Impact of a flood event on the zooplankton of an estuarine lake

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\textbf{ABSTRACT}

Shallow coastal lakes are prone to large fluctuations in physico-chemical variables such as salinity and turbidity. This is now escalating in response to global change. A flood event in March 2014 resulted in a silt plume spreading through part of Lake St Lucia (South Africa). To determine the impact of this event on zooplankton, the Narrows region of St Lucia was sampled on a monthly basis from March to September 2014. For comparative purposes, data from samples collected prior to the flood event were included in the analyses. Analysis of similarity (ANOSIM) revealed dissimilarities in zooplankton community structure among the sampling occasions. The March 2014–May 2014 period was characterized by the highest abundance of freshwater species. Conversely, the abundance of the resident St Lucia copepods \textit{Acartiella natalensis} and \textit{Oithona brevicornis} was lowest during this time, and highest in September 2014. The other dominant copepod \textit{Pseudodiaptomus stuhlmanni} prevailed in March 2014, but declined markedly in April. As of September 2014, \textit{P. stuhlmanni} had yet to regain its pre-flood densities. The BIOENV procedure, which relates biological and environmental data, revealed that turbidity, salinity and dissolved oxygen were responsible for the observed changes in zooplankton community structure during the study period. Careful management of turbidity and salinity is stressed, as both factors are major drivers of the biota of St Lucia and similar systems worldwide.

\textbf{Introduction}

The dynamic nature of coastal, estuarine lakes ensures that only species exhibiting a wide tolerance of various drivers are able to flourish (Elliot & Quintino 2007). However, anthropogenic activities exacerbate the situation and may result in altered species assemblages (Vitousek et al. 1997; Elliott & Quintino 2007). Lake St Lucia is the largest estuarine lake in Africa and forms an important part of the iSimangaliso Wetland Park, a World Heritage Site (Bate and Taylor 2008). St Lucia is known to experience cyclical wet and dry phases, which may last up to 10 years at a time (Bate & Taylor 2008). Six rivers feed into St Lucia, namely, the Mpati, Nyalazi, Hluhluwe, Mzinene, Mkhuze and Mfolozi (Whitfield & Taylor 2009). The Mfolozi mouth was permanently separated in 1952 (Cyrus et al. 2011; Whitfield et al. 2013). This, and freshwater abstraction in the other rivers that discharge into St Lucia, has led to an increased frequency, intensity and duration of the dry spells, which are characterized by low water levels and hypersalinity (Taylor 1991). The diversity of several important taxonomical groups within the system has been substantially reduced due to the harsh environmental conditions as well as the inadequate connectivity with the Mfolozi and the Indian Ocean (Forbes & Cyrus 1991; Mann & Pradervand 2007; Vivier & Cyrus 2009).

Early attempts at alleviating the low freshwater input in St Lucia included excavation of a narrow back channel in the late 1960s (Taylor 2013), which connects the Mfolozi River to the Narrows region of Lake St Lucia (Figure 1). There are currently other measures being taken to increase water inflow to St
Lucia. A beach spillway connecting St Lucia to the Mfolozi River became operational in 2012 (Whitfield et al. 2013) and allowed for the flux of both fresh water (from the Mfolozi) and sea water (when the Indian Ocean connection was maintained) into Lake St Lucia. Although a major step towards ecosystem restoration, the Mfolozi flows are often characterized by a high suspended sediment load during the rainy season. In March 2014, intense precipitation (∼210 mm rainfall) in northern KwaZulu-Natal region resulted in a small flood in the catchments of St Lucia, as sediment-laden water flowed from the Mfolozi as well as from the Mpate, a smaller freshwater source. Following this, a silt plume began to spread throughout the Narrows region of St Lucia. The crucial role of zooplankton in the energy transfer of aquatic food webs, combined with their quick generational turnover rate, make them important predictors of ecosystem health (Hays et al. 2005; Guo et al. 2012). A study was therefore undertaken with the aim of determining the effects of this flood event on the zooplankton of the Narrows region in St Lucia.

**Materials and methods**

**Sample collection**

Sampling was conducted at the Narrows region of Lake St Lucia (Figure 1). This site was chosen as the silt-laden water discharged from the back-channel at this point. Monthly sampling events were undertaken from March until September 2014. Additionally, zooplankton samples taken at the Narrows in May, July and November 2013 were included for pre-flood comparisons. These were chosen because they were the only pre-flood samples collected using the same sampling method as in the present study. Zooplankton, phytoplankton and microphytobenthos samples together with physico-chemical data were collected on each sampling occasion.

**Physico-chemical parameters**

Physico-chemical water quality measurements were taken with a YSI 6600-V2 water quality logger, fitted with temperature (°C), depth (m), turbidity (nephelometric turbidity units, NTUs), dissolved oxygen (mg l⁻¹), and salinity probes. Rainfall data were obtained from the Ezemvelo KwaZulu-Natal Wildlife conservation authority.

**Micro-algae, total suspended solids and particulate organic matter**

Microphytobenthos (MPB) cores (2 cm internal diameter, 1 cm depth) were collected and immediately transferred to 100 ml polyethylene bottles containing 30 ml 90% acetone for 48 h of cold–dark pigment (chlorophyll a and phaeopigment) extraction. Water samples were collected in order to measure phytoplankton biomass. The samples were kept in ice during transportation to the laboratory (∼3 h).

In the laboratory, 100 ml water subsamples were filtered through Whatman GF/F filters, which were then placed in 6 ml of 90% acetone for 48 h of cold–dark pigment (chlorophyll a and phaeopigment) extraction. Phytoplankton (mg pigm m⁻³) and MPB (mg pigm m⁻³) biomass were determined fluorometrically, using a Turner Designs 10-AU non-acidification system (Nozais et al. 2001). Additionally, the concentration of total suspended solids (TSS, mg l⁻¹) and particulate organic matter (POM, %) were measured. This was done by filtering 100 ml of estuarine water through pre-combusted (6 h, 420°C) Whatman GF/F filters. Once dried (48 h, 60°C), the filters were weighed to 0.1 mg using a Shimadzu AUW220D Uni Bloc balance, combusted in a muffle furnace (6 h,
420°C) and then re-weighed so that TSS and POM could be calculated (Carrasco et al. 2007).

Zooplankton

Duplicate daytime zooplankton tows were taken from a boat in the deep regions of the Narrows using a 100 μm mesh D-net mounted on a hyperbenthic sled (radius = 18.5 cm). The net was mounted on the sled so that it was held 7.5 cm above the sediment surface. The area of the D-net mouth was multiplied by the distance towed (27 m) to obtain the volume of water filtered (≈ 1.45 m³). The samples collected in the cod end were each immediately emptied into a 500 ml polyethylene bottle containing 5% phloxine-stained formalin.

In the laboratory, each sample was transferred to a 1–5 l solution, depending on the density of the zooplankton. The sample was then stirred to ensure a homogenous suspension of all the organisms, and a 10 ml plastic vial attached to a metal rod was used to withdraw six subsamples from mid-depth (Perissinotto & Woolridge 1989; Carrasco et al. 2010). Zooplankton within the subsamples were counted and identified under a Kyowa SDZ dissecting microscope (40×), using identification guides by Gibbons (1997), Grindley (1963) and Seaman et al. (1999) as well as by submitting specimens for analysis to experts of the relevant groups. Zooplankton density (ind m⁻³) was then calculated.

To estimate the dry biomass of each sample, a Folsom plankton splitter was used to split each sample into two equal portions. One of these was filtered onto pre-weighed Whatman GF/F filters and oven-dried (24 h, 60°C). Biomass was estimated as the total dry weight (mg DW m⁻³) of each sample.

Statistical analyses

Univariate statistical analyses were conducted with SPSS version 22 for Windows. The assumptions of normality and even distribution of residuals were tested with the Kolmogorov–Smirnov one-sample test and the Levene’s test, respectively. Data which did not meet the assumptions were log₁₀(x + 1) transformed, and the assumptions tested again, to ensure that they were met before performing the parametric test. One-way ANOVA was conducted to test for temporal differences in total zooplankton abundance, biomass and species richness. Where differences were found, Tukey post-hoc tests were applied to determine the source of the differences. Spearman’s Rank correlation analysis was used to test for a relationship between the environmental variables and the community parameters (total abundance, biomass and species richness).

Multivariate analyses were conducted using the PRIMER package version 6.0 (Clarke & Warwick 2001). Abundance data were fourth-root transformed in order to reduce the effect of the most abundant species. Analysis of similarity (ANOSIM) was conducted to check for temporal similarities in zooplankton community structure. Where dissimilarities were found, the similarity percentage (SIMPER) routine determined the magnitude of the dissimilarities between the sampling dates, and the different species’ contribution to the community structure on the different sampling occasions. A Bray–Curtis similarity matrix was then calculated for the different sampling periods, and cluster analysis (group average) was used to visually assess temporal differences in zooplankton community structure. The BIOENV Harmonic Spearman Correlation function was used to relate environmental variables to the zooplankton assemblages.

Results

Physico-chemical parameters

Water temperature ranged from 16.4 to 26.3°C throughout the study period (Figure 2). Salinity was highest in November 2013 (21.6) and declined dramatically following the flood, with the lowest value (0.5) recorded in May 2014. Dissolved oxygen content was lowest in April 2014, at 5.23 mg l⁻¹ and was relatively constant throughout the rest of the study duration, ranging from 5.2 to 6.8 mg l⁻¹. Rainfall was highest in March 2014 (209.6 mm), and the water column in the Narrows was 2 m deep during the March–May 2014 period. The lowest recorded turbidity was 3.4 NTU in May 2013. Turbidity reached its peak following the flood, with 962 and 308 NTU being recorded in March and April 2014, respectively (Figure 2).

Microalgae, total suspended solids and particulate organic matter

Highest phytoplankton biomass (22.9 mg m⁻³) and lowest MPB biomass (1.45 mg m⁻²) were recorded during March 2014, following the flood. The highest TSS concentration (426 mg l⁻¹) was also recorded after the flood. Percentage POM content was highest in May 2013 (41%, Figure 3). The lowest TSS (33 mg l⁻¹) and POM (13.7%) values were recorded in May and July 2013, respectively (Figure 3).
Zooplankton abundance, biomass and species richness

The total recorded zooplankton abundance ranged from $6.68 \times 10^4$ to $3.33 \times 10^5$ ind m$^{-3}$ throughout the study period. The lowest zooplankton densities coincided with the flood event in March 2014 (Figure 4). Zooplankton abundance showed significant differences between sampling occasions (ANOVA, $F_{9,10} = 28.8, p < 0.05$) with September 2014 values being significantly higher than those recorded on all other occasions (Tukey post-hoc test $p < 0.05$). In addition, the zooplankton abundance recorded during the March–May 2014 period was significantly different from those of all subsequent sampling occasions (Tukey post-hoc test, $p < 0.05$).

Total zooplankton biomass ranged from 50.7 to 239 mg DW m$^{-3}$ (Figure 4). Biomass varied significantly between sampling occasions (ANOVA, $F_{9,10} = 179, p < 0.05$). Similar to abundance, the month with the highest biomass was September 2014, and the difference was significant (Tukey post-hoc test, $p < 0.05$). The pre-flood months also exhibited a higher biomass than the March–August 2014 period.

Species richness was greatest in March 2014, with 18 taxa recorded on this sampling occasion (Table SI, supplementary material). However, with the exception of the copepod *Pseudodiaptomus stuhlmanni* (Poppe & Mrázek, 1895) and the cladoceran *Moina cf. micrura* Kurz, 1874, all other taxa occurred in very low numbers, thus explaining the low total abundance and biomass observed during this month. The lowest species richness was recorded during July 2013 (Figure 4). There was a significant difference in species richness between sampling occasions (ANOVA, $F_{9,10} = 30.9, p < 0.05$). The species richness recorded during the 2013 months did not significantly differ from one another (Tukey post-hoc test, $p > 0.05$), but differed

Figure 2. Physico-chemical parameters measured in the Narrows region during each sampling occasion. The arrow indicates the timing of the flood event.
from March, May, June and August 2014 (Tukey post-hoc test, \( p < 0.05 \)).

Correlation analyses revealed that neither total zooplankton abundance nor biomass was significantly correlated with any of the environmental parameters \( (p > 0.05) \). Species richness was significantly correlated only with salinity \( (r = 0.77; p < 0.01) \).

**Zooplankton community structure**

The abundance of the copepod *Pseudodiaptomus stuhlmanni* was highest in May 2013 \( (4.59 \times 10^4 \text{ ind m}^{-3}) \). This species’ lowest recorded abundance \( (1177 \text{ ind m}^{-3}) \) and contribution towards total abundance \( (< 1\%) \) were recorded during April 2014. *Pseudodiaptomus stuhlmanni* underwent a drastic population decline between March and April 2014, with about a third of the March abundance remaining by April. This was not unique to this particular species, as the abundance of the other dominant St Lucia copepods *Acartiella natalensis* (Connell & Grindley, 1974) and *Oithona brevicornis* Giesbrecht, 1891 also decreased markedly from March to April 2014 (Figure 5).

*Acartiella natalensis* was present on all sampling occasions, with the exception of April 2014. The relative abundance of this species was high on the sampling occasions preceding the flood event (i.e. May, July and November 2013). Following the flood event and silt plume, however, *A. natalensis* densities remained relatively low, until they peaked at \( 2.71 \times 10^4 \text{ ind m}^{-3} \) in September 2014 (Figure 5). The cyclopoid *O. brevicornis* occurred at densities of \( 3.12 \times 10^4 \text{ ind.m}^{-3} \) in November 2013 and was absent from the system in March and April 2014. Similar to *A. natalensis*, *O. brevicornis* peaked in September 2014, at \( 2.3 \times 10^5 \text{ ind.m}^{-3} \) (Figure 5).

Only one exclusively freshwater species was recorded prior to the flood event: the cladoceran *Moina* cf. *micrura* in July 2013 \( (74 \text{ ind m}^{-3}) \) and November 2013 \( (172 \text{ ind m}^{-3}) \). All other freshwater species were recorded for the first time in March 2014, following the flood. These include the cladocerans *Ceriodaphnia* sp. and *Bosmina* sp. In total, freshwater species accounted for 25.8% of all species recorded in March 2014, compared to \(< 1\%\) during the three pre-flood months. By April 2014, concurrent with the decline of the estuarine taxa, the abundance of the freshwater taxa had increased markedly, accounting for 95% of the total abundance. *Moina* cf. *micrura* was particularly...
prevalent, accounting for 65.9% of the total abundance recorded during this month (Figure 5).

ANOSIM revealed dissimilarities in zooplankton community structure among the sampling dates ($R = 0.92$, $p < 0.01$). Cluster analysis (Figure 6) showed that the March–May 2014 period was different from the rest of the sampling occasions. The March–May 2014 period was thereafter termed ‘disturbed’ and the rest of the sampling occasions ‘undisturbed’ (Figure 5). SIMPER analysis revealed five taxa that accounted for $\sim 90\%$ of the abundance in the undisturbed period. These were copepod nauplii, P. stuhlmanni, A. natalensis, O. brevicornis and the ostracod Cyprideis torosa (Jones, 1850). During the disturbed period, nine taxa accounted for $\sim 90\%$ of the abundance. The most dominant were M. cf. micrura, Ceriodaphnia sp., copepod nauplii and P. stuhlmanni (Figure 5).

The species generally responsible for the dissimilarity between the 2013 pre-disturbance months and June–August 2014 were A. natalensis, O. brevicornis and P. stuhlmanni. All three copepods were more abundant during the pre- compared to post-disturbance months. The BIOENV procedure identified turbidity, salinity and dissolved oxygen as the main environmental factors affecting the zooplankton communities ($R = 0.72$).

**Discussion**

At any given time, natural systems are impacted by an array of factors, which usually act in synergy to shape the prevailing community structure. Salinity and temperature are widely regarded as the dominant ‘ecological master factors’ driving estuarine biota (Kinne 1971; Dorgelo 1976). Anthropogenic activities have, however, acted to influence the effect of these variables, as well as increase the importance of others, such as oxygen content and turbidity (Vitousek et al. 1997; Donohue & Molinos 2009). In this study, salinity, turbidity and dissolved oxygen emerged as statistically significant drivers of the zooplankton assemblage at the Narrows region of Lake St Lucia.

Low salinity prevailed for longer (March–May 2014) than high turbidity (March–April 2014). The low-salinity regime was characterized by a unique zooplankton community, as it was during this time that the freshwater cladocerans Moina cf. micrura and Ceriodaphnia sp. were dominant while the St Lucia estuarine resident copepods Oithona brevicornis and Acartiella natalensis were virtually absent.

Oithona brevicornis has been recorded in St Lucia from as early as the 1970s (Grindley 1976). This cyclopoid mainly inhabits estuarine and marine environments (Wooldridge 1977; Boxshall et al. 2007) and Jerling et al. (2010a) found its highest abundance at St Lucia to coincide with the open-mouth phase. The distribution of O. brevicornis was also reported by
Grindley (1976, 1982) to be restricted to sites with salinities of five or above. Therefore, the fresh conditions and competitive exclusion by the freshwater cladocerans may have been primarily responsible for the decline of this species in March 2014.

Acartiella natalensis, however, is able to withstand low salinity (fresh to ~ > 70; Grindley 1982), and is a member of the Mfolozi River zooplankton community (Jerling et al. 2010b). The freshwater conditions in March 2014 were therefore not expected to negatively affect this species. It is possible that despite its euryhalinity, A. natalensis has a preference for higher salinities. Carrasco et al. (2013) investigated the turbidity tolerance of this species, and found that its ingestion and survival were significantly reduced by turbidity in the range 1000–2500 NTU. Apart from high turbidity and low salinity, competition imposed by the cladocerans may have contributed towards the population decline of this species.

In contrast to A. natalensis, Pseudodiaptomus stuhlmanni was present in high densities in March 2014 following the flood event. This was in agreement with both this species' recorded salinity and turbidity tolerances (Grindley 1976, 1982; Jones et al. 2015). Pseudodiaptomus stuhlmanni is the numerically dominant calanoid in both St Lucia and Mfolozi (Grindley 1976, 1982; Carrasco et al. 2010; Jerling et al. 2010a, 2010b), and has been demonstrated through laboratory experiments to exhibit a relatively high tolerance to elevated turbidity (Jones et al. 2015), as well as to hypo- and hypersaline conditions (< 5 to > 70, Grindley 1982). Due to this wide salinity tolerance, both Grindley (1982) and Jerling et al. (2010a) have suggested that factors other than salinity preference may influence the distribution of this calanoid in St Lucia.

Pseudodiaptomus stuhlmanni is an important food item for fish within St Lucia and Mfolozi. Suspended sediments may obscure the field of view of visual predators, thus reducing their feeding success (Vinyard & O’Brien 1976; Gardner 1981; Maes et al. 1998). Therefore, it is possible that the high turbidity in March 2015 shielded P. stuhlmanni from predators. By April turbidity had decreased, and P. stuhlmanni abundance had declined threefold. This might have been due to both increased predation pressure and the physiological after-effects of being exposed to high turbidity, as Jones et al. (2015) recorded a time lag between the occurrence of sublethal effects (inhibition of feeding and respiration) and mortality. Further, P. stuhlmanni individuals collected during the March 2014 sampling event were found to be hosting epibiotic peritrich ciliates (Salome Jones 2014, personal observation). Epibionts use the exterior surface of other organisms as an attachment site (Bickel et al. 2012). The St Lucia epibionts were observed to attach almost exclusively to P. stuhlmanni, in spite of the availability of other zooplankton species. The relationship epibionts have with their hosts may range from commensal to parasitic (Weissman et al. 1993; Visse 2007; Chatterjee et al. 2013). It is therefore possible that the St Lucia epibionts contributed towards the subsequent population decline of P. stuhlmanni.

The freshwater cladocerans M. cf. micrura and Ceriodaphnia sp. were able to thrive during the time that P. stuhlmanni declined. Cladocerans are generally more sensitive to turbidity than copepods (Kirk & Gilbert 1990; Koenings et al. 1990). Therefore, it is unlikely that the high turbidity in March 2014 favoured these cladocerans over the St Lucia copepods. The three-month persistence of the cladocerans may be attributed to both the low salinity during this period and niche availability following the population decline of the St Lucia resident species.

The high numbers of copepod nauplii observed from May 2014 onwards are an indication that the copepods can regain their characteristically high densities, but only after several months following the flood event. Oithona brevicornis attained its peak density in the last two months (August and September 2014) of this study. Acartiella natalensis also regained its pre-flood densities in September 2014. However, although P. stuhlmanni has been among the top four dominant species since June 2014, this species had, as of September 2014, not yet attained its pre-disturbance abundance. The quicker recovery of O. brevicornis and A. natalensis may also be attributable to their smaller body size (~ 400 and 650 µm, respectively) at maturity, which might mean that they have a quicker regeneration time than the larger (~ 1 mm) P. stuhlmanni. Species belonging to Oithonidae are known for their remarkably high reproductive output and low metabolic demands (Turner 2004). The decline of the cladocerans in June 2014 may have also resulted in more food availability for the St Lucia copepods.

The March–May 2014 period was characterized by the lowest concentration of dissolved oxygen, which might explain the BIOENV inclusion of this factor as a determinant of the community structure during this study. Sediments have a high oxygen demand (Sklar & Browder 1998; Donohue & Molinos 2009) and have been found to sequester as much as 16 times their volume of aerated water (Bruton 1985). Therefore, high turbidity, such as that experienced at St Lucia during the March–April 2014 period, is generally accompanied by decreased oxygen content
Further, there was a generally high concentration of particulate organic matter in the Narrows in the four months following the flood event. Large amounts of organic matter may result in a high ratio of water column community respiration: available dissolved oxygen content. Studies of the effect of turbidity on the respiration of *P. stuhlmanni* have revealed that this species requires more oxygen at high versus low turbidity (Jones et al. 2015). Therefore, turbidity per se results in low dissolved oxygen availability, while simultaneously increasing the oxygen requirements of this species.

The importance of the Mfolozi River as a source of freshwater for Lake St Lucia is well documented in the literature (Taylor 2013; Cyrus et al. 2010, 2011; Carrasco & Perissinotto 2011; Whitfield et al. 2013). However, in the current compromised state of this river, the freshwater aid it provides during the dry season is to some degree offset by the sediment it discharges into St Lucia during heavy rainfall events. The flood event and resulting silt plume, although temporary (~6 weeks), has had a long-lasting effect on the community structure of the zooplankton of the Narrows region. As this was an observational study, it is not possible to positively isolate any one variable as the driver of the St Lucia zooplankton during this study. However, at St Lucia, salinity and turbidity are arguably the two most important factors influencing biota; most management interventions since the onset of the agricultural activities at the Mfolozi River have been centred on maintaining both these factors at an ecologically healthy level within the system (Whitfield & Taylor 2009; Whitfield et al., 2013).

Given the role of zooplankton in linking primary to secondary producers, the effects of salinity and turbidity, in synergy and in isolation, on the zooplankton of St Lucia have implications for other functional groups. *Acartiella natalensis* and *P. stuhlmanni* are known to be staple food items of several planktivorous fish at St Lucia, including *Hilsea keele* (Cuvier, 1829), *Thryssa vitirostris* (Gilchrist & Thompson, 1908), *Gilchristella aestuaria* (Gilchrist, 1913), and *Ambassis ambassis* (Lacepède, 1802) (Grindley 1982; Peer et al. 2013; Dyer et al. 2015). Gut content analysis of benthic feeders suggests that the diel migration of *P. stuhlmanni* also makes it an important component of the benthic food web, as remains of this species have been found in the gut of the prawn *Penaeus indicus* (H. Milne Edwards, 1837), as well as being dominant in the stomach contents of the benthic fish *Leiognathus equulus* (Forskål, 1775) at both St Lucia and Mfolozi (Grindley 1982; Nhleko et al. 2012). Attempts should therefore be made to understand the consequence of all future management interventions on the zooplankton community of this and similar estuarine lakes worldwide.

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**References**

Appleby J, Scarratt DJ. 1989. Physical effects of suspended solids on marine and estuarine fish and shellfish with special reference to ocean dumping: a literature review. Canadian Technical Report of Fisheries and Aquatic Sciences 1681:1–33.

Arruda JA, Marzolf GR, Faulk RT. 1983. The role of suspended sediments in the nutrition of zooplankton in turbid reservoirs. Ecology 64(5):1225–35.

Bate G, Taylor R. 2008. Sediment salt-load in the St Lucia Estuary during the severe drought of 2002–2006. Environmental Geology 55(5):1089–98.

Bickel SL, Tang KW, Grossart H-P. 2012. Ciliate epibionts associated with crustacean zooplankton in German lakes: distribution, motility, and bacterivory. Frontiers in Microbiology 3(243):1–11.

Boxshall G, Boero F, Olenin S. 2007. Establishment of *Oithona brevicornis* Giesbrecht, 1892 (Copepoda: Cyclopoida) in the Black Sea. Aquatic Invasions 2(4):407–10.

Bruton M. 1985. The effects of suspensoids on fish. Hydrobiologia 125(1):221–41.

Carrasco NK, Perissinotto R. 2011. Temperature and salinity tolerance of *Mesopodopsis africana* in the freshwater-deprived St. Lucia Estuary, South Africa. Journal of Experimental Marine Biology and Ecology 399(1):93–100.

Carrasco NK, Perissinotto R, Miranda NAF. 2007. Effects of silt loading on the feeding and mortality of the mysid *Mesopodopsis africana* in the St. Lucia Estuary, South Africa. Journal of Experimental Marine Biology and Ecology 352(1):152–64.

Carrasco NK, Perissinotto R, Pillay D. 2010. Zooplankton of the St. Lucia Estuary during the current drought cycle: a comparison between open-and closed-mouth conditions. Marine Ecology Progress Series 399:157–71.
Carrasco NK, Perissinotto R, Jones S. 2013. Turbidity effects on feeding and mortality of the copepod Acartiella natalensis (Connell and Grindley, 1974) in the St Lucia Estuary, South Africa. Journal of Experimental Marine Biology and Ecology 446:45–51.

Chatterjee T, Kotov AA, Fernández-Leborans G. 2013. A checklist of epibiotic ciliates (Peritrichia and Suctoria) on the cladoceran crustaceans. Biologia 68(3):439–47.

Clarke KR, Warwick RM. 2001. Change in Marine Communities: An Approach to Statistical Analysis and Interpretation. PRIMER-E, 2nd edition. Plymouth: Plymouth Marine Laboratory. 172 pages.

Cyrus DP, Vivier L, Owen RK, Jerling HL. 2010. Ecological status and role of the Mfolozi–Msunduzi estuarine system within the iSimangaliso Wetland Park, a World Heritage Site on the south-east coast of South Africa. African Journal of Aquatic Science 35(2):109–16.

Cyrus D, Jerling H, MacKay F, Vivier L. 2011. Lake St Lucia, Africa’s largest estuarine lake in crisis: Combined effects of mouth closure, low levels and hypersalinity. South African Journal of Science 107(3-4):1–13.

Donohue I, Molinos JG. 2009. Impacts of increased sediment loads on the ecology of the lakes. Biological Reviews 84(4):517–31.

Dorigo J. 1976. Salt tolerance in Crustacea and the influence of temperature upon it. Biological Reviews 51(3):255–90.

Dyer DC, Perissinotto R, Carrasco NK. 2015. Temporal and spatial dietary dynamics of the longspine glassy (Ambassis ambassid) in the St Lucia Estuary, iSimangaliso Wetland Park. Water SA 41(1):91–104.

Elliott M, Quintino V. 2007. The estuarine quality paradox, environmental homeostasis and the difficulty of detecting anthropogenic stress in naturally stressed areas. Marine Pollution Bulletin 54(6):640–45.

Forbes AT, Cyrus DP. 1991. Recruitment and origin of penaeid prawn post-larvae in two south-east African estuaries. Estuarine, Coastal and Shelf Science 33(3):281–89.

Gardner MB. 1981. Mechanisms of size selectivity by planktivorous fish: a test of hypotheses. Ecology 62:571–78.

Gibbons MJ. 1997. An Introduction to the Zooplankton of the Benguela Current Region. Cape Town: Zoology Department, University of the Western Cape. 51 pages.

Grindley JR. 1963. The Pseudodiaptomidae (Copepoda: Calanoida) of Southern African waters, including a new species, Pseudodiaptomus chartari. Annals of the South African Museum 46(15):373–91.

Grindley JR. 1976. Zooplankton of St Lucia. In: Heydorn AEF, editor. St Lucia Scientific Advisory Council Workshop Meeting – Charter’s Creek. Paper 12. Pietermaritzburg: Natal Parks Board. 8 pages.

Grindley JR. 1982. The role of zooplankton in the St Lucia estuary system. In: Taylor RH, editor. St Lucia Research Review 256. Pietermaritzburg, South Africa: Natal Sharks Board, p 88–107.

Guo Z, Liu S, Hu S, Li T, Huang Y, Liu G, et al. 2012. Prevalent ciliate symbiosis on copepods: high genetic diversity and wide distribution detected using small subunit ribosomal RNA gene. PLoS One 7(9):e44847. 9 pages.

Hays GC, Richardson AJ, Robinson C. 2005. Climate change and marine plankton. Trends in Ecology and Evolution 20(6):337–44.

Jerling HL, Vivier L, Cyrus DP. 2010a. Response of the mesozooplankton community of the St Lucia estuary, South Africa, to a mouth-opening event during an extended drought. Estuarine, Coastal and Shelf Science 86(4):543–52.

Jerling HL, Vivier L, Cyrus D, Owen R. 2010b. Initial characterisation of the mesozooplankton community of the Mfolozi–Msunduzi estuarine system, KwaZulu-Natal, South Africa, during a low-flow period. African Journal of Aquatic Science 35(2):117–22.

Jones S, Carrasco NK, Perissinotto R. 2015. Turbidity effects on the feeding, respiration, and mortality rate of the copepod Pseudodiaptomus stuhlmanni in the St Lucia Estuary, South Africa. Journal of Experimental Marine Biology and Ecology 469:63–68.

Kinne O. 1971. Salinity: 3. Animals: 1. Invertebrates. In: Kinne O, editor. Marine Ecology: A Comprehensive, Integrated Treatise on Life in Oceans and Coastal Waters: 1(2). London: Wiley, p 821–995.

Kirk KL, Gilbert JJ. 1990. Suspended clay and the population dynamics of planktonic rotifers and cladocerans. Ecology 71(5):1741–55.

Koenings J, Burkett RD, Edmundson JM. 1990. The exclusion of limnetic Cladocera from turbid glacier-meltwater lakes. Ecology 71(1):57–67.

Maes J, Taillieu A, Van Damme PA, Cottenie K, Ollevier F. 1998. Seasonal patterns in the fish and crustacean community of a turbid temperate estuary (Zeeschelde Estuary, Belgium). Estuarine, Coastal and Shelf Science 47(2):143–51.

Mann BQ, Pradervand P. 2007. Declining catch per unit effort of an estuarine-dependent fish, Rhabdosargus sarba (Teleostei: Sparidae), in the marine environment following closure of the St Lucia Estuarine System, South Africa. African Journal of Aquatic Science 32(2):133–38.

Nhleko JBB, Cyrus DP, Vivier L. 2012. Diet of the demersal feeding Leioagnathus equula in the Mfolozi–Msunduzi estuarine system, South Africa, in response to an impoverished macrobenthic invertebrate community. African Journal of Aquatic Science 37(2):175–82.

Nozais C, Perissinotto R, Mundree S. 2001. Annual cycle of microalgal biomass in a South African temporarily-open estuary: nutrient versus light limitation. Marine Ecology Progress Series 223:39–48.

Peer N, Carrasco NK, Perissinotto R, du Plooy SJ. 2013. Flood effects on trophic linkages of selected fish species in the littoral zone of the St Lucia estuarine system, South Africa. African Journal of Aquatic Science 38(3):341–47.

Perissinotto R, Wooldridge T. 1989. Short-term thermal effects of a power-generating plant on zooplankton in the Swartkops Estuary, South Africa. Marine Ecology 10(3):205–19.

Seaman MT, Kok DJ, Watson M. 1999. Chapter 4: Cladocera. In: Day JA, Stewart BA, de Moor IJ, Louw AE, editors. Guides to the Freshwater Invertebrates of Southern Africa: Crustacea. WRC Report No. TT 121/00, South Africa, p 81–109.

Sklar FH, Browder JA. 1998. Coastal environmental impacts brought about by alterations to freshwater flow in the Gulf of Mexico. Environmental Management 22(4):547–62.

Taylor RH. 1991. The Greater St Lucia Wetland Park. Cape Town: Parke-Davis. 48 pages.

Taylor RH. 2013. Chapter 2: Management history. In: Perissinotto R, Stretch D, Taylor R, editors. Ecology and Conservation of
Estuarine Ecosystems: Lake St Lucia as a Global Model. New York: Cambridge University Press, p 21–45.

Turner JT. 2004. The importance of small planktonic copepods and their roles in pelagic marine food webs. Zoological Studies 43(2):255–66.

Vinyard GL, O’Brien WJ. 1976. Effects of light and turbidity on the reactive distance of bluegill (Lepomis macrochirus). Canadian Journal of Fishery and Aquatic Science 33(12):2845–49.

Visse M. 2007. Detrimental effect of peritrich ciliates (Epistylis sp.) as epibionts on the survival of the copepod Acartia bifilosa. Proceedings of the Estonian Academy of Science, Biology, Ecology 56(3):173–78.

Vitousek PM, Aber JD, Howarth RW, Likens GE, Matson PA, Schindler DW, et al. 1997. Human alteration of the global nitrogen cycle: sources and consequences. Ecological Applications 7(3):737–50.

Vivier L, Cyrus DP. 2009. Alternative nursery habitat for estuarine associated marine fish during prolonged closure of the St Lucia estuary, South Africa. Estuarine, Coastal and Shelf Science 85(1):118–25.

Weissman P, Lonsdale DJ, Yen J. 1993. The effect of peritrich ciliates on the production of Acartia hudsonica in Long Island Sound. Limnology and Oceanography 38(3):613–22.

Whitfield AK, Taylor RH. 2009. A review of the importance of freshwater inflow to the future conservation of Lake St Lucia. Aquatic Conservation: Marine and Freshwater Ecosystems 19(7):838–48.

Whitfield AK, Bate GC, Forbes T, Taylor RH. 2013. Relinkage of the Mfolozi River to the St. Lucia estuarine system – urgent imperative for the long-term management of a Ramsar and World Heritage Site. Aquatic Ecosystem Health and Management 16(1):104–10.

Wooldridge T. 1977. The zooplankton of Mgazana, a mangrove estuary in Transkei, southern Africa. Zoologica Africana 12(2):307–21.