

Zooplankton of the St. Lucia Estuary during the current drought cycle: a comparison between open- and closed-mouth conditions

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ABSTRACT: The St. Lucia Estuary is currently experiencing a drought-induced crisis, resulting in the system having been closed off from the sea for approximately 8 yr. This closure was interrupted by a brief open-mouth phase, induced by a unique combination of extreme climatic events. The primary aim of the present study was to compare zooplankton dynamics during open- and closed-mouth conditions. Sampling was undertaken during quarterly surveys from February 2006 to November 2008. During the closed-mouth phase, up to 70% of the lake bed was dry and salinities in the northern lakes often exceeded 90, making these areas largely uninhabitable for zooplankton. However, in the lower regions where drought effects were less harsh, zooplankton were characterized by high densities and biomass of typical estuarine taxa such as the copepods *Pseudodiaptomus stuhlmanni*, *Acartia natalensis* and the mysid *Mesopodopsis africana*. Of the 69 taxa recorded during the study period, only 27 were present during the closed-mouth phase. Under open-mouth conditions, previously excluded marine taxa (e.g. the prawn *Penaeus indicus* and fish larvae), once again re-entered the system, increasing its diversity significantly. A unique occurrence after mouth re-closure was the colonisation of the mouth area by swarms of the tunicate *Oikopleura dioica* ($>10^3$ ind. m^{-3}), while previously dominant zooplankton grazers virtually disappeared. These findings emphasize the complexity of the system and stress the need for further research into the potential impacts of environmental and climate changes on this key African estuarine lake.

KEY WORDS: Zooplankton · Drought · St. Lucia Estuary · Extreme events · *Oikopleura dioica*

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INTRODUCTION

The St. Lucia Estuary, on the eastern seaboard of South Africa, is a system that experiences periodic isolation from the Indian Ocean. This normally occurs during periods of low or no river inflow. Under such conditions, a sand berm may form across the estuary mouth (Taylor 2006). Similar estuaries are present in a variety of regions worldwide, e.g. Australia (Roy et al. 2001), Brazil and Uruguay (Bonilla et al. 2005), India and Sri Lanka (Ranasinghe & Pattiaratchi 2003) and the USA, particularly California and Texas and occasionally as far north as Long Island, New York (Gobler

et al. 2005). Within South Africa, approximately 70% of the currently functional estuaries are of this nature, with most of them being specifically classified as temporarily open/closed estuaries (Whitfield 1992).

The St. Lucia Estuary forms part of the iSimangaliso (formerly Greater St. Lucia) Wetland Park. iSimangaliso is South Africa's first World Heritage Site and has been designated a Ramsar Wetland of international importance (Begg 1978, Cyrus & Vivier 2006). It is the largest estuarine lake in Africa (Fielding et al. 1991, Cyrus & Vivier 2006). Covering an area of 325 km², it represents approximately 80% of KwaZulu-Natal's total estuarine area (Begg 1978). The lake system is

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governed by cyclical wet and dry periods, each lasting between 4 and 10 yr (Begg 1978). The St. Lucia Estuary is currently experiencing a drought cycle, with below average rainfall persisting since 2002. Prior to 1920, the Mfolozi River discharged into the St. Lucia Estuary and would buffer water loss during periods of drought, but in the 1930s a canal was excavated through the Mfolozi flats for agricultural purposes (Begg 1978, Whitfield & Taylor 2009). The natural filtration system of the swamps was, therefore, destroyed and the 2 systems have since been artificially maintained separately in an attempt to avoid the perceived threat of siltation from the Mfolozi. This alteration of the system's catchment has further exacerbated the severity of the current drought cycle.

The present drought has led to a drastic reduction in water levels and concomitant salinity increases. A reversed salinity gradient has persisted, with the occurrence of hypersaline conditions in the northern regions of the lake. The hypersaline conditions (70 to 90) that developed in the North Lake between 1969 and 1971 as a direct result of a previous drought led to a number of extraordinary changes in some of the basic trophic relations. These involved mainly: (1) a bloom of dinoflagellates (Grindley & Heydorn 1970); (2) the dominance of chironomid larvae and harpacticoid copepods in benthic-pelagic samples (Grindley 1982); (3) a population explosion of aerial spiders; and (4) the loss of most of the plankton present, leaving only few species with high salinity tolerance (Grindley 1981).

Breaching in temporarily open/closed estuaries usually occurs because of increased precipitation in the catchment and greater head pressure in the lower estuary, resulting in a break of the sandbar (Whitfield 1992). On the 3rd of March 2007, however, the St. Lucia Estuary breached from the seaward side due to the combined effects of Cyclone Gamede and a spring equinox. This resulted in exceptional wave energy development in the surf zone and the consequent breakage of the ~100 m sand berm (R. H. Taylor pers. comm.). This breaching event allowed seawater to enter the estuary for the first time in approximately 5 yr and was unique in that the estuary was still experiencing drought conditions in the region.

A range of studies have highlighted the importance of zooplankton as indicators of change in marine systems (e.g. Bonnet & Frid 2004, Beaugrand 2005). Their rapid response to ecosystem perturbations (Kjørboe & Nielsen 1994, Hays et al. 2005) is achieved through strong coupling between environmental change and plankton dynamics (Roemmich & McGowan 1995). In temporarily open/closed estuaries, maximum zooplankton abundance and biomass is generally recorded during closed-mouth conditions (Whitfield 1980, Kibirige & Perissinotto 2003, Kibirige et al. 2006), with

communities usually dominated by a few euryhaline taxa (Froneman 2004). Breaching events lead to the loss of zooplankton and their food resources, leaving low densities and biomasses during open-mouth conditions. Species richness, on the other hand, is typically greater during open phases, due to recruitment of marine neritic species within the estuary (Froneman 2004). Increases or decreases in precipitation and runoff may create extreme events—floods or droughts, respectively—and are increasing in frequency worldwide (Gleick 2003, Mirza 2003). The effects of such events remain unknown for estuarine communities, and are probably crucial for naturally variable systems such as the St. Lucia Estuary. From a zooplankton perspective, no comprehensive survey has been conducted in the St. Lucia Estuary, aside from the relatively outdated work by Grindley (1976, 1982). The present study, therefore, aims to determine the responses of zooplankton to open- and closed-mouth conditions, in terms of community structure, abundance and biomass. This knowledge would contribute significantly to the synthesis of information on the key producers of the St. Lucia Estuary, enhancing understanding of the ecology of this system, especially in response to environmental fluctuations.

MATERIALS AND METHODS

Quarterly surveys were undertaken at 5 representative stations within the St. Lucia Estuary, from February 2006 to November 2008. These stations were: the Mouth, Esengeni, Catalina Bay, Charters Creek and Listers Point (Fig. 1). The study period covered 3 different hydrological phases: a closed phase (Feb 2006 to Feb 2007), an open phase (Mar 2007 to Aug 2007) and a re-closed period (Nov 2007 to Oct 2008). Zooplankton, phytoplankton and microphytobenthic samples together with physicochemical data were collected at each site during each sampling season.

Physicochemical variables. Physicochemical measurements were made with a YSI 6920 water quality logger, fitted with temperature (°C), depth (m), salinity, dissolved oxygen (mg l^{-1}), pH and turbidity (Nephelometric Turbidity Units [NTUs]) probes. Where possible, measurements were made at both the surface and the bottom of the water column. In cases where the water level was <10 cm deep, the probe was placed horizontally so that all the sensors were submerged.

Pelagic and benthic microalgae. Subsurface water samples were collected at each of the 5 stations during each sampling season. Near-bottom water samples were collected with a pop bottle at sites where water levels were deep enough. One 250 ml subsample was filtered through a GF/F filter to determine the total

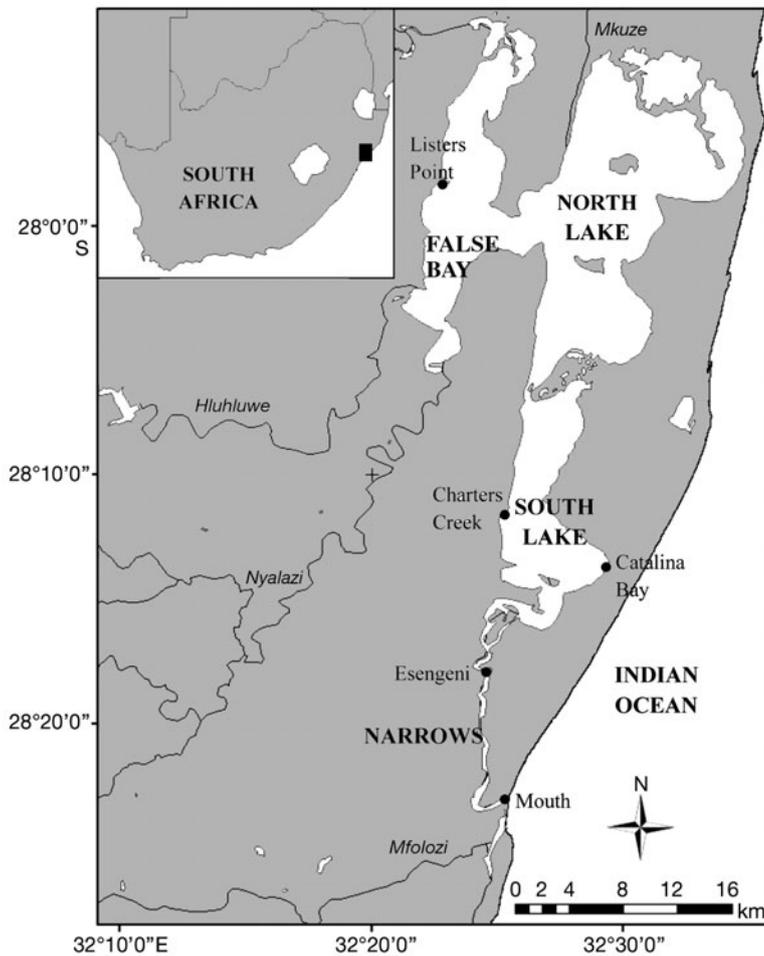


Fig. 1. St. Lucia Estuary, South Africa, and sampling sites

concentration of chlorophyll *a* (chl *a*). Phytoplankton biomass was determined fluorometrically (Turner Designs 10-AU) after cold extracting chl *a* and phaeopigments from filters in 10 ml 90% acetone for 48 h in the dark. Microphytobenthic cores (internal diameter = 2 cm, $n = 3$, depth = 1 cm) were collected on each sampling occasion at each station and placed in 100 ml polyethylene bottles containing 30 ml 90% acetone for microphytobenthic chl *a* extraction (Nozais et al. 2001). Biomass was again determined fluorometrically and expressed as mg chl *a* m^{-2} .

Zooplankton. Single daytime mesozooplankton samples were collected using an epibenthic sled fitted with 200 μm mesh (open area ratio $\approx 3:1$). This method was employed due to the shallow water levels and the diel migration pattern of many of the zooplankton taxa present in the system. The sled was towed in the nearshore shallow waters at all stations, except at Esengeni, where a boat was used. The mouth of the net was semi-circular in shape (radius = 18.5 cm) and was

mounted on a sled such that the net was raised 7.5 cm above the sediment surface. The volume of water filtered ($\approx 1.43 m^3$) was calculated by multiplying the area of the sled mouth by the distance towed (27 m). The sample was emptied into a 500 ml bottle containing 4% phloxine-stained formaldehyde. In regions where water depth was too shallow for the sled to be used, a hand held D-net (radius = 28 cm) with the same mesh size was driven over a 20 m transect.

In the laboratory, samples were suspended in 0.5 to 5 l solutions, depending on the density of organisms. The main sample was then stirred vigorously so that all the organisms remained in a homogenous suspension. A 20 ml plastic vial attached to a metal rod was then used to withdraw 3 to 6 subsamples from mid-depth (Perissinotto & Wooldridge 1989, Jerling & Wooldridge 1995). Zooplankton within the samples were identified and counted with a dissecting microscope (400 \times). In all cases, the coefficient of variation between subsamples was <10%. Zooplankton density was then calculated as ind. m^{-3} .

Biomass was estimated as the total dry weight (mg DW m^{-3}) of the sample. The sample was divided into 2 equal portions with a Folsom plankton splitter (McEwen et al. 1954). Large detritus and sediment particles were removed from the sample under a dissecting microscope (400 \times) and biomass was measured by oven drying half of each sample at 60°C for 24 h. For those samples that contained too much detritus, between 10 and 50 ind. of each species were oven-dried (24 h, 60°C) in pre-weighed tin capsules. Triplicate weights were recorded for each species. The average weight for each species was then multiplied by the respective abundance so as to obtain the average dry weight per sample.

Statistical analyses. Univariate statistical analyses were conducted with SPSS 15 for Windows. Data which did not satisfy the assumptions of parametric testing (i.e. normality and even distribution of residuals) were normalised using a $\log(x+1)$ transformation. Two-way ANOVA without replication (Zar 1996) was applied to test for possible spatial and temporal differences in total zooplankton abundance, biomass and diversity. Results from these tests showed no seasonal variation within each mouth state, allowing 1-way ANOVA with post hoc Tukey's tests to be used to test for differences (in phytoplankton and microphytobenthic biomass as well as zooplankton abundance, biomass and diversity) between stations and between mouth states. Spearman's rank correlations were used

to test for relationships between environmental variables and the 3 univariate community parameters.

Multivariate analysis was conducted on abundance data using the PRIMER package (version 6.0). All data were square-root transformed. Analysis of similarity (ANOSIM) showed no significant seasonal difference in zooplankton community structure within each hydrological phase (closed, open and re-closure). For this reason, densities of taxa during each season were averaged to give the mean abundance of each taxon at the different stations during each of the mouth phases. A Bray-Curtis similarity matrix was then calculated from the 5 stations sampled during the different mouth phases. Cluster analysis (group averaged) and multidimensional scaling (MDS) were used to visually assess spatio-temporal differences in zooplankton assemblages, which were then tested using ANOSIM. Where differences were found, the similarity percentage (SIMPER) routine determined the relative contribution of individual species to community structure between mouth states. The BIOENV function (using harmonic Spearman correlation) was then used to relate environmental variables to the zooplankton communities.

RESULTS

Physical environment

During the closed-mouth phase, >50% of the estuary was dry and the greatest water depth recorded was 2.48 m at the Mouth in April 2006. During the open-mouth phase, all sites were submerged or inundated and, while most northern lake stations were ini-

tially very shallow, by the time the mouth re-closed in August 2007, water levels approached 2003 levels (~0.9 m average).

During the closed phase, a reversed salinity gradient existed throughout the estuary (Table 1), ranging from

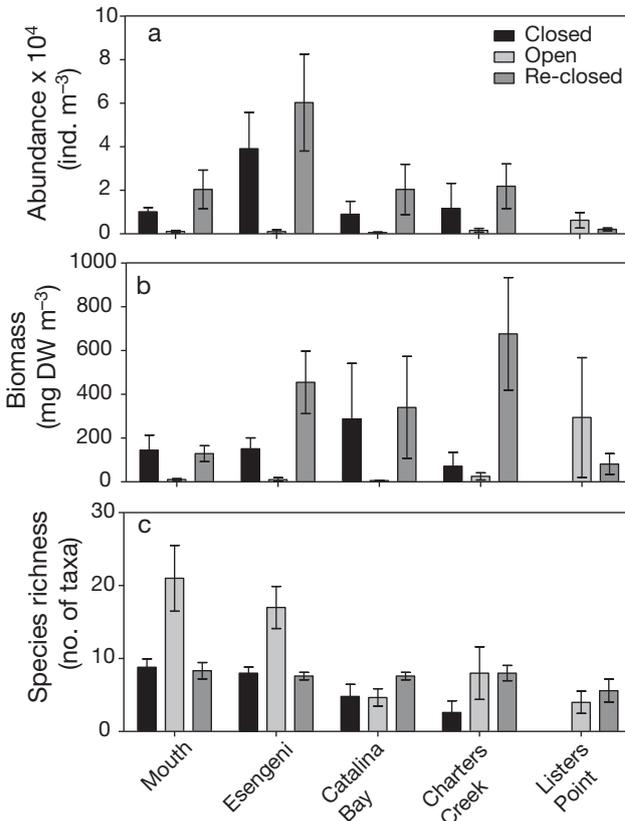


Fig. 2. Average (\pm SE) (a) total zooplankton abundance ($\times 10^4$), (b) biomass and (c) species richness during the closed, open and re-closed mouth phases of the St. Lucia Estuary

Table 1. Physicochemical variables, microphytobenthic (MPB) and phytoplankton (PPL) biomass measured at each station during the different mouth phases (mean \pm SE). NTU: Nephelometric Turbidity Units

Mouth phase	Station	MPB (mg chl a m ⁻²)	PPL (mg chl a m ⁻³)	Depth (m)	Oxygen (mg l ⁻¹)	Salinity (ppt)	Temperature (°C)	Turbidity (NTU)
Closed	Mouth	54.1 \pm 24.2	22.3 \pm 9.96	1.34 \pm 0.60	8.99 \pm 4.02	13.2 \pm 5.88	25.5 \pm 11.4	6.76 \pm 3.02
	Esengeni	43.7 \pm 19.6	25.0 \pm 11.2	0.83 \pm 0.37	7.75 \pm 3.47	6.45 \pm 2.88	24.5 \pm 11.0	28.7 \pm 12.8
	Catalina Bay	189 \pm 84.7	26.7 \pm 11.9	0.38 \pm 0.17	9.06 \pm 4.05	14.5 \pm 6.49	24.8 \pm 11.1	42.8 \pm 19.1
	Charters Creek	176 \pm 78.7	40.9 \pm 18.3	0.09 \pm 0.04	8.38 \pm 4.19	24.0 \pm 12.0	29.2 \pm 14.6	41.4 \pm 18.5
	Listers Point	143 \pm 63.9	116 \pm 52.0	0.12 \pm 0.05	4.96 \pm 2.48	44.0 \pm 22.0	29.8 \pm 14.9	85.8 \pm 38.4
Open	Mouth	19.9 \pm 11.5	13.4 \pm 7.75	0.13 \pm 0.08	7.57 \pm 4.37	34.6 \pm 20.0	23.1 \pm 13.3	24.4 \pm 14.1
	Esengeni	23.0 \pm 16.3	24.7 \pm 17.5	0.83 \pm 0.58	6.78 \pm 4.79	33.9 \pm 24.0	21.4 \pm 15.1	41.2 \pm 29.1
	Catalina Bay	86.2 \pm 49.7	7.09 \pm 4.09	0.72 \pm 0.42	7.50 \pm 4.33	29.1 \pm 16.8	23.7 \pm 13.7	8.37 \pm 4.83
	Charters Creek	154 \pm 89.0	26.7 \pm 15.4	0.29 \pm 0.17	8.51 \pm 4.92	29.7 \pm 17.2	25.5 \pm 14.7	20.7 \pm 12.0
	Listers Point	62.0 \pm 35.8	23.8 \pm 13.8	0.29 \pm 0.17	6.91 \pm 3.99	35.1 \pm 20.2	23.8 \pm 13.7	32.8 \pm 18.9
Re-closed	Mouth	23.2 \pm 10.4	15.9 \pm 7.10	0.58 \pm 0.26	5.24 \pm 2.62	24.5 \pm 11.0	21.6 \pm 9.7	20.9 \pm 10.5
	Esengeni	12.6 \pm 5.61	23.7 \pm 10.6	1.58 \pm 0.70	6.00 \pm 3.00	27.2 \pm 12.2	21.3 \pm 9.52	49.6 \pm 24.8
	Catalina Bay	26.1 \pm 11.7	1.96 \pm 0.88	1.52 \pm 0.68	5.04 \pm 2.52	37.1 \pm 16.6	24.1 \pm 10.8	10.6 \pm 5.28
	Charters Creek	10.4 \pm 4.65	7.25 \pm 3.24	0.22 \pm 0.10	7.16 \pm 3.58	49.4 \pm 22.1	23.7 \pm 10.6	186 \pm 93.1
	Listers Point	5.81 \pm 2.60	22.2 \pm 9.95	0.24 \pm 0.11	7.57 \pm 3.78	49.1 \pm 22.0	21.0 \pm 9.37	234 \pm 117

1.8 at Esengeni in February 2007 to 86.9 at Listers Point in February 2006. During the open phase, salinities were generally marine (35), but the reversed salinity gradient re-established once again after mouth re-closure.

Average water temperatures ranged between 15.2 and 34.8°C in summer, 19.7 and 25.2°C in autumn, 17.2 and 24.4°C in winter and 22.5 and 30.5°C in spring. Dissolved oxygen was highly variable throughout the survey, with values ranging from 1.92 mg O₂ l⁻¹ at Listers Point in November 2006 to 11.9 mg O₂ l⁻¹ at Esengeni in November 2006. Turbidity ranged from 1 NTU at Catalina Bay to 341 NTU at Charters Creek. The highest turbidities were generally recorded at Esengeni, Charters Creek and Listers Point (Table 1).

Phytoplankton and microphytobenthic biomass

Phytoplankton biomass ranged from 1.49 to 421 mg chl a m⁻³ during the study period. Biomass peaked during the closed phase, with maximum phytoplankton biomass recorded in the northern regions of the lake. Biomass in the Mouth and Narrows was substantially lower. During the open and re-closed mouth phases, biomass was generally uniform across all stations (Table 1).

Microphytobenthic biomass ranged from 0.47 to 451 mg chl a m⁻² during the study period. There was a significant difference between mouth states ($F_{2,58} = 6.75$, $p < 0.01$). Like phytoplankton biomass, microphytobenthic biomass was also greater in the closed phase and was also generally greater in the northern regions of the lake (Table 1). These variations were, however, not significantly different either spatially or seasonally ($p > 0.05$).

Zooplankton

Total recorded zooplankton abundance in the St. Lucia Estuary ranged from 53.5 to 13.4×10^4 ind. m⁻³ during the study period (Table 2). Abundance varied between mouth states ($F_{2,61} = 5.04$, $p < 0.01$, Fig. 2a), peaking after mouth re-closure. Abundance was greatest at the Mouth and Esengeni during the closed phase. During the open phase, zooplankton abundance was low throughout the lake system, showing no spatial variation ($F_{4,9} = 0.579$, $p > 0.05$). After mouth re-closure, densities escalated to a maximum of 13.4×10^4 ind. m⁻³ at Esengeni. While zooplankton were recorded at Charters Creek and Listers Point after the mouth breached, densities diminished by October 2008 when hypersaline conditions again persisted (Fig. 3).

Abundance of the mysid *Mesopodopsis africana* was greatest at the Mouth and Esengeni during the closed phase, but was virtually zero throughout the system during the open-mouth phase. After mouth re-closure, high densities of *M. africana* were recorded in the South Lake stations. Small populations were also recorded at Listers Point in November 2007 (Fig. 3b). The copepod *Pseudodiaptomus stuhlmanni* was present at all stations except Listers Point during the closed phase. Densities decreased during the open-mouth period and increased again after mouth re-closure at all stations except the Mouth. Densities during the re-closure period were higher than those previously recorded, especially at Esengeni (Fig. 3c). Abundance of another copepod, *Acartia natalensis*, was greatest at the Mouth and Esengeni during the closed phase and increased substantially to a maximum of 5.6×10^4 ind. m⁻³ in July 2008 (Fig. 3d).

Mean zooplankton biomass recorded by Grindley (1982) for the 5 main areas of the St. Lucia system during the period 1967–1974 are compared with biomass data generated from the present study in Fig. 4. There was an increase in biomass from 1967 to 1974 corresponding with an increase in freshwater flow. Although 2006 was during the peak of the drought, biomass during this year was within the range of that in 1974.

Data from the present study confirmed a significant difference in biomass between mouth states ($F_{2,60} = 7.21$, $p < 0.05$, Fig. 2b). Biomass during the re-closed phase was significantly greater than in the closed and open phases (post hoc Tukey's test, $p < 0.05$). Biomass was also generally greatest at the Mouth and Esengeni and lower in the lakes during the closed phases ($p < 0.05$). The opposite was true for the open phase (Fig. 2b); however, the differences were not significant ($p > 0.05$). Following mouth re-closure, average biomass ranged from 81.6 to 676 mg DW m⁻³, but spatial variation was not significant ($F_{4,20} = 2.01$, $p > 0.05$).

Zooplankton species richness was significantly higher during open-mouth conditions (post hoc Tukey's test, $p < 0.05$, Fig. 2c). During the closed phase, diversity at the Mouth and Esengeni was significantly greater than that at Charters Creek and Listers Point ($p < 0.05$). In the open phase, peaks in species richness were recorded at the Mouth and Esengeni. Following mouth re-closure, species richness was roughly uniform throughout the system, ranging from 5 taxa at Charters Creek to 13 taxa at the Mouth (Table 2).

Community structure

A total of 69 different taxa were recorded during the entire study period, 27 of which were present during the closed phase, 51 during the open phase and 33 dur-

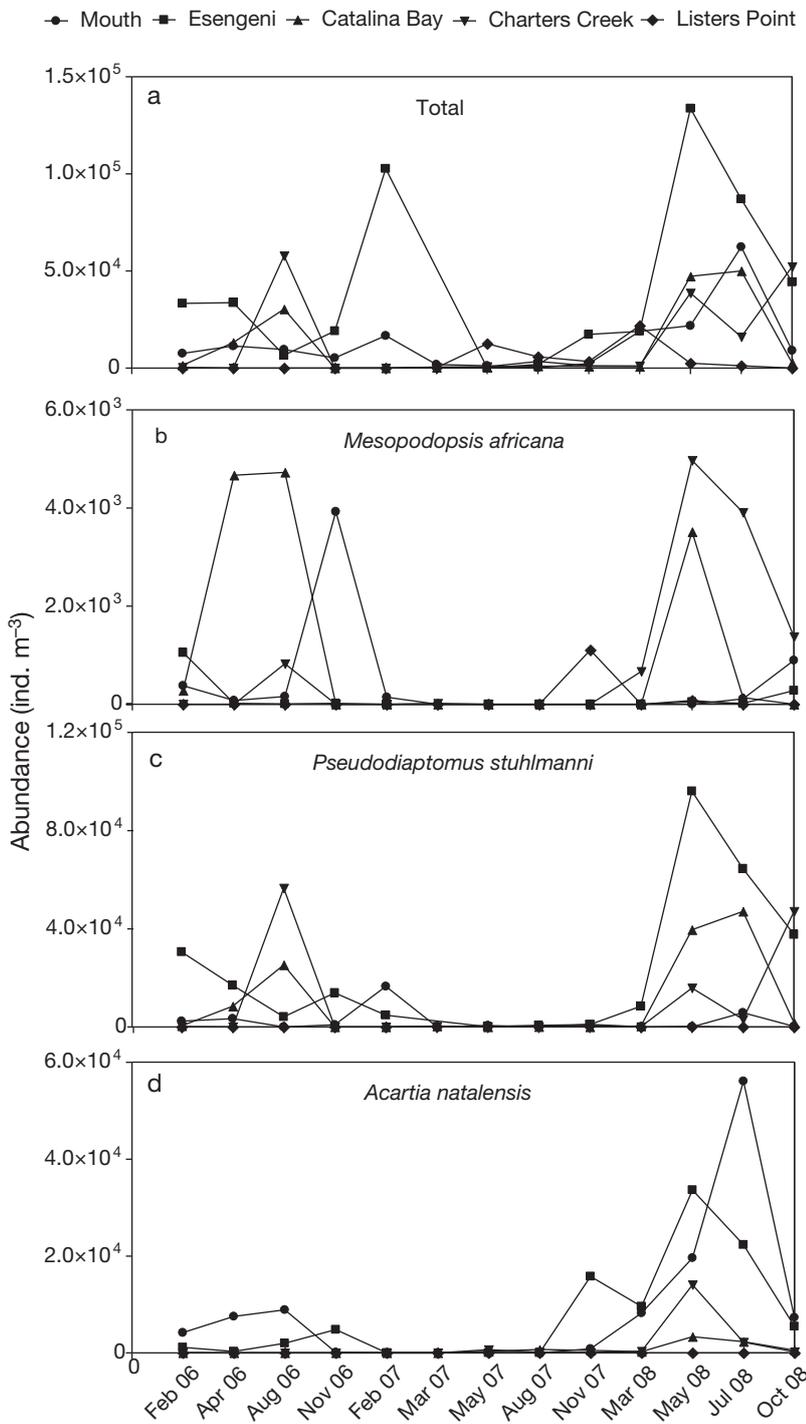


Fig. 3. *Mesopodopsis africana*, *Pseudodiaptomus stuhlmanni* and *Acartia natalensis*. Average seasonal densities of total zooplankton and the 3 most dominant taxa in the St. Lucia Estuary throughout the study period

ing the re-closed phase (Table 3). A number of taxa were introduced when the estuary mouth breached. These included various harpacticoid copepods, such as *Macrosetella* sp., *Euterpina acutifrons* and *Metis* sp., calanoids such as *Eucalanus* sp. and *Mesocalanus* sp.,

as well as poecilostomatoids, *Oncaea* spp. and *Corycaeus* spp. Other marine recruits which were previously excluded, such as the prawn *Penaeus indicus*, were also recorded following the breaching event.

Cluster analysis and MDS plots (Fig. 5) showed that zooplankton communities differed between the open and closed-mouth states, and was statistically confirmed by ANOSIM ($R = 0.838$, $p < 0.01$). Sites within the closed-mouth cluster showed between 40 and 80% similarity, while those in the open-mouth cluster were more dissimilar, showing only 15 to 55% similarity. The zooplankton community present at Listers Point subsequent to the re-closure of the estuary's mouth was an anomalous data point, as it grouped in the open-mouth cluster.

The dominant taxa during the closed phases were the calanoid copepods *Pseudodiaptomus stuhlmanni* and *Acartia natalensis*, contributing on average 74.1 and 17.9% to total zooplankton abundance, respectively. These taxa made a cumulative contribution of 92% to total zooplankton density. Although the abundance of *P. stuhlmanni* and *A. natalensis* decreased significantly during the open-mouth phase, they still accounted for 74% of the total zooplankton assemblage. The remaining contributors were *Euterpina acutifrons* (11.2%), gastropod veligers (3.07%) and copepod nauplii (2.9%).

Data analysis using the SIMPER routine revealed that 90.7% of the dissimilarity between the open and closed phases was due to 8 different taxa (Table 4). These included *Pseudodiaptomus stuhlmanni* (48.3%), *Acartia natalensis* (25%), *Mesopodopsis africana* (5.18%), *Halicyclops* spp. (3.77%), *Cletocamptus* spp. (3.27%), gastropod veligers (2.23%), polychaete larvae (1.54%) and *Euterpina acutifrons* (1.4%).

With the exception of Listers Point during the closed phase, cluster analysis showed all stations to be >30% similar during each of the mouth phases. Zooplankton communities at Catalina Bay and Charters Creek, as well as at the Mouth and Esengeni, consistently

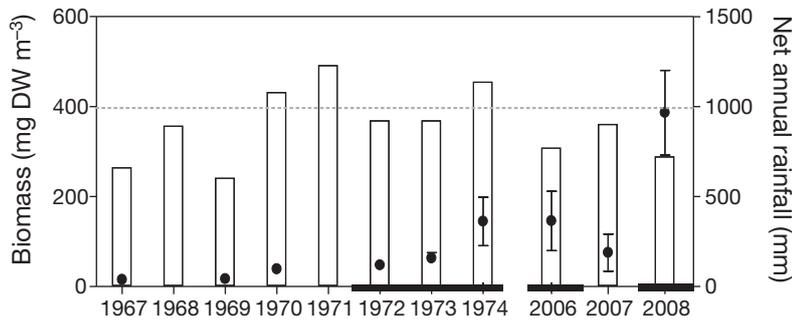


Fig. 4. Time series of average (\pm SE) zooplankton biomass (\bullet) from 1967 to 1974 (Grindley 1982) and from 2006 to 2008 in the St. Lucia Estuary. White bars show the net annual rainfall and the dotted line represents the average net annual rainfall for St. Lucia. Thick lines along the x-axis indicate periods of closed-mouth conditions

grouped together during each of the mouth phases, but communities at Listers Point were always separated from any of the above (Fig. 6). ANOSIM also confirmed significant spatial variability in zooplankton assemblages within each mouth state. Most notable was the difference between the Mouth and all other stations after mouth re-closure ($R = 0.29$, $p < 0.05$). While the zooplankton communities at all other stations were characterised by typical St. Lucia zooplankton, the Mouth was dominated by *Oikopleura dioica* and *Acartia natalensis*. *O. dioica* entered the estuary during the open-mouth state and, upon re-closure, appeared to flourish in co-existence with *A. natalensis*, reaching a maximum abundance of 10^4 ind. m^{-3} up to 5 mo after mouth closure. However, in May 2008, the *O. dioica* population dwindled, leaving *A. natalensis* as the single dominant species in the area. Only in July 2008 did the zooplankton community structure at the Mouth

start resembling that observed prior to mouth breaching, with *Mesopodopsis africana* and *Pseudodiaptomus stuhlmanni* once again making a substantial contribution to the total zooplankton biomass (Fig. 7).

The BIOENV procedure identified different environmental variables influencing the zooplankton communities. Overall, interactions between microphytobenthic biomass, phytoplankton biomass, salinity and temperature best explained the patterns observed in the zooplankton assemblages ($R = 0.37$). Within the closed phase, interactions between microphytobenthic biomass,

phytoplankton, dissolved oxygen, salinity and temperature best explained zooplankton distribution ($R = 0.31$). Microphytobenthic biomass and dissolved oxygen were the primary determinants during the open-mouth phase, while after mouth re-closure, water depth, salinity and temperature explained most of the variation in zooplankton ($R = 0.38$).

Spearman's rank correlation between environmental parameters and zooplankton diversity, density and biomass showed few significant correlations (Table 5). On the whole, zooplankton abundance, biomass and species richness were inversely related to microphytobenthic biomass. Zooplankton abundance and species richness correlated positively with water depth and negatively with temperature. Additionally, a negative relationship existed between zooplankton abundance and salinity. Within the closed phase, zooplankton biomass and species richness were also inversely related

Table 2. Total zooplankton abundance, biomass and species richness recorded across all stations within the St. Lucia Estuary during the study period. N/W: stations without water

Mouth phase	Station	— Abundance (ind. m^{-3}) —				— Biomass (mg DW m^{-3}) —				Species richness (no. of taxa)			
		Mean	SE	Min	Max	Mean	SE	Min	Max	Mean	SE	Min	Max
Closed	Mouth	10108	1954	5270	16768	145	67.9	24.5	391	8.8	1.2	6	13
	Esengeni	39093	16676	6619	10269	151	49.8	22.8	294	8	0.8	5	10
	Catalina Bay	9017	5890	0	30408	287	254	0	1302	4.8	1.7	0	10
	Charters Creek	11649	11553	0	57861	71.8	62.8	0	321	2.6	1.6	0	7
	Listers Point	N/W	N/W	N/W	N/W	N/W	N/W	N/W	N/W	N/W	N/W	N/W	N/W
Open	Mouth	1113	499	188	1901	10.7	3.3	4.1	14.9	21	4.5	16	30
	Esengeni	1045	859	186	1904	10.3	8.6	1.8	18.9	17	5	12	22
	Catalina Bay	625	196	404	1017	5.8	1.1	4.7	7.9	4.7	1.2	3	7
	Charters Creek	1612	900	623	3409	25	16.2	5.1	57	8	3.6	3	15
	Listers Point	6223	3589	223	12636	294	274	2	841	4	1.5	2	7
Re-closed	Mouth	20674	10914	2313	62394	114.5	40.9	23.2	253	9	1.1	7	13
	Esengeni	60270	22261	17372	133675	454	143	104	871	7.6	0.5	6	9
	Catalina Bay	20350	11585	782	50076	340	233	8.2	1215	7.6	0.5	6	9
	Charters Creek	21870	10224	1184	52213	676	257	16.7	1363	8	1	5	10
	Listers Point	2055	628	0	3419	81.6	47.5	0	260	5.6	1.6	0	9

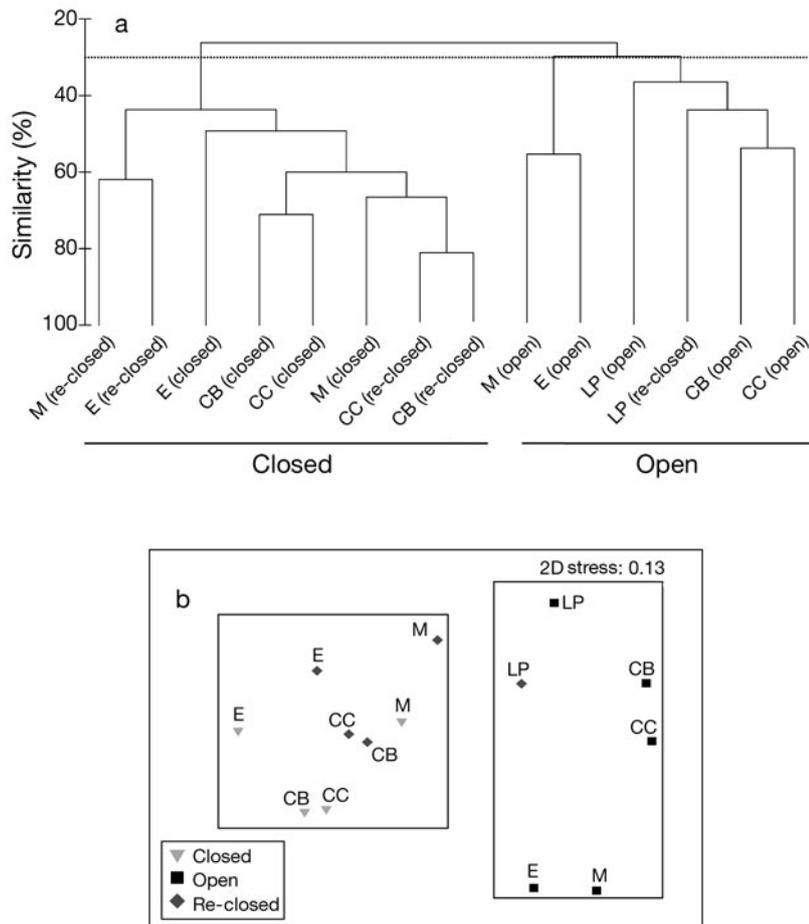


Fig. 5. (a) Dendrogram and (b) multidimensional scaling ordination showing the grouping of zooplankton communities during closed, open and re-closed mouth phases of the St. Lucia Estuary. Dotted line in (a) represents 35% similarity. M: Mouth; E: Esengeni; CB: Catalina Bay; CC: Charters Creek; LP: Listers Point

to microphytobenthic biomass, while negative correlations existed between zooplankton abundance and salinity as well as temperature. During the open-mouth and re-closure phases, microphytobenthic biomass was the only parameter to significantly correlate with zooplankton species richness, positively during the closed-mouth phase and negatively during the open-mouth phase.

DISCUSSION

As has been previously observed in most South African estuaries, maximum zooplankton abundance and biomass in the St. Lucia Estuary were recorded during the closed phase (Whitfield 1980, Kibirige & Perissinotto 2003, Kibirige et al. 2006). This is due to a combination of stable conditions, limited freshwater input and minimal exchange of water with the sea

(Gaughan & Potter 1995, Perissinotto et al. 2000). Low zooplankton abundance and biomass during open-mouth conditions are consistent with findings reported in the literature and are linked to the export of biomass-rich estuarine water into the ocean (Froneman 2004).

In Grindley's (1982) study of zooplankton biomass in the St. Lucia system (1967–1974), which covered both open- and closed-mouth phases and extreme salinity fluctuations, peaks in biomass corresponded with freshwater pulses (Grindley 1982). It is, therefore, not surprising to find no seasonal variation in total zooplankton biomass during the present study, since the survey took place during harsh drought conditions, with little freshwater input. Biomass was generally highest at the Mouth and Narrows and substantially lower in the lakes during the closed phase. This is because the northern regions were most severely affected by the drought, culminating in reduced water levels and greater salinity and temperature. Conversely, zooplankton biomass was greater in the lakes during open-mouth conditions. These findings correspond with those of Grindley (1982) and can be attributed to the lakes being a more stable environment under open-mouth conditions. Biomass levels recorded at the peak of the drought (2006) during the present study were generally within the range

of those recorded by Grindley (1982) in 1974, despite the above-average rainfall which the area received during that year. Comparisons between these studies must, however, be taken with caution for the following reasons. (1) Grindley (1982) used 2 different sampling methods, a ring-net (30 cm diameter, 90 μm mesh) and a Clarke Bumpus sampler (12.5 cm diameter, 125 μm mesh). (2) All samples were taken at the surface (hand-held) and next to the boat gunnels, thereby creating substantial disturbance (T. H. Wooldridge pers. comm.). (3) Sampling frequency and intensity were not consistent.

In this study, biomass peaked after mouth re-closure, exceeding levels which were recorded both during the present study and that of Grindley (1982). Inflowing marine water may have aided the buildup in zooplankton biomass during the subsequent closed phase, as was previously observed in the Kasouga Estuary (Froneman 2004). On a regional scale, biomass records

Table 3. Spatial variations in average zooplankton density during the different mouth phases at the 5 representative stations within the St. Lucia Estuary. M: Mouth; E: Esengeni; CB: Catalina Bay; CC: Charters Creek; LP: Listers Point. Unid.: unidentified

	CLOSED					OPEN					RE-CLOSED				
	M	E	CB	CC	LP	M	E	CB	CC	LP	M	E	CB	CC	LP
FORAMINIFERA															
CNIDARIA															
Hydrozoa															
Hydra/medusoid stage															
<i>Obelia</i> sp.															
Unid. hydromedusa 1															
Unid. hydromedusa 2															
Unid. hydromedusa 3															
Scyphozoa															
<i>Crambionella orsini</i>															
ANNELIDA															
Polychaeta															
<i>Capitella capitata</i>															
Capitellid larvae															
Nereid larvae															
Phyllodocid larvae															
Spionid larvae															
Unid. polychaete larvae															
Clitellata															
<i>Chaetogaster naididae</i>															
Unid. oligochaete															
ARTHROPODA															
Branchiopoda															
<i>Diaphanosoma</i> spp.															
<i>Evadne</i> sp.															
<i>Moina</i> sp.															
Malacostraca															
Euphausiacea															
<i>Calypterus</i> larvae															
Decapoda															
<i>Palaemon</i> sp.															
<i>Penaes indicus</i>															
Zoeae															
Mysida															
<i>Mesopodopsis africana</i>															
Mysid embryo															
Mysid juvenile															
<i>Rhopalaphthalmus tropicalis</i>															
Cumacea (unid.)															
Tanaidacea															
<i>Apseudes digitalis</i>															
Isopoda															
<i>Synidotea variegata</i>															
Amphipoda															
Amphipod larvae															
<i>Corophium</i> sp.															
<i>Grandidierella</i> sp.															
Talitridae sp.															
Unid. amphipod															
Maxillopoda															
Cirripede cypris															
Cirripede nauplius															

were generally within the range of those reported by Wooldridge (1999) for South African estuaries. In fact, even some of the lowest values recorded during the present study exceeded those documented in temperate north systems, such as the Patuxent River, Narragansett Bay and Westerschelde (Heip et al. 1995 and references therein).

Prolonged periods of mouth closure in temporarily open/closed estuaries are generally associated with

low levels of zooplankton taxonomic diversity (Froneman 2004, Perissinotto et al. 2004). In the present study, the lake zooplankton was, like most estuarine zooplankton assemblages in southern Africa (Wooldridge 1999), dominated by typical estuarine taxa, such as *Pseudodiaptomus stuhlmanni*, *Acartia natalensis* and *Mesopodopsis africana*, which often collectively contributed over 90% of the total zooplankton abundance. The zooplankton assemblages of the St. Lucia

Table 3 (continued)

	CLOSED					OPEN					RE-CLOSED				
	M	E	CB	CC	LP	M	E	CB	CC	LP	M	E	CB	CC	LP
Copepoda															
Nauplii															
Calanoida															
<i>Acartia natalensis</i>															
<i>Eucalanus</i> sp.															
<i>Mesocalanus</i> sp.															
<i>Paracalanus</i> spp.															
<i>Pseudodiaptomus stuhlmanni</i>															
<i>Temora discaudata</i>															
<i>Temora turbinata</i>															
Cyclopoida															
<i>Halicyclops</i> spp.															
<i>Oithona</i> spp.															
Poecilostomatoida															
<i>Corycaeus</i> spp.															
<i>Oncaea</i> spp.															
Harpacticoida															
<i>Cletocamptus</i> spp.															
<i>Euterpina acutifrons</i>															
Harpacticoid nauplii															
<i>Macrosetella</i> sp.															
<i>Metis</i> sp.															
Unid. harpacticoid copepod															
Ostracoda (unid.)															
Chelicerata															
<i>Hydracarina</i> sp.															
Insecta															
Chironomid larvae															
Dragonfly larvae															
Tricopteran larvae															
Unid. dipteran larvae															
MOLLUSCA															
Gastropoda															
Gastropod veliger															
Bivalvia															
Bivalve larvae															
ECTOPROCTA															
Cyphonautes larvae															
CHAETOGNATHA (unid.)															
CHORDATA															
Asciacea															
Ascidian larvae															
Appendicularia															
<i>Oikopleura dioica</i>															
Osteichthyes															
<i>Ambassis ambassis</i> (juvenile)															
Fish eggs															
Fish larvae															

Code					
Density (ind. m ⁻³)	1–9	10–99	100–999	1000–9999	10 000–99 999

Estuary, as described by Grindley (1982), were generally made up of: (1) a stenohaline marine component, consisting of copepods such as *Corycaeus* spp., which tidally accessed the mouth; (2) a euryhaline marine component, including species of *Paracalanus*, which were able to penetrate a little further; and (3) a freshwater component, consisting of species such as *Diaptomus* spp. and *Cyclops* spp., found at the mouths of inflowing rivers. Only 27 of the 95 previously recorded

taxa (Grindley 1976) were observed in the system during the closed-mouth phase. Missing components included marine and freshwater taxa, which were absent because of prolonged reduced freshwater input (Allanson & Read 1995) and the closed-mouth state which prevented tidal exchange. Primo et al. (2009) showed that dry periods in the downstream stations of the permanently open Mondego Estuary (Portugal) were also characterised by a lack of seasonality, low taxonomic

Table 4. Zooplankton taxa accounting for 90.7 % of the dissimilarity between the 2 clusters (viz. open and closed) identified using dendrograms and multidimensional scaling ordinations from SIMPER

Species	Average abundance (ind. m ⁻³)		% contribution	% cumulative contribution
	Closed	Open		
<i>Pseudodiaptomus stuhlmanni</i>	9883	261	48.3	48.3
<i>Acartia natalensis</i>	4061	1121	25.0	73.3
<i>Mesopodopsis africana</i>	612	1.54	5.18	78.5
<i>Halicyclops</i> spp.	1287	16.3	3.77	82.2
<i>Cletocamptus</i> spp.	3.98	213	3.27	85.5
Gastropod veliger	490	33.9	2.23	87.7
Polychaete larvae	29.3	185	1.54	89.3
<i>Euterpina acutifrons</i>	0.93	72.6	1.40	90.7

diversity and a high density of *Acartia* spp. However, in contrast to the St. Lucia system, marine taxa dominated the Mondego Estuary, probably due to its open mouth (Primo et al. 2009). The opening of the St. Lucia Estuary mouth in March 2007 led to a great increase in species richness. Marine taxa, such as the copepods *Corycaeus* spp., *Paracalanus* spp., juvenile *Penaeus indicus* and estuarine-dependent ichthyoplankton re-

cruited into the system. The timing of the mouth breaching allowed the autumn cohort of *P. indicus* to enter the estuary. This cohort would usually overwinter in the estuary and return to sea the next spring (Benfield et al. 1989), but was prevented from doing so due to the reformation of the beach berm by 24 August 2007.

Because this breaching event took place during a drought, it is not surprising that there was still a general lack of freshwater zooplankton. Groundwater seepage points along the eastern shores have been hypothesised to form

microhabitats of reduced salinity, capable of acting as reservoirs during dry cycles and providing refugia for estuarine species, for later recolonisation of the estuary (Taylor et al. 2005). However, data from an allied study carried out in 2005 (S. Singh unpubl. data) showed that the zooplankton communities of these refugia are significantly different from those of neighbouring sites and, therefore, probably not the primary source of recolonisation and recruitment. It is more likely that some species of zooplankton may be able to produce resting stages or eggs capable of surviving dry or hypersaline conditions for long periods of time (e.g. Uye 1985, William-Howze 1997, Engel 2005). Recolonisation could also have occurred from adjacent parts of the estuary that had not dried out completely during the drought (e.g. the Narrows or the southern part of South Lake).

Abundance of the mysid *Mesopodopsis africana* decreased drastically after the system breached, becoming almost entirely absent within a month. Possible explanations may include reduced water levels in the mouth region as a result of sediment deposition, populations being flushed out to sea (e.g. Wooldridge 1986, Kibirige & Perissinotto 2003) or increased predation

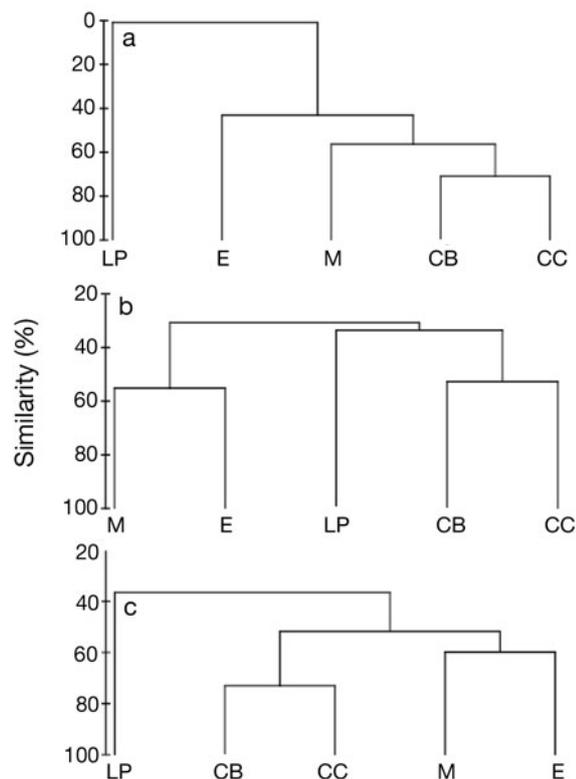


Fig. 6. Dendrograms showing spatial variation in community structure during the (a) closed, (b) open and (c) re-closed mouth phases of the St. Lucia Estuary during the study period. Station codes are as in Fig. 5

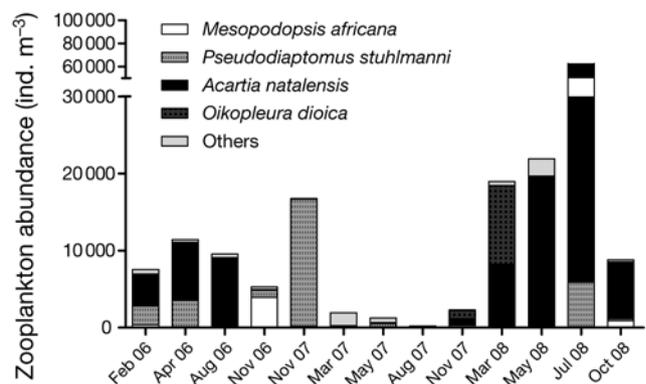


Fig. 7. Average abundance of the dominant zooplankton taxa at the Mouth of the St. Lucia Estuary during the study period

Table 5. Spearman's rank correlation between physicochemical parameters and diversity, abundance and biomass of zooplankton during the different mouth phases of the St. Lucia Estuary. MPB: microphytobenthic biomass; PPL: phytoplankton biomass; *: $p < 0.05$; **: $p < 0.01$

Mouth phase	Parameter	MPB	PPL	Depth	Oxygen	Salinity	Temperature	Turbidity
Closed	Biomass	-0.58**	-0.07	0.06	0.09	-0.37	-0.33	-0.09
	Abundance	-0.40	0.13	0.15	0.21	-0.46*	-0.45*	-0.03
	Diversity	-0.58**	0.03	0.48	0.22	-0.50	-0.41	-0.22
Open	Biomass	-0.34	0.18	-0.06	-0.05	-0.20	-0.32	-0.08
	Abundance	-0.35	0.13	-0.09	-0.10	-0.19	-0.33	-0.05
	Diversity	-0.58*	-0.01	0.24	-0.04	0.02	-0.47	0.16
Re-closed	Biomass	-0.27	0.15	0.09	-0.01	-0.18	0.15	0.26
	Abundance	-0.21	0.26	0.33	0.11	-0.34	0.01	0.06
	Diversity	0.57*	-0.12	0.18	-0.19	-0.19	0.17	-0.29
Overall	Biomass	-0.44**	0.04	0.16	0.07	-0.17	-0.22	0.10
	Abundance	-0.37**	0.12	0.27*	0.16	-0.27*	-0.31*	0.06
	Diversity	-0.38**	-0.01	0.36*	0.01	0.01	-0.33*	-0.05

pressure by fish that entered the estuary from the ocean. In the present study, mysid swarms were mostly restricted to the mouth region during the closed phase, but were recorded in low numbers, along with *Pseudodiaptomus stuhlmanni* and *Acartia natalensis* at Charters Creek and Listers Point after the estuary breached. It is likely that the more favourable conditions (viz. increased water level and decreased salinity) allowed for the development of these communities in the northern lakes, which was probably a more stable environment than the Mouth and the Narrows at the time.

Multivariate correlations showed weak associations of zooplankton with environmental parameters in the estuary. This is not uncommon in estuaries (Hastie & Smith 2006) and is probably a product of the highly dynamic nature of this system. Overall, the interaction between microphytobenthic biomass, phytoplankton biomass, salinity and temperature best explained the variation in community structure. In terms of univariate variables, microphytobenthic biomass was inversely related to zooplankton biomass, abundance and species richness. Reduced grazing pressure could have allowed for microphytobenthos proliferation, since biomass was generally greatest at Charters Creek and Listers Point, where conditions were often not favourable for the survival of zooplankton. Similar findings were reported by Pillay & Perissinotto (2008, 2009) for the benthic communities of the St. Lucia Estuary. Overall, zooplankton abundance and species richness correlated positively with water depth. Such a relationship is expected, since habitat for zooplankton increases with water depth. Additionally, the Mouth and narrows are deeper stations, partly protected from the effects of drought due to the freshwater inflow at Makakatana, Mfolozi and Mpate Rivers. Zooplankton abundance and salinity were negatively correlated, reflecting the negative impact of hypersaline condi-

tions on zooplankton abundance. Additionally, zooplankton abundance and species richness were greater in cooler waters. This could be a product of the shallower waters (e.g. Charters Creek and Listers Point) being more susceptible to heating. This negative correlation is, therefore, probably more related to depth than temperature itself, since water temperature decreases with depth. High temperature is nevertheless known and expected to negatively affect the physiology of many zooplankton species (e.g. Moore et al. 1996, Norberg & De Angelis 1997).

Zooplankton dynamics at the mouth of the St. Lucia Estuary followed a very unique pattern, particularly after mouth re-closure. High abundances of the appendicularian *Oikopleura dioica* ($>10^4$ ind. m^{-3}) were found. These tunicates live in individual mucous cases, which efficiently concentrate and collect particulate matter from the water (Deibel 1998). While appendicularians commonly occur in permanently open estuaries, there are no reports of *O. dioica* swarms thriving in estuaries under closed-mouth conditions. Studies have shown that other planktonic grazers are often rare or absent in swarms of planktonic tunicates (Fraser 1962, Berner 1967, Deibel 1980). Several factors may contribute to this apparent exclusion of other herbivores. Firstly, high reproductive rates enable planktonic tunicates to exploit food sources more rapidly (Heron 1972, Deibel 1980). Also, appendicularians are food generalists, capable of ingesting a wide size spectrum of naturally occurring particles (Deibel 1998). Particle consumption by tunicates may, therefore, reduce the food available to juvenile stages of other herbivores, decreasing recruitment of competing zooplankton. Finally, the exceptionally high filtering rates of most tunicates could reduce phytoplankton standing stocks to levels that would not support other grazers. In older swarms, both copepods and appendicularians may

coexist in high densities, suggesting that, given enough time and sufficient food, herbivores with longer generation times could also exploit the same phytoplankton stocks (Alldredge & Madin 1982).

With the arrival of *Oikopleura dioica* in the St. Lucia Estuary, the zooplankton community structure in the Mouth area shifted drastically from being dominated by *Mesopodopsis africana* and *Pseudodiaptomus stuhlmanni*, which used to make up the bulk of the biomass, to being dominated by *O. dioica* and *Acartia natalensis*. There are several possible explanations for the apparent exclusion of these larger taxa. Firstly, it is possible that changes in the physical environment associated with the re-closure of the estuary mouth (e.g. a decrease in turbidity and an increase in water level) favoured *O. dioica*, to the exclusion of the other grazers. Secondly, *O. dioica*, with its efficient feeding mode (Alldredge 1981, Deibel 1998) may have outcompeted *P. stuhlmanni*. Thirdly, the slower regeneration times of copepods such as *P. stuhlmanni* (e.g. *Paracalanus crassirostris* versus *O. dioica* ratio of $\approx 1:10$, Hopcroft & Roff 1995) may have made it vulnerable to predation, with the opposite being true for *O. dioica*. Lastly, heavy fish predation may have limited populations of *M. africana* and *P. stuhlmanni*. Both of these taxa are important components in the diet of a number of zooplanktivorous fish in the St. Lucia Estuary (Blaber 1979). While *Oikopleura* spp. are the preferred food type for many fish species because of their high carbon and nitrogen content, as well as their lack of a carapace and slow reaction times (Gorsky & Fenaux 1998), they also exhibit extremely fast generation rates (Deibel 1998). So, within the St. Lucia mouth, the effect of fish predation on *O. dioica* abundance may have been counterbalanced by their fast generation rates.

This community shift, however, lasted only for about 2 mo, as *Oikopleura dioica* disappeared completely from the estuary by the end of May 2008. A number of factors may have contributed to this. Firstly, the salinity dropped down to 23 ppt in May 2008, which, according to Uye & Ichino (1995), is outside its range of tolerance. Secondly, in the absence of *Pseudodiaptomus stuhlmanni* and *Mesopodopsis africana*, *O. dioica* may have become the primary target of fish predation. Lastly, it has been shown that copepods in high abundance may have a significant impact on the abundance of appendicularians by ingesting their eggs and juveniles (López-Urrutia et al. 2004). Whichever combination of factors it may be, the zooplankton community at the mouth of the estuary, 2 mo subsequent to mouth re-closure, was dominated by *Acartia natalensis*, with an average individual size of about 800 μm . Only in October 2008 did the zooplankton community at the Mouth start resembling that of its pre-breaching state: large numbers of immature *M. africana* were once again

recorded on this occasion, along with small populations of *P. stuhlmanni*.

Shifts in zooplankton community structure, especially the opportunistic dominance of *Oikopleura dioica* under closed-mouth conditions, emphasize the complexity and the erratic nature of the system in response to environmental variability. The unpredictable and extreme changes recorded in the present study concur with those reported by Grindley & Heydorn (1970), where blooms of spiders, midges or dinoflagellates signalled major environmental change. The only major difference between the 2 studies was the types of organisms that flourished. In spite of severe environmental perturbations, the St. Lucia Estuary has been reported as being extremely resilient in the past (Begg 1978, Taylor 2006), but it is now critical to monitor the extent and the time scale of its recovery from the present drought-induced crisis, once a new wet cycle sets in.

Acknowledgements. Our sincere gratitude to the iSimangaliso Wetland Park Authority and the management and staff of Ezemvelo KZN Wildlife for their continuous support throughout this study. Special thanks to R. Taylor, C. Fox and A. Myeza. S. Haripurshad, G. Kruger and N. Miranda are gratefully acknowledged for their help in the field. Funding for this study was provided by the National Research Foundation (NRF), Marine and Coastal Management (MCM) and WWF.

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Editorial responsibility: Otto Kinne, Oldendorf/Luhe, Germany

*Submitted: June 2, 2009; Accepted: October 5, 2009
Proofs received from author(s): January 18, 2010*