

Community structure and composition of meiofauna over a sea-induced mouth-breaching event in St Lucia Estuary, South Africa

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ABSTRACT: Mouth state significantly affects the ecology of temporarily open-closed estuaries. Breaching typically occurs due to river flooding during high rainfall periods, but occasionally a breach may be initiated by the sea due to storm surges and high sea levels. There is little information on the effects of this type of breach on estuarine ecosystems. St Lucia Estuary is one of the most important estuaries in South Africa in terms of biodiversity; however, it has been severely affected by drought and prolonged mouth closure since 2002, except for a 6 mo breaching event in 2007. Meiofauna are poorly known from the estuary, with virtually no studies prior to the drought. This study therefore examines the effects of a sea-induced breach on meiofauna communities in the St Lucia Estuary, with particular reference to the influence of mouth state and spatial variations between sites in different regions of the estuary. Samples were collected quarterly from August 2006 to May 2008. Four study sites were selected to represent the mouth area, the narrow channel joining the lakes, South Lake and the northernmost lake at False Bay. The breach had a significant impact on community structure and composition, with variations among sites. The greatest impact was at the mouth. Density increased, peaking after reclosure; however, taxon richness and diversity were significantly reduced throughout the open phase, likely due to sediment disturbance and strong flows. In contrast, density and richness generally increased in the shallow lakes, where water depths and salinity increased after the breach. Communities in the deeper estuary channel appear to be structured mainly by temperature and food availability, whereas salinity is likely the most important environmental driver in the shallow lakes.

KEY WORDS: Meiofauna · St Lucia Estuary · Mouth state · Breach · Community structure · Composition · Drought · Salinity

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INTRODUCTION

Temporarily open/closed estuaries (TOCEs) and their variously named equivalents are widespread around the world, being particularly important in southern Africa, Australia, India, Brazil, and the west and south coast of the USA (Perissinotto et al. 2010b). The state of the mouth (whether open or closed) and amount of freshwater inflow are the most important factors influencing physical and biological processes in such systems (Grange et al. 2000, Perissinotto et al. 2010a). Open and closed phases are generally governed by seasonal rainfall cycles, with the estuary

mouth usually closing during the dry season, when rainfall and river inflow are lowest, and opening in the wet season when the sandbar at the mouth is breached by rising water levels inside the estuary (Schumann et al. 1999, Perissinotto et al. 2010b). However, seasonal patterns may be overridden by large-scale climatic events, such as drought cycles and episodic flooding, and large systems may undergo mouth closure for several years during a drought (Schumann et al. 1999). Extreme events related to climate change are escalating (Beniston et al. 2007, Intergovernmental Panel on Climate Change 2007, Walsh et al. 2012), and it is therefore likely that the

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breaching pattern of TOCEs may undergo significant disruptions in the future.

Breaching events can have a significant impact on estuarine biota and overall functioning of the estuary (Whitfield et al. 2008, Perissinotto et al. 2010b). Normally, this occurs in response to heavy rainfall and/or flooding, and a particular consequence of this type of breach is that the whole system may be flushed and enter a fully freshwater phase, which can lead to large mortalities of freshwater-intolerant estuarine biota (e.g. McLachlan & Grindley 1974, Cyrus 1988). Sea-induced breaching occurs less frequently, generally as a result of extreme weather events causing high tides and strong coastal surges (Schumann et al. 1999). When water levels inside the estuary are lower than mean sea level, there will be a predominant inflow of seawater to the estuary (Cooper et al. 1999) rather than the strong initial outflow typical of flood-induced breaching (Whitfield et al. 2008). This can lead to increased salinities inside the estuary, particularly in periods of low river inflow, which can have important consequences for estuarine communities (Riddin & Adams 2010). Knowledge of the effects of sea-induced breaching on estuarine ecosystems is therefore important given that such events are likely to increase.

The St Lucia estuarine lake system forms part of the iSimangaliso Wetland Park on the north-east coast of South Africa. The area incorporates a rich diversity of habitats and wetland ecosystems supporting a number of rare, threatened and endemic species (A. S. Combrink & T. Kyle unpubl. report), and has therefore been recognised both as a Ramsar Wetland of International Importance (1989) and as South Africa's first UNESCO World Heritage Site (1999) (Taylor 2006). Due to the large size and shallowness of the system, it is particularly vulnerable to the influence of climatic conditions and large-scale fluctuations in physico-chemical conditions are a characteristic feature (Day et al. 1954, Boltt 1975, Owen & Forbes 1997). This has become particularly pronounced in recent years following the onset of a prolonged drought in 2001. The estuary mouth closed a year later and has remained closed to date, with the exception of a 6 mo breaching event in 2007. Although the biological community is considered to be resilient and capable of rapid recovery from stress (Boltt 1975), there is concern that conditions have reached such extremes in recent years that they may result in a permanent loss of biodiversity to the system (Whitfield & Taylor 2009).

Most components in the St Lucia Estuary have been well studied, e.g. zooplankton (Carrasco et al.

2010, Jerling et al. 2010), macrofauna (Owen & Forbes 1997, Pillay & Perissinotto 2008, MacKay et al. 2010) and fish (Whitfield et al. 2006, Vivier et al. 2010); however, meiofauna have generally received little attention (Pillay & Perissinotto 2009). Meiofauna are a key component in estuarine sediments. As grazers of benthic algae, bacteria and detritus, they contribute to decomposition and denitrification processes, and therefore nutrient and organic matter cycling in estuaries (Gerlach 1978, Coull 1999, Lillebø et al. 1999). Carbon assimilation by meiofauna can be high (Hodda & Nicholas 1990, Moens et al. 2002), and certain taxa are an important food source for macro-invertebrates and benthic-feeding adult and juvenile fish (Coull et al. 1995, Schlacher & Wooldridge 1996, Spieth et al. 2011). Meiofauna may therefore contribute significantly to secondary production and energy flow in estuaries, establishing an important link between the microbial food web and higher trophic levels (Hodda & Nicholas 1990, Heymans & Baird 1995).

The mouth of the St Lucia Estuary breached in March 2007, due to a combination of high wave conditions and strong storm surges generated by Cyclone Gamede (Whitfield & Taylor 2009, Cyrus et al. 2010). Due to the exceptionally low water levels in the estuary, the breach resulted in a continued flow of seawater into the system for a period of 6 mo before closing at the end of August 2007 (Cyrus et al. 2010). Only one previous study specifically examined the meiofauna in St Lucia Estuary during severe drought conditions in 2005 (Pillay & Perissinotto 2009). Density and diversity were substantially lower than that reported for other South African estuaries due to desiccation, high salinity and habitat fragmentation. The breaching event therefore provided an opportunity to measure both the impact of mouth state on the structure and composition of meiofauna communities and their potential for recovery from drought-related stress. As a group, meiofauna are generally poorly known in South Africa (Griffiths et al. 2010, Barnes et al. 2011, Todaro et al. 2011), and knowledge of their biodiversity in St Lucia Estuary during this reprieve is especially important given the current state of the system.

The aims of this study were therefore to examine the effect of a sea-induced breach on meiofauna community structure and composition and to determine whether this effect varied between sites in different regions of the estuary. No hypotheses were made *a priori*; however, it was expected that there would be variations between sites related to distance from the mouth and conditions prior to the breach.

MATERIALS AND METHODS

Study sites

St Lucia Estuary is located on the subtropical north-east coast of South Africa. The maximum length of the system is 61 to 66 km (28° 24' to 27° 52' S), with a maximum width of 22 km (32° 21' and 32° 34' E) and a total surface area of $\pm 350 \text{ km}^2$ (Begg 1978). The system consists of 3 shallow, interconnected lakes (False Bay, North Lake and South Lake) and a 21 km long estuary channel known as the Narrows that opens intermittently to the sea (Fig. 1). The estuary is very shallow, with an average depth of $<1 \text{ m}$ in the lakes and 1 to 4 m in the Narrows and mouth area. Average rainfall for the area is 1000 mm yr^{-1} , predominantly in summer (Taylor 2006).

Sampling was undertaken at 4 representative sites in the estuary (Perissinotto et al. 2010a), located several km apart and at increasing distance from the mouth. These were the Mouth, Esengeni in the Narrows, Charters Creek in South Lake and Listers Point in False Bay (Fig. 1). Samples were collected at quarterly intervals from August 2006 to May 2008, with an additional sample collected in March 2007, shortly after the mouth breached. The mouth remained open for 6 mo until August 2007. To determine the impact of this event, 3 quarterly sample dates were selected to represent each mouth phase, designated as the closed (before the mouth opened; August 2006, November 2006, February 2007), open (March 2007, May 2007, August 2007) and reclosed phases (after the mouth closed; November 2007, March 2008, May 2008). No samples were obtained from Listers Point in August and November 2006, when the lake was dry, nor from Esengeni, which is only accessible by boat, in March 2007, due to poor weather conditions.

Environmental variables

All samples were collected from the nearshore water edge, except at Esengeni where samples were taken by boat from the estuary channel. Temperature ($^{\circ}\text{C}$), depth (m), salinity, dissolved oxygen (mg l^{-1}), pH and turbidity (nephelometric turbidity units, NTUs) were measured on each occasion using a YSI 6920 multiprobe. At deeper sites ($>0.5 \text{ m}$), measurements were taken from surface and bottom waters, and only the latter were used in this study. At shallow depths the probe was placed horizontally when necessary to ensure that all sensors were submerged.

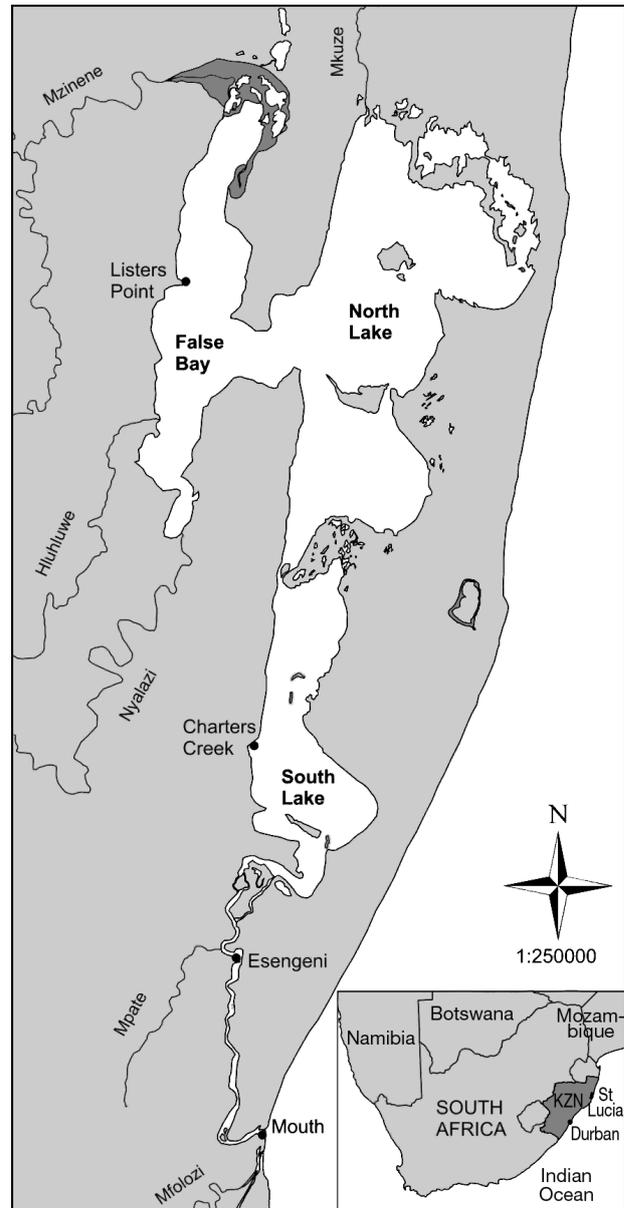


Fig. 1. The 4 study sites in different regions of the St Lucia Estuary on the north-east coast of KwaZulu-Natal (KZN), South Africa. Sampling sites were located at the Mouth, Esengeni in the Narrows, Charters Creek in South Lake and Listers Point in False Bay. Inset, location of KwaZulu-Natal on the east coast of South Africa. St Lucia Estuary map based on USGS EROS (2007) imagery

Rainfall data was obtained from 3 stations closest to the study sites (South African Sugarcane Research Institute [SASRI] weather website): St Lucia-Monzi (Mouth), Nyalazi River (Esengeni and Charters Creek) and Hluhluwe-GlenPark (Listers Point). Sediment characteristics for each site were summarised using averaged data from available samples. Mean

percentage sediment organic matter (SOM) was determined from samples collected between 2006 and 2008 (November 2006, February 2007, March 2008, October 2008) (2 replicates per site per occasion, 2 cores per sample). Grain size data were not obtained during this survey. Mean grain size composition for each site was therefore measured using sediments from meiofauna samples collected in March and May 2008 (excluding Esengeni), combined with grain size samples collected in November 2010 and July 2011. A separate long-term study of macrofauna in the estuary found no significant change in grain size composition after the breach, even at the mouth of the estuary (MacKay et al. 2010).

Microphytobenthic biomass

Three replicates of the top 1 cm of sediment were collected using a Perspex twin corer (internal diameter: 2 cm). Cores were incubated in 30 ml 90% acetone at 4°C for 48 to 72 h for chlorophyll *a* extraction. Chlorophyll *a* biomass was measured fluorometrically using a Turner Designs 10-AU fluorometer and biomass was measured as mg chl *a* m⁻².

Meiofauna

Following the protocol described in Nozais et al. (2005), 3 replicates of the top 1 cm of sediment were collected using a Perspex twin-corer (internal diameter: 2 cm). Samples were fixed with 10% formalin and stained with Phloxin-B. In the laboratory, each sample was washed through 2 sieves of 500 µm and 63 µm mesh size to isolate the meiofauna size fraction. This was then washed into 50 ml plastic centrifuge tubes. Meiofauna were extracted by mixing a suspension of 10 ml sediment plus distilled water and 20 ml of Ludox HS-40, followed by centrifugation at 900 rpm for 2 to 3 min (modified from Burgess 2001). The extraction was repeated 3 times per sample. Extraction efficiency was tested for the different sediment types of each site by processing the sediment residue (after meiofauna were extracted) of 3 samples per site. Extraction efficiency was 95 to 100% for virtually all taxa, with the exception of ostracods (10 to 100%). Thereafter, a portion of the sediment residue was checked for every sample. Samples were sorted under a dissecting microscope (40×), and the meiofauna were identified and transferred either to 5% formalin (soft-bodied taxa) or 70% alcohol (hard-bodied taxa) for storage.

Taxonomic identification

Specimens were either identified under the dissecting microscope or mounted on temporary slides in pure or anhydrous glycerol sealed with nail polish. Slides were examined under a standard compound microscope or using microscopes fitted with Differential Interference Contrast optics. Specimens were identified directly (see Appendix 1), or sent as specimens or photographs to taxonomic experts for identification/confirmation (see 'Acknowledgements'). Identification of ciliates generally requires examination of living specimens or advanced staining and microscope techniques to determine the details of oral and somatic ciliature (Taylor & Sanders 1991), which was not possible in our study. Preserved ciliates were therefore identified to the lowest possible taxonomic level based on morphological features visible with light microscopy, following the keys provided in Taylor & Sanders (1991). As noted by these authors, the guide is useful for identifying fixed specimens to genus or family level but only describes certain representative genera. Thus, whilst ciliate identifications were confirmed as far as possible with information gathered from other sources, they should be considered cautiously. A full list of identified taxa and groups is provided later in Table 5.

Statistical analyses

Tests for statistical differences in physico-chemical variables between sites and mouth phases were analysed using 1-way analysis of variance (ANOVA; Statistica 6.0, General Linear Models) for site and phase separately (sample sizes were too small for a combined analysis; $n = 1$ to 3 per site per phase).

Univariate community indices calculated were total meiofauna density (N), taxon diversity (Shannon-Wiener index, H') and taxon richness (Margalef's index, d), determined using Primer V6.1 software. To determine the effect of site and mouth phase on univariate community indices, individual replicates from within each mouth phase for each site were pooled and the data analysed using a factorial ANOVA with site and phase as fixed factors (unbalanced). Potential problems with this approach were that replicates from different dates within each phase would not be independent of each other, while the variability between dates within phases was unaccounted for, as indicated by the high error sum of squares (see Table 3). Averaging the 3 replicates per site and date and using date as the replicate for each phase was not

possible due to missing samples and the small sample size ($n = 1$ to 3). To test the validity of these results, the data were analysed using a nested ANOVA with site and phase as crossed factors, and date as a fixed factor nested within site and phase. The significance of the main effects and interaction term in this analysis were the same as those obtained with the factorial ANOVA using pooled replicates. Date (site \times phase) did have a highly significant effect in all cases; however, the results generally reflected the patterns summarised by variations with mouth phase. Since temporal variations within phases were not of primary interest in this study, results from the former analysis are presented. Density data were log-transformed to meet the assumptions of normality and homogeneity of variance. Indices of richness and diversity did not require transformation to meet these assumptions. Significant results were examined using Neuman-Keuls post-hoc comparisons ($p < 0.05$).

Multivariate analyses were performed using Primer V6.1 software. For the meiofauna, analyses were performed using counts of all taxa and groups identified to the lowest taxonomic level (see Table 5). Data were fourth root-transformed to balance the contribution of common and rare taxa (Clarke & Warwick 2001). Spatio-temporal patterns in community structure were represented using non-metric multidimensional scaling (MDS) ordination of Bray-Curtis similarities

between samples, matched with cluster analysis. Variability in community structure and composition between sites and between mouth phases was analysed using analysis of similarity (ANOSIM), a multivariate analogue for ANOVA. ANOSIM was always performed using all individual replicates (Clarke & Warwick 2001). To determine which taxa were most important in distinguishing significant spatio-temporal patterns in community structure, data were analysed using similarity percentage (SIMPER) analysis. Environmental data were normalised prior to analysis. To determine whether the measured environmental variables correlated with community structure, the BIOENV procedure was applied to averaged meiofauna data (average of 3 replicates per sample date). Final correlations only included the most important variables based on these analyses (temperature, salinity, microphytobenthic [MPB] biomass, depth).

RESULTS

Environmental variables

In August 2006, False Bay was completely dry and water levels at Charters Creek in South Lake were exceptionally low (Fig. 2). Esengeni and the Mouth had maintained relatively normal water levels. High

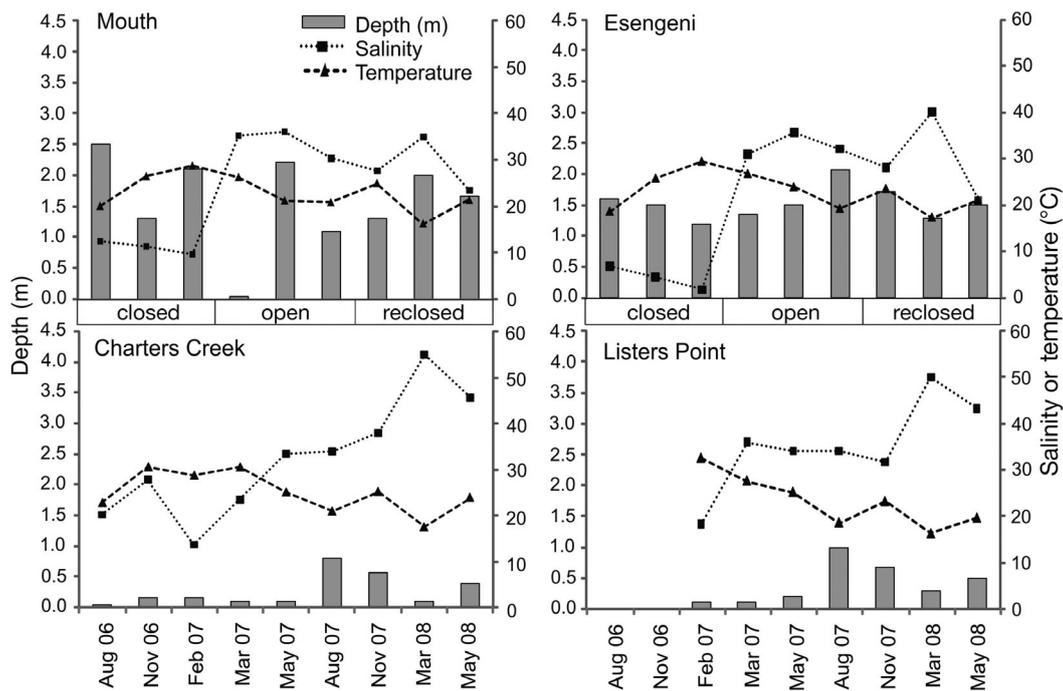


Fig. 2. Variations in sampling depth, salinity and temperature from quarterly samples collected between August 2006 and May 2008 at the 4 study sites in St Lucia Estuary (Mouth, Esengeni, Charters Creek, Listers Point). An additional sample was collected in March 2007 shortly after the estuary mouth breached. Mouth phase of estuary (close, open, reclosed) shown for all sites

rainfalls over summer 2006/2007 at all sites (621 to 733 mm, Table 1) resulted in a shallow accumulation of water in False Bay by February 2007. During the closed phase (August 2006 to February 2007), salinities were generally low, ranging from 9.7 to 12.4 at the Mouth, 1.8 to 6.8 at Esengeni, and 13.7 to 27.8 at Charters Creek, and 18 at Listers Point. During the open phase (March to August 2007), salinity changed immediately in the lower reaches and by May 2007, was that of seawater throughout the system. However, depth in the lakes only increased substantially towards the end of the open phase, as indicated by the significant rise in nearshore water depths in August 2007 (Fig. 2). In the reclosed phase (November 2007 to May 2008), water levels receded in the lakes, and a reversed salinity gradient developed by November 2007. There was a substantial increase in salinity in March 2008, which coincided with a drop in water temperature and depth. This was most severe in the lakes, with Charters Creek and Listers Point reaching 55 and 50, respectively. Temperature generally followed seasonal trends, particularly in the deeper sites at the Mouth and Esengeni, but this pattern was obscured by the uncharacteristically low temperatures recorded in March 2008 (Fig. 2). Ranges were also more extreme in the lakes (16.2 to 32.5°C) compared to the deeper sites (16.2 to 29.3°C).

One-way ANOVAs of the effect of site (phases pooled) and mouth phase (sites pooled) on environ-

mental variables indicated that sites were only differentiated by water depths during this survey, with significantly lower average depths in the lakes (0.33 ± 0.29 m) compared to the lower reaches (1.56 ± 0.6 m) ($F_3 = 35.81$; $p < 0.001$). However, salinity and temperature differed between mouth phases, with significantly lower salinity and higher temperatures during the closed phase than during either the open or reclosed phases ($F_2 = 27.2$; $p < 0.001$ and $F_2 = 5.46$; $p < 0.01$, respectively). No other measured environmental variables exhibited significant differences between sites or phases: dissolved oxygen content ranged from 4.09 to 13.0 mg l⁻¹, turbidity from 2 to 1179 NTUs and pH from 5.04 to 9.2 (Table 1). Overall, mean MPB biomass (chlorophyll *a*) was generally low (4 to 51 mg m⁻²), but higher means were observed during the closed phase at the Mouth and Esengeni (88.0 ± 98.3 and 64.1 ± 61.9 mg m⁻², respectively) and during the open phase at Charters Creek (121.8 ± 108.1 mg m⁻²), with a considerable overall range in values (0.5 to 258 mg m⁻²).

Sediments at the Mouth were well-sorted, composed mainly of medium sands (median particle size of 293 µm) and very low silt content (Fig. 3, Table 2). Sediments at Esengeni and Listers Point were similar, being moderately–poorly sorted, with a large percentage of mud and silt (75 and 53%, respectively) and small median particle size (50 and 107 µm, respectively). Charters Creek sediments were mod-

Table 1. Mean \pm SD of environmental variables measured on each sample occasion during the closed, open and reclosed phases at each site. Minimum and maximum values across all phases (Range) are also provided. Variables included dissolved oxygen (DO), pH, turbidity, microphytobenthic biomass (MPB), and cumulative rainfall. Note that measurements of salinity, temperature and depth are given in Fig. 2. NTU: nephelometric turbidity units

Site	Phase	DO (mg l ⁻¹)	pH	Turbidity (NTU)	MPB (mg chl <i>a</i> m ⁻²)	Rainfall (mm)
Mouth	Closed	7.2 \pm 2.0	7.8 \pm 0.8	37.7 \pm 47.0	88.0 \pm 98.3	730
	Open	7.7 \pm 1.1	8.1 \pm 0.2	26.3 \pm 30.3	16.4 \pm 12.4	357
	Reclosed	7.8	8.2 \pm 0.6	32.3 \pm 16.0	20.8 \pm 19.2	822
	Range	5.4–9.4	6.9–8.9	3.9–70.9	0.5–212.1	
Esengeni	Closed	8.4 \pm 4.5	8.4 \pm 0.3	42.0 \pm 4.8	64.1 \pm 61.9	621
	Open	6.7 \pm 0.9	7.5 \pm 0.1	59.2 \pm 49.2	14.1 \pm 14.9	311
	Reclosed	6.5	8.1 \pm 0.2	618.9 \pm 791.8	16.0 \pm 8.4	546
	Range	4.1–13.0	7.4–8.7	24.4–1179	0.5–145.5	
Charters Creek	Closed	8.8 \pm 2.3	8.7 \pm 0.5	39.2 \pm 22.4	41.1 \pm 20.6	621
	Open	8.5 \pm 2.0	8.1 \pm 0.4	27.5 \pm 28.6	121.8 \pm 108.1	311
	Reclosed	6.5 \pm 1.4	8.5 \pm 0.4	128.7 \pm 52.8	12.6 \pm 11.4	546
	Range	5.5–10.8	7.7–9.2	2.0–166.0	0.7–257.6	
Listers Point	Closed	6.5	8.3	75.0	51.2 \pm 49.6	733
	Open	7.5 \pm 1.0	7.1 \pm 1.8	32.8 \pm 30.7	42.6 \pm 49.9	427
	Reclosed	8.7 \pm 0.9	8.6 \pm 0.3	69.4 \pm 44.7	4.3 \pm 3.9	636
	Range	6.5–9.3	5.0–8.9	5.6–101.0	1.2–96.7	

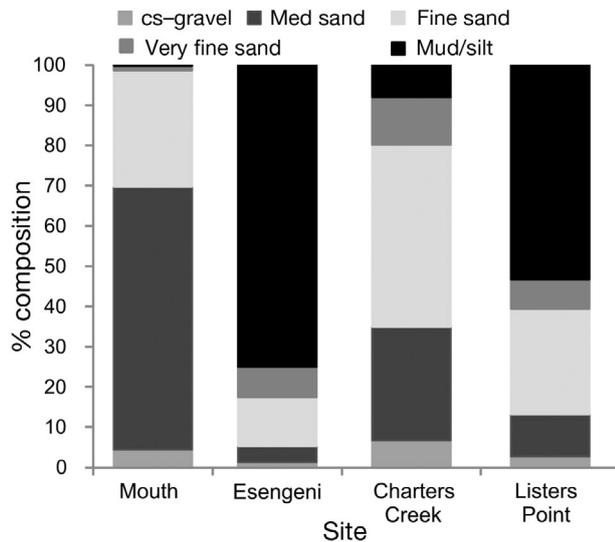


Fig. 3. Mean percentage composition of grain size classes at 4 sites in St Lucia Estuary (Mouth, Esengeni, Charters Creek, Listers Point). 'cs-gravel' includes 3 size classes: coarse sand, very coarse sand and gravel. Mean grain size was measured using sediments from meiofauna samples collected in May 2008 combined with grain size data from 2010 and 2011

erately sorted, with a greater proportion of fine-medium sands (median particle size of 213 μm) and low silt content. Average organic content was low at the Mouth (1.2%) and highest at Esengeni (7.6%), with intermediate values at Charters Creek and Listers Point (3.2 and 3.5%, respectively).

Meiofauna density, diversity and richness

Average densities varied among sites, and were 545 ± 910 ind. per 10 cm^2 at the Mouth, 394 ± 851 at Esengeni in the Narrows, 623 ± 510 at Charters

Table 2. Sediment characteristics at 4 sites in St Lucia Estuary (Mouth, Esengeni, Charters Creek, Listers Point), including sample size (n) and mean (\pm SD) median particle size (MPS), sorting class and percentage sediment organic matter (SOM). Mean MPS and sorting class were measured using sediments from meiofauna samples collected in May 2008 combined with grain size data from 2010 and 2011; mean % SOM was determined from random samples collected between 2006 and 2008 (November 2006, February 2007, March 2008, October 2008)

Site	Sediment features		
	MPS (μm)	Sorting	SOM (%)
Mouth	293 ± 0.01 (7)	0.49 ± 0.08 (7)	1.2 ± 1.8 (3)
Esengi	50 ± 0.001 (2)	0.96 ± 0.1 (2)	7.62 ± 1.5 (3)
Charters Creek	213 ± 0.05 (7)	0.78 ± 0.32 (7)	3.16 ± 3.0 (3)
Listers Point	107 ± 0.08 (7)	0.91 ± 0.47 (7)	3.48 ± 0.4 (2)

Creek in South Lake and 214 ± 164 at Listers Point, with an overall average of 457 ind. per 10 cm^2 . Minimum and maximum densities were 4 ± 7.4 and 2838 ± 1065 ind. per 10 cm^2 , both recorded at the Mouth (Fig. 4). Density peaked at the Mouth in the reclosed phase (November 2007) and in the closed phase (August 2006) at Esengeni, with comparatively low density on all other occasions. Charters Creek exhibited smaller, more gradual changes in density, with peaks in the closed (August 2006) and open phases (August 2007), and lows shortly after the mouth opened (March 2007) and in the reclosed phase when salinity reached 55 (March 2008). At Listers Point, density increased progressively after seawater entered the system, with a peak at the end of the open phase (August 2007), followed by a substantial drop and then recovery after reclosure.

The higher density at Charters Creek was significantly different (ANOVA $p < 0.001$; Table 3) from other sites. Mouth phase alone had no effect; however, there were differences between phases among sites as indicated by the significant interaction effect ($p = 0.002$). Post-hoc comparisons revealed that mouth phase only significantly influenced density at the Mouth, where there was a progressive increase after the mouth opened, with a significant difference between the closed and reclosed phases (Fig. 5). Although not significant, given the low mean density of meiofauna at Listers Point compared to other sites, the increase in density during the open phase at this site compared to the closed and reclosed phases (317 ± 200 ind. per 10 cm^2 , 94 ± 2 and 151 ± 77 ind. per 10 cm^2 , respectively) was considered important.

Taxon richness at the Mouth was considerably lower throughout the open phase and at the end of the reclosed phase compared to other times (Fig. 4). At Charters Creek, richness was generally high, but with notable decreases in the closed (August 2006) and open phases (March 2007). Esengeni and Listers Point had a low and fairly steady number of taxa, with peaks at Listers Point in the open (August 2007) and reclosed (May 2008) phases.

For diversity and richness, both main effects and the interaction between site and phase were significant (Table 3). Overall, taxon diversity and richness were significantly higher at Charters Creek than at all other sites, while the Mouth had significantly greater richness compared to the remaining sites. The interaction

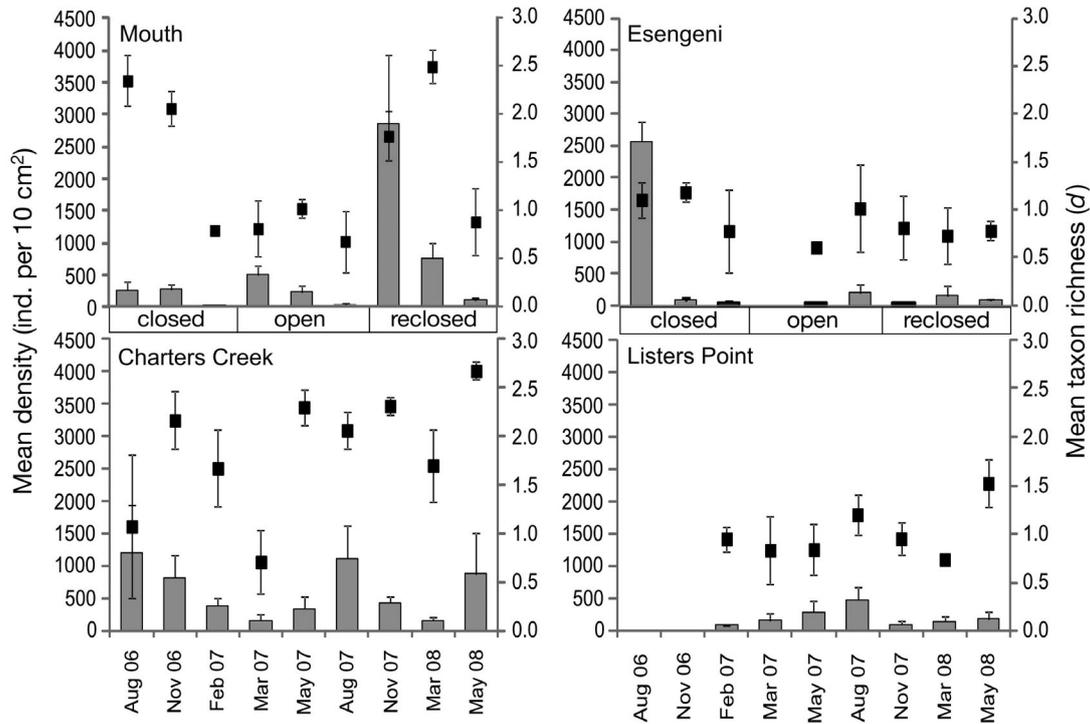


Fig. 4. Temporal variation in mean meiifauna density and taxon richness (Margalef's index, d) from quarterly samples collected between August 2006 and May 2008 at the 4 study sites in St Lucia Estuary (Mouth, Esengeni, Charters Creek, Listers Point). An additional sample was collected in March 2007, 10 d after the estuary mouth breached. Bars: density; ■: taxon richness. Error bars are SD. Mouth phase of estuary (closed, open, reclosed) shown for all sites

Table 3. Results of factorial ANOVAs examining the effects of site (Mouth, Esengeni, Charters Creek, Listers Point) and mouth phase (closed, open, reclosed) on density, taxonomic diversity (H') and richness (d) of meiifauna in St Lucia Estuary. Significant results are marked with an asterisk ($\alpha = 0.05$). Tests were performed using pooled replicates ($n = 3-9$)

Factors	SS	df	MS	F	p
Density					
Intercept	444.08	1.00	444.08	1348.35	<0.001
Site	6.85	3.00	2.28	6.93	<0.001
Phase	0.13	2.00	0.06	0.19	0.827
Site × Phase	7.57	6.00	1.26	3.83	<0.001*
Error	28.32	86.00	0.33		
Diversity					
Intercept	143.49	1.00	143.49	656.15	<0.001
Site	4.58	3.00	1.53	6.99	<0.000*
Phase	2.13	2.00	1.06	4.86	0.010*
Site × Phase	5.38	6.00	0.90	4.10	0.001*
Error	18.37	84.00	0.22		
Richness					
Intercept	148.07	1.00	148.07	610.02	<0.001
Site	14.46	3.00	4.82	19.86	<0.001*
Phase	2.64	2.00	1.32	5.44	0.006*
Site × Phase	5.29	6.00	0.88	3.63	0.003*
Error	20.39	84.00	0.24		

effect showed that there were no significant differences in diversity or richness between mouth phases at Esengeni and Listers Point (Fig. 5). However, both indices were significantly lower during the open phase at the Mouth, compared to the closed and reclosed phases. At Charters Creek, diversity was similar between the closed and open phases, but increased significantly after the mouth closed; the same pattern was observed for richness but was not significant.

Community structure

Two-way ANOSIM of the effects of site and mouth phase on meiifauna community structure showed that both factors had a highly significant effect ($R = 0.55$ and $R = 0.37$, respectively, $p = 0.001$; Table 4a). Pairwise comparisons revealed that the communities at each site were distinct and differed significantly from each other. Charters Creek, in particular, was clearly distinguished from the other sites as shown by the high R values. Similarly, the communities of each mouth phase were all significantly different from each other (Table 4a).

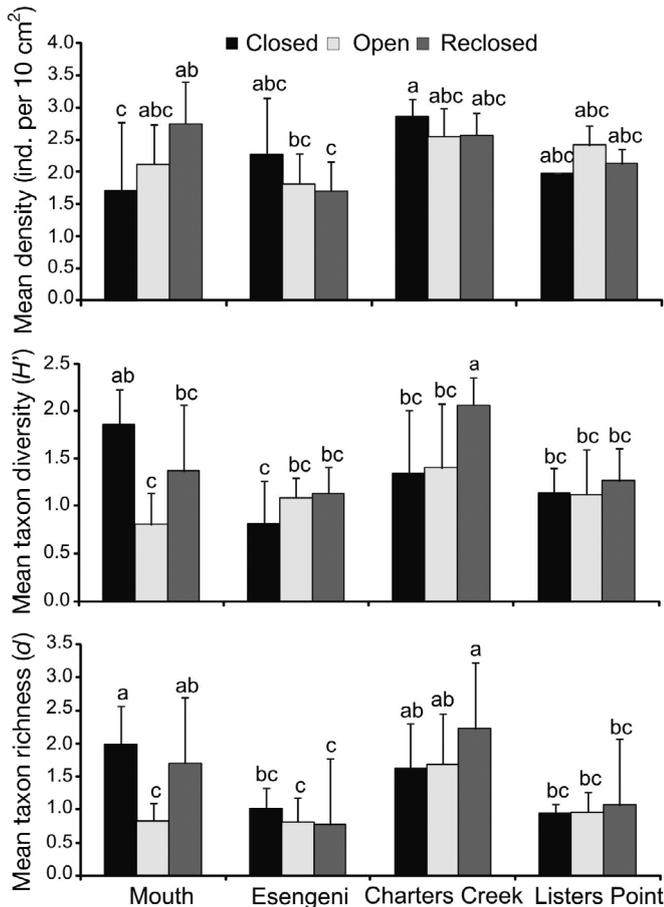


Fig. 5. Post-hoc test results showing the significant interaction effect of site and mouth phase (ANOVA) on density (log-transformed), diversity (Shannon-Weiner, H') and taxon richness (Margalef's index, d) of meiofauna in St Lucia Estuary. Similar letters indicate homogenous groups. Error bars are SD

For MDS ordinations, large sample sizes generally increase the complexity of the sample relationship, so that a successful 2-dimensional representation is unlikely (Clarke & Warwick 2001). This appeared to be the case when all replicates were used ($n = 96$) as the ordination resulted in a poor stress coefficient (0.24) and did not match the cluster analysis well. However, the same was true when replicates were averaged per site for each sampling date ($n = 33$). The most visible outcome of these plots was that samples grouped together primarily by site rather than mouth phase. Since phase did affect community structure as evidenced by ANOSIM, the difficulty in successfully mapping the data using MDS may therefore reflect a more complex interaction between these factors. Further spatial analysis examining the influence of mouth phase was therefore performed for each site separately. Similarly, application of the BIOENV procedure to the averaged data identified

no significantly correlating environmental parameters, i.e. when considered across all sites and phases, no variables could satisfactorily explain community patterns ($\rho = 0.117$; $p = 0.4$). Further assessment of the relationship with community patterns was therefore examined for individual sites.

When considered separately, there were distinct communities associated with different mouth phases, but not at all sites. The clearest differentiation was at the Mouth and Listers Point, where samples for each phase grouped separately at 55% similarity, although with outliers (Fig. 6a). This was supported by 1-way ANOSIMs, which found that communities between each phase were significantly different from each other at these sites (Table 4b). There was no correlation between environmental variables and community structure at the Mouth ($\rho = 0.08$, $p = 0.76$, BIOENV). Although slightly non-significant, environmental variables showed strong correlations with community structure at Listers Point ($\rho = 0.64$, $p = 0.06$). Salinity was the most important variable and when overlaid on the meiofauna MDS ordination, changes in salinity between mouth phases closely matched the clustering of samples (Fig. 6b).

At Esengeni, there was only a small cluster of open and reclosed-phase samples at 55% similarity in the MDS ordinations, all other samples being distinct (Fig. 6a). The closed-phase samples were generally the most dissimilar from the others, but also from each other. Overall, there was a significant difference in communities between the closed and reclosed phases only (Table 4b). Environmental variables were significantly correlated with community structure at this site ($\rho = 0.8$, $p = 0.001$). Temperature and MPB biomass were the most important, followed by a combination of these variables and salinity ($\rho = 0.78$). Temperature appeared to better explain the dispersion of samples in the MDS plot than mouth phase (Fig. 6b), with the exception of Sample 1 (August 2006, closed), which was differentiated by a substantially higher MPB biomass compared to other samples. At Charters Creek, samples did not cluster distinctly by mouth phase in the MDS ordination, but the closed- and reclosed-phase samples generally plotted furthest apart (Fig. 6a). Statistically, there was a significant change in communities only after mouth reclosure (Table 4b). Environmental variables were strongly correlated with variations in community structure ($\rho = 0.7$, $p = 0.001$). Salinity was the best predictor of community variation, followed by MPB biomass then temperature, but only salinity was well-matched with the clustering of samples in the MDS plot (Fig. 6b).

Table 4. Results of multivariate analysis of similarity (ANOSIM) on community structure and composition of meiofauna in the St Lucia Estuary, examining the effects of (a) site and mouth phase (2-way ANOSIM), and (b) mouth phase at each site separately (1-way ANOSIM). For the ANOSIM test statistic (R), a significance level of 5% corresponds to $p = 0.05$, Clarke & Warwick 2001). Significant results are marked with an asterisk ($\alpha = 0.05$)

	R	Significance
(a) Two-way ANOSIM (site and phase)		
Site		
Global test	0.549	0.1*
Pairwise tests		
Mouth, Esengeni	0.492	0.1*
Mouth, Charters Creek	0.533	0.1*
Mouth, Listers Point	0.519	0.1*
Esengeni, Charters Creek	0.634	0.1*
Esengeni, Listers Point	0.534	0.1*
Charters Creek, Listers Point	0.678	0.1*
Phase		
Global test	0.365	0.1*
Pairwise tests		
Closed, Open	0.34	0.1*
Closed, Reclosed	0.517	0.1*
Open, Reclosed	0.313	0.1*
(b) One-way ANOSIMS (phase)		
Mouth		
Global test	0.319	0.1*
Closed, Open	0.366	1.1*
Closed, Reclosed	0.291	2*
Open, Reclosed	0.316	1*
Esengeni		
Global test	0.284	0.3*
Closed, Open	0.204	6
Closed, Reclosed	0.534	0.1*
Open, Reclosed	0.028	35.2
Charters Creek		
Global Test	0.348	0.1*
Closed, Open	0.104	11.2
Closed, Reclosed	0.588	0.2*
Open, Reclosed	0.359	0.1*
Listers Point		
Global Test	0.544	0.1*
Closed, Open	0.823	0.5*
Closed, Reclosed	0.683	0.5*
Open, Reclosed	0.469	0.1*

Distinguishing taxa

A total of 61 taxa or groups were identified at various taxonomic levels (Table 5). Of the major groups, nematodes were generally dominant, contributing on average 44% to total meiofaunal abundance. Subdominant groups were more variable, but the most common were harpacticoid copepods, foraminiferans, ciliates, naupliar larvae, ostracods and turbellarians, with other taxa becoming important at spe-

cific sites or times, such as kinorhynch (Charters Creek) and nemertean (Mouth).

The spatio-temporal patterns of abundance of the most important groups distinguishing sites and phases (identified by SIMPER) are plotted in Fig. 7. These were nematodes, harpacticoid copepods, calcareous and allogromiid foraminiferans and ostracods, which were found at all sites but differed in their relative abundances in space and time. Nematode abundance was highest during the open phase at the Mouth and Listers Point and during the closed phase at Charters Creek and particularly at Esengeni in August 2006, where a substantial peak of 2414 ± 272 ind. per 10 cm^2 was observed (compared to a mean density of 28 ± 20 ind. per 10 cm^2 for all other times at this site). There were large increases in harpacticoid copepod abundance during the open phase at Charters Creek (275 ± 272 ind. per 10 cm^2) and the reclosed phase at the Mouth. Ostracods were virtually absent throughout the system while the mouth was open, with a peak in the lower reaches during the closed phase and in the lakes during the reclosed phase, reaching peak density at Charters Creek (199 ± 116 ind. per 10 cm^2). Similarly, calcareous foraminiferans were least abundant during the open phase, except at Listers Point where they exhibited the highest density at this time (153 ± 98 ind. per 10 cm^2). The opposite pattern was observed for allogromiid foraminiferans, which had substantially greater abundances during the open and/or reclosed phases at all sites (peak density 86 ± 95 ind. per 10 cm^2). Density of both foraminiferan groups was substantially greater in the lakes than in the lower reaches.

The strong distinction of communities between sites was emphasised by the high dissimilarities in the SIMPER analysis (61 to 68%). Some of the differences between phases were therefore better explained by taxa specific to those sites (or rare elsewhere). Community composition differed significantly between all 3 phases at the Mouth. In addition to ostracods, nemertean were important in distinguishing the closed phase community, being absent during the open phase and only reappearing at the end of the reclosed phase. The open phase was characterised by a high abundance and dominance of nematodes (78% of total meiofauna), while large numbers of ciliates, macrostomid turbellarians, harpacticoid copepods and naupliar larvae differentiated the reclosed phase. The closed phase at Esengeni was distinguished by a high density of nematodes and a higher abundance of ostracods, nereid polychaetes and the kinorhynch *Echinoderes maxwelli*. The change in communities after the mouth opened was largely due to the de-

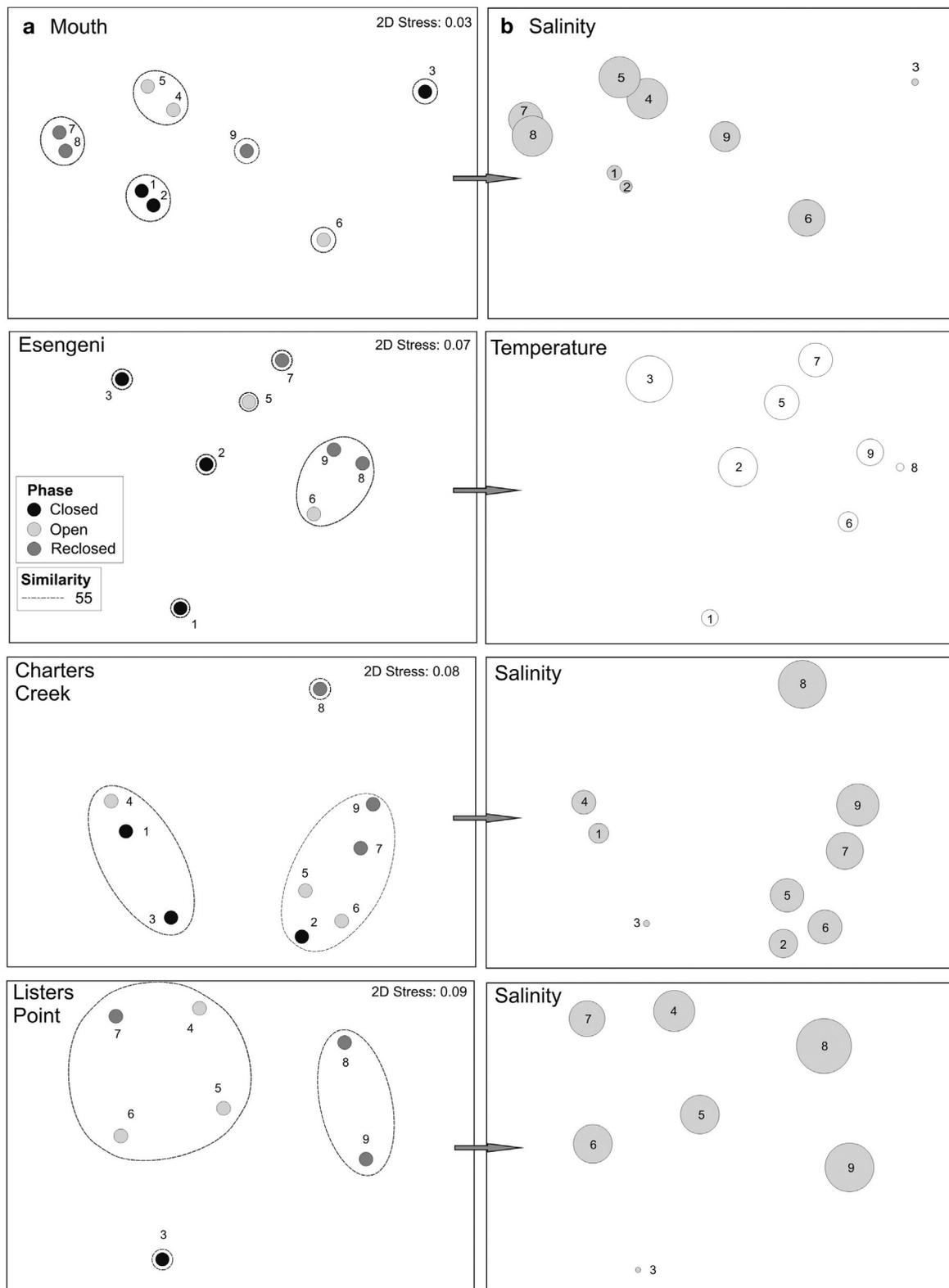


Fig. 6. Non-metric multidimensional scaling (MDS) ordinations for (a) meiofauna communities and (b) primary environmental variables, showing the distribution and grouping of samples according to the closed (1: August 2006; 2: November 2006; 3: February 2007), open (4: March 2007; 5: May 2007; 6: August 2007) and reclosed (7: November 2007; 8: March 2008; 9: May 2008) phases at each site. Results from cluster analysis are superimposed to show groups defined at 55% similarity

Table 5. Mean density (ind. per 10 cm²) of identified meiofauna groups and taxa in the St Lucia Estuary during the closed (C), open (O) and reclosed (R-C) mouth phases at 4 sites located at increasing distance from the estuary mouth (left to right). Major group categories are numbered (1 to 20). Total maiofauna values are means ± SD. *Identification tentative. Unid.: unidentified

Major groups & taxa		Mouth			Esengeni			Charters Creek			Listers Point		
		C (n=9)	O (n=9)	R-C (n=9)	C (n=9)	O (n=6)	R-C (n=9)	C (n=8)	O (n=9)	R-C (n=9)	C (n=3)	O (n=9)	R-C (n=9)
1. FORAMINIFERA													
Calcareous forams		–	2	16	2	5	10	47	13	45	1	84	6
Monothalamous forams													
Allogromiidae		2	–	10	2	19	2	5	28	38	–	32	1
Saccamminidae		–	–	2	–	–	–	–	1	8	–	–	–
2. CILIOPHORA													
Litostomatea													
Unid. haptorians		8	8	32	–	–	–	2	–	1	–	–	–
(Haptoria)													
Tracheliidae								1	20	42	–	–	–
<i>Dileptus</i> sp/p.		–	–	–	–	–	–	–	–	–	–	–	–
<i>Trachelius</i> sp/p.		4	–	3	–	–	–	–	–	0.4	–	–	–
Lacrymariidae													
<i>Lacrymaria</i> sp/p.*		–	–	7	–	–	–	–	–	–	–	–	–
Karyorelictea													
Karyorelictea spp.*		1	1	27	0.4	–	–	–	–	–	–	–	–
Nassophorea													
<i>Frontonia</i> -type		1	–	747	–	–	–	–	–	–	–	–	–
Heterotrichea													
<i>Condylostoma</i> sp.*		–	–	13	–	–	–	–	–	–	–	–	–
Ciliates													
Ciliate sp. 1		–	–	–	–	–	–	–	47	–	–	–	–
Unid. ciliates		4	6	28	2	1	10	20	16	13	–	7	6
3. CNIDARIA													
Cnidaria													
Unid. cnidarian juveniles		–	–	–	–	–	–	0.4	–	3	–	–	–
Hydrozoa													
Unid. hydrozoans		–	–	–	–	–	–	0.4	–	–	–	–	0.4
PLATYHELMINTHES													
4. Turbellaria													
Macrostomida													
(juveniles)		–	–	42	–	–	–	0.4	0.4	27	0	–	–
Proseriata		7	1	0.4	–	–	–	–	–	–	–	–	–
Rhabdozoa													
Unid. turbellarians		–	–	0.4	–	–	–	–	0.4	–	–	–	–
Unid. turbellarians		4	7	4	2	–	–	7	2	1	2	1	14
5. NEMERTEA													
Nemertea		13	0.4	16	–	–	–	–	–	–	–	–	–
6. NEMATODA													
Desmoscolecidae													
<i>Quadricoma</i> sp.*		–	–	–	–	–	–	–	0.4	12	–	–	–
Unid. nematodes		51	190	124	828	38	17	565	246	99	3	149	69
7. KINORHYNCHA													
Echinoderidae													
<i>Echinoderes maxwelli</i>		–	1	2	11	1	1	57	11	43	–	–	0.4
8. ROTIFERA													
Brachionidae													
<i>Brachionus rotundiformis</i>		–	–	–	–	–	–	–	–	–	5	3	0.4
Brachionidae sp. 1		–	–	–	–	–	–	–	–	0.4	–	–	–
Dicranophoridae													
<i>Enicentrum</i> sp. 1		–	–	8	–	–	–	–	–	–	–	–	–
Lecanidae													
<i>Lecane</i> cf. <i>grandis</i>		–	–	–	–	–	–	4	–	–	–	–	–
Testudinellidae													
<i>Testudinella</i> cf. <i>obscura</i>		–	–	–	0.4	–	–	–	–	–	–	–	–
ANNELIDA													
9. Oligochaeta													
Oligochaete sp. 1		–	–	–	1	–	0.4	–	–	–	–	–	–
Unid. oligochaetes		1	3	–	1	–	–	–	–	–	–	–	–
10. Polychaeta													
Capitellidae													
<i>Capitella capitata</i>		–	–	1	–	–	–	–	4	1	–	–	–
<i>Mediomastus</i> spp.*		–	–	–	–	–	–	–	0.4	0.4	–	–	–
Unid. capitellids		–	–	–	–	–	–	1	0.4	1	–	–	–
Nereidae													
Nereidae spp.		2	–	1	6	–	–	6	7	0.4	–	–	–

Table 5 (continued)

Major groups & taxa		Mouth			Esengeni			Charters Creek			Listers Point			
		C (n=9)	O (n=9)	R-C (n=9)	C (n=9)	O (n=6)	R-C (n=9)	C (n=8)	O (n=9)	R-C (n=9)	C (n=3)	O (n=9)	R-C (n=9)	
Protodrilidae*	Protodrilidae sp.	-	1	-	-	-	-	-	-	-	-	-	-	
Sabellidae	<i>Desdemonia ornata</i>	-	-	-	-	-	-	3	5	2	-	-	-	
	Unid. sabellids	-	-	-	0.4	-	-	-	0.4	0.4	-	-	-	
Spionidae	<i>Polydora</i> group ^a	0.4	-	0.4	-	-	-	-	-	-	1	11	1	
	<i>Prionospio</i> spp.	-	-	2	-	-	-	-	-	0.4	-	-	1	
	Unid. spionids	-	-	0.4	-	1	-	-	1	-	3	-	0	
Unid. postlarvae		0.4	-	-	0.4	-	-	1	-	-	-	0.4	0.4	
ARTHROPODA														
CRUSTACEA														
11.	Amphipoda	0.4	-	-	-	-	-	1	-	1	-	-	3	
12.	Cumacea	1	-	-	-	-	-	0.4	0.4	-	-	-	-	
13.	Copepoda													
	Calanoida	1	-	-	-	-	-	0.4	0.4	-	-	-	-	
	Cyclopoida	0.4	-	5	0.4	-	-	2	-	-	-	-	4	
	Harpacticoida	25	19	85	4	35	15	47	107	30	58	16	6	
14.	Ostracoda	29	-	1	32	3	-	0.4	3	67	-	1	20	
15.	Tanaidacea													
	Apseudidae	<i>Apseudes digitalis</i>	1	-	-	0.4	-	-	6	-	2	-	-	
	Unid. tanaid	Tanaidacea sp. 1	-	-	-	0.4	1	-	1	0.4	-	-	-	
16.	Naupliar larvae		0.4	1	40	2	4	26	77	24	22	15	10	6
HEXAPODA														
17.	Diptera													
	Ceratopogonidae	Ceratopogonid larvae	-	-	-	-	-	-	1	-	-	-	-	
	Chironomidae	Chironomid larvae	2	-	-	-	-	-	2	2	1	-	-	0.4
	Dolichopodidae	Dolichopodid larvae*	-	-	-	-	-	-	0.4	-	-	-	-	
	Unid. dipteran larvae		-	-	-	-	1	0.4	-	-	-	-	-	
CHELICERATA														
18.	Acari													
	Astigmata													
	Acaridae	<i>Tyrophagus putrescentiae</i>	0.4	1	1	2	-	-	-	1	3	3	2	0.4
	Prostigmata													
	Halacaridae	<i>Copidognathus africanus</i>	0.4	0.4	-	-	-	-	0.4	1	2	-	-	-
		<i>Copidognathus</i> sp. 1	-	0.4	-	-	-	-	-	-	-	-	-	-
		<i>Acarothrix umgenica</i>	-	-	-	-	-	-	-	-	6	1	-	-
	Mesostigmata													
	Uropodidae	<i>Uroobovella</i> sp.	-	-	-	-	-	-	-	-	-	1	0.4	-
MOLLUSCA														
19.	Bivalvia	Bivalve postlarvae	0.4	-	-	-	-	-	-	-	-	-	-	-
20.	Gastropoda													
	Assiminea	<i>Assiminea</i> sp/p.	7	-	-	-	-	-	-	-	15	-	-	13
OTHER (Unid.)														
			2	-	9	1	1	-	1	1	5	-	-	-
TOTAL MEIOFAUNA														
			167	243	1226	896	108	81	858	544	493	94	317	151
			±142	±218	±1356	±1268	±128	±91	±553	±516	±445	±2	±200	±77
	Cysts		1	-	0.4	-	-	-	-	3	0.4	-	-	-
	Eggs		363	39	42	121	72	110	237	90	145	101	98	58

^aPolydora group: complex of spionid polychaete genera defined by the number and structure of modified spines on setiger 5 (Delgado-Blas 2011); includes the genera *Boccardia*, *Polydora* and *Dipolydora*, which have been recorded in St Lucia Estuary (Millard & Broekhuysen 1970, Pillay & Perissinotto 2008, McKay et al. 2010)

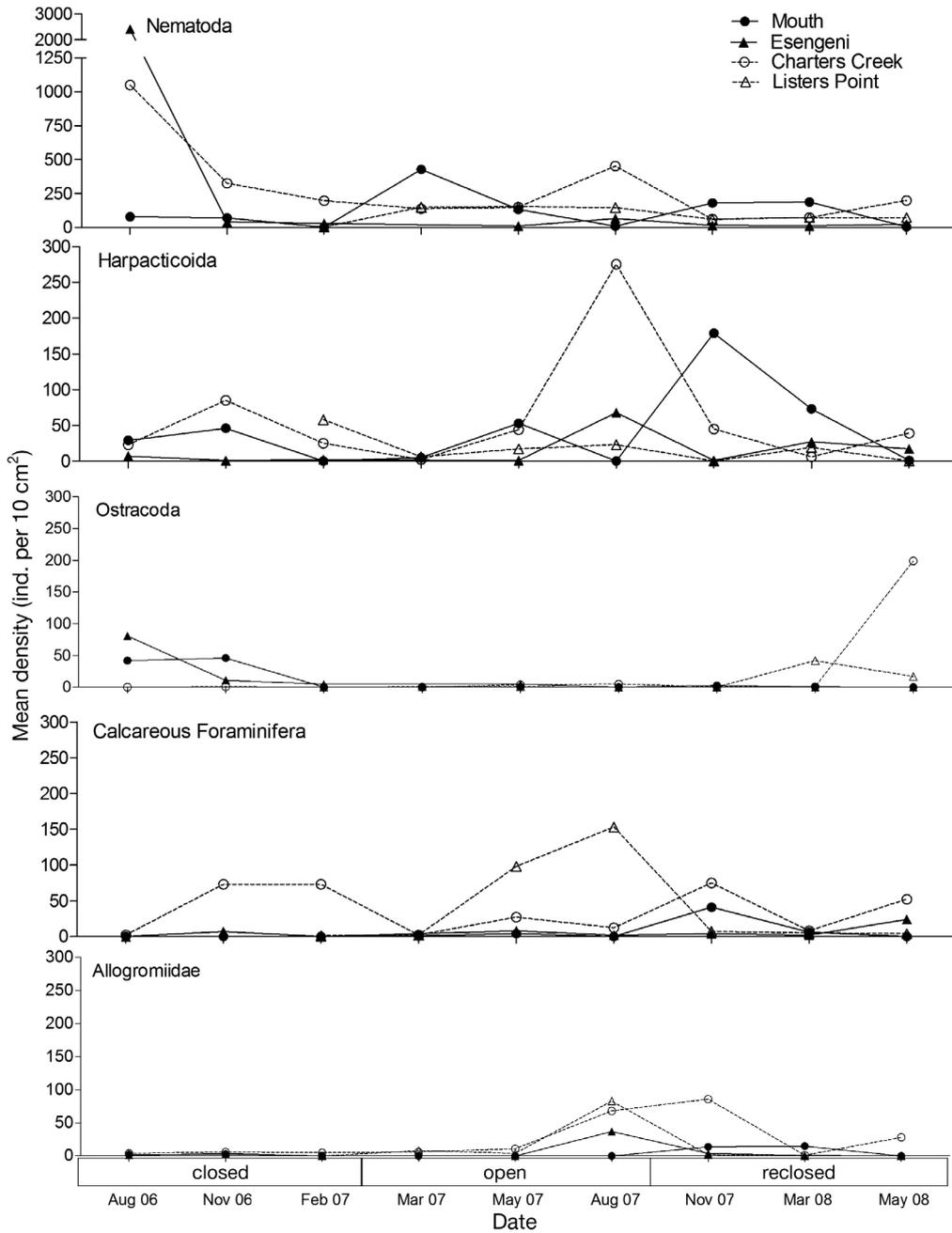


Fig. 7. Temporal variations in mean density of dominant taxa (n = 3) based on quarterly samples collected between August 2006 and May 2008 at 4 sites in St Lucia Estuary (Mouth, Esengeni, Charters Creek, Listers Point). An additional sample was collected shortly after the mouth breached in March 2007. Mouth phase of estuary (closed, open, reclosed) shown for all sites. Note that maximum density values (y-axis) differ in the first graph (Nematoda)

crease/absence of these taxa and the increase in allogromiid foraminiferans and harpacticoid copepods, while the reclosed phase was characterised by a large number of naupliar larvae.

At Charters Creek, *Echinoderes maxwelli*, in particular, was a regular and important component of the biota (1 to 17% of meiofauna) and contributed significantly to dissimilarity with other sites and be-

tween phases at this site (5 to 6.7%). Average density of *E. maxwelli* ranged from 0 to 139 ind. per 10 cm² and was substantially lower during the open phase compared to the closed and reclosed phases (Table 5). Density of harpacticoid copepods, allogromiid foraminiferans and most polychaete taxa increased substantially during the open phase. However, the change in community composition was only significant in the

reclosed phase, which could be attributed to the high abundance of several taxa that were generally rare or absent before this. These included macrostomid turbellarians, the nematode, cf. *Quadricoma* sp., both of which contributed the most to dissimilarity between phases (5.5 to 7.8%), the ciliate genus *Dileptus*, *E. maxwelli*, ostracods and the mite *Acarothrix umgenica*. At peak salinity (55), taxon richness and diversity were substantially reduced (Fig. 4) and only macrostomid turbellarians, *E. maxwelli*, cf. *Quadricoma* sp. and other nematodes persisted in reasonably high densities (12 to 62 ind. per 10 cm²). Communities also changed significantly between each mouth phase at Listers Point, the most distant site from the sea. The closed phase samples were dominated by harpacticoid copepods and naupliar larvae (78%). The open phase was distinguished by high densities of nematodes, allogromiid and calcareous foraminiferans and a peak in recruitment of juvenile polychaetes of the *Polydora* group. The reclosed phase was characterised by the appearance of gastropods and amphipods for the first time, an increase in ostracod abundance and the lower abundance of dominant open-phase taxa.

DISCUSSION

The sea-induced breaching event recorded at St Lucia Estuary in 2007 had a significant impact on community structure and composition of meiofauna, but with varying effects between sites in different regions of the estuary. This partly reflected the distance of sites from the mouth and differences in important environmental variables among sites. Distinct differences in community structure and composition between sites further contributed to the differential effects of mouth phase.

Spatial variations in meiofauna community structure

Mean densities varied among sites, and were 545 ± 910 ind. per 10 cm² at the Mouth, 394 ± 851 at Esengeni in the Narrows, 623 ± 510 at Charters Creek in South Lake and the lowest mean density of 214 ± 164 ind. per 10 cm² was recorded at Listers Point. Similarly, taxon richness and diversity of meiofauna were highest at Charters Creek and the Mouth, with significantly lower indices at Esengeni and False Bay, corresponding with meiofaunal richness patterns previously recorded in the estuary (Pillay & Perissinotto 2009).

In most estuaries, meiofauna density and richness decrease with distance from the mouth, which is generally attributed to the salinity gradient moving from marine to freshwater at the head of the estuary (Alves et al. 2009, Hourston et al. 2009). However, in this study the salinity gradient was reversed, with the exception of the open phase when salinity was marine throughout. This is typical for St Lucia Estuary during periods of low rainfall (Day et al. 1954, Bolt 1975, Pillay & Perissinotto 2009). The lakes are particularly susceptible to high rates of evaporative water loss, which leads to higher salinities and greater variability in conditions compared to the deeper sites of the estuary channel (Bolt 1975, Pillay & Perissinotto 2009, Whitfield & Taylor 2009). The higher density and richness observed at Charters Creek may reflect this reversed salinity gradient. Community structure was significantly correlated with salinity at this site, and salinity variations are usually less extreme than in the northern lakes (Pillay & Perissinotto 2009). Similarly, near-freshwater salinities at Esengeni during closed-mouth conditions may contribute to reduced density and richness there (e.g. Adão et al. 2009, Alves et al. 2009, Hourston et al. 2009).

Meiofauna density generally decreases from the mouths to the inner reaches in Australian intermittently open and closed coastal lakes and lagoons (ICOLLs), which is considered to reflect the greater isolation of these areas from the sea (Dye 2005). The lowest density in St Lucia Estuary was at the northernmost site in False Bay, which can be partly attributed to the greater isolation of this site from the rest of the system and the sea (e.g. Millard & Broekhuysen 1970, Bolt 1975). The northern lakes are also the most sensitive to desiccation and hypersalinity (Pillay & Perissinotto 2009) and therefore exhibit the most extreme variations in environmental conditions. Extreme salinity ranges, rather than absolute salinity, can reduce meiofauna populations (Attrill 2002, Hourston et al. 2009). Distance from population sources and more variable and extreme conditions may therefore explain the low abundance and diversity of meiofauna there.

Sediment characteristics may interact with and override salinity effects (Soetaert et al. 1995, Alves et al. 2009). Sediment structure can directly determine the type of organisms likely to be found at a site (Fenchel 1978), and combined with the influences of isolation and salinity gradient, likely contributed to the differences in community structure and composition between sites. Charters Creek and the Mouth were composed of fine to medium sandy sediments (>200 µm median particle size [MPS]), which gener-

ally support higher densities and diversity of meiofauna, whereas richness and diversity are generally low in fine, muddy sediments with high organic content, as observed at Listers Point and Esengeni (53 to 72% mud/silt; <110 μm MPS) (Fenchel 1978, Schratzberger & Warwick 1998, Vanaverbeke et al. 2011). Other factors known to influence meiofauna, but which were not important at the spatial and temporal scales examined in this study, include dissolved oxygen (Vanaverbeke et al. 2011) and pH (Kapusta et al. 2006). In shallow estuaries, waters are usually well mixed by wind action and oxygen content is rarely limiting (Perissinotto et al. 2010b).

Effect of mouth state on meiofauna community structure and composition

There is very little information on the effect of mouth-breaching on meiofauna. In the Mdloti Estuary, South Africa, meiofauna density peaked after prolonged mouth closure, but decreased substantially when the mouth breached due to high rainfalls (Nozais et al. 2005). This was largely attributed to substantial scouring of sediments that is typical of flood-induced breaching (Perissinotto et al. 2006, Whitfield et al. 2008). In St Lucia Estuary, the Mouth site was the most severely affected in terms of all aspects of community structure and was the only site to exhibit a negative impact of the breach. Diversity and richness of meiofauna were significantly reduced throughout the open phase. However, in contrast to the study in the Mdloti Estuary, density increased and peaked after mouth reclosure. Density and diversity at other sites in the estuary were either unaffected by mouth state, or increased during the open or reclosed phases. This likely reflects the greater physical disturbances in the mouths of estuaries during open phases (Perissinotto et al. 2010b), which may be reduced with distance from the mouth. Sediment scouring may also be less severe in a sea-induced breach, disturbances instead being generated by tidal currents and sediment transport/inflow from the sea (Perissinotto et al. 2010b).

Strong tidal flows can reduce meiofauna density and diversity in surface sediments (Heip et al. 1985, Chen et al. 1999) due to sediment erosion, increased suspension of meiofauna in the water column (Palmer & Gust 1985, Commito & Tita 2002) or migration of meiofauna deeper into the sediment (Palmer & Molloy 1986, Steyaert et al. 2001). The meiofaunal community during the open phase became strongly dominated by nematodes (78%), which increased in density, while many other taxa disappeared (e.g.

nemertean and ostracods). Certain meiofaunal groups may be more susceptible to sediment disturbance than others (e.g. foraminiferans) (Palmer 1988). Nematodes have been found to be variously more resistant or susceptible to disturbance with increased tidal flows compared to other taxa, such as harpacticoid copepods, which appears to reflect species-specific differences (Fleeger et al. 1984, Palmer & Gust 1985, Palmer & Molloy 1986, Steyaert et al. 2001, Commito & Tita 2002). Certain (presumably) 'disturbance-tolerant' nematode species are also known to migrate towards the surface as tidal flows increase (Steyaert et al. 2001, Schratzberger et al. 2009, Maria et al. 2011). Thus, different tolerances to physical disturbance and/or resuspension may explain the lower overall diversity but increased density of nematodes in surface sediments at the Mouth

MPB biomass was lower during the open phase at the Mouth, suggesting that low food availability, possibly due to increased tidal flows (e.g. Perissinotto et al. 2006), may have led to reduced taxonomic richness. However, MPB biomass was still within the range reported for most other occasions in the estuary and the absence of any correlation with meiofauna patterns indicates that it did not significantly influence meiofauna communities at this site. Sudden changes in salinity can be detrimental to meiofauna (Richmond et al. 2007, Bollmohr et al. 2009, Duggan et al. 2010). The rapid increase in salinity at the Mouth after the breach (11 to 35) may therefore have contributed to the loss of certain taxa, whereas estuarine nematodes are known to be particularly tolerant to substantial salinity fluctuations (Forster 1998, Moens & Vincx 2000a,b). This may have been exacerbated by prolonged closure in St Lucia Estuary prior to the breach, during which communities may have acclimated to the persistently low salinities at this site. This could also be an artefact of the frequency of breaching, rather than salinity itself (Lill et al. 2011), the impact on estuarine communities being greater when breaching occurs infrequently (De Decker 1987, Lill et al. 2011), e.g. extended periods of mouth closure in the Bot River Estuary (South Africa) leads to the development of a macrofauna assemblage dominated by 'lagoonial' species that are subsequently eliminated when the mouth breaches (De Decker 1987).

Esengeni in the Narrows was less affected by the breach compared to other sites. There were no significant differences in density, diversity or richness between mouth phases. Although community composition was significantly different before and after the breach (ANOSIM), changes in community structure in MDS ordinations were more strongly associated

with environmental variables (BIOENV) that did not necessarily correspond with mouth state. Community variations were mainly correlated with temperature and MPB biomass, followed by salinity. MPB biomass strongly differentiated samples on one occasion in the closed phase. It is generally not considered to be a limiting resource for meiofauna (Pinckney et al. 2003, Nozais et al. 2005); however, a substantial bloom at this site, where MPB biomass is normally low (Perissinotto et al. 2010a), was associated with a considerable increase in the density of nematodes (28 ± 20 ind. per 10 cm^2 to 2414 ind. per 10 cm^2), juvenile nereid polychaetes, ostracods and kinorhynchs, suggesting that food availability may be a limiting factor at certain sites or for certain species (e.g. Vanaverbeke et al. 2004, Hourston et al. 2009).

Water levels at Esengeni were deeper and reasonably constant, and hence seasonal temperature patterns were more pronounced than at other sites, which may explain the greater influence of temperature on populations there. Seasonal patterns are common in meiofauna in estuaries, and temperature can be particularly important in controlling reproductive cycles (Coull & Dudley 1985, Moens & Vincx 2000b, Hourston et al. 2009). Harpacticoid copepod abundance was greatest during the open phase, followed by a substantial peak in naupliar larvae in the reclosed phase at this site. Since the breach occurred in winter, this may reflect seasonal reproductive cycles (e.g. Coull & Dudley 1985) and/or the change from near-freshwater to marine salinities (e.g. Gonçalves et al. 2012). Allogromiid (monothalamous) foraminiferans also increased substantially in abundance during the open and/or reclosed phases at all sites, which likely reflects the change to marine salinities. Although known from freshwater environments (Holzmann & Pawlowski 2002), most monothalamous foraminiferans are marine (Sabbatini et al. 2010).

At Charters Creek (South Lake), density did not differ significantly between phases. However, this could largely be attributed to a substantial peak in nematode density at the beginning of the closed phase in close association with a filamentous algal mat present only at this time. Excluding this sample, mean meiofaunal density increased from 175 ± 4.5 ind. per 10 cm^2 in the closed phase to 544 ± 516 ind. per 10 cm^2 in the open phase. There was some evidence to suggest that increased flow through South Lake during the open phase disturbed certain taxa, while benefitting others. In particular, there were substantial increases in densities of harpacticoid copepods, allogromiid foraminiferans and a strong recruitment of most polychaete taxa (e.g. the

filter-feeding polychaete *Desdemona ornata*). However, calcareous foraminiferans and the kinorhynch *Echinoderes maxwelli* were both abundant in the closed and reclosed phases but decreased substantially while the mouth was open. There is typically a reversed net flow of water through the system during dry periods, when the mouth is open (Owen & Forbes 1997), which was evident in the current study due to the substantial rise in nearshore water depths at both lake sites at the end of the open phase. Kinorhynchs and foraminiferans are small, burrowing deposit feeders (Ruppert et al. 2004). Their lower abundance while the mouth was open may therefore reflect stronger water flows, either due to direct disturbance or to decreased sediment organic content (Dunn et al. 2008). Similarly, benthic ostracods, which are also mainly burrowing detritivores, were virtually absent throughout the system while the mouth was open, possibly for the same reason.

Taxon richness and diversity were similar in the closed and open phases but increased significantly in the reclosed phase. Salinity was the most important variable correlating with community structure at this site and there was an overall increase in salinity from the closed to the reclosed phase when community composition changed significantly. This was largely attributed to certain taxa that only emerged or became abundant at this time, suggesting a preference for the higher salinity and/or the calmer conditions. This could also reflect the lower abundance of open-phase groups and hence reduced competition for resources, allowing rarer, possibly more salinity-tolerant, species to increase (e.g. Medina et al. 2007, Schratzberger et al. 2009). When salinity peaked at 55, density and richness decreased as most taxa became scarce or absent. Similar effects of increased salinity on meiofauna communities have been reported for other estuarine lake/lagoonal systems (Montagna & Kalke 1992, Doulgeraki et al. 2006). Communities become impoverished, in this case being reduced to a small selection of taxa including macrostomid turbellarians, the nematode cf. *Quadricoma* sp. and *Echinoderes maxwelli*. None of these taxa are typical of hypersaline environments; however, macrostomids are known to occur at high salinities (Kuperman et al. 2002).

Listers Point in False Bay was dry at the start of the study. High summer rainfalls resulted in water entering the lake and sampling was initiated at this site shortly before the mouth breached. There were significant changes in community composition between mouth phases, which were correlated with changes in salinity, but no significant differences in univariate

community indices. The community before the breach was dominated by harpacticoid copepods and naupliar larvae. Harpacticoids are known to be early colonisers due to their high dispersal ability (Comito & Tita 2002, da Fonsêca-Genevois et al. 2006), and the high number of naupliar larvae suggests a rapid and opportunistic response to the input of water. Although not significant, mean density was substantially higher while the mouth was open compared to the closed and reclosed phases (317 ± 200 , 94 ± 2 and 151 ± 77 ind. per 10 cm^2 , respectively). This was due to the increased abundance of nematodes and recruitment of taxa such as polychaetes and foraminiferans, which have planktonic larvae or propagules (Ruppert et al. 2004, Murray 2006) and are able to disperse more rapidly (e.g. Schratzberger et al. 2008). The continual inflow of seawater throughout the open phase presumably facilitated recruitment of these taxa, which supports the suggestion that the southern portions of North Lake and South Lake may act as a reservoir for recolonisation of northern areas (Boltt 1975). Furthermore, richness only peaked at the end of the survey, when the gastropods *Assimineia* cf. *ovata*, amphipods and ostracods appeared for the first time. These groups have direct development and are therefore dependent on sediment suspension for dispersal, so that recolonisation is slower than for taxa with planktonic larvae (Palmer 1988, Norkko et al. 2010). This may also reflect the increase in salinity in the reclosed phase. Ostracods and *Assimineia* cf. *ovata* are known to favour higher salinities in the lakes (Boltt 1975, Pillay & Perissinotto 2008). Both were also only present in South Lake in the reclosed phase, which may suggest they are only able to reproduce at higher salinities. Thus, reproductive cycles of individual taxa could increase recruitment time to this site.

Recovery of meiofauna

Overall, there was a substantial recovery of meiofauna populations in the system compared to a previous survey when the fauna were subject to severe drought stress (Pillay & Perissinotto 2009). This highlights the importance of freshwater inflow and an open connection with the sea for benthic populations in the estuary. Density and richness of meiofauna increased at all sites, particularly in the lakes where conditions were most extreme. Seven additional major taxonomic groups were also recorded during the current survey (excluding Foraminifera, which were not previously included). Mean density was

457 ind. per 10 cm^2 , ranging from 4 to 2838 ind. per 10 cm^2 , which is similar to densities reported for many shallow, subtropical estuaries and ICOLs (Montagna & Kalke 1992, Gómez Noguera & Hendrickx 1997, Dye 2005, Kapusta et al. 2006). Very little information is available on meiofauna in St Lucia Estuary prior to the drought. However, the mean densities of calcareous foraminiferans (1 to 152 ind. per 10 cm^2) recorded during this survey compare well with estimates from surveys conducted in 1972 and 1973 when the mouth of the estuary was open (Phleger 1976).

Although some progress was made in terms of improving the taxonomic knowledge of meiofauna, the 2 dominant and most diverse groups, nematodes and harpacticoid copepods, largely remain unidentified beyond group level. Taxa that were identified to species and that represent new distribution records for South Africa and for the St Lucia Estuary include the kinorhynch *Echinoderes maxwelli*, the benthic rotifers *Lecane* cf. *grandis* and *Testudinella* cf. *obscura*, as well as 3 mite species: *Tyrophagus putrescentiae* (Astigmatidae), *Copidognathus africanus* (Halacaridae) and *Acarothrix umgenica* (Halacaridae).

Echinoderes maxwelli was originally described from the Kleinemonde Estuary, on the south coast of South Africa (Omer-Cooper 1957a,b), its only record until now, and this may suggest it is endemic to southern Africa. It was an important component of the benthic fauna at Charters Creek, where it contributed 1 to 17% of the meiofauna population, attaining a maximum density of 139 ind. per 10 cm^2 . Little is known of the biology of this species, but in the St Lucia Estuary it was found in a range of sediment types from medium sands to fine mud and at salinities of 2 to 55.

The rotifer *Lecane* cf. *grandis* was found in reasonably high densities (18 ± 16 ind. per 10 cm^2) on only 1 occasion at Charters Creek after high rainfalls, when salinity was low (14). *L. grandis* is a cosmopolitan species found mainly in tropical and subtropical marine and brackish littoral habitats (De Manuel 1994, Segers 1996, Fontaneto et al. 2008). In the St Lucia Estuary, it was found in sublittoral sandy sediments as part of the meiobenthos and appears to favour brackish conditions and/or higher temperatures (29°C).

Testudinella cf. *obscura* is known from several coastal and estuarine environments worldwide, but has not previously been reported from South Africa (De Smet 2009). It appears to prefer warmer waters (15 to 38°C) and is considered to be strictly marine (De Smet 2009). Only a single specimen of *T. cf. obscura* was found at Esengeni at low salinity (7), and therefore this record should be treated with caution.

Tyrophagus putrescentiae (common mould mite) is cosmopolitan in marine and terrestrial environments. In South Africa, it has previously been recorded from the Mdloti Estuary, KwaZulu-Natal, where it was found to be an important component of the meiofauna (Marshall et al. 2001, Nozais et al. 2005). *T. putrescentiae* was found throughout St Lucia Estuary at a wide range of salinities (2 to 55), with the highest abundance in the lakes, but did not contribute significantly to meiofauna populations in this study.

Copidognathus africanus (formerly *C. baiirdi*) is also a cosmopolitan species known from various tropical and temperate shorelines in the Indian and Atlantic oceans, and has a widespread distribution in rocky littoral habitats on the south and east coasts of South Africa (Procheş & Marshall 2002). *C. africanus* was only recorded at the Mouth and Charters Creek, suggesting a preference for sandy sediments within a salinity range of 12 to 55.

Acarothrix umgenica was described relatively recently from sediments and algae in mangrove pneumatophores (*Avicennia marina*) on the east coast of South Africa at salinities of ≤ 35 (Procheş et al. 2001, Procheş 2002). No specimens were found in benthic sediments of these mangrove habitats (Procheş et al. 2001). This species was found in sublittoral benthic sediments at St Lucia Estuary, and only in the lakes (mainly Charters Creek). The salinity range in this study was 18 to 55; however, density decreased significantly at 55.

CONCLUSIONS

The breaching of St Lucia Estuary was unusual in that it occurred from the sea during a period of extreme drought and low water levels in the estuary. The resultant inflow of seawater, higher salinities and increased water levels led to a substantial recovery of meiofauna populations, with similar effects reported for zooplankton and fish populations in the estuary (Carrasco et al. 2010, Jerling et al. 2010, Vivier et al. 2010). The impact of the breach on meiofauna communities differed between sites in the estuary. Physical disturbances due to tidal currents and sediment erosion were most prevalent at the mouth, but results suggest that disturbances generated by sea-induced breaching may be less severe than in a fluvial breach where meiofauna populations were substantially reduced by sediment scouring (Nozais et al. 2005). There was an overall positive effect in the lakes, where density and diversity of meiofauna generally increased after the breach. Thus, the effects of

breaching on benthic communities may vary depending on a range of variables, including conditions inside the estuary prior to the breach and both the direction and magnitude of the breach.

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Appendix 1. List of identification guides used in this study

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