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Benthic macrofauna of an estuarine lake during a drought: spatio-temporal drivers under different hydrological states

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ABSTRACT: Mouth state is a key determinant of estuarine processes in arid and semi-arid regions. While this factor is well researched for periodically open systems, it is much less researched for estuarine lakes. Here we used a 4-year data set to determine spatio-temporal patterns in responses of benthic macrofauna to changes in mouth state in a subtropical estuarine lake system during a drought cycle, with a focus on understanding the ecological mechanisms driving community change. We also assessed the effects of changes in mean levels of environmental factors relative to their statistical variability (measured as standard deviation, SD) in driving changes in species richness and abundance of dominant macrofauna. Results showed that greatest variability in physico-chemical factors and macrofaunal assemblages occurred in the upper lake sections, especially under closed mouth conditions. At the community level, changes in salinity under different mouth states played an important structuring role, but were less important at the level of individual species, being important for only 1 of the 6 dominant species. Low oxygen levels under closed mouth conditions, particularly in the lake complex, were also an important determinant of macrofaunal community structure and species richness. A major finding was that variability (SD) in environmental factors was more important in determining species richness and abundance of dominant macrofauna than changes in mean levels. This suggests that, while dominant species in the systems can tolerate significant environmental changes, the rate and magnitude of change exert an important control over species abundance.

KEY WORDS: St Lucia Estuary · Benthos · Drought · Mouth dynamics · Environmental variability

INTRODUCTION

Mouth dynamics play a major role in determining environmental and assemblage variability in estuarine ecosystems (Teske & Wooldridge 2003, Perissinotto et al. 2010a). In open estuaries, spatio-temporal variability is imposed on a daily basis through changing tides and freshwater inflow, while seasonal changes and inter-annual fluctuations act over larger scales (Little 2000). In many arid or semi-arid parts of the world, however, estuaries do not always connect to the sea on a permanent basis because of low rainfall (Allanson & Baird 1999, Perissinotto et al. 2010b, Meerhoff et al. 2013). Such systems function differently to permanently open systems, with freshwater inputs and the state of the mouth (whether opened or closed) being the most influential determinants of community structure and spatiotemporal variability (Teske & Wooldridge 2003, Perissinotto et al. 2010a). In periodically closed systems, freshwater inputs are strongly linked

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with the state of the mouth, with high freshwater inputs often leading to open-mouth conditions.

The influence of changing mouth states has received significant attention for temporarily open/closed estuaries (e.g. Young et al. 1997, Young & Potter 2002, Smakhtin 2004, Perissinotto et al. 2010a), but this is poorly understood for estuarine lake systems. The latter are types of estuaries that are typically formed from drowned river valleys, and still retain some degree of connectivity with the sea (Whitfield 1992). Such systems are usually composed of lake complexes, with high surface areas in the upper reaches, that discharge into the ocean via a channel. These systems can be much larger than permanently open or periodically open estuaries, and in some cases account for roughly 80% (300 to 350 km^2) of local estuarine area (Begg 1978). The intermittent state of their connection with the sea in conjunction with high levels of variability in geomorphology and hydrology result in estuarine lakes being very complex ecosystems (Dye & Barros 2005).

The ecological functioning of estuarine lakes is dependent on a number of variables, but the most influential is the balance between freshwater inflow, evaporative water loss and the frequency and duration of the marine link (Bally & McQuaid 1985). However, because of the large size and changing morphology along the length of these systems, responses to mouth opening and closure are likely to be highly modified by spatial location from the mouth to the uppermost reaches of the lakes. Under open-mouth conditions, tidal action is not certain to affect the lake compartments because of the small cross-sectional area of the channel connecting the lakes to the ocean (Whitfield 1992). Under closed conditions, wind is the main force responsible for water movement (Whitfield 1992), but may not always be strong or persistent enough for the exchange of water between the lakes and the channel. Under both open and closed phases, fragmentation of water masses, especially in the lakes, can restrict exchange between these fragmented water masses and the sea (Whitfield 1992, Pillay & Perissinotto 2008, Whitfield & Taylor 2009).

This study aimed to address 3 issues regarding the ecological effects of alternating mouth states on the St Lucia Estuary, a sub-tropical estuarine lake system in South Africa, during a drought phase. The system typically undergoes alternating phases of droughts and flooding, each lasting several years (Whitfield & Taylor 2009, Perissinotto et al. 2013). During these phases, environmental characteristics can change dramatically, including switching between open and closed mouth states and brackish to severe hypersaline (>100) conditions. The first aim was to identify patterns in benthic macrofaunal communities and physico-chemical variables under different mouth states, and to determine if these are modified spatially along the length of the system. We predicted that the lake sections of the system would display greatest extremes and variability in physico-chemical properties, leading to greater variability in macrofaunal community structure. The second aim was to identify the main environmental determinants of macrofaunal community structure across different mouth states, and to determine if the contribution of these factors is altered along the length of the system. We hypothesized that water depth and salinity will become more influential in determining macrofaunal community structure from the lower (mouth) to upper reaches (lakes) of the estuary. This is based on previous observations that the lake sections of the system experience the most extreme fluctuations in water depth and salinity (Pillay & Perissinotto 2008, 2009). The last aim was to identify the main environmental determinants of macrofaunal richness and abundance, as well as the abundance of dominant macrofaunal species in the system. In this present study, we specifically assess the importance of changes in mean levels of environmental factors relative to their statistical variability (measured as standard deviation) in driving patterns in macrofaunal richness and species abundance. Because of the dynamic and variable nature of the St Lucia Estuary, it is likely that dominant species have evolved physiological and life-history strategies to deal with wide variations in environmental conditions. However, the abundance of dominant species may be limited by the rates and magnitudes of environmental change, which can be measured by the standard deviation of environmental data. We therefore hypothesized that the abundance of numerically dominant species would be more affected by the degree of statistical variability in environmental data than changes in mean levels.

MATERIALS AND METHODS

Study area

The St Lucia Estuary is situated in northern Kwazulu-Natal on the east coast of South Africa (Fig. 1, between 27° 52′ S–28° 24′ S and 32° 21′ E–32° 34′ E). The system is composed of 3 shallow lakes (viz. South Lake, North Lake and False Bay) that connect to the Indian Ocean via a 21 km channel called the Narrows (Fig. 1). Depending on water levels, the

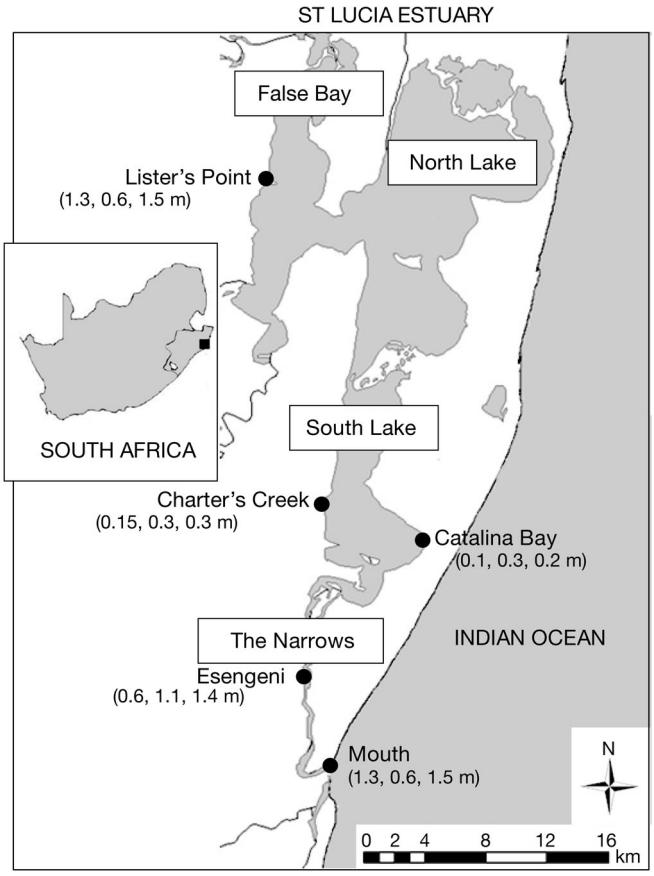

Fig. 1. Map of the St Lucia Estuary showing sampling sites and geographical position within South Africa. Values in parentheses under site names indicate mean water levels during the closed, open and reclosed phases, respectively

St Lucia Estuary and lake complex cover an area between 300 and 350 km^2 (Begg 1978). The St Lucia Estuary is the largest estuarine system in Africa (Fielding et al. 1991, Cyrus & Vivier 2006) and was declared a RAMSAR site in 1992. The system forms a major component of the iSimangaliso Wetland Park, which was granted UNESCO World Heritage Site status in 1999, in acknowledgement of the richness and diversity of the habitat.

Biotic samples and physico-chemical data were collected at 5 sites 4 times a year (spring, summer, autumn and winter) between 2006 and 2009 (Fig. 1). These sites were chosen as representative of the major biotopes (False Bay, South Lake, Narrows and Mouth) within the system (Perissinotto et al. 2013). Because of the very low water levels during the study, especially in North Lake, access to sampling sites by boat was restricted. The investigation occurred during a drought phase, which has persisted since 2002 (Carrasco et al. 2010). The duration of the study covered 3 different mouth states: a closed state (Feb 2006 to Feb 2007), an open phase (Mar 2007 to Aug 2007) and a re-closed state (Nov 2007 to Nov 2009). The opening of the estuary was caused by an unusual breaching that occurred from the seaward side of the estuary, due to very high wave heights caused by a combination of storm activity (Cyclone Gamede) and spring equinoxial tides.

Physico-chemical data

In situ measurements of physico-chemical variables such as salinity, temperature, turbidity, pH and dissolved oxygen (DO) were made using a portable YSI 6920 multiprobe system. Measurements of physico-chemical data were made at the sediment-water interface at all sites (see Fig. 1 for mean water levels).

Microphytobenthos

Surface samples of sediment were collected to a depth of 1 cm using a corer with an internal diameter of 2 cm. Extracted cores were placed in 50 ml polyethylene bottles containing 30 ml of 90% acetone for extraction over a 24 to 48 h period. At each site, 3 replicate cores were collected. Microphytobenthic biomass was measured as chlorophyll *a* (chl *a*) concentration using a fluorometer (10-AU Turner Designs) fitted with the narrow-band, non-acidification system of Welschmeyer (1994).

Phytoplankton

Under shallow conditions (<0.5 m deep), subsurface water was collected from each site using a 500 ml polyethylene bottle and filtered on GF/F filters. Individual filters were then placed in polyethylene test tubes containing 10 ml of 90% acetone for chl *a* extraction. Test tubes containing acetone and filters were refrigerated over a 24 to 48 h period for pigment extraction. Again, chl *a* concentrations were measured using a Turner Designs 10-AU fluorometer. At deeper sites (>0.5 m depth), near-bottom water samples were collected using a 'pop-bottle', consisting of a weighted glass bottle fitted with a stopper that can be released once at the sediment-water interface. Phytoplankton biomass was estimated using the methods described for microphytobenthos.

Benthic macrofauna

A Zabalocki-type Ekman grab (sampling area = 0.0236 m^2, depth = 15 cm) was used to sample benthic macrofauna (Kajak 1971). Three replicate samples per site were collected, with each sample comprising 3 individual grabs. Replicate benthic samples were transferred to buckets to which water was added and stirred vigorously to suspend benthic invertebrates. The supernatant was then passed through a 500 µm sieve. The process of stirring and sieving was repeated 5 times and the material retained on the sieve was transferred into a plastic jar. This procedure has been shown to be effective in extracting more than 95% of the macrofauna in each sample (Cyrus & Martin 1988). The sediment remaining in each bucket after 5 sieves was washed through a 2000 µm sieve to collect larger macrofaunal groups such as bivalves, gastropods or crustaceans (Cyrus & Martin 1988). Macrofauna samples were preserved using a formaldehyde solution (4%) and stained with Phloxine-B. Organisms were sorted and identified to the lowest possible taxonomic level in the laboratory using available identification guides.

Statistical analyses

Multivariate analyses were undertaken in PRIMER-E v. 6 (Clarke & Gorley 2006). Macrofaunal abundance data were fourth-root transformed to reduce the contribution of the dominant taxa. A zero-adjusted Bray-Curtis similarity measure was used to generate resemblance matrices. CAP (canonical analysis of principal co-ordinates) analysis was performed to visually assess trends in communities in relation to site and mouth state PERMANOVA+ (permutational multivariate analysis of variance; 2-way crossed design) was used to test the effects of site, mouth state and their interaction on macrofaunal assemblages. Pairwise tests, which are the multivariate equivalents of univariate post-hoc tests, were performed for comparisons of assemblages under different mouth states at each of the sites sampled. A SIMPER analysis was undertaken to identify macrofaunal taxa that dominated the overall macrofaunal assemblage in the St Lucia Estuary. DIVERSE was used to calculate the total number of species (species richness) and total abundance for each mouth state per sampling site. DISTLM (distance based linear modelling) was used to identify environmental variables that accounted for variability in macrofaunal assemblages per site and across different mouth states, as well as to quantify the proportion of variance explained by each variable. Where required, environmental data were fourth-root transformed for this analysis.

Univariate analyses were undertaken using SPSS v. 20. Differences in macrofaunal community measures and physico-chemical variables between different sites and mouth states, as well as the interactions between the latter variables, were assessed using a 2-way analysis of variance (ANOVA). Post-hoc Tukey tests were applied to highlight statistically significant differences between levels of the factors. Normality and homogeneity of variance were assessed using the Kolmogorov-Smirnov and Levene tests, respectively. In instances where these assumptions were not met, data were transformed [log(x + 1)] for parametric testing. Multiple linear regressions were used to highlight the environmental variables that accounted for variability in richness (S) and abundance (N) of macrofauna and abundance of individual taxa over the 3 mouth stages. In these analyses, the effects of changes in mean levels of environmental variables and the variability in the latter (measured as the standard deviation, SD) were tested against mean changes in community descriptors (S and N) and abundance of taxa as well as variability (SD) in the latter. Where required, data were transformed [log(x + 1)].

Table 1. Results of 2-way analysis of variance (ANOVA) testing the individual and interactive effects of site and mouth state on physico-chemical variables and macrofaunal community descriptors. Values in bold indicate significant differences

	Mouth state (M)		Site (S)		M × S	
	F	p	*F*	p	*F*	p
Water depth	14.47	**<0.0001**	70.1	**<0.0001**	7.6	**<0.0001**
Salinity	34.1	**<0.0001**	10.0	**<0.0001**	7.2	**<0.0001**
Temperature	8.5	**<0.0001**	5.7	**0.002**	0.9	0.46
Dissolved oxygen	1.9	0.19	2.7	**0.03**	2.9	**0.004**
pH	23.4	**<0.0001**	8.6	**<0.0001**	6.1	**<0.0001**
Microphytobenthic biomass	12.9	**<0.0001**	4.1	**0.003**	1.4	0.19
Phytoplankton biomass	0.9	0.37	2.1	0.081	4.4	**<0.0001**
Richness	4.34	**0.014**	5.49	**<0.0001**	3.38	**0.001**
Abundance	8.4	**<0.0001**	10.90	**<0.0001**	11.1	**<0.0001**

RESULTS

Microalgae and physico-chemical environment

The majority of variables measured differed significantly between different mouth states as well as between sites (Table 1, Figs. 2, 3 & 4). Except for water temperature and microphytobenthic biomass, all variables were affected by the interaction between mouth state and site, indicating that the influence of mouth state on the above variables was altered by spatial location. Except for water depth, sites in the lake basins showed most variability between different mouth phases.

Water depths at the estuary mouth and in the Narrows (Esengeni) were generally 3 to 4 times greater than at the remaining 3 sites located in the lake system. Mouth opening resulted in a decline in water depth at the mouth, but led to increases in water depths at the other sites. Salinity was greatest during the open phase (marine salinity: 35) at the Mouth and Esengeni, but waters became mesohaline (salinity range: 10 to 20) during the closed and reclosed stages. Following mouth re-closure, salinity was greatest at sites in the lakes, with evidence of hypersaline conditions developing. Dissolved oxygen levels were similar between different mouth states at most sites, with the exception of False Bay (Lister's Point), where oxygen levels were significantly reduced during the closed phase of the system. Apart from the Mouth, pH levels were significantly reduced at all sites during the open phase.

Microphytobenthic and phytoplankton biomass showed different responses to mouth state as well as site (Table 1, Fig. 4). Both factors significantly affected microphytobenthos levels, with no significant interactive effects. In terms of spatial patterns, microphytobenthos biomass peaked at Catalina Bay, especially during the closed mouth phase. In contrast to patterns observed for microphytobenthos biomass, neither mouth state nor site influenced phytoplankton concentrations, but there was a significant interaction effect.

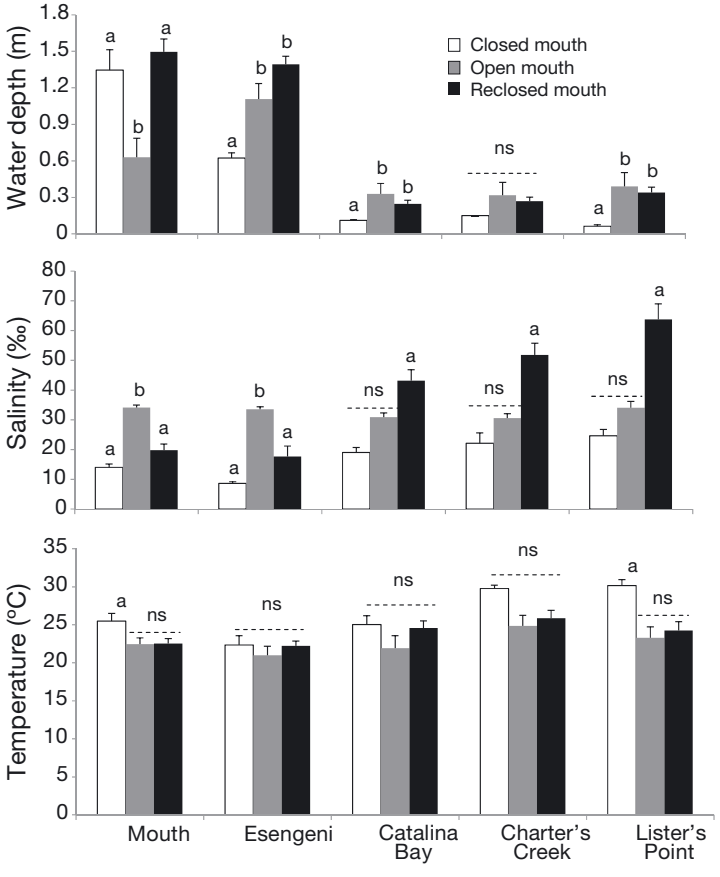

Fig. 2. Spatial variation (means ± SE) in water depth, salinity and temperature across different mouth states in the St Lucia Estuary. Different letters above bars indicate significant differences; ns: no significant difference

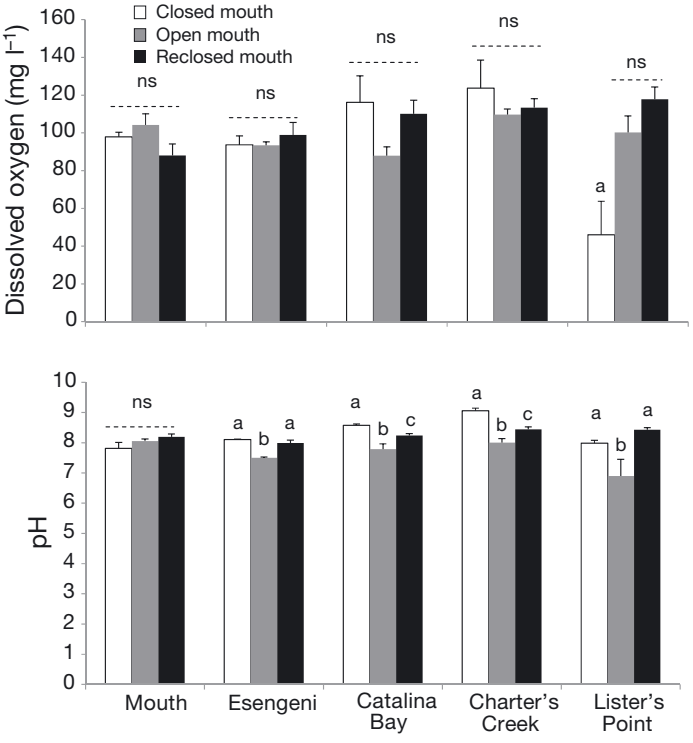

Fig. 3. Spatial variation (means ± SE) in dissolved oxygen and pH across different mouth states in the St Lucia Estuary. Different letters above bars indicate significant differences; ns: no significant difference

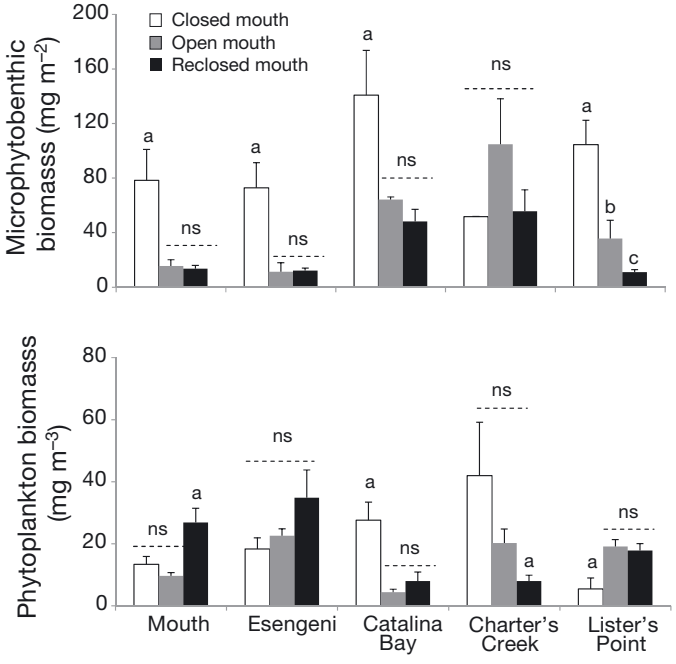

Fig. 4. Spatial variation (means ± SE) in microphytobenthic and phytoplankton biomass across different mouth states in the St Lucia Estuary. Different letters above bars indicate significant differences; ns: no significant difference

Macrofaunal communities

Under closed mouth conditions, macrofaunal assemblages were dominated by the polychaete *Ceratonereis keiskamma* (59%), the tanaid *Apseudes digitalis* (18%), the amphipod *Grandidierella bonnieroides* (12%) and chironomids (3.4%), with these taxa cumulatively accounting for 92% of community structure (SIMPER analysis). Upon closure, *A. digitals* (35%) increased and *C. keiskamma* (27%) decreased their respective contribution to community structure, while *Polydora* sp. (Polychaeta) and *G. bonnieroides* contributed 20 and 9.9%, respectively. When the estuary closed again, the polychaete *Prionospio sexoculata* (42%) became the most dominant species, followed by *A. digitals* (25%), *C. keiskamma* (9.8%), *Polydora* sp. (9%) and the mysid *Mesopodopsis africana* (5%).

Macrofaunal assemblages were significantly affected by mouth state (Pseudo-$F_{2,198}$ = 8.02, p = 0.001), site (Pseudo-$F_{4,198}$ = 6.7, p = 0.001) and the interaction between them (Pseudo-$F_{4,198}$ = 2.8, p = 0.001). Assemblages at each of the sites responded differently to closure, opening and reclosure of the estuary mouth (Table 2, Fig. 5), indicating that there were site-specific factors that influenced responses of assemblages to mouth state. Assemblage structure at the Mouth differed only between closed and reclosed phases, but differed among all mouth phases at Esengeni and Catalina Bay. The tight grouping of macrofaunal samples during each of the mouth phases at Esengeni and Catalina Bay is shown in Fig. 5. At Charter's Creek, assemblages did not differ between closed and open mouth states, while at Lister's Point, assemblages were statistically indistinguishable between the closed and reclosed phase (Table 2, Fig. 5). Assemblages at the 2 northernmost sites in the system (Charter's Creek and Lister's Point) showed greatest variability in macrofaunal communities during the closed mouth phase. The latter mirrors the variability observed in the physico-chemical data (Figs. 2 & 3).

Mouth state was the most important structuring agent of assemblages across all sites, but made different contributions to explaining overall community variance across sites (Table 3). At the Mouth, mouth state explained only 9.3% of macrofaunal community variability, but explained roughly 20% of community variance at the remaining sites. Water depth was also an important determinant of community structure, but its contribution to overall assemblage variation declined from the mouth (6.9%) to the northernmost site, Lister's Point (2.8%). With the exception of the Mouth, dissolved oxygen level was a significant contributor to variability at all sites, generally increasing in contribution from the Narrows to the lakes. Salinity and pH made variable contributions in explaining macrofaunal variability in the system, with no obvious spatial patterns regarding their statistical contributions.

Phytoplankton biomass was a significant contributor to macrofaunal variability at all sites of the estuary, with its contribution being greatest at Lister's Point (10.8%). Microphytobenthic biomass con-

Table 2. Results (p-values) of pairwise tests on the effect of mouth state on macrofaunal assemblages per site. Distances of sampling sites from the mouth are given in parentheses. Significant p-values are indicated in **bold**

Pairwise test	Mouth (0)	Esengeni (11 km)	Catalina Bay (24 km)	Charter's Creek (26 km)	Lister's Point (58 km)
Closed vs. Open	0.09	**0.002**	**0.022**	0.148	**0.004**
Open vs. Reclosed	0.32	**0.026**	**0.000**	**0.003**	**0.002**
Closed vs. Reclosed	**0.006**	**0.002**	**0.001**	**0.006**	0.059

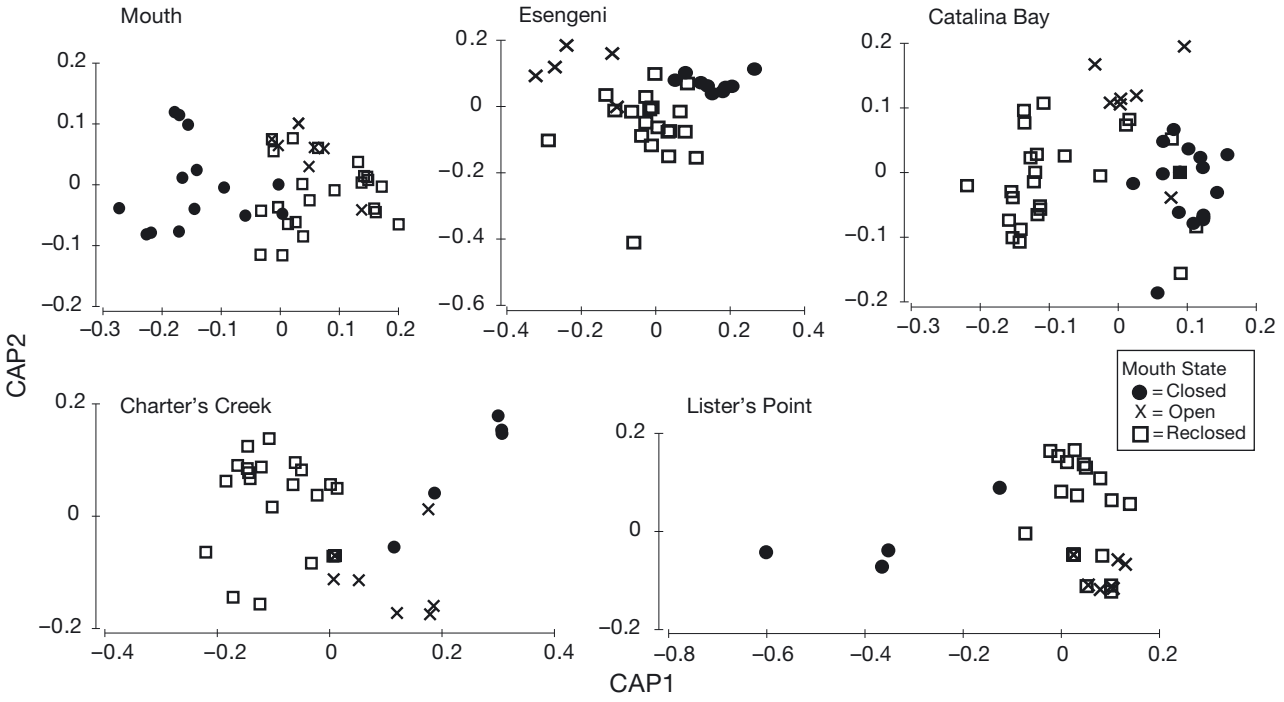

Fig. 5. CAP (canonical analysis of principal components) results showing variability in macrofaunal assemblages at each site in the St Lucia Estuary during different mouth states

tributed significantly to variance in assemblage structure at the 3 lake sites (Catalina Bay, Charter's Creek and Lister's Point), but not at the deeper sites of the Mouth and Esengeni. The contribution of microphytobenthic biomass in determining overall community structure generally increased from the Mouth to the northern parts.

Richness and abundance

Macrofaunal richness and abundance were significantly affected by mouth state, site and the interaction between these variables (Table 1, Fig. 6). Richness did not differ between mouth phases at the Mouth and Esengeni, but did differ at the remaining 3 lakes sites. At Catalina Bay, richness increased with mouth opening and re-closure, but was reduced upon mouth opening at Charter's Creek, while it increased at Lister's Point when the mouth closed again. Macrofaunal abundance showed 4 main patterns related to different mouth states. At the mouth, opening resulted in a decline in abundance relative to the closed and reclosed phases, whereas at Esengeni and Catalina Bay, abundance was elevated by roughly 5 and 3 times respectively during mouth opening. In contrast, abundance was greatest at Charter's Creek during the closed phase of the system, while no statistically discernible differences were apparent at Lister's Point.

The main determinant of macrofaunal richness in the St Lucia across all mouth phases and sites was dissolved oxygen, with increases in levels of the latter variable promoting richness (Table 4). Variability in species richness (as standard deviation, SD) was positively related to variability in salinity, and negatively to water temperature. None of the variables measured could be related to macrofaunal abundance, indicating a high degree of statistical 'noise' within the dataset or that other variables outside of those measured were in operation. Variability in macrofaunal abundance was negatively related to variability in salinity, water depth, temperature and variability in microphytobenthic biomass. In contrast, increasing phytoplankton and microphytobenthic biomass enhanced variability in macrofaunal abundance.

SIMPER identified 9 taxa that dominated the macrobenthic fauna in the system (Table 5). Based on their responses to different mouth states, species could be classed into 3 groups—Group 1: species that decreased in abundance when the estuary opened and then reclosed (*Ceratonereis keiskamma*, chironomids); Group 2: species that increased in

Table 3. Variable combinations (identified by DistLM) accounting for most of the variability in macrofaunal assemblages at sampling sites in the St Lucia Estuary. Significant p-values are indicated in **bold**; asterisks denotes statistical significance; *p < 0.05, **p < 0.01, ***p < 0.001

Site Variable	Pseudo-*F*	p	Proportion (%)	Cumulative (%)
Mouth				
Mouth state***	2.1929	**0.009**	9.26	9.26
Salinity***	4.7004	**0.001**	9.13	18.39
Water depth**	3.7953	**0.002**	6.91	25.30
Phytoplankton**	3.6707	**0.001**	6.28	31.58
Temperature**	3.7985	**0.002**	6.07	37.65
pH**	3.5189	**0.005**	5.28	42.94
Microphytobenthos	1.3336	0.23	1.98	44.92
Dissolved oxygen	0.85445	0.513	1.29	46.42
Esengeni				
Mouth state**	4.2289	**0.002**	21.44	21.44
Salinity*	13.782	**0.001**	24.73	46.17
pH**	4.4454	**0.005**	4.19	50.35
Phytoplankton*	2.7848	**0.03**	4.49	54.84
Water depth*	2.8523	**0.031**	4.31	59.16
Dissolved oxygen *	2.8411	**0.035**	4.02	63.18
Microphytobenthos	2.3315	0.068	3.14	66.32
Temperature	1.0171	0.41	1.37	67.69
Catalina Bay				
Mouth state***	6.3731	**0.001**	20.98	20.98
Phytoplankton**	5.8687	**0.002**	8.77	29.75
Dissolved oxygen*	2.7199	**0.019**	3.92	33.68
Microphytobenthos*	2.7806	**0.017**	3.86	37.53
Water depth	1.781	0.07	2.43	39.97
Temperature	1.8234	0.1	2.44	42.41
pH	1.2009	0.284	1.60	44.01
Salinity	1.03	0.389	1.37	45.38
Charters Creek				
Mouth state***	4.2968	**0.001**	20.66	20.66
pH***	12.1	**0.001**	21.77	42.43
Dissolved oxygen***	7.4838	**0.001**	11.19	53.63
Temperature***	8.8239	**0.001**	10.54	64.17
Phytoplankton***	3.872	**0.001**	4.22	68.39
Microphytobenthos**	3.7091	**0.003**	3.70	72.08
Water depth**	3.7981	**0.004**	3.44	75.53
Salinity**	4.5851	**0.004**	3.67	79.20
Listers Point				
Mouth state**	3.5007	**0.002**	20.00	20.00
Dissolved oxygen***	9.3181	**0.001**	20.52	40.53
Phytoplankton**	5.8226	**0.002**	10.88	51.41
Salinity**	5.9087	**0.002**	9.29	60.70
Microphytobenthos**	3.8264	**0.007**	5.40	66.10
Temperature**	5.1872	**0.002**	6.24	72.34
Water depth*	2.5054	**0.038**	2.83	75.17
pH*	3.2144	**0.016**	3.30	78.46

abundance upon opening of the system (*Prionospio sexoculata*, *Mesopodopsis africana*, *Solen cylindraceus*); Group 3: species that were unaffected or showed either increases or decreases in abundance based on location (*Apseudes digitalis*, *Polydora* sp.).

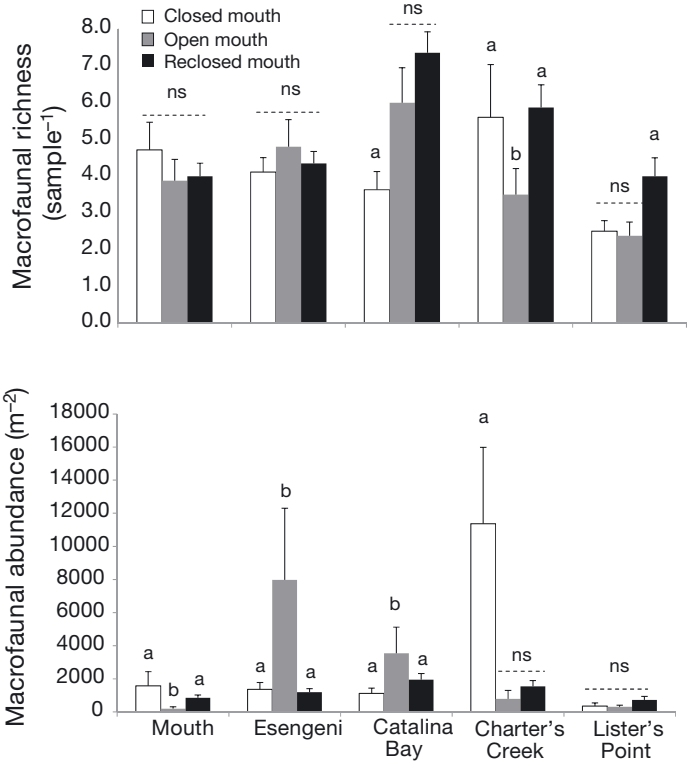

Fig. 6. Spatial variation (means ± SE) in macrofaunal richness and total abundance across different mouth states in the St Lucia Estuary. Different letters above bars indicate significant differences; ns: no significant difference

Of Group 1, densities of *C. keiskamma* were most affected by the combined effects of salinity, pH and variability in both DO and water temperature (Table 4). Increasing salinity and DO variability negatively influenced the abundance of this species, indicating a low tolerance to high salinity and variability in DO levels. Chironomid abundance was positively affected by DO levels. In Group 2, all species were affected by variability in salinity to different degrees. *P. sexoculata* density was additionally negatively linked with variability in microphytobenthic biomass, while *S. cylindraceus* density was negatively linked with phytoplankton biomass and positively with DO levels. Water depth and variability in DO levels were the other measures linked to *M. africana* densities. Among Group 3 species, *A. digitalis* density was positively influenced by DO levels and negatively by pH variability, while the density of *Polydora* sp. was enhanced by increasing salinity variability.

Of the physico-chemical variables that were identified as key determinants of densities of specific taxa, variable fluctuations (standard deviation) were more

Table 4. Variable combinations accounting for most variability in abundance of dominant macrofaunal species and community descriptors in the St Lucia Estuary per site across different mouth phases. Significant p-values are indicated in bold. β = standardized coefficient. 'Whole model' shows summary statistics for the effects of variable combinations on dominant macrofaunal species and community descriptors

	Explanatory variables	p	β	Whole model
Community measure				
Species richness	Dissolved oxygen	**0.04**	0.48	r = 0.48, p = 0.04
SD Species richness	SD Salinity	**<0.0001**	0.81	
	Water temperature	**0.034**	−0.39	r = 0.61, p = 0.001
Total abundance	None			
SD Total abundance	SD Salinity	**<0.0001**	−0.76	r = 0.96, p < 0.0001
	Water depth	**0.001**	−0.34	
	Phytoplankton biomass	**<0.0001**	0.34	
	Microphytobenthic biomass	**0.001**	0.49	
	Water temperature	**0.004**	−0.29	
	SD Microphytobenthic biomass	**0.032**	−0.17	
Taxon				
Caratonereis keiskama	Salinity	**0.003**	−0.57	R = 0.72, p = 0.001
	pH	**0.001**	0.78	
	SD Dissolved oxygen	**0.013**	−0.48	
	SD Water temperature	**0.014**	0.43	
Apseudes digitalis	Dissolved oxygen	**0.011**	0.57	R = 0.48, p = 0.008
	SD pH	**0.02**	−0.52	
Prionospio sexoculata	SD Salinity	**<0.0001**	0.92	R = 0.59, p = 0.002
	SD Microphytobenthic biomass	**0.027**	−0.49	
Polydora sp.	SD Salinity	**0.012**	0.62	R = 0.34, p = 0.012
Mesopodopsis africana	SD Salinity	**0.006**	0.36	R = 0.60, p = 0.004
	Water depth	**0.012**	0.57	
	SD Dissolved oxygen	**0.032**	0.56	
Chironomids	SD Dissolved oxygen	**0.032**	0.25	R = 0.60, p = 0.032
Solen cylindraceus	Phytoplankton biomass	**<0.0001**	−0.85	R = 0.68, p = 0.001
	Dissolved oxygen	**0.025**	0.46	
	SD Salinity	**0.042**	0.38	

Table 5. Abundance of dominant macrofaunal species in the St Lucia Estuary per site across different mouth states. Values in bold indicate significant differences (p < 0.05)

Site	Taxon	Mouth state			Taxon	Mouth state		
		Closed	Open	Reclosed		Closed	Open	Reclosed
Mouth	*Ceratonereis*	311	73	59	*Apseudes*	32	32	67
Esengeni	*keiskamma*	**403**	11	28	*digitalis*	**873**	**7629**	**1259**
Catalina Bay	(Polychaeta)	388	156	**64**	(Tanaidacea)	154	558	598
Charters Creek		101	260	**38**		**4511**	**317**	**90**
Listers Point		3	**0**	7		0	4	115
Mouth	*Prionospio*	**0.1**	64	103	*Polydora* sp.	0.2	4	**62**
Esengeni	*sexoculata*	0.2	0.8	39	(Polychaeta)	0.6	0.8	6
Catalina Bay	(Polychaeta)	0	24	**649**		7	8	**64**
Charters Creek		0.6	0.4	700		207	129	67
Listers Point		0.2	0.3	**254**		**0.9**	294	175
Mouth	*Grandidierella*	**117**	0.2	30	*Mesopodopsis*	1	5	**318**
Esengeni	*bonnieroides*	50	11	31	*africana*	0.6	0.2	**121**
Catalina Bay	(Amphipoda)	129	**2064**	30	(Mysidacea)	11	0.6	5
Charters Creek		**1470**	62	12		0.2	0.9	**107**
Listers Point		0.5	2	0.9		8	5	8
Mouth	Chironomids	24	2	76	*Solen cylindraceus*	**2**	**0.2**	**2**
Esengeni	(Chironomidae)	0.1	0.3	0.8	(Bivalvia)	**0.6**	**0.5**	**0.9**
Catalina Bay		**346**	134	95		**0.7**	563	62
Charters Creek		**692**	0.6	0.8		0.1	9	**245**
Listers Point		**150**	2	32		0.2	0.1	**27**

prominent than changes in mean values (Table 4). Salinity, for example, was an important determinant of abundance for one taxon only, whereas variability in salinity was important for 4 taxa. Taken collectively, the results given in Table 4 suggest that variability in the physical environment was potentially more important in determining species abundance than changes in mean levels alone.

DISCUSSION

The results of this investigation indicate a strong influence of spatial location (site) and mouth status as drivers of spatio-temporal patterns in physico-chemical and trophic variables, as well as community structure and descriptors. These results concur with findings from other studies highlighting the importance of spatial location and mouth state individually (Carrasco et al. 2010, Perissinotto et al. 2010a). As predicted, highest variability in the physico-chemical environment was observed in the lake sections of the St Lucia Estuary, and was mirrored by variability in benthic macrofaunal communities. The interaction recorded between spatial location and mouth status indicates that the influence of mouth state is modified by spatial location in terms of both community structure and environmental variables. With respect to the physical habitat, the latter is best exemplified by effects on salinity, where mouth opening shifted salinity from mesohaline to marine at the sites in the Narrows, while re-closure resulted in a reversion to mesohaline conditions. At the lake sites, however, salinities were elevated further following mouth reclosure. The development of hypersaline conditions in the lakes of the St Lucia Estuary and other similar systems are well documented, and may be especially severe under closed mouth conditions (Boltt 1975, Blaber et al. 1983, Owen & Forbes 1997, Pillay & Perissinotto 2008, Perissinotto et al. 2010b, Lake 2011).

Several patterns emerged concerning the role of environmental variables in structuring macrofaunal communities. As hypothesized, water depth became more important as a determinant of macrofaunal community structure from the mouth to the lake section of the estuary. Low water levels in the lakes can influence macrofauna by indirectly causing increases in water temperature and salinity, which under some conditions can reach extreme levels (Carrasco & Perissinotto 2012) and can exert strong physiological constraints upon organisms. Our hypothesis of increasing importance of salinity in determining macrofaunal community structure with increasing distance from the mouth was not upheld. Cycling between periods of low and very high salinity, often leading to the development of hypersaline conditions, is a dominant feature of the St Lucia Estuary and it is likely that dominant species have evolved physiological mechanisms to tolerate very wide ranges in salinity. Salinity may therefore not be of primary importance as a determinant of the abundance of dominant species.

Mouth state was the most important variable governing community structure at most sites in the St Lucia Estuary. However, the contribution of mouth state in explaining macrofaunal variability was least at the Mouth, explaining only 9%, compared with its contribution elsewhere (±20% of community variance). Because of the coarse, organically poor and highly mobile sediments that frequently dominate at estuary mouths, it is likely that a few specialist species dominate the macrofaunal assemblage of this area (Day et al. 1954) and persist over various hydrological phases with little change in species composition. This is supported by results of the pairwise analysis, which indicated that only 1 of the 3 comparisons of mouth states was statistically significant (Table 2).

With the exception of the Mouth, changes in dissolved oxygen levels was a significant contributor to variability at all sites, generally increasing in importance from the Narrows to the lakes. Most variability in dissolved oxygen levels across different mouth phases occurred in the lake sections of the estuary, and lowest mean levels were recorded at Lister's Point during the closed phase of the estuary. Under closed conditions, water movement between the different components of the system can be reduced significantly, with portions becoming fragmented, thereby limiting the potential for oxygenation through mixing (Whitfield 1992, Pillay & Perissinotto 2008). These outcomes may indicate that the lake compartments of the estuary and other similar systems are potentially more prone to variable oxygen levels and hypoxic conditions, due to the shallow water-column and limited circulation that typify these areas under closed mouth conditions.

In terms of trophic drivers, benthic microalgal biomass was not a significant explanatory component of variability in macrofaunal assemblages at the Mouth and Narrows, but did feature more prominently in the lakes. As was the case with salinity and dissolved oxygen levels, most variability in microphytobenthic biomass was observed in the lakes, especially during the open and reclosed phases. In contrast, phyto-

plankton biomass was more influential at the Mouth and Narrows, as well as at Lister's Point. These results suggest that under shallow conditions, benthic microalgae may be more influential in determining macrofaunal variability, whereas in deeper sections, phytoplankton assumes greater importance. The latter is supported in part by the study of Govender et al. (2011), which showed that benthic and planktonic food webs in lakes were supported primarily by benthic microalgae, whereas food webs were more dependent on suspended solids at deeper sites in the Narrows.

It is interesting to note that none of the variables measured could be linked with changes in benthic macrofaunal abundance, which may reflect a high level of variability within the current data, or that factors outside of those measured may be more influential. Fish predation under open-mouth conditions, for example, may potentially be a significant determinant of macrofauna abundance. Most estuarine-dependent marine fish species that recruit into the estuary are very reliant on benthic macrofaunal sources for their diet and energy balance (Carrasco et al. 2012, Cyrus 2013, Pillay et al. 2013). Sediment granulometry could also have been influential in determining spatio-temporal patterns of macrofaunal abundance, although our previous work identified negligible or weak effects of sediment granulometry at the community level, and no effect on macrofaunal abundance (Pillay & Perissinotto 2008). Dye & Barros (2005) also did not find any correlation between sediment granulometry and meiofaunal abundance in their study of Australian intermittently open lakes and lagoons.

Variability in macrofaunal abundance was explained by a suite of interacting factors. Of these, increases in mean levels of trophic factors (microphytobenthic and phytoplankton biomass) enhanced variability in macrofaunal abundance, while water depth and temperature and variability in salinity and microphytobenthic biomass lowered variance in abundance. Increasing water temperature and fluctuations in salinity reduced variability in macrofaunal abundance, most likely by eliminating intolerant species and selecting for a set of species with wide tolerances. Increasing water depth probably reduced variability in macrofaunal abundance by buffering environmental unpredictability and extremes. The lake sections of the St Lucia Estuary, which are shallower than the rest of the system, are more variable habitats than the Narrows and Mouth. During severe droughts, environmental conditions can become extreme (Pillay & Perissinotto 2008, Carrasco et al. 2010, Carrasco & Perissinotto 2012), being characterised by hypersalinity (max ≈ 200), anoxia (O_2 min ≈ 0.1 mg l^{-1}) and high water temperatures (max ≈ 49°C), which can impose physiological constraints on species with low tolerance.

DO was the only variable that could statistically be linked with macrofaunal richness. The positive relationship between richness and dissolved oxygen indicates that the low oxygen levels periodically recorded in the system, especially in the northernmost areas under closed mouth conditions, exert an important control on macrofaunal diversity. Dauer et al. (1992) reported a reduction in macrofaunal diversity and biomass related to low oxygen levels in Chesapeake Bay, as well as dominance of opportunistic species.

Variability in macrofaunal richness was enhanced with increasing salinity variance, but was reduced with increasing water temperature. Previous work on the Thames Estuary demonstrated that macrofaunal diversity was negatively affected by variability in salinity (Attrill 2002), indicating that fewer species could persist under fluctuating salinities. Our study, along with that of Attrill (2002), indicate that under certain conditions, rapidly changing salinity can reduce macrofaunal diversity and increase its variability. Increasing water temperature can reduce variability in macrofaunal richness by eliminating species intolerant of high temperatures. Temperatures approaching 50°C have been observed in the shallowest parts of the St Lucia estuarine lake at the peak of summer (Perissinotto et al. 2010b, 2013), which may exert strong physiological constraints on macrofaunal species.

In terms of drivers of species abundance, changes to mean levels of environmental factors featured less prominently than variability in those measures. Salinity emerged as important for only one of the 8 dominant species in the system. These results may indicate that the dominant species within the system can tolerate a wide range of salinities (Millard & Broekhuysen 1970, MacKay et al. 2010), and that changes in mean levels do not significantly influence the abundance of these species. Under the current conditions, salinity appears to be more influential at the community level, most likely by affecting the physiology and survival of sub-dominant species. Variability in salinity however, was far more influential, being an important determinant of abundance patterns of 4 of the dominant species. In all cases, variability in salinity was linked to increases in abundance of species, which is possibly an indication of wide salinity tolerances by these 4 species

and their ability to proliferate opportunistically in the absence of stenohaline species, which may be competitors.

Two of the dominant macrofaunal taxa (the tanaid *Apseudes digitalis* and the bivalve *Solen cylindraceus*) were positively linked with increasing DO levels, suggesting a potential intolerance for low oxygen conditions. Variability in oxygen levels however, positively affected 2 taxa (*Mesopodopsis africana*, chironomids) and negatively affected another one (*Ceratonereis keiskamma*). Positively affected groups are most likely tolerant to highly variable oxygen levels and thrive under these conditions, while negatively affected species are those with very specific DO requirements. One species (*C. keiskamma*) was positively linked to pH levels, indicating a preference for alkaline conditions, while another species (*A. digitalis*) was negatively affected by variability in pH, which may indicate a poor tolerance by this species to highly variable pH conditions. Sporadic fluxes of hydrogen sulphide from the anoxic sediments that characterise most of the St Lucia system may play an important role in the occurrence of periodic acidic events and spatio-temporal variability in pH (Taylor 2006).

Our finding that variability in physico-chemical variables may be more important in determining patterns of species abundance than changes in mean levels is in agreement with our hypothesis. Species that occur commonly in estuaries are known to have wide tolerances to changes in physico-chemical variables (Elliot & Quintino 2007, Millard & Broekhuysen 1970, MacKay et al. 2010), and it would be expected that dominant species in the most dynamic of estuarine systems would have tolerance levels proportional to the level of variability inherent in the system. This could explain why in the present study, changes in mean levels of environmental variables featured less prominently as determinants of species abundance patterns. In spite of these high tolerances, our data suggest that the rate at which environmental change occurs, coupled with the magnitude of change, can be important controls of species abundance and distribution, especially in very dynamic estuarine ecosystems.

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