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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 ‰ 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 ‰ 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 (Boltt 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*. 1989*a*; 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 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

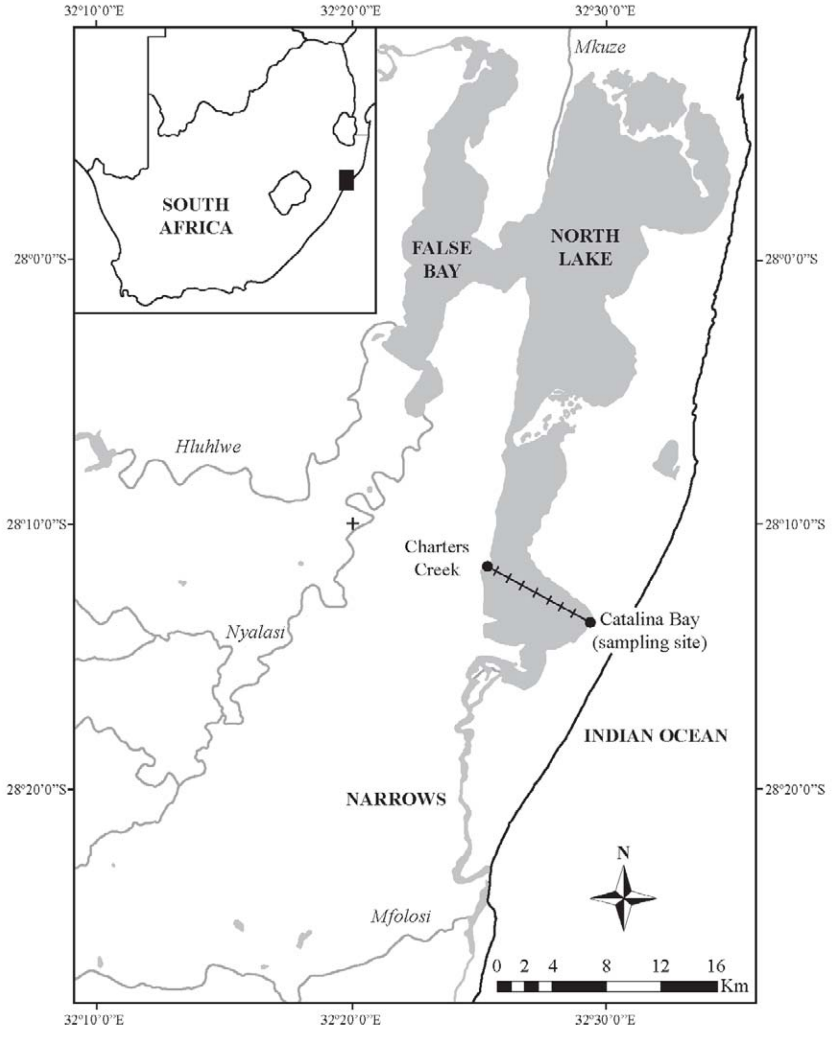

Fig. 1. Geographic position of the St Lucia Estuary showing the sampling site, Catalina Bay, and the abundance transect occupied in June 2010 (adapted from Carrasco *et al.* 2010).

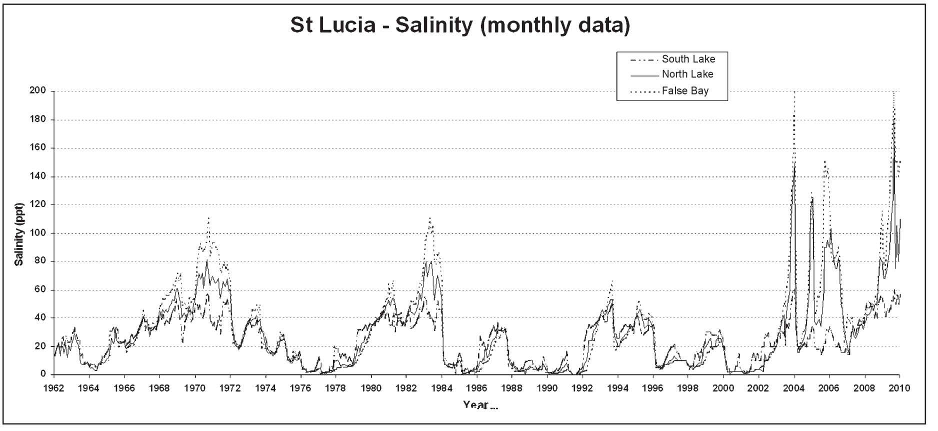

Fig. 2. Changes in salinity (ppt) recorded in False Bay and the South and North lakes of the St Lucia Estuary during the period 1960–2010.

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 km^2 (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 predetermined 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 m^2, 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).

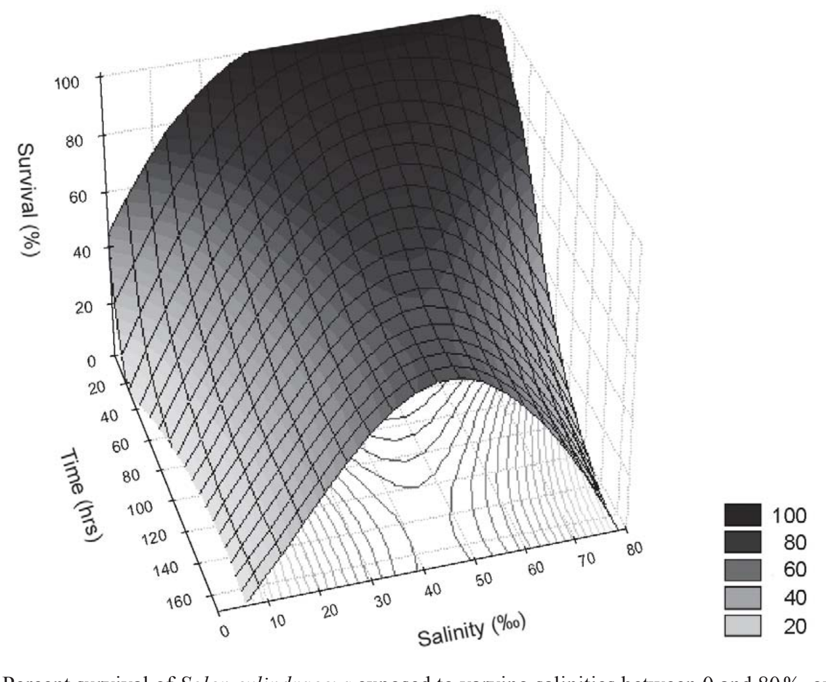

Fig. 3. Percent survival of *Solen cylindraceus* exposed to varying salinities between 0 and 80 ‰ over time (hrs), after being acclimated to 50 ‰ (shock change test).

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	*F*	*GG*
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

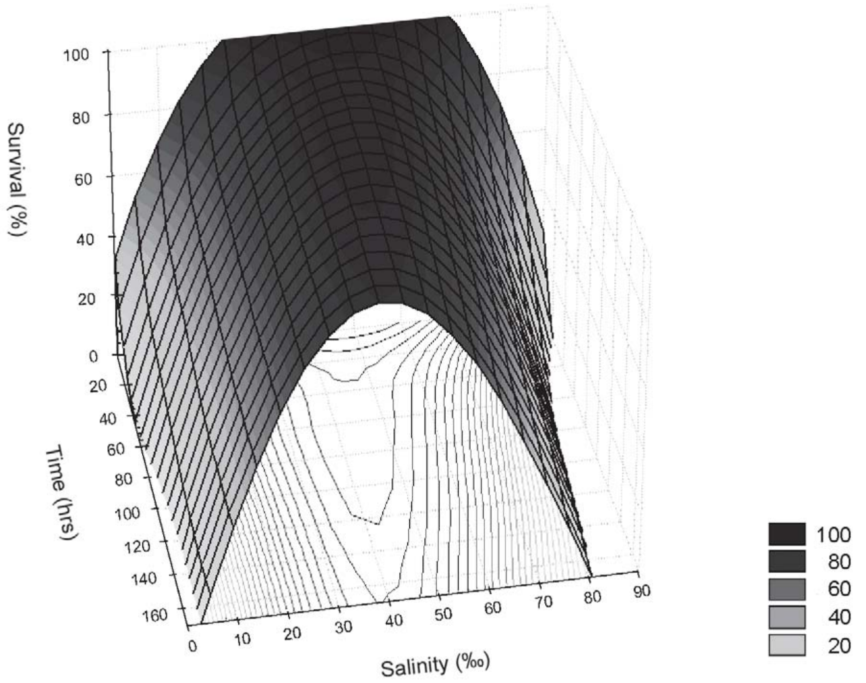

Fig. 4. Percent survival of *Solen cylindraceus* for varying salinities between 0 and 80‰ over time (hrs), after acclimation to varying salinities (gradual change test).

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
S. cylindraceus (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*. (1989*b*) 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 overlying 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.

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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. 1989*a*. 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. 1989*b*. 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. & Cattrijsse, 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.