The benthic macrofauna of the St. Lucia Estuary during the 2005 drought.

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Abstract

The St. Lucia Estuary is the largest estuarine system in Africa. The estuary is part of the Greater St. Lucia Wetland Park, which has been declared a World Heritage Site. This ecosystem has been subjected to severe drought conditions over the last four to five years, resulting in its mouth being closed off from the ocean in June 2002 for a period of over 4 years. The main aim of this study was to document the effects of the prevailing drought on the macrofauna of the system, since the last work on this benthic component had been undertaken over a decade ago, during a normal-to-wet phase. Macrofauna samples together with physico-chemical data were collected at representative sites in the Narrows, the South and North lakes in February, April, August and October 2005. The drought exerted a strong influence on the system, leading to hypersaline conditions developing in its northern regions (maximum of 126 ‰ at Hells Gate), and to the loss of aquatic habitat. Ordinations and clustering indicated that the macrofauna of the system could generally be separated into three clusters viz. (1) the Narrows and the southern

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portion of South Lake, (2) the northern half of South Lake, and (3) the North Lake-False Bay complex. Multivariate correlations indicated weak relationships between macrofaunal community structure and physico-chemical parameters. The distinction in macrofaunal assemblages between these clusters was probably caused by these habitats being physically separated at the peak of the drought, with no water flow between them, thereby preventing exchange of planktonic larvae and retarding colonisation of habitats. There was a northward decline in taxonomic richness and diversity of macrofauna in the system, which correlated positively with water depth and negatively with the biomass of microphytobenthos. It is evident that the drought structured macrofauna communities primarily through its effects on water depth and habitat fragmentation. The results of this investigation provide valuable information regarding the effects of droughts on estuarine-lake systems and the possible mechanisms by which they occur.

Keywords: drought, hypersalinity, habitat fragmentation, macrofauna, estuarine lake, South Africa.

1. Introduction

The St. Lucia estuarine lake (hereafter referred to as the St. Lucia Estuary) is the largest estuarine system in Africa (Fielding et al. 1991, Cyrus and Vivier 2006a), and makes up roughly 80% of the overall estuarine area in the province of KwaZulu-Natal (Begg 1978). The St. Lucia Estuary forms part of the Greater St. Lucia Wetland Park, which was declared a RAMSAR site in 1991, and granted World Heritage status in 1999, in view of the biological diversity and richness of this ecosystem.

Ecologically, the St. Lucia Estuary functions as a nursery for many fish (Wallace and van der Elst 1975) and invertebrate species (Begg 1978, Benfield et al. 1989). From a commercial and socio-economic point of view, the estuary has also supported a commercial prawn bait fishery since 1952 (Fielding et al. 1990), as well as other subsistence and recreational fisheries (Mann 1995).

The St. Lucia Estuary is a naturally variable system, as large-scale spatial and temporal variations in physical and chemical parameters have been documented through its history (Begg 1987, Fielding et al. 1991). The system has been typified by intermittent periods of flooding, droughts and mouth closure, but in spite of such disturbances, the system has nevertheless supported rich and diverse fauna and flora (Fielding et al. 1991). Such unpredictability in the physico-chemical habitat, allied with the diversity of biota in the system, have resulted in the system being well researched relative to other systems in South Africa. Studies on phytoplankton (Fielding et al. 1991), zooplankton (Grindley and Heydorn 1970), fish (Blaber 1979, Cyrus and Vivier 2006a & b) and macrofauna (Forbes and Cyrus 1992, Owen and Forbes 1997) have been undertaken in the system.

However, the St. Lucia Estuary has been subjected to severe drought conditions over the last four to five years, which have resulted in the mouth of the estuary being permanently cut off from the Indian Ocean in June 2002 (Cyrus and Vivier 2006a). Since then, the only link the estuary has had with the ocean is via the adjacent Mfolozi River during a flood event (Cyrus and Vivier 2006a). Due to high evaporation rates and reduced fresh water inflow into the system, parts of the estuary have became hypersaline, with salinities of 200 and 90 ‰ being recorded in the North and South lakes, respectively (Cyrus and Vivier 2006a).

So far, the only published work documenting the biological effects of this drought has dealt with the fish community, but there is as yet no information available on its effects on invertebrates, specifically macrofauna. The primary aim of this investigation was, therefore, to examine the effects of the prevalent drought conditions of the macrofauna of the St. Lucia system, as no study has specifically addressed this issue. The secondary aim was to update knowledge of benthic macrofauna in the St Lucia Estuary, since the last published work on macrofauna was undertaken roughly a decade ago. From a global perspective, literature regarding the effects of droughts on estuaries and estuarine lakes is scarce, and the mechanisms by which they influence these ecosystems are poorly understood (eg Hastie and Smith 2006). The present study was intended to add to current knowledge of drought effects on estuarine systems, and to understand the fundamental causative mechanisms.

2. Materials and Methods

2.1. Study Area

The St. Lucia Estuary is situated in northern Kwazulu-Natal and lies between 27°52’S to 28°24’S and 32°21’E to 32°34’E. The system is made up of three shallow lakes connected to the Indian Ocean by a 21 km meandering channel referred to as the Narrows (Fig 1). In total, the St. Lucia Estuary and lake system cover an area between 300 and 350 km^2, depending on water levels (Begg 1978). The system is sub-divided into the Mouth, Narrows, South Lake, North Lake and False Bay (Fig 1).

2.2. Sampling procedure

Samples were collected in February, May, August and October 2005. 13 representative sites were sampled during each season (Fig 1). An additional four sites were sampled in the North Lake only in December 2006 (Sites H1 – H4). The drought conditions prevented access to these four sites by boat, and could only be accessed by a helicopter. The expense incurred in chartering the helicopter prevented sampling these sites more regularly.

2.2.1. Physico-chemical parameters

A portable YSI 556 multiprobe system was used to measure *in-situ* physico-chemical variables such as salinity, temperature and dissolved oxygen. Measurements were made at the sediment-water interface at all sites. For sediment particle size analyses, pre-weighed (dry-weight) sediment was passed through a 2000 µm sieve. The sediment that passed through this sieve was then analysed by a Malvern Analyser, which could detect fractions between 2 and 2000 µm. Sediments retained by the 2000 µm sieve were weighed and incorporated with the data obtained from the Malvern Analyser to determine median particle sizes. Sediments were classified according to the Wentworth classification system (Morgans 1956). Silt (< 63 µm) content was determined from data obtained from the Malvern Analyser.

2.2.2. Benthic macrofauna

In February 2005, macrofauna samples were collected using a stainless steel corer (sampling area = 0.00442 m^2, depth = 20 cm). The corer proved difficult to operate in very muddy substrates, and resulted in considerable delays in extracting cores. To overcome this problem, benthic samples were subsequently collected using a Zabalocki-type Ekman grab (sampling area = 0.0236 m^2, depth = 15 cm) for the rest of the survey, and proved more efficient in muddy substrata. In February, single samples comprising three cores were collected at each site. For the remaining sampling trips, three replicate samples were collected at each site, with each sample comprising three grabs. Replicate sediment samples were emptied into buckets to which water was added, and stirred vigorously, thereby suspending benthic invertebrates. The supernatant was then washed through a 500 µm sieve. This process of adding water, stirring and sieving was repeated five times, and any material retained on the sieve was emptied into a plastic jar. This procedure has been shown to extract more than 95% of the macrofauna in each sample (Cyrus & Martin 1988). The remaining sediment was washed through a 2000 µm sieve in order to collect larger macrofauna such as bivalves, gastropods or crustaceans (Cyrus & Martin 1988). All the macrofauna samples were preserved in 4% formaldehyde solution and stained with Phloxin-B. In the laboratory, organisms were sorted and identified to the lowest possible taxon.

2.2.3. Microphytobenthos

Sediment surface samples were collected using a corer (internal diameter = 2 cm, depth = 1 cm, n = 3) and placed into 50 ml polyethylene bottles containing 30 ml of 90%

acetone. Microphytobenthic biomass was measured as chlorophyll-*a* (chl-*a*) concentration using a 10-AU Turner Designs fluorometer fitted with the narrow-band, non acidification system of Welschmeyer (1994) (Nozais et al. 2001).

2.2.4. Phytoplankton

Surface water was collected from each site using a 500 ml polyethylene bottle, and filtered on GF/F filters. Each filter was placed in a polyethylene test tube containing 10 ml of 90% acetone for chl-*a* extraction. Samples were refrigerated for pigment extraction over a 24 - 48 hour period. Again, chl-*a* concentrations were measured fluorometrically (Turner Designs 10-AU model). At deeper sites (> 0.5m depth), bottom water samples were collected using a pop-bottle, and phytoplankton biomass determined as above.

2.3. Statistical Analysis

All multivariate analyses were performed using the PRIMER (Plymouth Routines in Multivariate Ecological Research) v5 statistical package. Cluster analysis and MDS ordinations were used to visually assess spatial differences in macrobenthic communities in the St. Lucia Estuary (Clarke & Warwick 1994). MDS ordination and dendrograms were constructed from similarity matrices generated from Bray-Curtis similarities, after fourth root transformations and row standardization of abundance data. A one-way analysis of similarity (ANOSIM) procedure was used to determine any temporal difference in the structure of macrofaunal communities, with pair-wise analyses for

inter-treatment comparisons. The BIOENV function was used to highlight the key factors, or combination of factors, that accounted for macrobenthic community patterns. SIMPER was used to identify taxa that dominated or characterised clusters generated from clustering and ordination techniques. The DIVERSE function was used to calculate the following community parameters at each sampling site: total abundance, taxonomic richness (expressed as total number of taxa) and Shannon-Weiner diversity (H´, as log to the base e). For univariate statistical testing, data were transformed (log + 1, arcsin), but did not always result in normality of data or homogeneity of variance. Non-parametric testing was therefore used for all analyses. Mann-Whitney U tests were used to test if abundance, richness and diversity differed between clusters identified by ordinations and dendrograms. Correlation analyses (Spearman) were performed between physico-chemical parameters, phytoplankton, microphytobenthos and abundance, richness and diversity of macrofauna.

3. Results

3.1. Physical Environment

3.1.1. Salinity

A reversed-salinity gradient persisted in the system over the whole survey period, with salinities at the mouth and Narrows ranging from 10.1 to 17.9 ‰ and from 5.3 to 16.7 ‰ respectively. Salinity ranged from 17.3 to 72 ‰ in the South Lake, and from 0 to 125.6 ‰ in the North Lake (Table 1). Hypersaline conditions were most extreme in February, when maxima of 113.7 and 125.6 ‰ were recorded at Lister’s Point and Hell’s Gate, respectively. Salinities declined over the April and August sampling periods, with

few cases of extreme hypersalinity remaining. In October however, at the peak of the drought phase, extreme hypersalinities of 108.1 and 66.8 ‰ were measured at sites H2 and H1. Salinities at the False Bay stream outlet never exceeded 14.8 ‰, as it was heavily influenced by freshwater flow.

3.1.2. Temperature

Seasonal variations in temperature were marked during the survey, with temperatures ranging between 27.2 and 36.6°C in February, 19.3 to 26.5°C in April, 17.4 to 26.7°C in August and between 21.35 and 28.6°C in October (Table 1).

3.1.3. Oxygen

Oxygen levels were highly variable within the system, ranging from 0.1 to 12.6 $mg.l^{-1}$ (Table 1). Hypoxic and anoxic conditions were measured at Listers Point and Hells Gate in February, and in the False Bay stream outlet, H1 and H2 in October. Oxygen levels ranged between 5.4 and 12.8 $mg.l^{-1}$ in the Narrows, between 3.7 and 8.4 $mg.l^{-1}$ in the South Lake, and between 0 and 12.6 $mg.l^{-1}$ in the North Lake. Dissolved oxygen levels were positively correlated with depth ($r = 0.439$, $p < 0.001$,).

3.1.4. Depth

Water depths at most sites were generally less than 0.2 m during the survey (Table 1). The only sites at which water depths were consistently greater than 0.5 m were in the Narrows, viz. the Bridge, the Public Jetty, and at the Mouth. In October, at the peak of

the drought, the pelagic habitat at Makakatana in the South Lake, as well as Hell's Gate, Lister's Point and H4 in the North Lake had completely dried out.

3.1.5. Sediment

Sediment was generally medium to very fine sand fine at the mouth (Table 1), but was finer in the Narrows, and was classed as very fine sand to coarse silt. Sediments in the South Lake were classed as fine to very fine sand. Finest sediments were recorded at Lister's Point and Lister's Point Seepage, where they were classed as fine and course silt, respectively. Silt content was positively correlated with sediment phi values ($r = 0.68$, $p < 0.001$) indicating that silt levels increased as sediment became finer.

3.1.6. Phytoplankton

There was a trend of a northerly increase in phytoplankton biomass in the system, averaging 14.6 ± 2 mg chl-a.m^{-3} in the Narrows, 27 ± 13.7 mg chl-a.m^{-3} in the South Lake and 55.3 ± 15 mg chl-a.m^{-3} in the North Lake. Phytoplankton biomass was positively correlated with salinity ($r = 0.358$, $p < 0.01$).

3.1.7. Microphytobenthos

There was also a trend of a northerly increase in microphytobenthic biomass in the system. Biomass averaged 52.2 ± 9.6 mg chl-a.m^{-2} in the Narrows, 113.2 ± 21.6 mg chl-a.m^{-2} in the South Lake, and 554 ± 113 mg chl-a.m^{-2} in the North Lake. Microphytobenthic biomass was inversely correlated with depth ($r = -0.402$, $p < 0.01$),

and confirmed field observations that microphytobenthos flourish in very shallow or even dry conditions.

3.2. Macrofauna

A total of 23 benthic taxa was recorded in the system over the entire survey period (Table 2). The dominant taxa over the whole survey were tanaidaceans (61 951ind.m^{-2}), and the polychaetes *Ceratonereis* sp. (34 699 ind.m^{-2}), *Dendronereis arborifera* (35 744 ind.m^{-2}) and *Dendronereides zululandica* (12 633 ind.m^{-2}), which cumulatively contributed 75% to the overall macrobenthic assemblage. There was statistical evidence of temporal variability in macrofaunal assemblages between sampling seasons (ANOSIM global p = 0.009), with the most significant differences occurring between February and August (pairwise analyses p = 0.046), February and October (p = 0.03) and April and August (p = 0.01). 75% of the difference between the February and August samples was attributed to the greater abundance of *Ceratonereis* sp., *D. arborifera*, *Paramoera capensis* (isopod), *D. zululandica*, *Grandidierella bonnieroides* (amphipod), *Ampelisca brevicornis* (amphipod) and *Tellina* sp. (bivalve) in February, and tanaidaceans in the August samples. The differences between the February and October samples were due to increased proportions of tanaidaceans, *Ceratonereis* sp., *D arborifera* and *Assiminea* sp. (gastropod) in October and *Tellina* sp. in February. The April and August samples were statistically different because of the increase in densities of tanaidaceans, *Ceratonereis* sp., *D. arborifera*, *P. capensis*, *D. zululandica* and ingolfiellid amphipods in August.

Cluster analysis and MDS ordinations indicated that the macrofauna of the St. Lucia Estuary could be divided into three distinct spatial clusters (Fig 2). Cluster 1 comprised macrofauna from the mouth of the estuary, the Narrows, as well as the stations of Makakatana, Catalina Bay, Charter's Creek and Fanies Island in the southern half of South Lake, and H4 and Lister's Point in the North Lake-False Bay complex (Figs 2 & 3). This group was dominated by the polychaetes *D. arborifera*, *Ceratonereis* sp. and tanaidaceans. Minor contributions were made to this assemblage by two other polychaetes *D. zululandica* and *Glycera* sp., the isopod *P. capensis* and the bivalve *Solen cylindraceus*. Cluster 2 comprised macrofauna from sites in the middle (Dead Tree Bay) and northern half (H1) of South Lake as well as Hell's Gate and Lister's Point Seepage from the southern margin of the North Lake-False Bay area (Figs 2 & 3). Tanaidaceans, and the polychaetes *Ceratonereis* sp. and *Boccardia ligerica* were the dominant macrofauna of cluster 2, and contributed 100% to the composition of this group. The third group was made up of macrofauna from the False Bay stream outlet together with H2 and H3, all of which were in the North Lake-False Bay complex. No macrofauna were recorded at any of these sites, making the characterization of this group on the basis of dominant species impossible (Table 2).

Abundance (Z = -3.73, $p < 0.001$,), taxonomic richness (Z = -2.26, $p < 0.05$) and diversity (Z = -3.971, $p < 0.001$) of macrofauna were statistically greater in cluster 1 than in cluster 2. Further statistical comparisons with cluster 3 were not undertaken because variance was zero in this group for the above-mentioned parameters. Abundance, taxonomic richness and diversity of macrofauna were positively related to depth (r = 0.317, $p < 0.05$ for abundance, r = 0.31, $p < 0.05$ for richness, r = 0.351, $p < 0.01$ for

diversity), but was inversely related to microphytobenthic biomass (r = -0.4, $p < 0.01$ for abundance, r = -0.447, $p < 0.001$ for richness, r = -4.64, $p < 0.001$ for diversity). The northward decline in richness and diversity of macrofauna, indicated by Fig 4 would therefore be related to the northward decrease in water depth and secondarily to an increase in microphytobenthic biomass.

Multivariate correlation analyses revealed weak associations between macrofaunal assemblages and physico-chemical parameters, which are indicative of the highly variable nature of the biotic and abiotic factors acting on the macrofauna of the system. On the whole, interactions between salinity, temperature, water depth, phytoplankton and microphytobenthic biomass (r = 0.126) best explained the variance observed in the macrofaunal assemblages of the system. From a temporal point of view, different factors influenced macrofauna during each sampling seasons. Water depth (r = 0.047) was the main determinant of community structure in February, while interactions between sediment silt content, dissolved oxygen and water depth (r = 0.273) best explained macrofaunal distributions in April. In August, water temperature, salinity, dissolved oxygen and microphytobenthic biomass (r = 0.443) explained most of the variation in macrofauna, whereas salinity (r = 0.159) was the primary determinant of community structure in October. Multivariate correlations indicated that the structure of macrofaunal assemblages of specific clusters identified by ordination techniques, was determined by different variables. Cluster 1 was most affected by temperature (r = 0.27) whereas cluster 2 was most influenced by the combined effects of water depth and sediment silt levels (r = 0.438). Further correlation analyses including cluster 3 could not

be undertaken since no macrofauna were recorded at the stations making up this cluster, thus resulting in zero variance.

4. Discussion

The results of this investigation indicate a significant effect of the prevailing drought on the physical environment and macrofauna of the St. Lucia Estuary. The most noteworthy effects on the physical habitat are the reductions in total areas of inhabitable substrate available to macrofauna, as well as the development of hypersaline conditions in parts of the South and North lakes. The 5 year period of mouth closure, and the consequent loss of seawater intrusion into the system, allied with extended periods of low rainfall, have led to more than 50% of the estuary drying out (Taylor 2007), and probably being uninhabitable by macrofauna. Secondly, as evaporation rates increase and precipitation rates decrease, salt loads in the water column increase, resulting in hypersaline conditions developing in parts of the system (Cyrus and Vivier 2006a, Taylor 2007). It is evident from this study that in 2005 both effects were most severe in the North Lake-False Bay complex and parts of the South Lake, whereas the mouth and the Narrows were relatively unaffected. These drought-induced effects have been previously recorded in the St. Lucia system, and are a dominant feature of this ecosystem (Fielding et al. 1991, Owen and Forbes 1997).

Both of these effects were also the likely primary determinants of macrofaunal community structure in the system during the drought phase under study. Evidence for this comes from ordinations and cluster plots which indicate that sites in the North Lake, viz. the False Bay stream outlet, H2 and H3, were spatially distinct from the remaining

sites and were devoid of macrofauna during any sampling season (Fig 2). In contrast, macrobenthic organisms were more abundant and communities more diverse in the South Lake and the Narrows, where hypersaline conditions and habitat loss were less severe. Further evidence arises from correlation analyses, showing that diversity and richness of macrofauna were positively related to depth. Water depth was greatest in the Narrows and mouth of the system, but declined northwards, partially explaining the trend of a northerly reduction in richness and diversity of macrofauna within the system.

Reductions in water depth may have affected macrofauna directly in extreme cases, where water had completely evaporated and the area become completely uninhabitable by macrofauna. Indirect effects could also have played a role, because at the peak of the drought there was discontinous flow of water between clusters identified by ordinations and clustering. This resulted in different parts of the system being fragmented and physically separated from each other. During the peak of the drought, the Narrows was completely cut off from the South Lake, and the South Lake in turn was cut off from the North Lake (Taylor 2007), creating discrete habitats.

The ecological effects of such habitat fragmentation is varied, and includes effects such as discontinuous nutrient, organic matter and phyto- and zooplankton flow between these habitats. Significantly, fragmentation would have also prevented circulation and interchange of macrofaunal larvae and other propagules between parts of the system. Processes governing larval settlement ecology are key structuring agents of benthic communities (Eckman 1996), and fragmentation of habitats would have impeded the spread of various species and colonization of sediments, by negatively affecting larval circulation across the system.

Multivariate correlations indicated weak associations of macrofauna with physico-chemical parameters in the system. This is indicative of the high degree of variability in both physical and biotic components of the system. Such variability is common in estuaries (Hastie and Smith 2006), and is probably compounded by the unpredictability imposed by extended periods of drought. When the system was split into regional groups as identified by cluster analysis and ordinations, it was evident that different factors operated on each of these groups. Macrofauna of cluster 2, which comprised sites mainly in the northern regions of South Lake and southern regions of North Lake, were influenced primarily by the combined effects of sediment silt content, and water depth. In contrast, macrofauna in Cluster 1, comprising sites in the Narrows and the southern region of the South Lake, were influenced principally by water temperature. The latter result indicates that under drought conditions, these habitats functioned differently, with different physical factors determining the structure of macrofaunal assemblages between them. This further supports the hypothesis that habitat fragmentation imposed by the drought may be a key determinant of macrofaunal assemblages in the system.

Macrofaunal density and richness usually increase with salinity in most typical estuaries (eg Montagna and Kalke 1992), with elevated salinities favoring many marine associated species and concurrently negatively effecting non-marine species (Hastie and Smith 2006). The results of this study, however, show that abundance, richness and diversity of macrofauna were not correlated with salinity. This does not necessarily indicate that the effect of salinity on these parameters was negligible, but probably reflects the high degree of variability in macrofauna and the physical habitat in the system. Hypersaline conditions, which were especially severe in the northern regions of

the estuary would have been a significant structuring agent of macrofauna by eliminating stenohaline marine species, and selecting for species with salinity tolerances greater that 35‰ (Forbes and Cyrus 1993). In the Guadalupe and Nueces estuaries, Texas, Montagna et al. (2002) showed a peak in abundance of macrofauna at salinities of 32 ‰ and a peak in diversity at 9 ‰. These parameters declined drastically between salinities of 40 to 120 ‰ (Montagna et al. 2002), probably due to the mechanism stated above.

The negative correlation between density, richness and diversity of macrofauna and biomass of microphytobenthos is surprising, as one would have expected macrofauna to be positively influenced by food availability in the form of benthic microalgae (Miller et al. 1996). An alternate interpretation of this result is that microphytobenthos may have been positively affected by reductions in density of macrofauna because of a decline in grazing pressure. It is probable that factors such as lethally low water levels and hypersaline conditions may have killed off macrofauna, but recruits may not have been able to colonise the available habitat due to its fragmentation. This would have resulted in a grazer-free environment for microphytobenthos to flourish.

Bivalves have historically been numerically and gravimetrically important components of the St. Lucia benthos (Blaber et al. 1983, Weerts 1993), but were comparatively less abundant in this survey. A possible reason is that salinity was highly variable in the system during the survey, both temporally and spatially and this may have negatively affected bivalves. The bivalves recorded in this system previously have been shown to occur in high densities when salinities are stable and marine in nature (25 to 50 ‰), but are found in low numbers during low salinity conditions (Weerts 1993). This is especially so for *Solen cylindraceus*, which is sensitive to low or rapid changes in salinity

(Owen & Forbes 1997). It is therefore possible that the decline *S. cylindraceus* and other bivalve species, may have been attributed to unpredictable and rapid changes in salinity recorded in this system.

Similarly, the crab *Paratylodiplax blephariskios*, which was a dominant member of the Narrows benthos under marine conditions (Owen 1999), was poorly represented in the Narrows during this survey, contributing less than 1% to the total number of individuals in this area. This species has a salinity tolerance of 3 to 60 ‰ (Owen 1999) and it is, therefore, unlikely that its decline was salinity-related, since salinity in the Narrows ranged between 5.3 and 16.7 ‰. The species has a marine larval dispersive phase, and it is more likely that the recorded decline in density was due to the extended period of mouth closure, thus preventing recruitment of juvenile *P. blephariskios*. This mechanism could also explain the relative decline in bivalve numbers in the system or other species with marine-dependent juveniles.

Despite the ongoing drought conditions affecting the St. Lucia Estuary, there was evidence of strong resilience in the system based on the macrofauna sampled. The 23 taxa recorded in this survey compare well with the 22 taxa recorded by Weerts (1993) during a prolonged period of low salinities, and the 33 recorded during a period of marine salinities (Weerts 1993). This resilience has been previously noted in the system, though the precise mechanisms by which the system rebounds from, or resists, disturbances such as floods, cyclones and droughts remain obscure (Forbes and Cyrus 1992). Clarifying these mechanisms should be the target for future research.

More recent developments have shown that the system's complexity is far from resolved. During 2006, two previously unrecorded macrofaunal species were recorded in

the system. One is the opistobranch gastropod *Haminoea natalensis*, which was found in extremely high densities (maximum 300 ind.m^{-2}) in Catalina Bay and Charter's Creek. This is the first documentation of the existence of this species in the system. A more serious ecological and management finding was the presence of the alien invasive gastropod *Tarebia granifera* in parts of the system, where densities of up to 3000 ind.m^{-2} were measured at the end of 2006. This is a species with extreme reproductive efficiency that could pose an unprecedented threat to the ecosystem integrity of the St. Lucia Estuary. Its biology and ecology, particularly its ability to cope with the extreme salinity variations of the St. Lucia system are currently being studied.

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Table Captions

Table 1: Physico-chemical variables, phytoplankton and microphytobenthic biomass measured in the St. Lucia Estuary during the survey.

Table 2: Spatial and temporal variations in macrofaunal density (ind.m^{-2}) at sites occupied in the St. Lucia Estuary.

Table 3: Macrofaunal taxa characterising the clusters identified using dendrograms and MDS ordinations from SIMPER.

Table 4: Significance (*p*) and goodness of fit (*r*) from non-parametric correlations (Spearman) between physico-chemical variables, phytoplankton and microphytobenthic biomass, and macrofaunal taxonomic richness, abundance and diversity. Values in bold indicate significant associations.

Table 5: Results of multiple correlation analysis between physico-chemical variables, phytoplankton and microphytobenthic biomass and macrofaunal community structure over the entire survey and for each sampling period.

Figure Captions

Figure 1: Map of the St. Lucia Estuary showing sampling sites and its geographical position within South Africa.

Figure 2: Dendrogram (A) and MDS ordination (B) constructed from Bray-Curtis similarities showing spatial variations in macrofaunal assemblages in the St. Lucia Estuary.

Figure 3: Map of the St. Lucia Estuary with clusters identified from ordinations and cluster analysis superimposed.

Figure 4: Differences in density, taxonomic richness and diversity of macrofauna between sites in the St. Lucia Estuary. Vertical lines = means + SE.

Figures

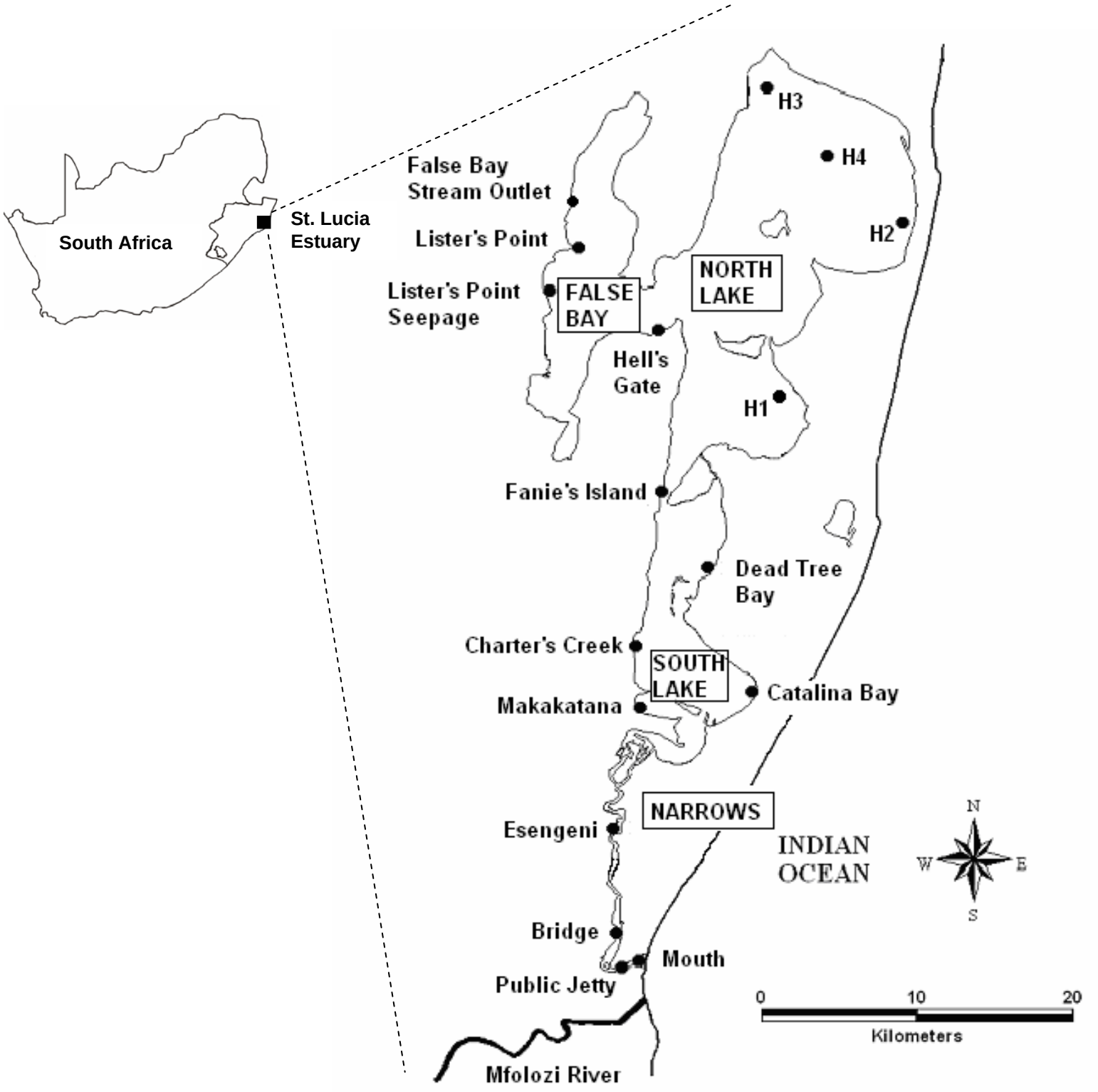


Figure 1.

Table 1

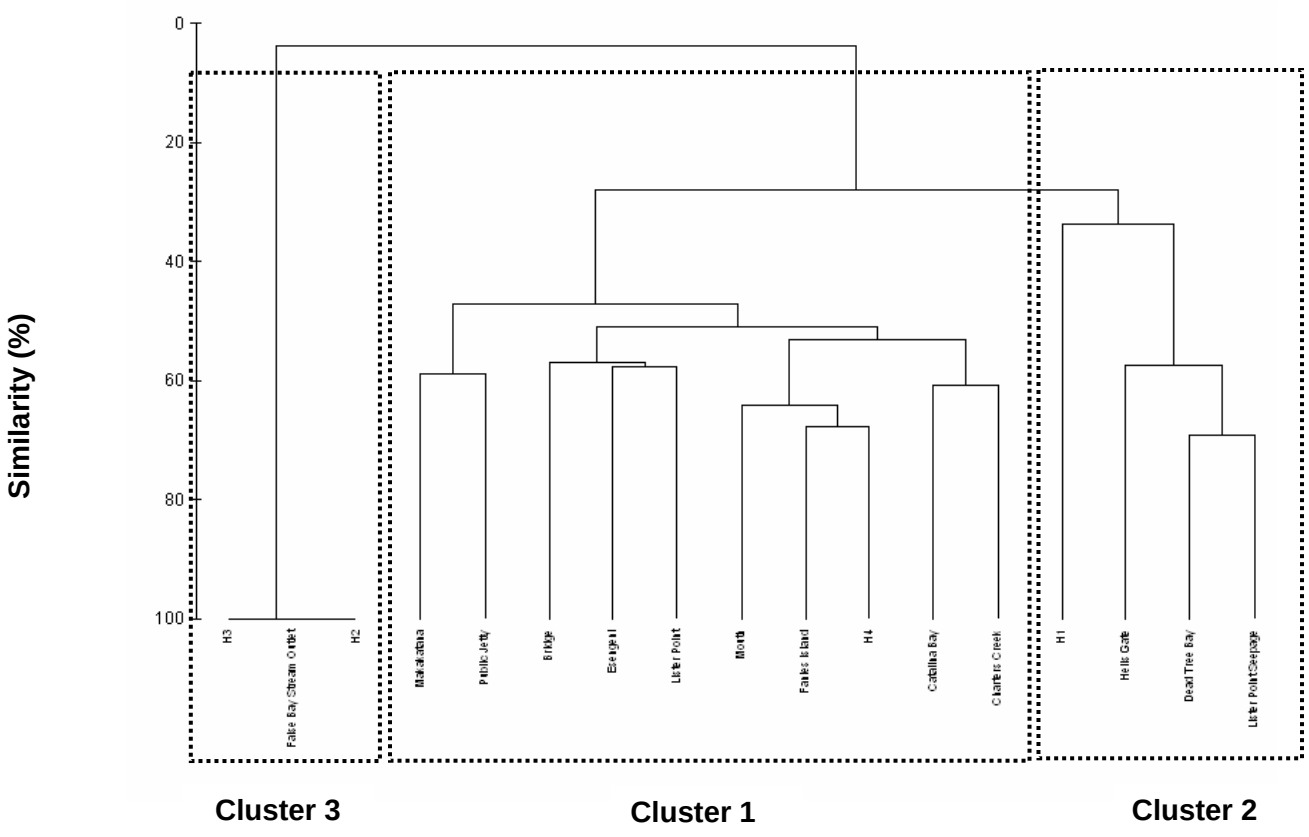
	Site	Sediment median particle size (phi)	Silt (%)	Temperature (^{o}C)	Salinity (ppt)	Dissolved Oxygen (mg.L^{-1})	Depth (m)	Phytoplankton Biomass (mg chl-*a*.m^{-3})	Microphytobenthic Biomass (mg chl-*a*.m^{-2})
February	**Mouth**	1.6	0.0	28.6	10.5	6.0	4.00	23.0	39.0
	Public Jetty	1.5	11.8	30.1	8.7	6.3	1.50	21.6	57.4
	Bridge	2.2	17.6	30.5	7.2	5.8	1.50	0.1	0.2
	Esengeni	2.4	29.9	30.9	9.8	5.4	0.50	15.2	70.9
	Makakatana	2.2	16.5	36.5	17.3	6.1	0.10	12.2	95.1
	Catalina Bay	1.8	8.8	29.0	32.7	5.1	0.10	2.1	24.8
	Charters Creek	2.0	15.9	33.8	32.5	4.8	0.15	9.0	123.9
	Dead Tree Bay	2.0	12.8	30.8	72.4	4.5	0.10	21.6	365.6
	Fanies Island	3.2	37.6	36.3	38.6	8.4	0.15	268.5	108.5
	Hell's Gate	5.8	74.6	34.7	125.6	0.1	0.01	13.1	216.2
	Lister Point Seepage	1.1	15.1	36.6	28.9	12.0	0.05	7.1	1990.4
	Lister Point	6.7	88.4	33.6	113.7	0.5	0.01	107.5	88.1
	False Bay Stream Outlet	1.2	11.7	31.0	9.7	4.9	0.05	16.4	204.5
April	**Mouth**	3.6	0.0	21.4	10.1	7.3	0.40	13.2	17.5
	Public Jetty	1.3	35.1	22.1	9.0	6.4	0.20	2.9	85.1
	Bridge	4.7	52.7	21.4	8.0	6.6	0.15	10.8	27.7
	Esengeni	2.7	41.6	20.4	5.3	6.2	2.00	22.3	52.2
	Makakatana	4.0	7.6	24.7	9.9	8.2	0.10	8.8	157.7
	Catalina Bay	1.9	3.6	22.3	13.8	5.9	0.01	1.8	22.7
	Charters	2.1	16.0	23.9	18.1	4.2	0.15	4.2	53.0
	Dead Tree Bay	2.0	10.3	22.9	29.6	5.4	0.01	3.5	192.4
	Fanies Island	3.0	39.6	19.4	26.8	5.3	0.20	17.9	80.6
	Hell's Gate	2.6	39.8	22.7	33.4	6.7	0.05	67.5	64.8
	Lister Point Seepage	5.7	42.7	25.0	51.9	5.8	0.05	14.6	195.6
	Lister Point	8.2	78.6	26.5	22.3	9.2	0.10	9.4	1392.3
	False Bay Stream Outlet	6.4	57.1	23.4	14.1	6.6	0.05	210.0	1719.7
August	**Mouth**	3.5	0.0	20.7	12.5	7.3	4.00	23.6	70.3
	Public Jetty	6.0	56.0	21.0	10.8	7.2	1.00	2.0	95.8
	Bridge	5.4	72.3	20.6	9.7	7.1	1.00	10.5	36.8
	Esengeni	4.2	56.0	19.3	6.8	12.8	1.30	16.4	84.1
	Makakatana	3.9	8.7	24.5	10.4	6.9	0.10	8.2	73.5
	Catalina Bay	2.0	5.5	20.5	16.7	6.3	0.05	0.8	71.6
	Charters	2.0	9.3	18.1	17.9	4.8	0.10	8.4	53.6
	Dead Tree Bay	2.0	0.6	24.3	22.8	6.2	0.05	7.3	294.3
	Fanies Island	2.2	24.1	25.6	28.5	7.8	0.15	29.8	55.6
	Hell's Gate	2.4	30.6	26.7	39.5	5.6	0.05	49.0	45.2
	Lister Point Seepage	4.1	0.0	25.1	21.0	12.6	0.05	6.7	1219.7
	Lister Point	4.2	57.9	23.0	63.6	5.6	0.05	182.0	94.9
	False Bay Stream Outlet	4.3	62.0	17.4	14.8	3.4	0.10	36.7	366.6
October	**Mouth**	3.7	0.0	22.8	17.9	9.8	0.80	9.3	8.8
	Public Jetty	3.6	10.0	23.5	16.7	10.0	0.80	9.2	147.0
	Bridge	6.3	52.9	22.8	14.4	10.1	1.20	14.9	23.0
	Esengeni	5.8	35.8	22.3	10.7	10.5	1.14	39.7	19.4
	Makakatana	5.4	32.7			**No Water**			89.3
	Catalina Bay	3.8	2.0	23.4	21.7	7.7	0.10	9.0	67.0
	Charters	3.8	7.2	25.5	44.1	3.7	0.10	20.4	207.3
	Dead Tree Bay	4.5	9.1	28.6	40.7	6.7	0.04	27.5	99.5
	Fanies Island	8.4	94.1	23.9	59.9	5.2	0.05	53.5	4.7
	Hell's Gate	6.3	60.2			No Water			55.2
	Lister Point Seepage	4.0	23.1	24.1	0.0	11.7	0.10	21.3	605.7
	Lister Point	7.4	68.6			**No Water**			72.7
	False Bay Stream Outlet	5.6	51.0	22.8	9.6	2.1	0.10	28.5	563.7
	H1	n/s	n/s	26.3	66.8	1.8	0.01	103.0	818.5
	H2	n/s	n/s	24.7	108.1	1.5	0.20	187.0	264.6
	H3	n/s	n/s	23.9	6.3	6.2	0.50	47.5	123.3
	H4	n/s	n/s			**No Water**			778.3

1 Table 2

	Site	Bl	Cer	Da	Dz	G	Ab	Ci	C	Gb	Lr	Pc	Pb	M	Tan	Ant	Ing	Vl	As	Sc	T	Ub	N	S
February	Mouth					117																		
	Public Jetty			20909																				
	Bridge			1591	3182							11288										9621		
	Esengeni			1591	4848	4848	16061			23182		83												
	Makakatana		2748								83													
	Catalina Bay			3182	83									6439						3182			4848	1591
	Charters Creek			3182	83	83				23182		83				19318	4848			1450	7415	3182		
	Dead Tree Bay																							
	Fanies Island						117														1061			
	Hells Gate																							
	Lister Point Seepage																							
	Lister Point																							
	False Bay Stream Outlet																							
April	Mouth																	14						
	Public Jetty																							
	Bridge		235						14						221									
	Esengeni			471																				
	Makakatana											14					25			14				
	Catalina Bay		14									47			363		47							
	Charters Creek	9							28	13		99		9	22									
	Dead Tree Bay	47	33																					
	Fanies Island																			28				
	Hells Gate																							
	Lister Point Seepage																							
	Lister Point																							
	False Bay Stream Outlet																							
August	Mouth	433		33	532	268	47					18								24				
	Public Jetty	146	6	18	18	1	14	33				38	31				31							
	Bridge		574	18	14		297				19	85		19						19				
	Esengeni		21	177																				
	Makakatana		165	325				99					381				687							
	Catalina Bay	28	132		14									8						6	28			
	Charters Creek	66		12					235	18		124		99						28				
	Dead Tree Bay	52	25																					
	Fanies Island	165		19		268														99				
	Hells Gate														631									
	Lister Point Seepage														2472									
	Lister Point	27	193		377		574					1422			2721		24							
	False Bay Stream Outlet																							
October	Mouth					6							36		4									
	Public Jetty		14962	332	3197																			
	Bridge		4732	532									66	65	18126					33	33			
	Esengeni		77	4											1497									
	Makakatana	165	9332												14694					466				
	Catalina Bay	33	33			499							66		33					33	132			
	Charters Creek	99	284	3197	21	998									2359	1332				165	1832			
	Dead Tree Bay												33		17928									
	Fanies Island	66	198		165										32						932			
	Hells Gate																		65					
	Lister Point Seepage																							
	Lister Point																		631					
	False Bay Stream Outlet																							
	H1		935												598									49
	H2																							
	H3																							
	H4	52		151	99	348									25									

Table 2:

Codes for macrofauna: **Bl**: *Boccardia ligerica*, **Cer**: *Ceratonereis* sp., **Da**: *Dendronereis arborifera*, **Dz**: *Dendronereides zululandica*, **G**: *Glycera* sp., **Ab**: *Ampelisca brevicornis*, **Ci**: *Cirolana imposta*, **C**: Cumacea, **Gb**: *Grandidierella bonnieroides* **Lr**: *Leucothoe richiardi* **Pc**: *Paramoera capensis* **Pb**: *Paratylodiplax blephariskios* **M**: Mysidacea, **Tan**: Tanaidacea, **Ant**: Anthurid isopods, **Ing**: Ingolfiellid amphipods, **Vl**: *Varuna litterata*, **As:** *Assiminea* sp., **Sc**: *Solen cylindraceus*, **T**: *Tellina triangularis*, **Ub**: Unidentified bivalves, **N**: Nemertea, **S**: Sipunculida.


Similarity (%)
0
20
40
60
80
100
H3
False Bay Stream Outlet
H2
Makakatana
Public Jetty
Bridge
Esengeni
Lister Point
Mouth
Fanies Island
H4
Catalina Bay
Charters Creek
H1
Hells Gate
Dead Tree Bay
Lister Point Seepage
Cluster 3
Cluster 1
Cluster 2

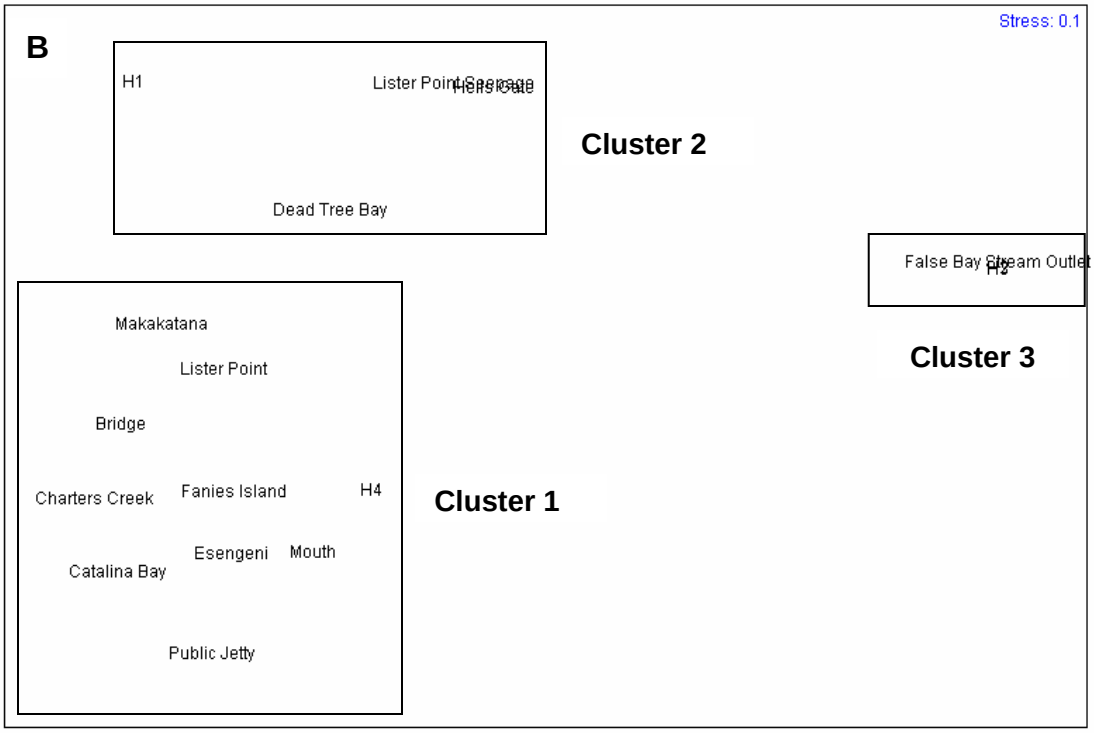

B
Stress: 0.1
H1
Lister Point Seepage
Hells Gate
Dead Tree Bay
Cluster 2
False Bay Stream Outlet
H2
Cluster 3
Makakatana
Lister Point
Bridge
Charters Creek
Fanies Island
H4
Esengeni
Mouth
Catalina Bay
Public Jetty
Cluster 1

Figure 2

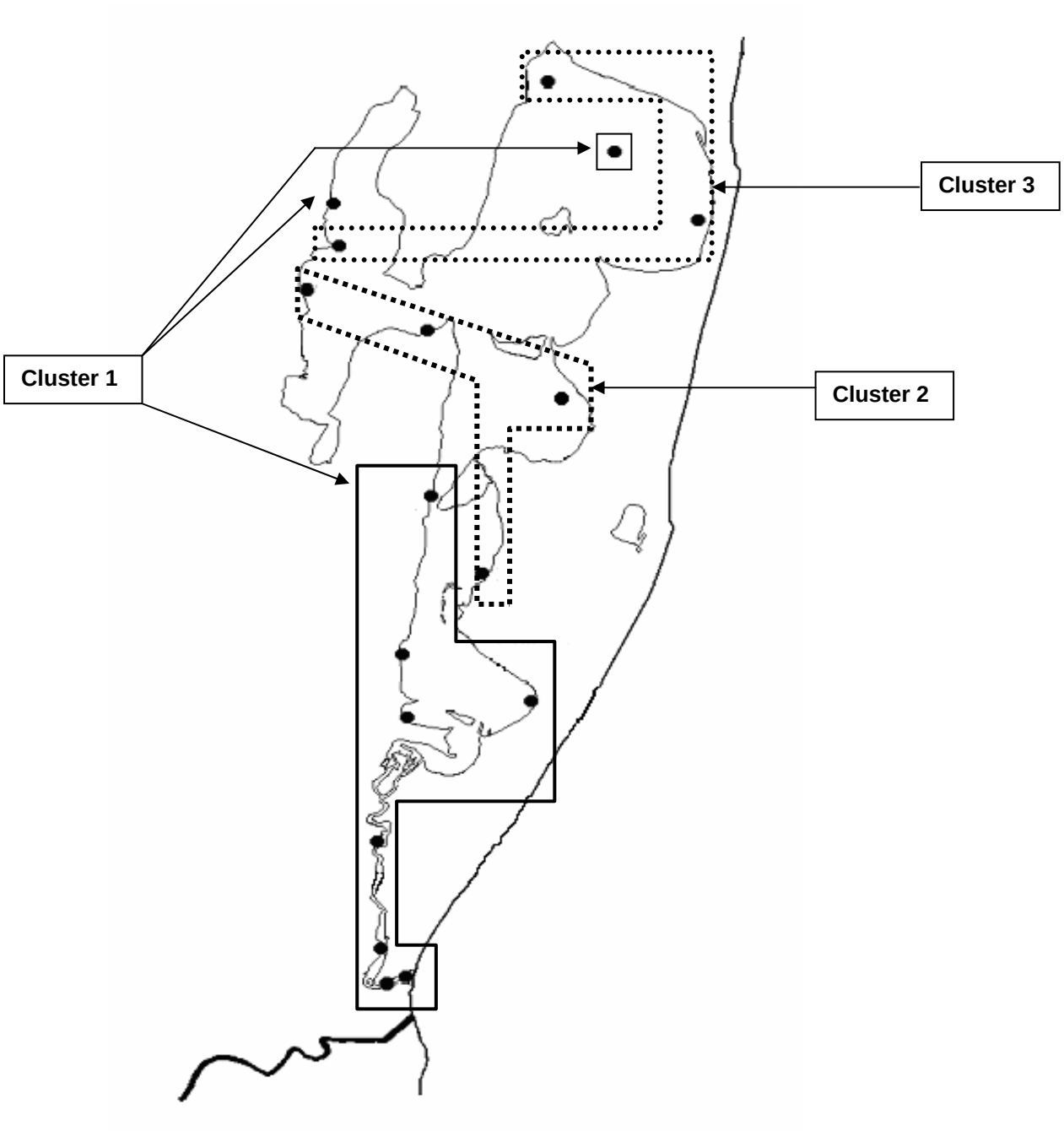


Figure 3.

Table 3.

	Taxon	Average Abundance (ind.m^{-2})	Contribution (%)	Cumulative Contribution (%)	Average similarity
Cluster 1	***Dendronereis arborifera***	3448	22.40	22.40	1.70
	Tanaidacea	15634.45	20.98	43.38	1.59
	***Ceratonereis* sp.**	9778.31	18.84	62.22	1.43
	Dendronereideis zululandica	2099.80	8.51	70.73	0.64
	***Glycera* sp.**	993.77	7.88	78.61	0.6
	Paramoera capensis	1482.39	6.26	84.86	0.47
	Solen cylendraceus	734.74	3.11	87.98	0.24
	Boccardia ligerica	357.31	2.85	90.82	0.22
Cluster 2	**Tanaidacea**	14973.92	48.89	48.89	1.43
	***Ceratonereis* sp.**	6867.67	43.55	92.44	1.28
	Boccardia ligerica	68.45	7.56	100	0.22

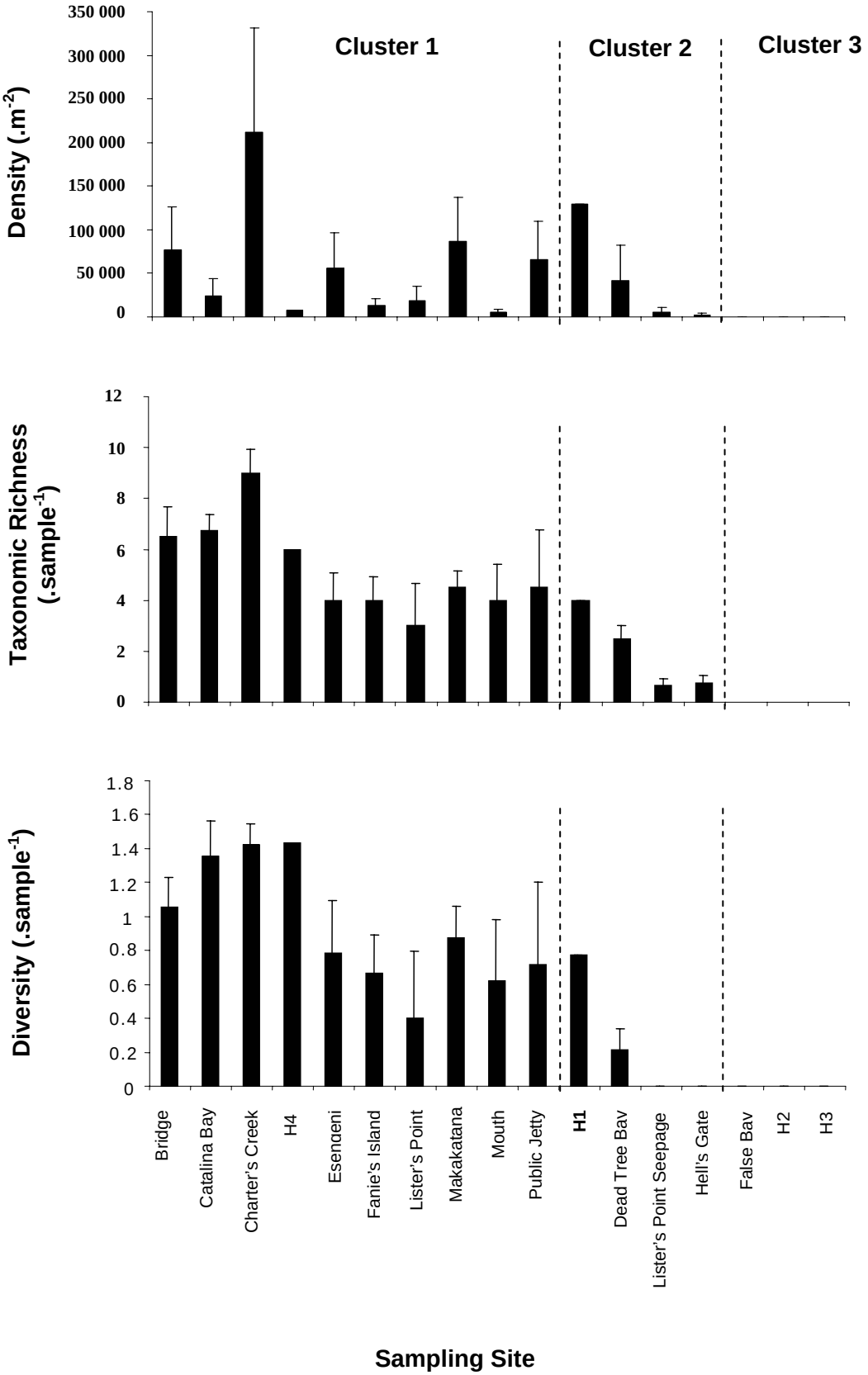

Cluster 1
Cluster 2
Cluster 3
Density (.m-2)
350 000
300 000
250 000
200 000
150 000
100 000
50 000
0
Taxonomic Richness (.sample-1)
12
10
8
6
4
2
0
Diversity (.sample-1)
1.8
1.6
1.4
1.2
1
0.8
0.6
0.4
0.2
0
Bridge
Catalina Bay
Charter's Creek
H4
Esengeni
Fanie's Island
Lister's Point
Makakatana
Mouth
Public Jetty
H1
Dead Tree Bay
Lister's Point Seepage
Hell's Gate
False Bay
H2
H3
Sampling Site

Figure 4.

Table 4:

	Taxonomic Richness		Abundance		Diversity	
Variable	**R**	**p**	**R**	**p**	**R**	**p**
Sediment Particle Size	0.08	0.53	0.12	0.35	0.03	0.81
Sediment Silt Content	-0.13	0.34	-0.07	0.57	-0.15	0.25
Temperature	-0.11	0.4	0.02	0.88	-0.11	0.39
Salinity	0.009	0.94	0.01	0.89	-0.01	0.89
Dissolved Oxygen	0.15	0.26	0.19	0.15	0.14	0.29
Depth	**0.31**	**0.02**	**0.31**	**0.01**	**0.35**	**0.008**
Phytoplankton Biomass	-0.23	0.09	-0.05	0.71	-0.24	0.06
Microphytobenthic Biomass	**-0.44**	**p < 0.001**	**-0.39**	**0.002**	**-0.46**	**0.0003**

Table 5:

	February	**April-May**	**August**	**October**	**Combined**
Variable Combination	Depth	Silt, Dissolved Oxygen, Depth	Temperature, Dissolved Oxygen, Salinity, MPB	Salinity	Temperature, Salinity, Water Depth, Microphytobenthos, Phytoplankton
Correlation coefficient	0.047	0.273	0.443	0.159	0.126