

Diversity of Bivalve Molluscs in the St Lucia Estuary, with an Annotated and Illustrated Checklist

Authors: Nel, H. A., Perissinotto, R., and Taylor, R. H.

Source: African Invertebrates, 53(2): 503-525

Published By: KwaZulu-Natal Museum

URL: https://doi.org/10.5733/afin.053.0210

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

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

H. A. Nel^{1*}, R. Perissinotto¹ and R. H. Taylor^{1,2}

¹School of Life Sciences, University of KwaZulu-Natal, Westville Campus, P. Bag X5, Durban, 4000 South Africa

²Ezemvelo KZN Wildlife, P. Bag X01, St Lucia, 3936 South Africa

*Corresponding author: hollynel1988@gmail.com

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 molluses 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, Mactra cuneata, Martesia striata, Meretrix meretrix, Saccostrea forskahlii and Tellina s.l. bertini. Single shells of another two previously unrecorded species, Anodontia edentula and Timoclea layrani, 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 physicochemical 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-

http://www.africaninvertebrates.org.za urn:lsid:zoobank.org;pub:FA87C9EF-195A-4ED1-9F6A-F8A83244BCB1

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). Boltt (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 (Hampel *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; Boltt 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 $0.0236\,\mathrm{m}^2$; 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 $500\,\mu\mathrm{m}$ sieve.

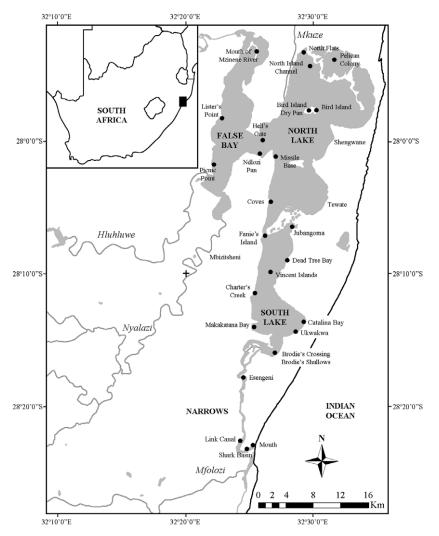


Fig. 1. Map of the St Lucia Estuary, showing the sampling sites where bivalves were collected from 1925 to 2011; and its geographical position relative to South Africa (adapted from Carrasco *et al.* 2010).

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 serveys 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 Mactra 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.

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

Ī

1

TABLE 2

Chambardia wahlbergi, Dh – Dosinia hepatica, Ds – <u>Dendostrea sandvichensis</u>, Ep – Eumarcia paupercula, Ff – <u>Fulvia fragilis</u>, Ii – Irus irus, Ml – Salmacoma Aa – Anomia achaeus, Ac – Arcuatula capensis, An – Anadara natalensis, Bm – Barnea manilensis, Bv – Brachidontes virgiliae, Cf – Corbicula fluminalis, Cw – Bivalve species reportedly found dead along the shores of the St Lucia estuary during the Natal Parks Board bivalve survey of 1982/83. Abbreviations: Species: litoralis, Mr – Macomopsis moluccensis, Sc – Solen cylindraceus, Sf – <u>Saccostrea forskahlii,</u> Sl – Soletellina lumulata, Sp – Siliqua cf. polita, Tb – <u>Tellina s. I. bertini,</u> Fi - Timoclea lavrani, TI - Theora lata, Tr - Tellina cf. rousi; Abundance: A - abundant, C - common, P - present, X - present but relative abundance unknown. Species underlined represent new records for the St Lucia Estuary.

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 lunulata*, 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
ake	Hell's Gate to Fanie's	-	-	-	-	-	X	-	-	-	-	-
North Lake	Tewate to Shengwane	-	-	-	X	X	-	X	X	X	X	-
Nor	Jubangoma to Tewate	-	X	-	X	X	-	-	X	X	X	-
	Fanie's Island to Charter's Creek	X	X	X	X	X	-	X	X	X	X	X
Lake	Catalina Bay to the Narrows	-	-	-	X	X	-	-	X	X	X	-
th L	Jubangoma to Vincent Island	-	-	-	X	X	-	-	X	X	X	-
South	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 lunulata, Tb – Tellina s.l. bertini.

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

TABLE 4b

Bivalve species collected from St Lucia and held at the NMSA. Abbreviations: Mc – <u>Mactra cuneata</u>, Ml – <u>Salmacoma litoralis</u>, Mm – <u>Meretrix meretrix</u>, Mr – <u>Macomopsis moluccensis</u>, Ms – <u>Martesia striata</u>, Sc – <u>Solen cylindraceus</u>, Sp – <u>Siliqua</u> cf. <u>polita</u>, Tl – <u>Theora lata</u>, Tr – <u>Tellina</u> cf. <u>rousi</u>. 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	-
	West bank opposite Fanie's Island	-	11/1971	-	2/1971	-	2/1971	-	-	-
	Catalina Bay	-	-	-	-	-	12/2005	-	-	-
South	Catalina Bay (Old Jetty)	-		12/2005	12/1982	-	-	-	12/1981	-
Lake	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	Shark Basin	-	-	-	-	-	-	-	-	6/1987; 8/1987
Mouth	St Lucia Lake	-	-	9/2003	7/1925	-	6/1962	-	-	-

IABLE 3

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	-	7/1948	-	-	-	7/1948	-
Mouth	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 sandvichensis* 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. *Mactra 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 – *Macomopsis 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, Cardiidae, 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 (Boltt 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 (Boltt 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. Lamellibranchiata. 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. & CATTRUSSE, 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 Lamarck, 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.

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.

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.

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.









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* (Jousseaume, 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

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); freshlydead 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.

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 souther

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.

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 Duri

Distribution: Tropical Indo-Pacific to Durban Bay. 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.m⁻²) but not alive during three surveys of 1983/83, 2005 and 2011. Found throughout western shores, wherever cretaceous sandstone is available for burrowing.

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).





