops Estuary, which exhibits a stable physico-chemical environment (McLachlan 1974). According to both McLachlan (1974) and Kilburn & Rippey (1982), it

can reach a maximum size of 95 mm in length; however, specimens currently found alive in St Lucia are seldom larger than 55 mm (H.A. Nel, pers. obs.).

Despite *S. cylindraceus* being considered a dominant member of the St Lucia benthos (Begg 1978), its growth rates and morphometric data have not yet been measured in the system. McLachlan (1974) investigated the growth of *S. cylindraceus* in the Swartkops Estuary using size frequency histograms. This indirect method of investigating species growth may become difficult if there is more than one recruitment event yearly, or growth varies greatly between years and/or individuals (Matthews & Fairweather 2003; Moura *et al.* 2009). Other studies have used annual growth lines to determine the age of bivalves (Breen *et al.* 1991; Gasper *et al.* 1999; Barón *et al.* 2004; Palmer 2004; Moura *et al.* 2009). However, this technique is not feasible in the study of *S. cylindraceus* growth, as the lines are too indistinct and irregular to be of any use (McLachlan 1974). In addition, Palmer (2004) reported that disturbance marks are common in razor clams; this would make using growth lines impossible in a variable system such as St Lucia. The present study adopted a more direct method of monitoring the shell length of *S. cylindraceus* individuals *in situ*. The objectives were to investigate the growth of both caged and uncaged *S. cylindraceus* spat, and provide preliminary morphometric estimates.

MATERIALS & METHODS

Study area

The growth rate of *Solen cylindraceus* was determined by analysing the changes in shell length of caged and uncaged animals in the St Lucia estuarine system, specifically at Charter's Creek (Fig. 1). Situated in the iSimangaliso (previously referred to as Greater St Lucia) Wetland Park, St Lucia is the largest estuarine lake in Africa, covering 80% of the estuarine area of KwaZulu-Natal (Begg 1978). The estuarine lake is situated in the northern parts of KwaZulu-Natal, between 27°52'S to 28°24'S and 32°21'E to 32°34'E and is subdivided into three shallow lakes (namely False Bay, North Lake and South Lake) and a 21 km channel known as The Narrows (Fig. 1). It has a total surface area of approximately 300 to 350 km² depending on the water levels (Begg 1978).

The experiment was initiated on 19 March 2011 and terminated on 12 March 2012, at the onset of

mass mortality due to salinity precipitating below the tolerance range recorded for this species. On all occasions salinity and temperature data were measured using a YSI 6920 water quality logger. *Solen cylindraceus* individuals were collected by shovelling sediment from a water depth of half a metre, from Charter's Creek (sampling site). This sediment was then washed through a 2 mm sieve. Animals with a shell length ranging from 14 to 27 mm were collected and placed in individual jars.

In situ growth rate of Solen cylindraceus

Initially, 50 experimental chambers, pre-washed 1 l wide-mouthed plastic jars, were used to house individual *Solen cylindraceus*. On the day of deployment, individual jars were filled to the lip with naturally occurring sediment from Charter's Creek. The sediment was sieved through a 2 mm mesh, to eliminate all bivalve juveniles and hard detrital material. The jars were then sealed with a 2 mm mesh, so that animals could not relocate during the experiment, but were still able to extend their siphons into the water column. The jars were buried *in situ*, so that the opening was at the interface between sediment and water, as in the natural condition. The jars were kept in a mesh-enclosed area serving to deter hippos and crocodiles from damaging them. Additionally, the enclosure allowed the jars to be easily located during each measurement. At fortnightly intervals, the animals were gently removed from the jars and both length and width were measured to the nearest 0.1 mm using Vernier callipers. From 28 July 2011 to the end of the experiment, length and width measurements were checked only monthly. Simultaneously, at each time interval, 20 to 60 animals (uncaged) were also removed from outside the mesh-enclosed area, measured using the same method and returned to their natural environment. In addition, a further 300 specimens were collected and frozen for length data. Wet and dry weights were measured to the nearest 0.01 mg, using an analytical balance. Dry weight was recorded after animals were dried at 60°C for 24 h, as this timeframe proved to be sufficient to dry animals of every size to constant weight.

Growth determination

The von Bertalanffy growth equation (von Bertalanffy 1957) was fitted to the observed length-at-age data for uncaged *Solen cylindraceus*,

$$L_t = L_\infty (1 - e^{-k(t-t_0)}), \quad (1)$$

where: L_t = mean length at age t ; k = growth constant; t_0 = theoretical age at zero length and L_∞ = theoretical maximum length.

The age of *S. cylindraceus* was estimated assuming that spat with a mean size and standard deviation of 9.98 ± 1.40 mm had settled from the water column approximately two months prior, as suggested by McLachlan (1974). The von Bertalanffy model was run separately using two scenarios. The first assuming $L_\infty = 55$ mm, which was the largest specimen collected alive in St Lucia (H.A. Nel, pers. obs.). The second scenario assumed that the theoretical maximum length of *S. cylindraceus* was 70 mm. This was the largest dead specimen found along the shorelines of St Lucia during a bivalve census undertaken by Nel *et al.* (2012). Therefore the parameters (k and t_0) were estimated by calculating the sum of squared difference between observed and predicted lengths, which was then minimized (Brash & Fennessy 2005). This was done using Solver in Microsoft Excel 2007.

Statistical analyses

The relationship between the log-transformed length (mm) and log-transformed width (mm) of *Solen cylindraceus* was determined using a regression analysis. This transformation was performed after a one-sample Kolmogorov-Smirnov normality test was not satisfied ($P < 0.05$). Thereafter the assumptions were re-tested on the residuals and both the one-sample Kolmogorov-Smirnov normality and Levene's test were satisfied ($P > 0.05$). Regressions were also performed between the log-transformed length (mm) and log-transformed wet and dry weight (g) data of *S. cylindraceus*. A one-sample Kolmogorov-Smirnov normality and Levene's test were satisfied on both sets of residuals ($P > 0.05$). The wet (October–April) and dry seasons (May–September) are the two typical climatic conditions experienced on the KwaZulu-Natal coast, which largely coincide with summer and winter, respectively (Carrasco & Perissinotto 2011b). The mean growth rates (mm/d) of both wet and dry seasons for caged animals were compared using a paired sample t -test, after normality was met ($P > 0.05$). All analyses were performed using SPSS 19.0 for Windows.

RESULTS

The initial shell lengths and standard deviation of the caged and uncaged animals were 18.3 ± 3.5

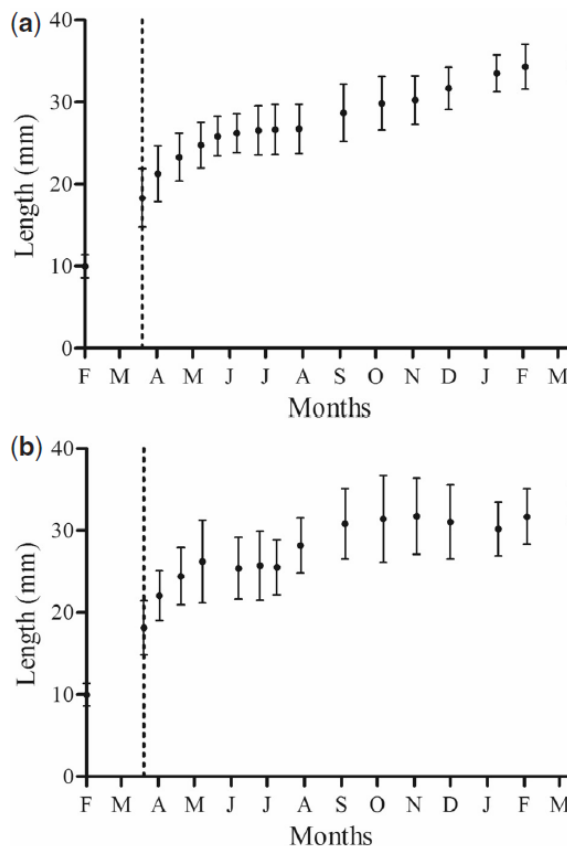


Fig. 2. a, Increase in mean shell length \pm S.D. (mm) of *Solen cylindraceus* kept in individual cages *in situ*, from March 2011 to March 2012. b, Increase in mean shell length \pm S.D. (mm) of naturally occurring animals, from March 2011 to March 2012 (b). The dotted lines represents the beginning and end of the experimental period.

and 18.1 ± 3.3 mm, respectively. Caged animals showed a clear increase in shell length from the start of the experiment, in March, to mid-May; thereafter, no major increase was evident until September (Fig. 2a). From September until February, shell length continued to increase (Fig. 2a). Uncaged animals displayed a similar increasing trend in shell length from the start of the experiment to mid-May, reaching a plateau around mid-May to July (Fig. 2b). A more moderate increase was seen thereafter, until October, but from this point till the end of the experiment there was a fluctuation in shell length, with no major increase (Fig. 2b). Caged and uncaged animals had final lengths of 34.5 ± 2.1 and 33.5 ± 2.2 mm, respectively. Therefore, during the experiment, caged and uncaged animals grew 16.2 and 15.4 mm, respectively.

With settlement of spat in the sediment occurring around November/December 2010, two von Bertalanffy growth curve equations were fitted to

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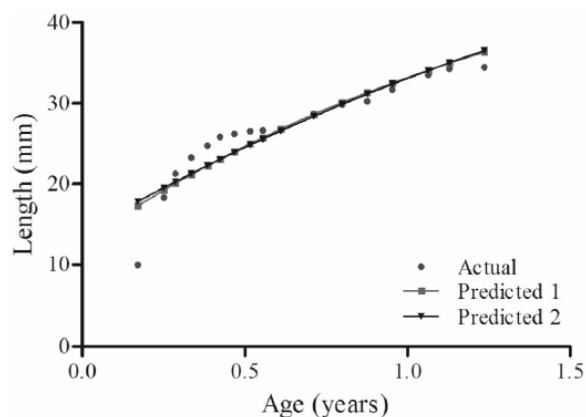


Fig. 3. von Bertalanffy growth curves estimated for *Solen cylindraceus* from *in situ* shell length measurements taken at St Lucia from March 2011 to March 2012. 'Predicted 1' was derived from a theoretical maximum length for *S. cylindraceus* of 55 mm, while 'Predicted 2' was derived from a theoretical maximum length of 70 mm.

the observed age-length data for uncaged animals only (Fig. 3). Assuming $L_{\infty} = 55$ mm, the equation produced was $L_t = 55(1 - e^{-0.66(t-0.27)})$, while $L_t = 70(1 - e^{-0.42(t-0.22)})$ was produced when the theoretical maximum length of *Solen cylindraceus* was 70 mm. This resulted in the growth parameters: $k = 0.66/\text{year}$ and $t_0 = 0.27/\text{year}$ and $k = 0.42/\text{year}$ and $t_0 = 0.22/\text{year}$, respectively. Using both von Bertalanffy growth curve equations, the estimated length of *S. cylindraceus* after its first year was 33.2 and 33.1 mm, respectively (Fig. 3). Additionally, caged and uncaged *S. cylindraceus* grew 31.0 ± 4.5 and 31.7 ± 2.3 mm, respectively, in their first year.

There was a significant relationship between the log-transformed length (mm) and width (mm) data ($F = 1505.39$, d.f. = 1, $P < 0.05$). This relationship was described by the equation $y = 0.883x - 0.721$ (Fig. 4a). The coefficient of determination obtained, $R^2 = 0.726$, suggested that about 73% of the width data can be explained by the length data. A significant regression was also found between the log-transformed length (mm) and wet weight (g) ($y = 0.038x - 0.635$) and the length and dry weight (g) ($y = 0.013x - 0.220$) data ($F_{\text{Wet}} = 422.64$, $F_{\text{Dry}} = 329.54$, d.f. = 1, $P < 0.05$). The length of *S. cylindraceus* explained 90 and 85% of the wet and dry weight data, respectively, as the coefficient of determinations obtained were $R^2 = 0.899$ and $R^2 = 0.845$, respectively.

Although the mean wet season growth rate (mm/d) was higher than that recorded in the dry season (Table 1), there was no significant difference between the two ($t = 0.734$, d.f. = 6, $P > 0.05$). The overall growth rate calculated for

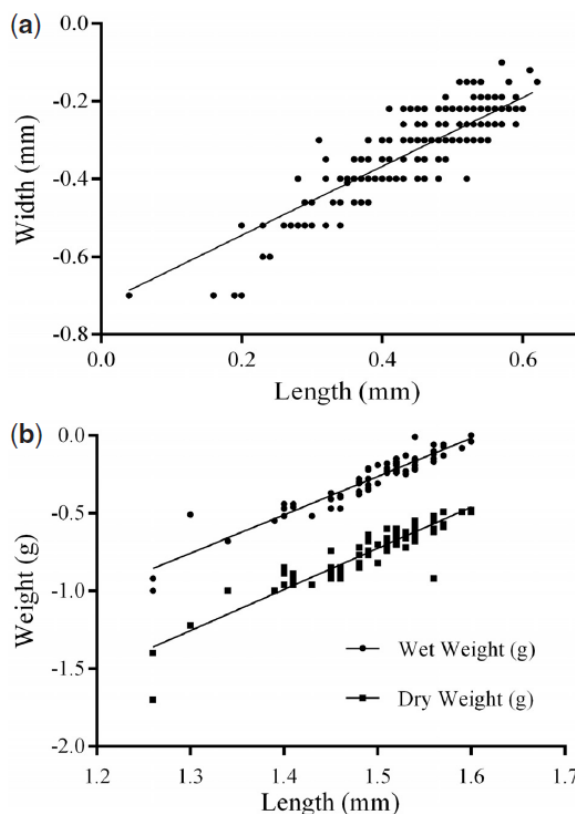


Fig. 4. a. Linear relationship between the shell length (mm) and width (mm) of *Solen cylindraceus* on log scale. **b.** Relationship between shell length (mm) and wet weight (g) and dry weight (g) of *S. cylindraceus* on log scale.

Table 1. Growth rate (mm/d) estimates for the bivalve *Solen cylindraceus* in St Lucia during the experimental period March 2011 – March 2012. S.D. = standard deviation; N = number of sampling occasions.

	N	Min	Max	Mean	S.D.
Wet season	7	0.004	0.232	0.060	0.078
Dry season	7	0.004	0.082	0.038	0.033
Overall	14	0.004	0.232	0.049	0.059

caged *S. cylindraceus* was 0.049 ± 0.059 mm/d, with a maximum and minimum growth rate of 0.232 and 0.004 mm/d, respectively (Table 1).

DISCUSSION

Solenid bivalves are regarded as key components of shallow estuarine ecosystems, because of their large density and ability to burrow rapidly in soft sandy or muddy sediments (Hodgson & de Villiers 1986; Huber 2010). Their role as powerful filter-feeders makes them potentially important in elim-

inating silt particles from the water-column, but also highlights their critical function as a link between primary producers and predators in estuarine food webs (Gerritsen *et al.* 1994; Hwang *et al.* 2004).

This study represents the first growth rate and morphometric data estimates for *Solen cylindraceus* in a subtropical region. In this study, caged and uncaged *S. cylindraceus* reached a size of 31.0 ± 4.5 and 31.7 ± 2.3 mm within their first year, respectively. This is less than the 40 mm estimated by McLachlan (1974) for *S. cylindraceus* in the Swartkops Estuary (warm-temperate region). However, McLachlan (1974) used size frequency histograms to infer growth rate data, while this study used a more direct method of measuring them *in situ*. Differences in latitude and physico-chemical parameters prevailing in the system at the time of the experiment may have an effect on the growth of bivalves (da Costa & Martínez-Patiño 2009; Moura *et al.* 2009). A faster growth rate may have been expected in St Lucia, due to it being positioned in a subtropical area. However, this was not seen, possibly due to the stressful conditions prevailing in the system at the time.

St Lucia is characterized by cyclic changes in hyper- and hyposaline conditions occurring because of alternations between drought and wetter than average years. A study on the growth of two different bivalves, *Chione cortezi* and *C. fluctifraga*, in the Colorado River Estuary showed that a reduction in freshwater inflow into the system, due to damming further upstream, resulted in an increase in salinity, which in turn caused an increase in the growth rate of these two species (Schöne *et al.* 2003). Holland & Dean (1977) suggested that increased physiological stress would cause a decrease in the size of bivalves. Large *S. cylindraceus* (40–55 mm shell length) have an experimental salinity tolerance ranging from 15 to 65 ppt (Nel *et al.* 2011). Mass mortality can occur when environmental conditions exceed the species tolerance range (Nel *et al.* 2011), resulting in bivalves being unable to reach their maximum shell length. Because St Lucia is a very variable system, salinity seldom remains within the tolerance range of *S. cylindraceus* for periods approaching 5 years (i.e. resulting in bivalves being unable to reach their estimated lifespan). During this experiment, salinities ranged from 9.7 to 35.4 ppt. Some *S. cylindraceus* individuals were alive at a salinity of 9.7 ppt, which was outside the range recorded by Nel *et al.* (2011). This suggests that a very gradual

fall in salinity may allow an expansion in its tolerance range. However, sub-lethal effects, which were not investigated, may have affected the physiology of *S. cylindraceus* individuals in this study, during the lower mesohaline period. Estuarine and marine bivalves often exhibit a decrease in growth rate when exposed to lower salinity levels (Niamaimandi 2012).

In December 2010, St Lucia experienced high rainfall that reduced the salinity at Charter's Creek from 55 to 10 ppt by January 2011. This caused mortality in larger *S. cylindraceus* individuals, and resulted in a new cohort (size range: 5–15 mm) being recruited in the gap (Nel *et al.* 2012). Matthews & Fairweather (2003) stated that bivalves may have different degrees of resilience at varying size/age cohorts. This is important in estuaries that exhibit dynamic physico-chemical conditions, as it allows the persistence of bivalve species during extreme environmental events. It is possible that *S. cylindraceus* is utilizing the same growth strategy as *Soletellina alba* in the Hopkins River Estuary (Matthews & Fairweather 2003), which accelerates growth in order to reach sexual maturity before the onset of the annual winter flooding event. Matthews & Fairweather (2003) found that bivalves often reach sexual maturity when they are approximately half their maximum size. From the estimation of size after its first growth year, it can be confidently assumed that *S. cylindraceus* will reach sexual maturity within its first year of development. Similarly, *S. dactylus* reaches sexual maturity at 46 mm, which is half its maximum length of between 101 and 108 mm (Saeedi *et al.* 2009).

This numerically and gravimetrically dominant bivalve in the St Lucia system had an overall growth rate for the first year of 0.049 ± 0.059 mm/d (Table 1). The growth rate of bivalves varies seasonally, with higher growth occurring in the summer and lower in winter (McLachlan 1974; Gasper *et al.* 1999; Urban 2002; Moura *et al.* 2009). McLachlan (1974) reported this variation in both *S. cylindraceus* and *Salmacoma litoralis* in the Swartkops Estuary. This trend was also exhibited by *S. brevis* in Iran (Niamaimandi 2012). The present study, with mean wet season growth rate of 0.060 ± 0.078 mm/d, compared to 0.038 ± 0.033 mm/d in the dry season, showed a higher growth rate in the warmer season (Table 1). However, there was no significant difference between them. During this study, mean temperature in St Lucia was $28.81 \pm 4.15^\circ\text{C}$ for the wet period and $19.89 \pm 1.75^\circ\text{C}$ during the dry period. The higher

growth rate observed in the wet season is likely due to the increased water temperature, leading to an increase in shell and tissue growth (Garton & Johnson 2000). An increase in freshwater inflow during the wet season may also result in higher food availability, which inevitably would affect the growth of bivalves. However, neither the relationship between growth rate and environmental factors nor between growth and food availability were investigated in this study.

Nel *et al.* (2011) reported that large *S. cylindraceus* found in Catalina Bay during 2010 ranged between 40 and 55 mm. Shells collected in December 1982 along the banks of St Lucia exhibited the largest length of 70 mm. The von Bertalanffy growth parameters obtained using the above information were: $L_{\infty} = 55$ mm, $k = 0.66$ /year and $t_0 = 0.27$ /year and $L_{\infty} = 70$ mm, $k = 0.42$ /year and $t_0 = 0.22$ /year. A similar growth constant of 0.7/year was estimated for *S. brevis* (Niamaimandi 2012). The k values estimated in this study fell within the range found for *Ensis directus* (0.31–0.64/year), which is regarded as a short-lived bivalve (Palmer 2004). Cranfield & Michael (2001) reported k values for *Spisula aequilatera*, *Macra murchisoni* and *M. discors* of 0.80, 0.60 and 0.35/year, respectively. Barón *et al.* (2004) determined a k value ranging from 0.20 to 0.25/year for *E. macha* in Argentina, which was lower than that recorded in the present study. Similarly, Breen *et al.* (1991) investigated the growth parameters of *Panopea zelandica* in New Zealand and obtained a low k value of 0.16/year. The high k value obtained in this study is in accordance with *S. cylindraceus* being considered a fast growing species with a short lifespan of about five years (McLachlan 1974).

Solen cylindraceus is a dominant bivalve in St Lucia, especially during dry periods when salinities may exceed the tolerance limits of other species. Although not tolerant of low salinity levels, *S. cylindraceus* appears to persist even after high rainfall events. This study showed that *S. cylindraceus* may reach sexual maturity within its first growth year. This strategy is important to ensure that it remains dominant in the system. However, it does not appear to reach its potential maximum size and age within St Lucia.

ACKNOWLEDGEMENTS

The iSimangaliso Wetlands Park Authority and Ezemvelo KZN Wildlife are gratefully acknowledged for supporting this project with logistical

and field assistance. We also thank K. Tirok, N.A.F. Miranda, D.C. Dyer, N.K. Carrasco, R. Jackson, R. Harmer, M. (Sabelo) Ngubane for their invaluable assistance in the field and laboratory. This project was funded by the National Research Foundation (NRF, Pretoria), the South African–Netherlands Research Programme on Alternatives in Development (SANPAD, Durban) and the University of KwaZulu-Natal (UKZN, Durban).

REFERENCES

- BARÓN, P.J., REAL, L.E., CIOCCO, N.F. & RÉ, M.E. 2004. Morphometry, growth and reproduction of an Atlantic population of the razor clam *Ensis macha* (Molina, 1782). *Scientia Marina* 68: 211–217.
- BEGG, G.W. 1978. *The Estuaries of Natal*. (Part II). Natal Town and Regional planning Commission Report 41: 1–657.
- BLABER, S.J.M., KURE, N.F., JACKSON, S. & CYRUS, D.P. 1983. The benthos of South Lake, St Lucia following a period of stable salinities. *South African Journal of Zoology* 18: 311–319.
- BOLTT, R.E. 1975. The benthos of some southern African Lakes Part V: The recovery of the benthic fauna of St Lucia Lake following a period of excessively high salinity. *Transactions of the Royal Society of South Africa* 41: 295–323.
- BRANCH, G.M., GRIFFITHS, C.L., BRANCH, M.L. & BECKLEY, L.E. 2010. *Two Oceans: a Guide to the Marine Life of Southern Africa*. Struik Nature, Cape Town, South Africa.
- BRASH, J.M. & FENNESSY, S.T. 2005. A preliminary investigation of age and growth of *Otolithes ruber* from KwaZulu-Natal, South Africa. *Western Indian Ocean Journal of Marine Science* 4: 21–28.
- BREEN, P.A., GABRIEL, C. & TYSON, T. 1991. Preliminary estimates of age, mortality, growth, and reproduction in the Hiatellid clam *Panopea zelandica* in New-Zealand. *New Zealand Journal of Marine and Freshwater Research* 25: 231–237.
- CARRASCO, N.K. & PERISSINOTTO, R. 2011a. Temperature and salinity tolerance of *Mesopodopsis africana* O. Tattersall in the freshwater-deprived St. Lucia Estuary, South Africa. *Journal of Experimental Marine Biology and Ecology* 399: 93–100.
- CARRASCO, N.K. & PERISSINOTTO, R. 2011b. The comparative diet of the dominant zooplankton species in the St Lucia Estuary, South Africa. *Journal of Plankton Research* 33: 479–490.
- CRANFIELD, H.J. & MICHAEL, K.P. 2001. Growth rates of five species of surf clams on a southern North Island beach, New Zealand. *New Zealand Journal of Marine and Freshwater Research* 35: 909–924.
- CYRUS, D. & VIVIER, L. 2006. Status of the estuarine fish fauna in the St Lucia Estuarine System, South Africa, after 30 months of mouth closure. *African Journal of Aquatic Science* 31: 71–81.
- DA COSTA, F. & MARTÍNEZ-PATIÑO, D. 2009. Culture potential of the razor clam *Solen marginatus* (Pennant, 1777). *Aquaculture* 288: 57–64.
- DAY, J.H., MILLARD, N.A.H. & BROEKHUYSEN, G.J. 1954. The ecology of South African estuaries part IV:

- the St Lucia system. *Transactions of the Royal Society of South Africa* **34**: 129–156.
- DE VILLIERS, C.J., ALLANSON, B.R. & HODGSON, A.N. 1989. The effect of temperature on the filtration rate of *Solen cylindraceus* (Hanley) (Mollusca: Bivalvia). *South African Journal of Zoology* **24**: 11–17.
- GARTON, D.W. & JOHNSON, L.E. 2000. Variation in growth rates of the zebra mussel, *Dreissena polymorpha*, within Lake Wawasee. *Freshwater Biology* **45**: 443–451.
- GASPAR, M.B., FERREIRA, R. & MONTEIRO, C.C. 1999. Growth and reproductive cycle of *Donax trunculus* L., (Mollusca: Bivalvia) off Faro, southern Portugal. *Fisheries Research* **41**: 309–316.
- GERRITSEN J, HOLLAND, A.F & IRVINE, D.E. 1994. Suspension-feeding bivalves and the fate of primary production – An estuarine model applied to Chesapeake Bay. *Estuaries* **17**: 403–416.
- HODGSON, A.N. & DE VILLIERS, C.J. 1986. Notes on the biology of ‘pencil-bait’ (*Solen capensis* and *Solen cylindraceus*). *The Naturalist* **30**: 16–19.
- HOLLAND, A.F & DEAN, J.M. 1977. Biology of stout razor clam *Tagelus plebeius*: II. Some aspects of population dynamics. *Chesapeake Science* **18**: 58–66.
- HWANG, S.J., KIM, H.S., SHIN, J.K., OH, J.M. & KONG, D.S. 2004. Grazing effects of a freshwater bivalve (*Corbicula leana* Prime) and large zooplankton on phytoplankton communities in two Korean lakes. *Hydrobiologia* **515**: 161–179.
- HUBER M. 2010. *Compendium of bivalves*. ConchBooks, Hackenheim, Germany.
- KILBURN, R. & RIPPEY, E. 1982. *Sea Shells of Southern Africa*. Macmillan South Africa, Johannesburg.
- MACKAY, F, CYRUS, D. & RUSSELL, K.L. 2010. Macrobenthic invertebrate response to prolonged drought in South Africa’s largest estuarine lake complex. *Estuarine, Coastal and Shelf Science* **86**: 553–567.
- MATTHEWS, T.G. & FAIRWEATHER, P.G. 2003. Growth rates of the infaunal bivalve *Soletellina alba* (Lamarck, 1818) (Bivalvia: Psammobiidae) in an intermittent estuary of southern Australia. *Estuarine, Coastal and Shelf Science* **58**: 73–885.
- McLACHLAN, A. 1974. Notes on the biology of some estuarine bivalves. *Zoologica Africana* **9**: 15–34.
- McLACHLAN, A. & ERASMUS, T. 1974. Temperature tolerances and osmoregulation in some estuarine bivalves. *Zoologica Africana* **9**: 1–13.
- MILLARD, N.A.H. & BROEKHUYSEN, G.J. 1970. The ecology of South African estuaries Part X: St Lucia: a second report. *Zoologica Africana* **5**: 277–307.
- MOURA, P., GASPAR, M.B. & MONTEIRO, C.C. 2009. Age determination and growth rate of a *Callista chione* population from the southwestern coast of Portugal. *Aquatic Biology* **5**: 97–106.
- NEL, H.A., PERISSINOTTO, R., TAYLOR, R.H. & CARRASCO, N.K. 2011. Salinity tolerance of the bivalve *Solen cylindraceus* (Hanley, 1843) (Mollusca: Euheterodonta: Solenidae) in the St Lucia Estuary. *African Invertebrates* **52**: 575–586.
- NEL, H.A., PERISSINOTTO, R. & TAYLOR, R.H. 2012. Diversity of bivalve molluscs in the St Lucia Estuary, with an annotated and illustrated checklist. *African Invertebrates* **53**: 503–525.
- NIAMAIMANDI, N. 2012. Biological parameters and abundance of the razor clam, (*Solen brevis*), from the Bushehr area of the Persian Gulf. *Agriculture, Forestry and Fisheries* **1**: 1–6.
- OWEN, R.K. & FORBES, A.T. 1997. Salinity, floods and the infaunal macrobenthic community of the St Lucia Estuary, KwaZulu-Natal, South Africa. *African Journal of Aquatic Science* **23**: 14–30.
- PALMER, D.W. 2004. Growth of the razor clam *Ensis directus*, an alien species in the Was on the east coast of England. *Journal of the Marine Biological Association of the United Kingdom* **84**: 1075–1076.
- PILLAY, D. & PERISSINOTTO, R. 2008. The benthic macrofauna of the St Lucia Estuary during the 2005 drought year. *Estuarine, Coastal and Shelf Science* **77**: 35–46.
- SAEEDI, H., RAAD, S.P., ARDALAN, A.A., KAMRANI, E. & KIABI, B.H. 2009. Growth and reproduction of *Solen dactylus* (Bivalvia: Solenidae) on northern coast of the Persian Gulf (Iran). *Journal of the Marine Biological Association of the United Kingdom* **89**: 1635–1642.
- SCHÖNE, B.R., FLESSA, K.W., DETTMAN, D.L. & GOODWIN, D.H. 2003. Upstream dams and downstream clams: growth rates of bivalve mollusks unveil impact of river management on estuarine ecosystems (Colorado River Delta, Mexico). *Estuarine, Coastal and Shelf Science* **58**: 715–726.
- URBAN, H.J. 2002. Modeling growth of different developmental stages in bivalves. *Marine Ecology – Progress Series* **238**: 109–114.
- VON BERTALANFFY, L. 1957. Qualitative laws in metabolism and growth. *Qualitative Review of Biology* **32**: 217–231.

Responsible Editor: D. Pillay

Marine & Freshwater Research: Manuscript in review

Ingestion rates and grazing impact of the Brackwater mussel, *Brachidontes virgiliae*, in Lake St Lucia, iSimangaliso Wetland Park, South Africa.

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Abstract

Bivalves feed on a combination of phytoplankton and zooplankton and as such, can have a significant impact on the planktonic biomass, especially when they occur in high densities, such as in oyster and mussel beds. *Brachidontes virgiliae* (Barnard, 1964) is currently numerically dominant within Africa's largest estuarine lake, St Lucia. The ingestion rates and grazing impact of this small mussel (maximum size = 2.5 cm) was determined for both the wet and dry seasons using an *in situ* gut fluorescence technique. Ingestion rates were higher during the wet season (5.78 $\mu\text{g pigm.ind}^{-1}.\text{d}^{-1}$) as opposed to the dry season (4.44 $\mu\text{g pigm.ind}^{-1}.\text{d}^{-1}$). This may be explained by the increased water temperature and food availability during the wet season. Due to the patchy distribution of mussel populations, there may be higher localised grazing impact near mussel aggregations. This study showed that mussel populations attached on the sediment had a grazing impact of 2.5 (wet season) and 8% (dry season) of the available phytoplankton biomass, while mussels clustered on dead oyster shells have the potential to consume 3 to 8 times the available phytoplankton biomass per day. This high grazing impact may affect the levels of phytoplankton measured in St Lucia. This needs to be factored into the management strategy for the system, as increased flood events may increase the spread and dominance of this mussel throughout the estuary.

Additional keywords: Suspension-feeding bivalves, estuarine lake, climate change, population feeding impact, diel variations.

Introduction

Suspension-feeding bivalves (i.e. mussels, oysters and clams) are often dominant constituents of estuarine benthic communities (Gerritsen *et al.* 1994; Pilditch and Grant 1999). Since bivalves utilise microalgae as a dietary component, grazing enforces a top-down control that may alter the quality and quantity of available phytoplankton standing stocks (Gerritsen *et al.* 1994; Nakamura and Kerciku 2000; Inoue and Yamamuro 2000; Rouillon and Navarro 2003; Hwang *et al.* 2004). This forms a link between the primary producers and the higher trophic consumers including crabs, fish and birds (Kamermans 1994).

Phytoplankton consumption indirectly affects water clarity by the removal of suspended particles from the surrounding environment (Gerritsen *et al.* 1994; Vaughn and Hakenkamp 2001; Hwang *et al.* 2004; Frau *et al.* 2013). This subsequently increases light availability, which may cause a positive feedback effect by promoting phytoplankton growth (Naddafi *et al.* 2007). Release of nutrients through excretion and microbial degradation of biodeposits may also stimulate microalgal growth via bottom-up forces (Newell 2004). In addition, sedimentation of faeces and pseudofaeces are important in coupling the benthic and pelagic environments (Fanslow *et al.* 1995; Pilditch and Grant 1999; Inoue and Yamamuro 2000). Lonsdale *et al.* (2009) highlighted the complexity of food web dynamics, as bivalves not only graze on phytoplankton but are simultaneously competing for, and preying on, planktonic species, such as copepod eggs and nauplii and heterotrophic protists.

A high diversity of bivalve molluscs (24 species) has historically been recorded in the St Lucia estuarine system, however due to adverse conditions, St Lucia has recently lost the majority of this community (Nel *et al.* 2012). For example, the bivalve *Barnea manilensis* (maximum size = 7.8 cm) was considered a major filter-feeder within the system, occurring at densities in excess of 100 ind.m⁻² (Nel *et al.* 2012). As a result of low water levels and hypersaline conditions prevailing during the decade 2002–2011, this bivalve no longer occurs in St Lucia. Additionally, Nel *et al.* (2012) reported three oyster species within St Lucia, none of which has been recorded alive recently. Currently, *Brachidontes virgiliae* and *Solen cylindraceus* are the two dominant bivalve species within Lake St Lucia (Nel *et al.* 2012). de Villiers *et al.* (1989) suggested that *S. cylindraceus* may have a filtration rate between 10 to 20 ml.min⁻¹. Additionally, Tirok and Scharler (2013) calculated that *S. cylindraceus* may filter the entire St Lucia volume 2.88 times per day, when found at densities of 100 ind.m⁻². The gastropod, *Tarebia granifera* also found in high densities within St Lucia has an estimated potential to consume 35% of the total microphytobenthic biomass per day (Miranda *et al.* 2011). Therefore, both molluscs playing a major role on ecosystem structure and function.

Brachidontes virgiliae (maximum size = 2.5 cm) is an estuarine mussel that attaches to stones, drift logs, roots and submerged macrophytes (Kilburn and Rippey 1982; Appleton 1996; Branch *et al.* 2010). Endemic to southern Africa, this species is currently widespread in the St Lucia estuarine system (Begg 1978; Branch *et al.* 2010; Huber 2010), an integral component of the iSimangaliso Wetland Park. St Lucia typically experiences fluctuations from wet to dry phases (Begg 1978). Due to the above average rainfall the system has recently been receiving, coupled with the recent reconnection of the St Lucia Estuary with the Mfolozi River, the system has undergone a regime shift from a dry hypersaline to a wet phase. St Lucia is presently dominated by oligohaline to polyhaline (< 25) conditions. This has resulted in *B. virgiliae* becoming widespread throughout the system, as it thrives under near-freshwater conditions (H.A. Nel, unpubl. data). Nel *et al.* (2012) recorded the maximum benthic density of *B. virgiliae* at 51 ind.m⁻², however, this does not take into account the extremely dense aggregations currently observed on macrophytes, boat hulls and dead oyster beds (H.A. Nel, pers. obs.). Davies (1982) recorded densities ranging from 1 x 10³ to 1 x 10⁶ ind.m⁻² as surface area for attachment increased in Swartvlei.

This study used an *in situ* gut fluorescence technique, which is typically utilized in the study of zooplankton feeding dynamics (e.g. Perissinotto 1992; Froneman 2000; 2001 & 2004; Carrasco and Perissinotto 2010), although recently Miranda *et al.* (2011) and Diaz *et al.* (2012) successfully employed this technique when investigating the grazing impact of the gastropods *Tarebia granifera* and *Littorina littorea*, respectively. Given the extremely high localised densities of *B. virgiliae*, there was a need to establish the effect this mussel may have on the available phytoplankton biomass. Thus, the overarching aim of the present study was to investigate the ingestion rate of the epifaunal bivalve, *B. virgiliae* in the St Lucia estuarine system and determine the impact this species may have on the available phytoplankton standing stock.

Materials and methods

Brachidontes virgiliae were collected from the lower reaches of the Narrows, St Lucia estuarine system (Fig. 1). Mussels with a size range between 0.6 and 1.9 cm were individually removed from the macrophyte *Stukenia pectinata* or from stationary boats located at the sampling area (Fig. 1). A single area was investigated in this study, due to their poor accessibility in most areas of the system because of the presence of crocodiles and hippos. On all occasions physico-chemical data were measured using a YSI 6600V2-D water quality logger, fitted with temperature, salinity, dissolved oxygen, pH and turbidity probes.

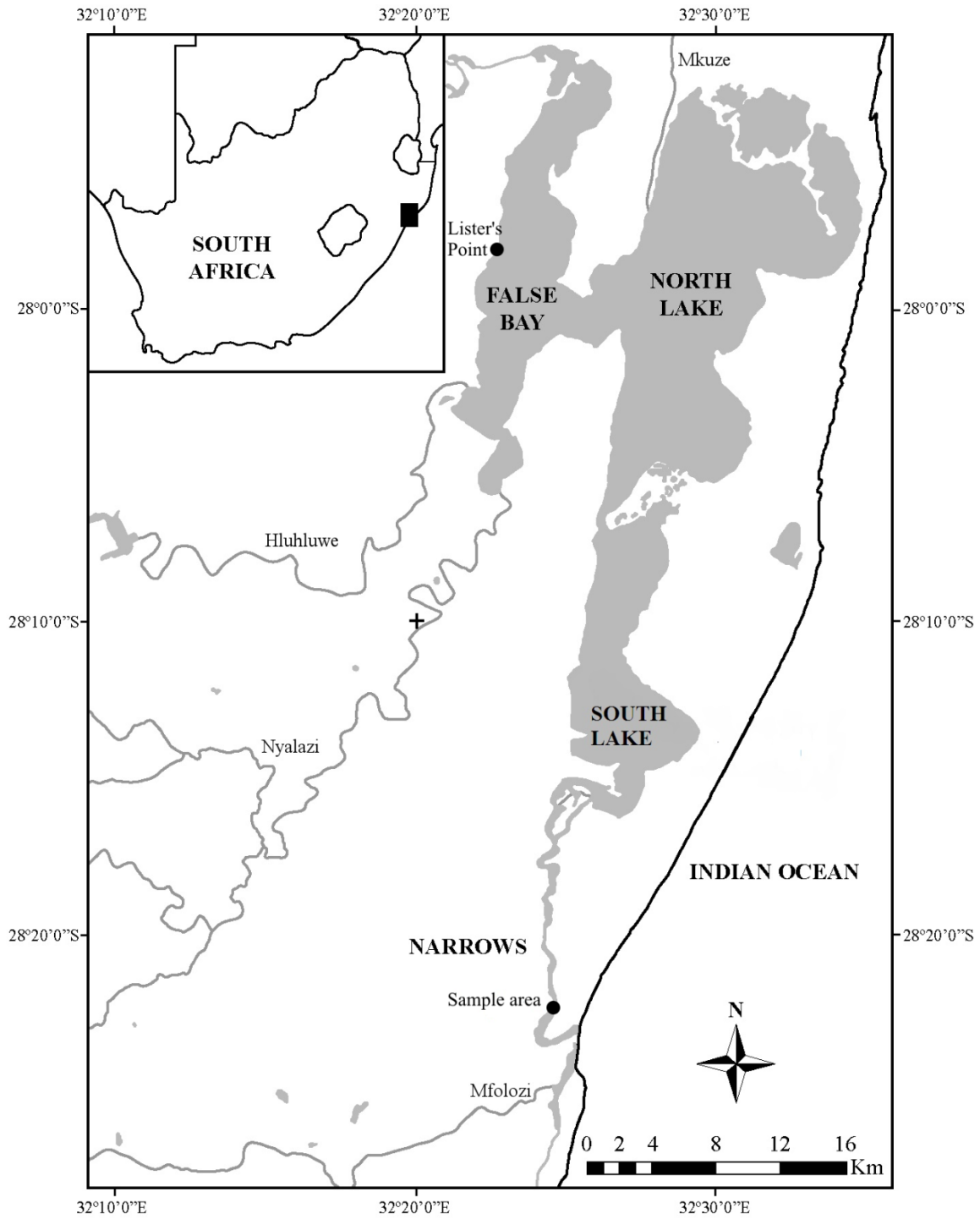


Fig. 1: Map showing the collection site of *Brachidontes virgiliae* used in the feeding experiments during both wet and dry seasons within the St Lucia estuarine system, as well as the sampling site of Lister's Point in the northern reaches (adapted from Carrasco and Perissinotto 2010).

Gut pigment content

The variation in *B. virgiliae* day/night gut pigment concentrations were determined during both November 2012 (wet season) and June 2013 (dry season). Ten individual bivalves were collected at 3 hr intervals for a period of 24 hrs. Bivalves were rinsed using filtered estuarine water (0.2 μm) and epizoic algae were gently removed. Valves were opened and the soft mass was excised and placed in individual test tubes containing 8 mL of 90% acetone solution. Test tubes were then stored at 4°C for 48 hrs in the dark, to allow for pigment extraction. Chlorophyll *a* and phaeopigments were measured using a Turner Designs 10-AU fluorometer, fitted with a non-acidification system (Nozais *et al.* 2001). Thereafter, measurements of total pigments (chl *a* and phaeopigment combined) were size standardized to account for differences in animal size ($\mu\text{g pigm.ind}^{-1}$). For this purpose, an animal size with mean and standard deviation of 1.07 ± 0.20 cm was used, on the basis of surveys conducted through the area prior to the study. Simultaneously, triplicate subsurface water samples were collected using 1 L polyethylene bottles. A 250 mL subsample was filtered through a GF/F glass fiber filter to determine total phytoplankton biomass. Filters were placed in individual test tubes and chlorophyll pigment equivalents were extracted and determined using the same method as above. An independent sample t-test was performed in SPSS version 21 for Windows, to investigate differences between day and night in gut pigment contents and water-column phytoplankton biomass. The period from 06:00 to 18:00 was included in the day sample during the dry season and from 05:30 to 18:30 in the wet season (Carrasco and Perissinotto 2010). The t-test was run after both the one-sample Kolmogorov-Smirnov normality and Levene's test were satisfied ($p > 0.05$).

Ingestion rates

Ingestion rates ($\mu\text{g pigm.ind}^{-1}.\text{d}^{-1}$) were estimated using the *in situ* gut fluorescence approach that utilises the equation (Perissinotto 1992),

$$I = kG/(1-b),$$

where: *I* = ingestion rate, *k* = gut evacuation rate constant (h^{-1}); *G* = integrated gut pigment concentration for a 24 hr period ($\mu\text{g pigm.ind}^{-1}$) and *b* = gut pigment assimilation/destruction index (%).

All gut evacuation experiments were conducted during November and December 2012 (wet season), and June and early September 2013 (dry season). The gut evacuation rate (*k*) was estimated using freshly caught bivalves that had been rinsed in filtered estuarine water and cleaned of epizoic algae. Bivalves were individually placed in separate 100 mL plastic vials, each containing a solution of filtered estuarine water and non-flourescent corn starch. The estuarine water was filtered through both a GF/F filter (0.7 μm) and a 0.22 μm Millipore filter, in order to eliminate any other grazers or algal material. Corn starch was added to the medium in order to allow the bivalves to feed continuously and displace previously ingested food (Perissinotto 1992). Animals were removed from the incubations

every ten minutes for the first 30 minutes, then every 30 minutes for the next three hours and every hour thereafter. The final incubation time was six hours. At each time interval, the entire tissue mass was excised from the valves and placed in 8 mL 90% acetone for chlorophyll pigment extractions, as described above. Ten replicates were used for the zero time intervals and five for each subsequent time interval thereafter. The results were assumed to follow a negative exponential model, thus 10% outliers were removed accordingly (Perissinotto and Pakhomov 1996; Miranda *et al.* 2011). The gut evacuation rate constant (K) was then estimated from the regression slope calculated by the change in log-transformed gut pigment content versus time (Perissinotto and Pakhomov 1996).

To calculate the gut assimilation/destruction efficiency (*b*) the two-compartment (water and grazer) pigment budget approach was used (Lopez *et al.* 1988). Prior to the experiment, bivalves were allowed to empty their guts for 48 to 72 hrs in a filtered estuarine water and corn starch solution (as above). The experiment consisted of five replicate 250 mL plastic jars that each contained a single bivalve in naturally occurring estuarine water. The estuarine water was sieved through a 55 µm mesh in order to remove larger metazoan grazers. Five replicates without grazers served as the control. After a 1 hr incubation period, each replicate was individually filtered through a GF/F filter and tissue mass was removed from each animal. Phytoplankton biomass and gut pigment content were determined using the methods described above. The loss of pigments by absorption/destruction was estimated from measurements of decrease in pigment content of grazing bottles and in gut measurements of animals incubated in the bottles, as no fecal pellets were produced throughout the experiment. Gut assimilation/destruction efficiency was calculated using the following equation (Perissinotto 1992),

$$b(\%) = \{[(G_t - P_b)/P] - 1\} 100,$$

where: G_t = gut pigment content (ng pigm.ind⁻¹) at the end of the incubation; P_b = background fluorescence (ng pigm.ind⁻¹) and P = total amount of pigment ingested (mg chl a .m⁻³), P is derived from the difference between the control (C_t) and experimental (E_t) bottles at the end of the incubation divided by (n) the number of animals in the grazing bottle.

Mussel abundance and grazing impact

Quantitative samples were taken to estimate mussel densities within St Lucia. Highest densities were estimated by removing five randomly selected oyster shells from Lister's Point (Fig. 1). Mussels within the size class 6 – 19 mm were gently removed and counted. Thereafter, the oyster shell was cleaned and surface area was estimated using the paraffin wax coating method (Naumann *et al.* 2009). Paraffin wax (ACE, paraffin wax refined) was melted, inside a water bath, at 80°C in a 250 mL glass jar. Oysters were dipped into the melted paraffin wax for 4 s and weighed. Subsequently, they were re-dipped for 4 s and re-weighed. The difference between the initial and final weight (x) was used to determine the surface area (y) using the following regression relationship: $y = 0.001x + 0.017$, $R^2 =$

0.973 (Y. Kisten, pers. comm.). The lowest density was estimated using a Zabalocki-type Ekman grab (sampling area 0.0236 m²; depth 15 cm). A single sample comprised three grabs and three replicate samples were taken at Lister's Point (Fig. 1). The method used followed the procedure described in Nel *et al.* (2012).

Brachidontes virgiliae population grazing impact was calculated as the product of bivalve abundance and individual ingestion rates for each season. Grazing impact was then expressed as a percentage of the mean phytoplankton standing stock consumed per day.

Results

Gut pigment content

The diel variation in gut pigment concentration of *Brachidontes virgiliae* ranged from 0.49 to 2.58 $\mu\text{g pigm.ind}^{-1}$ during the wet season, and from 0.18 to 1.12 $\mu\text{g pigm.ind}^{-1}$ during the dry season. A two-fold higher gut pigment content was recorded during the wet in comparison to the dry season, $1.30 \pm 0.47 \mu\text{g pigm.ind}^{-1}$ versus $0.62 \pm 0.22 \mu\text{g pigm.ind}^{-1}$, respectively (Table 1). Figure 2 shows no visible difference between day/night samples for both wet and dry seasons. However, there was a significant difference between the day and night gut contents during the dry season ($t = -2.001$, $df = 78$, $p < 0.05$), although this was not the case for the wet season data ($t = -1.398$, $df = 77$, $p > 0.05$). However, there was a high degree of variability among individuals within this study. Total phytoplankton biomass revealed average values of $3.568 \pm 1.781 \text{ mg.m}^{-3}$ and $1.235 \pm 0.227 \text{ mg.m}^{-3}$ for the wet and dry season, respectively (Table 1). A significant difference between the day and night was found for both wet and dry seasons ($t_{\text{WET}} = 5.410$, $t_{\text{DRY}} = 3.202$, $df = 22$, $p < 0.05$).

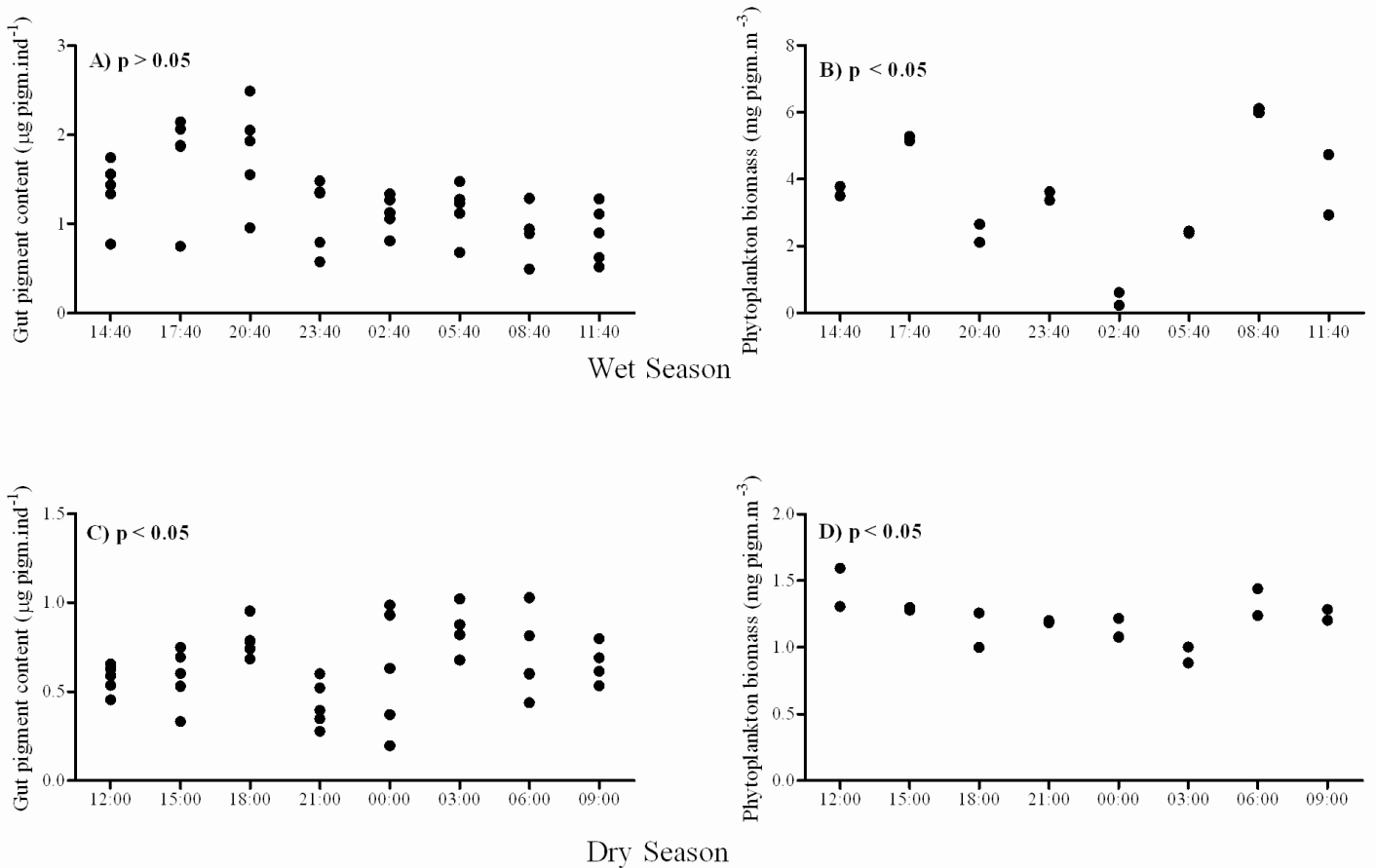


Fig. 2: Diel variations in gut pigment content ($\mu\text{g pigm.ind}^{-1}$) of *Brachidontes virgiliae* collected in the Narrows during the wet (A, November 2012) and dry season (C, June, 2013); as well as phytoplankton biomass (mg.m^{-3}) at the same locality during the wet (B, November 2012) and dry season (D, June 2013).

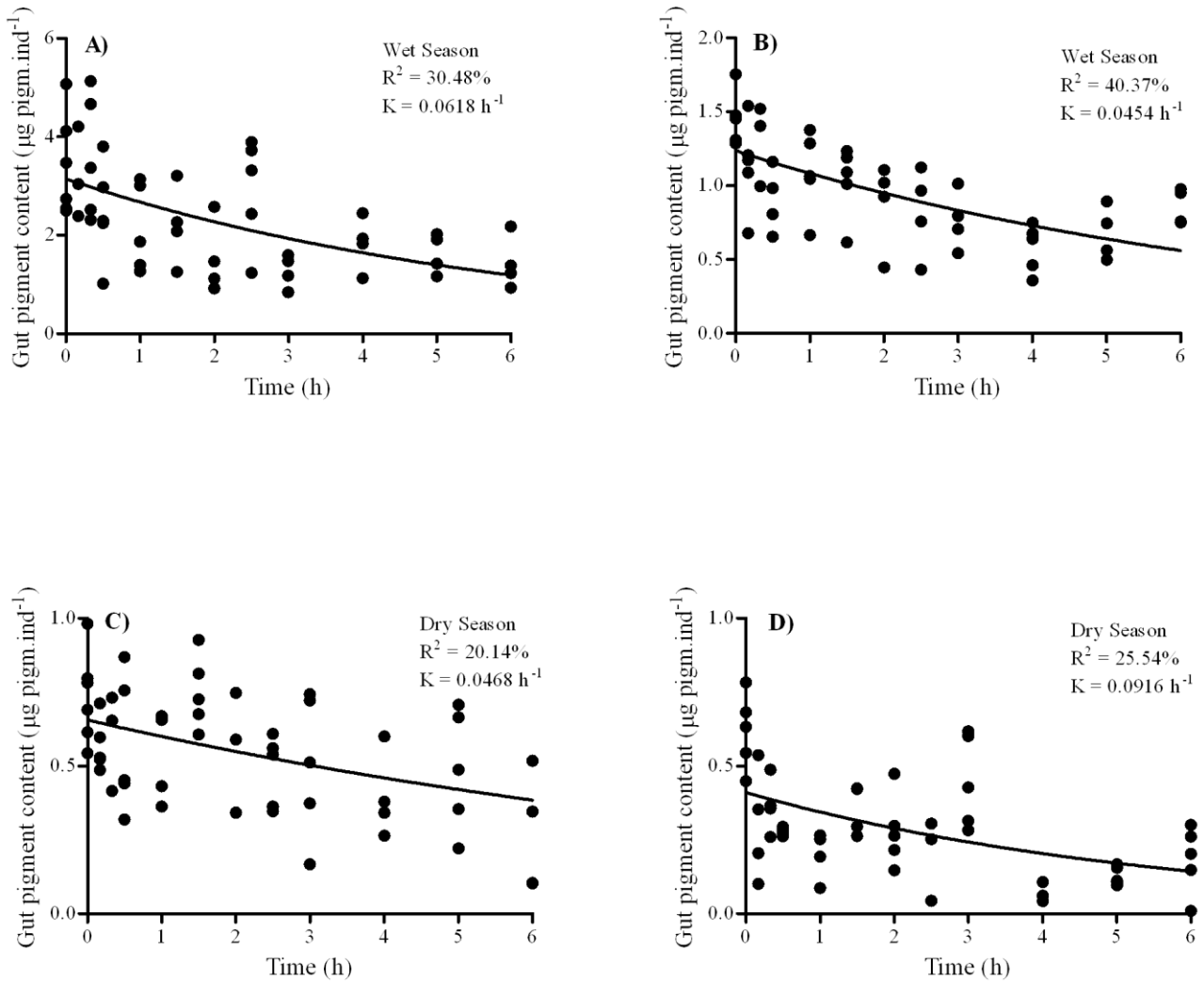


Fig. 3: Gut evacuation rates (K , h^{-1}) of *Brachidontes virgiliae* (mean individual size; 1.07 ± 0.6 cm) collected in the Narrows during the wet season (A, November and B, December 2012) and the dry season (C, June and D, September 2013).

Ingestion rates

In all four experiments, a negative exponential model was fitted to the declining gut pigment concentration over the 6 hour feeding period (R^2 values ranged from 32.0 to 33.7% for the wet season and 22.9 to 27.0% for the dry season). The initial gut pigment concentration was higher during both wet season experiments, as compared to the dry season (Fig. 3). The calculated gut evacuation rate constant (K) was low in both seasons (Fig. 3), with the wet season showing values of 0.0618 and 0.0454 h^{-1} , and the dry season of 0.0468 and 0.0916 h^{-1} (Fig. 3). These values correspond to the following gut passage time: 16.18 – 22.03 h (wet season) and 21.38 – 10.92 h (dry season).

The gut pigment assimilation/destruction efficiency (b) was calculated at 71% for the wet season and 78% for the dry season. This resulted in an overall ingestion rate for *B. virgiliae* of 5.78 and 4.44 $\mu\text{g pigm.ind}^{-1}.\text{d}^{-1}$ for the wet and dry season, respectively.

Mussel abundance and grazing impact

Dense aggregations were observed attached to substrates such as stones/rocks, submerged logs, dead oyster beds and macrophyte fronds. An estimate of the highest density was calculated for oyster shells at Lister's Point, amounting to $2178 \pm 742 \text{ ind.m}^{-2}$ (Fig. 4). The lowest density was estimated for mussels attached to scattered objects on the sediment. This was calculated at $20 \pm 27 \text{ ind.m}^{-2}$. The population feeding impact was calculated at 0.116 and 0.089 $\text{mg pigm.m}^{-2}.\text{d}^{-1}$, using the lowest density. This resulted in a grazing impact of 2.5 and 8.0% consumption of phytoplankton biomass per day. Using the maximum density, the population feeding impact was 12.6 and 9.67 $\text{mg pigm.m}^{-2}.\text{d}^{-1}$ for the wet and dry season, respectively. This equated to a grazing impact of 271 and 870% of phytoplankton biomass for the wet and dry season, respectively.



Fig. 4: Dense aggregations of brack-water mussels, *Brachidontes virgiliae* on dead oyster beds along the shoreline of False Bay, Lister's Point 14 April 2013 (Photo: Lynette Clennell).

Table 1: Physico-chemical variables (salinity, temperature and turbidity), phytoplankton biomass (PP, mg.m⁻³; mean \pm SD), and mean estimates of gut pigment content (G, ng pigm.ind⁻¹), gut evacuation rates (k, h⁻¹), gut pigment destruction (*b*, %) and ingestion rates (I, μ g pigm.ind⁻¹.d⁻¹) measured on each sampling occasion.

	Salinity	Temp (°C)	Turbidity (NTU)	PP (mg.m ⁻³)	G (μ g pigm.ind ⁻¹)	k (h ⁻¹)	<i>b</i> (%)	I (μ g pigm.ind ⁻¹ .d ⁻¹)
Wet Season	1.52 \pm 0.37	26.76 \pm 0.90	31.37 \pm 10.95	3.568 \pm 1.781	1.30	0.0537	71	5.78
Dry Season	22.8 \pm 0.54	16.50 \pm 5.87	6.55 \pm 1.34	1.235 \pm 0.227	0.62	0.0660	78	4.44

Discussion

Atkinson *et al.* (2013) highlighted that the spatially heterogeneous nature of mussel distribution results in their effect on the surrounding communities being equally heterogeneous. During this study, densities in excess of 2000 ind.m⁻² were recorded on dead oyster beds at Lister's Point (Fig. 4). This is in contrast to the low densities found within the sediment (20 ± 27 ind.m⁻²). The results of the present study indicate that *Brachidontes virgiliae* may exert a substantially lower grazing impact when scattered on the sediment, with 2.5 and 8.0% consumption of phytoplankton per day, for the wet and dry season respectively. Conversely, mussels aggregated on dead oyster beds have the potential to consume 3 to 8 times the available phytoplankton standing stock. Carrasco and Perissinotto (2010) reported that the grazing impact of the mysid *Mesopodopsis africana* at Charter's Creek and the Mouth of St Lucia was estimated at 3.05% and 11.0% of phytoplankton biomass per day, at the respective sites. Additionally, the gastropod, *Tarebia granifera* showed a 0.5 to 1.8% consumption of microphytobenthic biomass per day at Catalina Bay during freshwater conditions, and 3.6 to 23.9% during brackish states (Miranda *et al.* 2011). Thus, the grazing effect of mussels is within the range of other St Lucia grazers, although localised areas with high densities show an elevated grazing impact possibly causing localised biological oligotrophication (Vaughn and Hakenkamp 2001).

Bivalves have globally been recognised as ecosystem engineers, shaping the planktonic community. Notable decreases in chlorophyll-a concentration were recorded as water come into close proximity with mussel beds in two Dutch estuaries (Dame *et al.* 1991). The zebra mussel, *Dreissena polymorpha*, population within Saginaw Bay, U S A, was able to filter the volume of the inner bay 1.3 times per day in 1992 and 0.2 times in 1993 (Fanslow *et al.* 1995). In addition, the mussel population in two Korean lakes had a significant effect on both phytoplankton density and biomass (Hwang *et al.* 2004). Frau *et al.* (2013) used mesocosm experiments to illustrate the reduction in both phytoplankton and zooplankton in the presence of *Limnoperna fortunei*. The blue mussel, *Mytilus galloprovincialis* in Spain caused a severe depletion in chlorophyll *a* and zooplankton in the waters surrounding cultivation rafts (Petersen *et al.* 2008). Bivalves not only feed on primary producers but prey on heterotrophic protists (flagellates and ciliates), bacteria, and crustacean zooplankton mainly as copepod eggs and/or nauplii (Pace *et al.* 1998; Davenport *et al.* 2000; Lonsdale *et al.* 2009). Therefore, although mussel aggregations in St Lucia have the potential to consume 3 to 8 times the available phytoplankton standing stock, they have the ability to utilise alternate sources of energy as well.

Situated in a subtropical region, the St Lucia estuarine system is strongly influenced by the shift between wet (October – April) and dry (May – September) seasons, rather than seasonal temperature variations (Tirok and Scharler 2013). However, a higher temperature was recorded in this study

during the wet season, which broadly coincides with the late spring to summer months. Kamermans (1994) investigated the similarity between deposit and suspension-feeding bivalves and suggested that the higher temperatures associated with summer may influence bivalve feeding mechanisms (Table 1). Generally, suspension-feeding activity does show a pronounced seasonal pattern, with the most activity in spring and summer (Gerritsen *et al.* 1994). Although it is well documented that temperature has an effect on the uptake and release rates of bivalve species (Dame *et al.* 1991; Widdows 2001), food concentration also significantly affects bivalve filtration rates. The reduced phytoplankton biomass observed during the colder winter months can in part be attributed to the effect of lower water temperatures on the growth rates of phytoplankton. Similar to what was obtained by Kamermans (1994), in the current study maximum pigment content of mussel stomachs corresponded with the months of maximum phytoplankton biomass. A phytoplankton biomass of $3.57 \pm 1.78 \text{ mg}\cdot\text{m}^{-3}$ was recorded during the wet season. This was higher than that of $1.24 \pm 0.23 \text{ mg}\cdot\text{m}^{-3}$ associated with the dry season. This correlates with a two-fold increase in gut pigment content during the wet season (Table 1). Freshwater input, or re-suspension of bottom-regenerated nutrients, is widely accepted as controlling phytoplankton biomass in most South African estuaries (Pinckney *et al.* 2001). Salinity also varies between seasons, with a lower salinity level expected during the wet period as a result of higher rainfall (Tirok and Scharler 2013). This was evident in the current study, as a salinity of 22.82 ± 0.54 was associated with the dry season, while near freshwater conditions prevailed during the wet period. Increased water inflow, may also result in increased macronutrients entering the system, thus leading to increased phytoplankton production (Froneman 2004).

Temperature, salinity and initial gut content have been known to affect the gut evacuation rate (k) of filter-feeding species (Pakhomov *et al.* 1997; Irigoien 1998; Froneman 2004). In this study, *B. virgiliae* had a gut evacuation rate of 0.054 and 0.066 h^{-1} for the wet and dry season, respectively (Table 1). This equates to a gut passage time of 18.52 h for the wet season and 15.15 h for the dry season. These values do not fall within the range reported for any zooplankton species: e.g. *Acartia longipatella* and *Pseudodiaptomus hessei* had values ranging from 0.38 – 0.58 and 0.29 – 0.77 h^{-1} , respectively; *Euphausia superba* between 0.133 and 0.424 h^{-1} ; mixed mesozooplankton between 0.97 and 1.96 h^{-1} (Perissinotto 1992; Pakhomov *et al.* 1997; Froneman 2004). These extremely low gut evacuation rates also fall out of the range reported by Miranda *et al.* (2011) for the gastropod *Tarebia granifera* (0.36 - 0.62 h^{-1}). A possible explanation for the low k values observed in *B. virgiliae* is the sessile lifestyle of mussels. Gili and Coma (1998) highlighted that filter-feeding mussels use minimal energy while foraging for food and generally exhibit very low metabolic activity. The gut evacuation experiment also requires individuals to continuously feed, but this becomes difficult when animals are disturbed and remain tightly shut for some time. This may result in very low gut evacuation rates been measured. Miranda *et al.* (2011) reported similar responses in *T. granifera*, with periods of quiescence in the field resulting in high variability amongst individual gut pigment content.

A wide variation in individual gut pigment data was reported in the current study. This may be attributed to the cluster formation within mussel beds, resulting in individuals within the population receiving alternate restrictions in food availability (Tuchman *et al.* 2004). This variability was also seen in the study of Miranda *et al.* (2011) and was attributed to the complexity in the feeding history experienced by each individual. Individual feeding variability has been widely reported for molluscs and this may result in individual grazing impacts to differ (Miranda *et al.* 2011). Bricelj and Malouf (1984) suggested an individual variability in clearance rate for the clam *Mercenaria mercenaria*. MacDonald and Ward (2009) and Pilditch and Grant (1999) highlighted the fact that there are many exogenous and endogenous factors that may affect individuals. For instance micro-variations in food availability will change an individual feeding history and, therefore, the local grazing impact (Pilditch and Grant 1999). Fanslow *et al.* (1995) also mentioned that individuals may have an influence on each other, which results in laboratory determination of filtration rates to be generally inaccurate. Newell (2004) even highlighted the possible competition between bivalves and zooplankton as compounding inter-individual variability.

In summary, the estimated grazing impact for *Brachidontes virgiliae* at a background density of 20 ± 27 ind.m⁻² was 2.5 and 8.0% consumption of phytoplankton per day. However, when the densest mussel concentrations observed in the St Lucia estuarine lake system are considered, the population can consume 3 to 8 times the phytoplankton standing stock. This shows the significant effect *B. virgiliae* may have as a major top-down player during wet phases in Lake St Lucia. This may be underestimated, as smaller and larger mussels were not included in the calculations of grazing impact. More work needs to be done to investigate the extent to which secondary consumers and even detritus may contribute to the diet of *B. virgiliae*. Additionally, nutrient enrichment via mussel excretion needs to be determined, with a view to the role that this may play as “fertiliser” in phytoplankton growth, especially near mussel aggregations. Overall, brackwater mussels play an important role in structuring phytoplankton biomass within St Lucia and this needs to be recognised when estimating energy budgets for the system.

Acknowledgements

iSimangaliso Park Authority and Ezemvelo KZN Wildlife staff and management supported this project and are thus greatly appreciated. A special thanks to Ricky Taylor, Roy Jackson, Nelson Miranda, David Dyer, Nasreen Peer and Salome Jones for assisting with the collection of mussels and physico-chemical data in the field. The National Research Foundation (NRF, Pretoria), the South African Netherlands Research Programme on Alternatives in Development (SANPAD, Durban) and the University of KwaZulu-Natal (UKZN, Durban) provided the necessary funding for this project.

References

- Appleton, C.C. (1996). 'Freshwater Molluscs of Southern Africa.' (University of Natal Press: Pietermaritzburg.)
- Atkinson, C.L., Vaughn, C.C., Forshay, K.J., and Cooper, J.T. (2012). Aggregated filter-feeding consumers alter nutrient limitation: consequences for ecosystem and community dynamics. *Ecology* **94**, 1359-1369.
- Begg, G. W. (1978). 'The estuaries of Natal. Natal Town and Regional Planning Report 41.' (Blackhouse, Pietermaritzburg).
- Branch, G.M., Griffiths, C.L., Branch, M.L., and Beckley, L.E. (2010). 'Two Oceans: a Guide to the Marine Life of Southern Africa.' (StruikNature: Cape Town).
- Bricelj, V.M., and Malouf, R.E. (1984). Influence of algal and suspended sediment concentrations on the feeding physiology of the hard clam *Mercenaria mercenaria*. *Marine Biology* **84**, 155-165.
- Carrasco, N.K., and Perissinotto, R. (2010). *In situ* feeding rates and grazing impact of *Mesopodopsis africana* O. Tattersall in the St Lucia Estuary, South Africa. *Journal of Experimental Marine Biology and Ecology* **396**, 61-68.
- Dame, R., Dankers, N., Prins, T., Jongsma, H., and Smaal, A. (1991). The influence of mussel beds on nutrients in the Western Wadden Sea and Eastern Scheldt estuaries. *Estuaries* **14**, 130-138.
- Davenport, J., Smith, R., and Packer, M. (2000). Mussels *Mytilus edulis*: significant consumers and destroyers of mesozooplankton. *Marine Ecology Progress Series* **198**, 131-137.
- Davies, B.R. (1982) Studies on the zoobenthos of some southern Cape coastal lakes. Spatial and temporal changes in the benthos of Swartvlei, South Africa, in relation to changes in the submerged littoral macrophyte community. *Journal of the Limnological Society of Southern Africa* **8**, 33-45.

- De Villiers, C.J., Allanson, B.R., and Hodgson, A.N. (1989). The effect of temperature of the filtration rate of *Solen cylindraceus* (Hanley) (Mollusca: Bivalvia). *South African Journal of Zoology* **24**, 11-17.
- Diaz, E.R., Kraufvelin, P., and Erlandsson, J. (2012). Combining gut fluorescence technique and spatial analysis to determine *Littorina littorea* grazing dynamics in nutrient-enriched and nutrient-unenriched littoral mesocosms. *Marine Biology* **159**, 837-852.
- Fanslow, D.L., Nalepa, T.F., and Lang, G.A. (1995). Filtration rates of the zebra mussel (*Dreissena polymorpha*) on natural seston from Saginaw Bay, Lake Huron. *Journal of Great Lakes Research* **21**, 489-500.
- Frau, D., Molina, F.R., Devercelli, M., and de Paggi, S.J. (2013). The effect of an invading filter-feeding bivalve on a phytoplankton assemblage from the Parana system: a mesocosm experiment. *Marine and Freshwater Behaviour and Physiology* **45**, 303-316.
- Froneman, P.W. (2000). Feeding studies on selected zooplankton in a temperate estuary, South Africa. *Estuarine, Coastal and Shelf Science* **51**, 543-552.
- Froneman, P.W. (2001). Feeding ecology of the mysid, *Mesopodopsis wooldridgei*, in a temperate estuary along the eastern seaboard of South Africa. *Journal of Plankton Research* **23**, 999-1008.
- Froneman, P.W. (2004). *In situ* feeding rates of the copepods, *Pseudodiaptomus hessei* and *Acartia longipatella*, in a temperate, temporarily open/closed Eastern Cape estuary. *South African Journal of Science* **100**, 577-583.
- Gerritsen, J., Holland, A.F., and Irvine, D.E. (1994). Suspension-feeding bivalves and the fate of primary production – An estuarine model applied to Chesapeake Bay. *Estuaries* **17**, 403-416.
- Gili, J.M., and Coma, R. (1998). Benthic suspension feeders: their paramount role in littoral marine food webs. *Trends in Ecology and Evolution* **13**, 316-321.
- Huber, M. (2010). 'Compendium of Bivalves.' (ConchBooks: Hackenheim.)

- Hwang, S.J., Kim, H.S., Shin, J.K., Oh, J.M., and Kong, D.S. (2004). Grazing effects of a freshwater bivalve (*Corbicula leana* Prime) and large zooplankton on phytoplankton communities in two Korean lakes. *Hydrobiologia* **515**, 161-179.
- Inoue, T., and Yamamuro, M. (2000). Respiration and ingestion rates of the filter-feeding bivalve *Musculista senhousia*: implications for water-quality control. *Journal of Marine Systems* **26**, 183-192.
- Irigoiien, X. (1998). Gut clearance rate constant, temperature and initial gut contents: a review. *Journal of Plankton Research* **20**, 997-1003.
- Kamermans, P. (1994). Similarity in food source and timing of feeding in deposit-feeding and suspension-feeding bivalves. *Marine Ecology Progress Series* **104**, 63-75.
- Kilburn, R., and Rippey, E. (1982). 'Sea Shells of Southern Africa.' (Macmillan South Africa: Johannesburg).
- Lonsdale, D.J., Cerrato, R.M., Holland, R., Mass, A., Holt, L., Schaffner, R.A., Pan, J., and Caron, D.A. (2009). Influence of suspension-feeding bivalves on the pelagic food webs of shallow, coastal embayment's. *Aquatic Biology* **6**, 263-279.
- Lopez, M.D.G., Huntley, M.E., and Sytles, P.F. (1988). Pigment destruction by *Calanus pacificus*: impact on the estimation of water column fluxes. *Journal of Plankton Research* **10**, 715-734.
- MacDonald, B.A., and Ward, J.E. (2009). Feeding activity of scallops and mussels measured simultaneously in the field: Repeated measures sampling and implications for modelling. *Journal of Experimental Marine Biology and Ecology* **371**, 42-50.
- Miranda, N.A.F., Perissinotto, R., and Appleton, C.C. (2011). Feeding dynamics of the invasive gastropod *Tarebia granifera* in coastal and estuarine lakes of northern KwaZulu-Natal, South Africa. *Estuarine, Coastal and Shelf Science* **91**, 442-449.
- Naddafi, R., Pettersson, K., and Eklov, P. (2007). The effect of seasonal variation in selective feeding by zebra mussels (*Dreissena polymorpha*) on phytoplankton community composition. *Freshwater Biology* **52**, 823-842.

- Nakamura, Y., and Kerciku, F. (2000). Effects of filter-feeding bivalves on the distribution of water quality and nutrient cycling in a eutrophic coastal lagoon. *Journal of Marine Systems* **26**, 209-221.
- Naumann, M.S., Niggli, W., Laforsch, C., Glaser, C., Wild, C. (2009). Coral surface area quantification-evaluation of established techniques by comparison with computer tomography. *Coral Reefs* **28**, 109-117.
- Nel, H.A., Perissinotto, R., and Taylor, R.H. (2012). Diversity of bivalve molluscs in the St Lucia Estuary, with an annotated and illustrated checklist. *African Invertebrates* **53**, 503-525.
- Newell, R.I.E. (2004). Ecosystem influences of natural and cultivated populations of suspension-feeding bivalve molluscs: A review. *Journal of Shellfish Research* **23**, 51-61.
- Nozais, C., Perissinotto, R., and Mundree, S. (2001). Annual cycle of microalgal biomass in a South African temporarily-open estuary: nutrient versus light limitation. *Marine Ecology Progress Series* **223**, 39-48.
- Pace, M.L., Findlay, S.E.G., and Fischer, D. (1998). Effects of an invasive bivalve on the zooplankton community of the Hudson River. *Freshwater Biology* **39**, 103-116.
- Pakhomov, E.A., Perissinotto, R., Froneman, P.W., and Miller, D.G.M. (1997). Energetics and feeding dynamics of *Euphausia superba* in the South Georgia region during the summer of 1994. *Journal of Plankton Research* **19**, 399-423.
- Petersen, J.K., Nielsen, T.G., van Duren, L., and Maar, M. (2008). Depletion of plankton in a raft culture of *Mytilus galloprovincialis* in Ria de Vigo, NW Spain. I. Phytoplankton. *Aquatic Biology* **4**, 113-125.
- Perissinotto, R. (1992). Mesozooplankton size-selectivity and grazing impact on the phytoplankton community of the Prince Edward Archipelago (Southern-Ocean). *Marine Ecology Progress Series* **79**, 243-258.
- Perissinotto, R., and Pakhomov, E.A. (1996). Gut evacuation rates and pigment destruction in the Antarctic krill *Euphausia superba*. *Marine Biology* **125**, 47-54.

- Pilditch, C.A., and Grant, J. (1999). Effect of variations in flow velocity and phytoplankton concentration on sea scallop (*Placopecten magellanicus*) grazing rates. *Journal of Experimental Marine Biology and Ecology* **240**, 111-136.
- Pinckney, J.L., Paerl, H.W., Tester, P., and Richardson, T.L. (2001). The role of nutrient loading and eutrophication in estuarine ecology. *Environmental Health Perspectives* **109**, 699-706.
- Rouillon, G., and Navarro, E. (2003). Differential utilization of species of phytoplankton by the mussel *Mytilus edulis*. *Acta Oecologica-International Journal of Ecology* **24**, 299-305.
- Tirok, K., and Scharler, U.M. (2013). Dynamics of pelagic and benthic microalgae during drought conditions in a shallow estuarine lake (Lake St. Lucia). *Estuarine, Coastal and Shelf Science* **118**, 86-96.
- Tuchman, N.C., Burks, R.L., Call, C.A., and Smarrelli, J. (2004). Flow rate and vertical position influence ingestion rates of colonial zebra mussels (*Dreissena polymorpha*). *Freshwater Biology* **49**, 191-198.
- Vaughn, C.C., and Hakenkamp, C.C. (2001). The functional role of burrowing bivalves in freshwater ecosystems. *Freshwater Biology* **46**, 1431-1446.
- Widdows, J. (2001). Bivalve clearance rates: inaccurate measurements or inaccurate reviews and misrepresentation? *Marine Ecology Progress Series* **221**, 303-305.

General Discussion

Estuaries are characterized by large temporal and spatial fluctuations in physico-chemical parameters. In particular, the St Lucia estuarine lake undergoes natural cycling from wet to dry phases. This balance has, however, been disrupted due to water abstractions and the separation and subsequent reconnection of the Mfolozi River from the St Lucia Estuary (Begg 1978; Ngqulana *et al.* 2010). Seasonal rainfall is highly variable in many parts of the world, including southern Africa and Australia, which results in estuaries being exposed to a combination of drought-induced stress as well as periodic flooding events (Matthews 2006; Davis 2011). Historically, the Hopkins River Estuary in Australia has experienced floods annually, but this cycle has been dramatically altered by a recent drought (Matthews 2006). The Coorong, also in Australia, has undergone severe salinity increases over the last decade (Lester & Fairweather 2009). In addition, global climate change is expected to cause increases in extreme weather conditions (flood and drought events) in these regions (Lumsden *et al.* 2009; Mather *et al.* 2013). Lester and Fairweather (2009) stated that an estuary may only be managed successfully once an understanding of the ecosystem under different climatic conditions is obtained. The present thesis, thus, investigated how oscillations between wet and dry phases may affect the sessile and slow-moving bivalves present within Lake St Lucia, a World Heritage Site and RAMSAR Wetland of International Importance.

Bivalve species richness is very poorly documented in southern African estuarine studies, the majority of which have focused on macrofaunal communities (e.g. Davies 1982; MacKay & Cyrus 1998; Teske & Wooldridge 2001; Ngqulana *et al.* 2010). Chapter 1 provided the first bivalve census for Lake St Lucia, illustrating twenty-four bivalve species that have occurred recently within the system. The large majority of these species disappeared during the recent drought (2002–2011), as salinity levels increased and parts of Lake St Lucia were exposed due to decreased water levels. Although there have been a number of studies investigating the benthic community of Lake St Lucia (Day *et al.* 1954; Millard & Broekhuysen 1970; Bolt 1975; Blaber *et al.* 1983; Owen & Forbes 1997; Pillay & Perissinotto 2008; MacKay *et al.* 2010; Pillay & Perissinotto 2013), twelve of the twenty-four bivalve species recorded during this study had not been reported previously in the literature. Pillay *et al.* (2013) stated that it is important to provide an updated, taxonomically correct list of benthic fauna in St Lucia, as there is a potential to harbour both new and endemic species in this system. For example, Todaro *et al.* (2011) and Daly *et al.* (2012) identified new species of gastrotrichs and of burrowing anemone (*Edwardsia isimangaliso*) within St Lucia, respectively. The present study also resulted in the identification of two new bivalve species in the estuarine lake, *Tellinides kilburni* (previously reported as *Tellina cf. rousi*), and *Siliqua herberti* (previously reported as *Siliqua cf. polita*). Both of them are currently in description (M. Huber, pers. comm.).

The clam *Meretrix meretrix* being reported south of Mozambique for the first time was described in Chapter 1. Defined as a cryptogenic species, as it is neither clearly native nor a proven alien (Miranda & Adams 2013), this species appears to no longer be present within St Lucia. However, monitoring the benthic fauna is necessary to allow detection of further introductions and/or re-establishment thereof. The recognition of large numbers ($> 100 \text{ ind.m}^{-2}$) of *Barnea manilensis* shells embedded in cretaceous sandstone was also reported in this study. This large species (maximum size = 78 mm) may have been a major filter-feeder in the system in the past, however it has subsequently disappeared, probably due to drought conditions. It is fundamental to establish the role of key taxa within the system, allowing the evaluation of species loss through prolonged drought or major flood events (Pillay *et al.* 2013).

Of the twenty-four bivalve species recorded in Lake St Lucia, only six were reported in the most recent bivalve survey, conducted in March 2011. This annotated and illustrated checklist will minimise the occurrence of erroneous identifications and provide an identification guide for managers and future researchers. It has also highlighted the significant loss of bivalve species richness as a result of severe drought within St Lucia, which has subsequently not been reported for this region. In contrast, Henninger and Froneman (2011) highlighted the presence of the euryhaline bivalves, *Solen cylindraceus*, *Arcuatula capensis* and *Macoma litoralis* in the freshwater-deprived permanently open Kariega Estuary. Although this estuary is freshwater deprived, the bivalve community has remained the same for the last three decades (Henninger & Froneman 2011). This may highlight the importance of the ocean connection in sustaining estuarine stability. The current situation, with the Mfolozi mouth open to the ocean and a beach spillway connecting the Mfolozi River with St Lucia since July 2012, may allow recruitment into the estuary. However, restocking from the Mfolozi alone is unlikely due to the very low bivalve species richness within the system (Owen *et al.* 2010). Ngqulana *et al.* (2010) showed the lack of any bivalve species, apart from *Eumarcia paupercula*, in the Mfolozi River. Thus, it is imperative to maintain/conservate the St Lucia benthic community as the Mfolozi is an unlikely source of recolonization (Owen *et al.* 2010). However, *E. paupercula* was historically recorded in St Lucia, therefore this population may be restored by the Mfolozi/St Lucia link. Evaluating the bivalve community in St Lucia must continue as this may indicate whether an increase in bivalve species richness occurs as a result of the marine intrusion.

The two dominant species emerging from the diversity census, i.e. *Solen cylindraceus* and *Brachidontes virgiliae*, were designated for focused ecophysiological studies as presented in Chapters 2-5. The bivalve community within Lake St Lucia is strongly structured by salinity. This is seen in the shift in dominance from *S. cylindraceus* (dry phase) to *B. virgiliae* (wet phase). *Solen cylindraceus* was restricted to the South Lake during the hypersaline period and subsequently migrated to the

northern reaches as a result of the system becoming freshwater dominated. In contrast, *B. virgiliae* was restricted to the Narrows during periods of high salinity, however it has now become ubiquitous with the onset of the wet phase. The experimental salinity tolerance of *S. cylindraceus* was investigated in the second chapter, using both a shock and gradual change test to mimic flood and drought conditions, respectively. In the shock test, animals were able to tolerate salinity levels between 30 and 60, which suggested that this species may be vulnerable to flooding events. This dramatic decrease in salinity within the system has been known to cause mass mortality in bivalves (Matthews & Fairweather 2004; Nel *et al.* 2011). The gradual change test expanded the above tolerance range, as this species was able to withstand salinities from 15 to 65, highlighting the importance of acclimation. Salinity levels were adjusted over two weeks, however salinities may gradually increase over a period of months in the field resulting in an even wider tolerance range. Animals found at salinities around 10 in the field substantiated this claim, although the long-term persistence and sub-lethal effects are unclear (Chapter 2; Nel *et al.* 2013). In addition, *S. cylindraceus* may burrow deep within the sediment, thereby achieving the protection of a stable environment for a short period (de Villiers & Allanson 1989; Matthews & Fairweather 2004). The third chapter determined the experimental salinity tolerance for the mussel, *B. virgiliae*, using animals collected at two localities with substantially different salinity regimes (Lister's Point \approx 20 and Esengeni \sim 0). The results showed that this mussel has a preferred tolerance range from freshwater to 20, although when gradually exposed to an increase in salinity over a monthly period, animals were able to tolerate salinities up to 50. However, it must be noted that mussels have the ability to remain shut when exposed to unfavourable conditions, thereby allowing populations to withstand short salinity spikes (Davies 1980; Berger & Kharazova 1997). With the wide salinity tolerance suggested in Chapter 3, it is important to note that this species may be a potential biofouling threat, as it readily attaches to boat hulls and other hard structures. Additionally, as its spread and dominance are predicted to increase as St Lucia remains in a wet phase, understanding how this key species may affect overall ecosystem function is pivotal.

Although sub-lethal effects were not investigated in the above studies, estuarine and marine bivalves often exhibit a decrease in growth rate when exposed to salinity levels outside their tolerance range (Niamaimandi 2012). In St Lucia, *S. cylindraceus* is often exposed to salinity levels outside the range reported in Chapter 2. Although this species has the potential to reach a maximum size of 95 mm (McLachlan 1974; Kilburn & Rippey 1982), specimens in Lake St Lucia are seldom larger than 55 mm (Nel *et al.* 2011). *Solen cylindraceus* shells collected along the banks of Lake St Lucia have a maximum length of 70 mm, but this size has not been reported for any live specimens within the system. Another Solenidae found in southern Africa, *S. capensis*, has a maximum size of 160 mm (Kilburn & Rippey 1982; Branch *et al.* 2010). *Solen dactylus* found on the coast of the Persian Gulf reaches larger sizes than *S. cylindraceus*, with a maximum length estimated between 101 and 108 mm

(Saeedi *et al.* 2009). Additionally, the razor clams, *Tagelus plebeius* and *Ensis macha* attain a maximum length of 90 and 165 mm, respectively (Holland & Dean 1977, Baron *et al.* 2004).

Chapter 4 described how a dramatic decrease in salinity caused the disappearance of larger species, while a single cohort of juvenile *S. cylindraceus* (5 to 15 mm) remained. The growth rate of *S. cylindraceus* was determined *in situ* using a direct method of measuring shell length of individuals within this cohort (Chapter 4; Nel *et al.* 2013). Results suggested that *S. cylindraceus* in this system reach smaller lengths within its first growth year than previously reported for this species in the Swartkops Estuary (McLachlan 1974). Within their first year, caged and uncaged animals reached a size of 31.0 ± 4.5 and 31.7 ± 2.3 mm, respectively (Nel *et al.* 2013). This is substantially less than the shell length of 40 mm obtained by Robinson and Richardson (1998) for the razor clam, *E. arcuatus*. After 4 months in natural conditions and 1 year under culture, *S. marginatus* reached a size of 38 mm (da Costa and Martínez-Partiño 2009). *Ensis arcuatus* and *S. marginatus* reached a size of between 90 – 100 and 78 mm after 2 years, respectively (da Costa and Martínez-Partiño 2009). In addition, *S. cylindraceus* in the Swartkops Estuary reached a size of 60 mm after a 2 year growth period (McLachlan 1974). This may suggest that *S. cylindraceus* in the St Lucia Estuary has a reduced growth rate within their second year, but this needs to be investigated further. In addition, they may be eliminated by unfavourable environmental conditions before maximum size is reached. This was seen in the experiment, as it was terminated after a year, due to salinities decreasing below the tolerance range of *S. cylindraceus* and a high mortality rate occurring within the area.

The commencement of a wet phase has resulted in the St Lucia receiving higher than average rainfall since December 2011. This has resulted in an increase in abundance of the freshwater tolerant mussel, *B. virgiliae*. Nel *et al.* (2012) recorded the maximum benthic density of *B. virgiliae* at 51 ind.m⁻², however this does not take into account the extremely dense aggregations currently observed on macrophytes, boat hulls and dead oysters ($> 2178 \pm 742$ ind.m⁻²; Chapter 5). The last chapter thus looked at the grazing impact these localised aggregations may have on the available phytoplankton standing stock. A relatively low mussel grazing impact, between 2.5 and 8% consumption of phytoplankton biomass per day, was calculated using the average density found in the sediment. However a grazing impact of 3 to 8 times the available phytoplankton standing stock was found for animals aggregated on dead oyster beds. This showed the significant effect *B. virgiliae* may have as a major top-down grazer during wet phases. This study used an *in situ* gut fluorescence technique, which is typically utilised in the study of zooplankton feeding dynamics (e.g. Perissinotto 1992; Froneman 2000; 2001 & 2004; Carrasco and Perissinotto 2010), although Miranda *et al.* (2011) and Diaz *et al.* (2012) successfully employed this technique when investigating the grazing impact of the gastropods *Tarebia granifera* and *Littorina littorea*, respectively. Thus, to our knowledge this is the first study involving bivalve taxa. The grazing impact of *S. cylindraceus* within St Lucia also needs to

be investigated, as both species occur in the northern reaches, thus resulting in a possible competitive effect. This is, however unlikely due to the relatively large phytoplankton biomass in the overlying water-column.

In conclusion, this thesis emphasized the significant role salinity plays in structuring bivalve species within Lake St Lucia, therefore affecting overall ecosystem functioning. The onset of drought conditions (high salinity and low water levels) resulted in a severe loss of bivalve species richness. Thus, mitigation strategies need to be in place if this were to occur in the future, either by increasing flow via tributaries or by periodical freshwater release through a link canal and or back channel. Currently, *S. cylindraceus* and *B. virgiliae* are the two dominant bivalve species in the system. Both, strongly influenced by the climatic shift from hypersaline to meso/oligohaline conditions, associated with the fluctuations between dry and wet phases, respectively. With drought and flood events predicted to increase in frequency, extent and magnitude, understanding how key species react to climatic conditions is pivotal for informed management decisions to be made.

Future research

Results reported in this thesis revealed two undescribed bivalve species within St Lucia, as well as 12 species not recorded in previously published literature. It is, therefore, critical to continue providing updated annotated and illustrated checklists of all major estuarine groups. This may further reveal major biodiversity loss due to drought-induced crises experienced in the past, misidentifications and new/endemic species within the area. This may also reveal resilient species, which are able to persist within the harsh environment. This resilience may be due to the use of refuge areas that provide protection from unfavourable conditions (Lancaster & Belyea 1997; Taylor *et al.* 2006). These areas are important during natural disturbances (i.e. drought and flood events), allowing the persistence of species in a highly variable ecosystem (Magoulick & Kobza 2003). Taylor *et al.* (2006) hypothesized that *Solen cylindraceus* and other estuarine bivalves in St Lucia rely on populations surviving within the system for recolonization. It is, thus, important to identify and protect these refuge areas as they support the resilience of the estuary (Taylor *et al.*, 2006). Additionally, future studies should investigate the rate at which these areas act as nuclei from which recolonization of the remaining lake can occur.

Bayne *et al.* (1976) stated that the early life stages (i.e. larval phase) of a bivalve may be more susceptible to fluctuations in the surrounding environment. Therefore, although *S. cylindraceus* has a wide salinity tolerance, it is essential to establish the vulnerability of its larval phase. This also needs to be done with *B. virgiliae*. In addition, the sub-lethal effects (e.g. decrease in growth rate and

movement) need to be investigated for a combination of abiotic parameters. The decrease in salinity as a result of flood events may positively affect *B. virgiliae*, however the effect of an increased silt load into the estuary on bivalves such as *B. virgiliae* and *S. cylindraceus* needs to be investigated. While the re-connection of the Mfolozi River with the St Lucia Estuary is largely positive and a major step towards ecosystem recovery, the high silt loads that accompany the Mfolozi water remains a threat. The effect that these high silt loads could have on the bivalve community are largely unknown. While silt may interfere with the filter-feeding and/or respiration of some species (Adam 1986; Thrush *et al.* 2004), bivalves also have the potential to settle large amounts of suspended sediment and thus increase water clarity (Gerritsen *et al.* 1994; Vaughn & Hakenkamp 2001; Hwang *et al.* 2004). It is necessary to investigate this process as a possible mechanism to alleviate excessive siltation within Lake St Lucia.

A loss of bivalves will have detrimental effects on ecosystem functioning, as bivalves not only feed on primary producers but prey on heterotrophic protists (flagellates and ciliates), bacteria, copepod eggs and/or nauplii (Pace *et al.* 1998; Davenport *et al.* 2000; Lonsdale *et al.* 2009). The effect of mussel filtration on the heterotrophic planktonic community needs to be investigated. In addition, determining the ingestion rates and grazing impact of *S. cylindraceus* is an important gap which needs filling. This species currently occurs in high densities throughout Lister's Point, thus exerting a strong grazing impact on the planktonic community.

Chapter 4 determined the basic growth rate data for *S. cylindraceus* in the St Lucia estuarine system, using a direct method of following an individual cohort. This method was chosen as McLachlan (1974) suggested that growth lines in this species are too indistinct and irregular to be of any use. Additionally, there is difficulty in distinguishing between annual lines and disturbance marks (Palmer 2004; Cardoso *et al.* 2013). Thus in future studies, isotope sclerochronology may be used in combination with traditional methods, to eliminate the error introduced by disturbance marks (Cardoso *et al.* 2013). This progressive technique will be useful in a variable system, such as St Lucia. Additionally, it may be used to analyze bivalve populations found in areas with substantially different environmental conditions (e.g. the Kariega and St Lucia Estuary). The breeding strategies of both *S. cylindraceus* and *B. virgiliae* are still largely unknown. Although *S. cylindraceus* and *B. virgiliae* juveniles of similar sizes have been found throughout the year, suggesting that there may not be a particular breeding season but rather a set of parameters that induce spawning.

References

- Adam ME (1986) The Nile bivalves – How do they avoid silting during the flood. *Journal of Molluscan Studies* 52: 248–252.
- Barón PJ, Real LE, Ciocco NF, Ré ME (2004) Morphometry, growth and reproduction of an Atlantic population of the razor clam *Ensis macha* (Molina, 1782). *Scientia Marina* 68: 211–217.
- Bayne BL, Thompson RJ, Widdows J (1976) Physiology I. Pp. 121–206. In: Bayne BL (ed.), *Marine Mussels: Their Ecology and Physiology*. Cambridge Scientific Press, UK.
- Begg GW (1978) The estuaries of Natal. (Part II). Natal Town and Regional planning Commission Report. 41: 1–657.
- Berger VJ, Kharazova AD (1997) Mechanisms of salinity adaptations in marine molluscs. *Hydrobiologia* 355: 115–126.
- Bolt RE (1975) The benthos of some Southern African Lakes Part V: The recovery of the benthic fauna of St Lucia Lake following a period of excessively high salinity. *Transactions of the Royal Society of South Africa* 41: 295–323.
- Blaber SJM, Kure NF, Jackson S, Cyrus DP (1983) The benthos of South Lake, St Lucia following a period of stable salinities. *South African Journal of Zoology* 18: 311–319.
- Branch GM, Griffiths CL, Branch ML, Beckley LE (2010) *Two Oceans: a Guide to the marine Life of Southern Africa*. Cape Town, South Africa: Struik Nature.
- Cardoso J, Nieuwland G, Witbaard R, van der Veer HW, Machado JP (2013) Growth increment periodicity in the shell of the razor clam *Ensis directus* using stable isotopes as a method to validate age. *Biogeosciences* 10: 4741–4750.
- Carrasco NK, Perissinotto R (2010) *In situ* feeding rates and grazing impact of *Mesopodopsis africana* O. Tattersall in the St Lucia Estuary, South Africa. *Journal of Experimental Marine Biology and Ecology* 396: 61–68.
- da Costa F, Martínez-Patiño D (2009) Culture potential of the razor clam *Solen marginatus* (Pennant, 1777). *Aquaculture* 288: 57–64.

- Daly M, Perissinotto R, Laird M, Dyer D, Todaro A (2012) Description and ecology of a new species of *Edwardsia* de Quatrefages, 1842 (Anthozoa, Actiniaria) from the St Lucia Estuary, South Africa. *Marine Biology Research* 8: 233–245.
- Davenport J, Smith R, Packer M (2000) Mussels *Mytilus edulis*: significant consumers and destroyers of mesozooplankton. *Marine Ecology Progress Series* 198: 131–137.
- Davies BR (1980) The identification of the mytilids *Musculus virgiliae* Barnard, *Arcuatula capensis* (Krauss) and *Brachidontes variabilis* Krauss, with corrections to the literature and a note on their distribution. *Transactions of the Royal Society of South Africa* 44: 225–235.
- Davies BR (1982) Studies on the zoobenthos of some southern Cape coastal lakes. Spatial and temporal changes in the benthos of Swartvlei, South Africa, in relation to changes in the submerged littoral macrophyte community. *Journal of the Limnological Society of Southern Africa* 8: 33–45.
- Davis CL (2011) *Climate Risk and Vulnerability: A Handbook for Southern Africa*. Council for Scientific and Industrial Research, Pretoria, South Africa, Pp. 92.
- Day JH, Millard NAH, Broekhuysen GJ (1954) The ecology of South African estuaries. Part IV: the St Lucia system. *Transactions of the Royal Society of South Africa* 34: 129–156.
- de Villiers CJ, Allanson BR (1989) Osmotic properties of an infaunal estuarine bivalve *Solen cylindraceus* (Hanley). *Journal of Molluscan Studies* 55: 45–51.
- Diaz ER, Kraufvelin P, Erlandsson J (2012) Combining gut fluorescence technique and spatial analysis to determine *Littorina littorea* grazing dynamics in nutrient-enriched and nutrient-unenriched littoral mesocosms. *Marine Biology* 159: 837–852.
- Froneman PW (2000) Feeding studies on selected zooplankton in a temperate estuary, South Africa. *Estuarine, Coastal and Shelf Science* 51: 543–552.
- Froneman PW (2001) Feeding ecology of the mysid, *Mesopodopsis wooldridgei*, in a temperate estuary along the eastern seaboard of South Africa. *Journal of Plankton Research* 23: 999–1008.

- Froneman PW (2004) *In situ* feeding rates of the copepods, *Pseudodiaptomushessei* and *Acartia longipatella*, in a temperate, temporarily open/closed Eastern Cape estuary. South African Journal of Science 100: 577–583.
- Henninger TO, Froneman PW (2011) Macrofaunal community structure in the littoral zone of a freshwater-deprived, permanently open Eastern Cape estuary. African Zoology 46: 263–279.
- Holland AF, Dean JM (1977) Biology of Stout Razor clam *Tagelus plebeius*: II. Some aspects of population dynamics. Chesapeake Science 18: 58–66.
- Hwang SJ, Kim HS, Shin JK, Oh JM, Kong DS (2004) Grazing effects of a freshwater bivalve (*Corbicula leana* Prime) and large zooplankton on phytoplankton communities in two Korean lakes. Hydrobiologia 515: 161–179.
- Gerritsen J, Holland AF, Irvine DE (1994) Suspension-feeding bivalves and the fate of primary production: an estuarine model applied to Chesapeake Bay. Estuaries 17: 403–416.
- Kilburn R, Rippey E (1982) *Sea shells of southern Africa*. Johannesburg: Macmillan South Africa.
- Lancaster J, Belyea LR (1997) Nested hierarchies and scale-dependence of mechanisms of flow refugium use. Journal of the North American Benthological Society 16: 221–238.
- Lester RE, Fairweather PG (2009) Modelling future conditions in the degraded semi-arid estuary of Australia's largest river using ecosystem states. Estuarine, Coastal and Shelf Science 85: 1–11.
- Lonsdale DJ, Cerrato RM, Holland R, Mass A, Holt L, Schaffner RA, Pan J, Caron DA (2009) Influence of suspension-feeding bivalves on the pelagic food webs of shallow, coastal embayment's. Aquatic Biology 6: 263–279.
- Lumsden TG, Schulze RE, Hewitson BC (2009) Evaluation of potential changes in hydrologically relevant statistics of rainfall in Southern Africa under conditions of climate change. Water SA 35:649–656.
- Mackay CF, Cyrus DP (1998) A review of the macrobenthic fauna of the Mhlathuze Estuary: Setting the ecological reserve. Southern African Journal of Aquatic Sciences 24: 111–129.

- MacKay F, Cyrus D, Russell KL (2010) Macrobenthic invertebrate responses to prolonged drought in South Africa's largest estuarine lake complex. *Estuarine, Coastal and Shelf Science* 86: 553–567.
- Magoulick DD, Kobza RM (2003) The role of refugia for fishes during drought: a review and synthesis. *Freshwater Biology* 48: 1186–1198.
- Mather AA, Stretch DD, Maro AZ (2013) Climate change impacts. Pp. 397–412 In: Perissinotto R, Stretch DD, Taylor RH (eds.), *Ecology and Conservation of Estuarine Ecosystems: Lake St Lucia as a Global Model*. New York: Cambridge University Press.
- Matthews TG, Fairweather PG (2004) Effect of lowered salinity on the survival, condition and reburial of *Soletellina alba* (Lamarck, 1818) (Bivalvia: Psammobiidae). *Austral Ecology* 29: 250–257.
- Matthews TG (2006) Spatial and temporal changes in abundance of the infaunal bivalve *Soletellina alba* (Lamarck, 1818) during a time of drought in the seasonally-closed Hopkins River Estuary, Victoria, Australia. *Estuarine, Coastal and Shelf Science* 66: 13–20.
- McLachlan A (1974) Notes on the biology of some estuarine bivalves. *Zoologica Africana* 9: 15–34.
- Millard NAH, Broekhuysen GJ (1970) The ecology of South African estuaries. Part X: St Lucia: a second report. *Zoologica Africana* 5: 277–307.
- Miranda NAF, Adams JB (2013) Alien and invasive species. Pp. 367–379 In: Perissinotto R, Stretch DD, Taylor RH (eds.), *Ecology and Conservation of Estuarine Ecosystems: Lake St Lucia as a Global Model*. New York: Cambridge University Press.
- Miranda, N.A.F., Perissinotto, R., and Appleton, C.C. (2011). Feeding dynamics of the invasive gastropod *Tarebia granifera* in coastal and estuarine lakes of northern KwaZulu-Natal, South Africa. *Estuarine, Coastal and Shelf Science* 91: 442–449.
- Nel HA, Perissinotto R, Taylor RH, Carrasco NK (2011) Salinity tolerance of the bivalve *Solen cylindraceus* (Hanley, 1843) (Mollusca: Euheterodonta: Solenidae) in the St Lucia Estuary. *African Invertebrates* 52: 575–586.

- Nel HA, Perissinotto R, Taylor RH (2012) Diversity of bivalve molluscs in the St Lucia Estuary, with an annotated and illustrated checklist. *African Invertebrates* 53: 503–525.
- Nel HA, Perissinotto R, Taylor RH (2013) *In situ* growth rate of *Solen cylindraceus* (Mollusca: Euheterodonta: Solenidae) in the St Lucia estuarine lake, South Africa. *African Zoology* 48: 266–273.
- Ngqulana SG, Owen RK, Vivier L, Cyrus DP (2010) Benthic faunal distribution and abundance in the Mfolozi-Msunduzi estuarine system, KwaZulu-Natal, South Africa. *African Journal of Aquatic Science* 35: 123–133.
- Niamaimandi N (2012) Biological parameters and abundance of the razor clam, (*Solen brevis*), from the Bushehr area of the Persian Gulf. *Agriculture, Forestry and Fisheries* 1: 1–6.
- Owen RK, Forbes AT (1997) Salinity, floods and the infaunal macrobenthic community of the St Lucia Estuary, KwaZulu-Natal, South Africa. *African Journal of Aquatic Science* 23: 14–30.
- Owen RK, Cyrus DP, Vivier L, Jerling HL (2010) The potential for zoobenthic fauna dispersal into the St Lucia Estuary from the Mfolozi-Msunduzi estuarine system, KwaZulu-Natal, South Africa. *African Journal of Aquatic Science* 35: 135–140.
- Pace ML, Findlay SEG, Fischer D (1998) Effects of an invasive bivalve on the zooplankton community of the Hudson River. *Freshwater Biology* 39: 103–116.
- Palmer D W (2004) Growth of the razor clam *Ensis directus*, an alien species in the Wash on the east coast of England. *Journal of the Marine Biological Association of the United Kingdom* 84: 1075–1076.
- Perissinotto R (1992). Mesozooplankton size-selectivity and grazing impact on the phytoplankton community of the Prince Edward Archipelago (Southern-Ocean). *Marine Ecology Progress Series* 79: 243–258.
- Pillay D, Perissinotto R (2008) The benthic macrofauna of the St Lucia Estuary during the 2005 drought year. *Estuarine, Coastal and Shelf Science* 77: 35–46.

- Pillay D, Perissinotto R (2013) Benthic macrofauna of an estuarine lake during a drought: spatio-temporal drivers under different hydrological states. *Marine Ecology Progress Series* 492: 111–123.
- Pillay D, Bownes SJ, Nel HA (2013) Benthic Invertebrates. Pp. 226–245 In: Perissinotto R, Stretch DD, Taylor RH (eds.), *Ecology and Conservation of Estuarine Ecosystems: Lake St Lucia as a Global Model*. New York: Cambridge University Press.
- Saeedi H, Raad SP, Ardalan AA, Kamrani E, Kiabi BH (2009) Growth and reproduction of *Solen dactylus* (Bivalvia: Solenidae) on northern coast of the Persian Gulf (Iran). *Journal of the Marine Biological Association of the United Kingdom* 89: 1635–1642.
- Taylor R, Kelbe B, Haldorsen S, Botha GA, Wejden B, Vaeret L, Simonsen MB (2006) Groundwater-dependent ecology of the shoreline of the subtropical Lake St Lucia estuary. *Environmental Geology* 49: 586–600.
- Teske PR, Wooldridge T (2001) A comparison of the macrobenthic faunas of permanently open and temporarily open/closed South African estuaries. *Hydrobiologia* 464: 227–243.
- Thrush SF, Hewitt JE, Cummings V, Ellis JI, Hatton C, Lohrer A, Norkko A (2004) Muddy waters: elevating sediment input to coastal and estuarine habitats. *Frontiers in Ecology and the Environment* 2: 299–306.
- Todaro MA, Matteo DZ, Bownes SJ, Perissinotto R (2011) First records of Gastrotricha from South Africa, with description of a new species of *Halichaetonotus* (Chaetonotida, Chaetonotidae). *ZooKeys* 142: 1–13.
- Vaughn CC, Hakenkamp CC (2001) The functional role of burrowing bivalves in freshwater ecosystems. *Freshwater Biology* 46: 1431–1446.