

UNIVERSITY OF KWAZULU-NATAL

Impact of turbidity on *Pseudodiaptomus stuhlmanni*, a dominant copepod in Lake St Lucia,
iSimangaliso Wetland Park

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Abstract

Although the St Lucia Estuary is a Ramsar Wetland of International Importance, it has historically been subjected to human-accelerated ecological stressors. One of these is high turbidity resulting from excessive sediment inputs. Laboratory-based studies have revealed a negative turbidity effect on the feeding and mortality rate of two dominant zooplankton species, the mysid *Mesopodopsis africana* and the calanoid copepod *Acartiella natalensis*. The first aim of this study was to determine the effect of turbidity on the feeding, respiration, and mortality rate of another important calanoid, *Pseudodiaptomus stuhlmanni*. Although this species was negatively affected by high turbidity, it was substantially more tolerant than *M. africana* and *A. natalensis*. The second aim was to test the field response of the dominant St Lucia zooplankton to a silt plume-causing flood event that occurred in March 2014. As *M. africana* was not abundant in the system prior to this event, attention was paid to the copepods. The field response of *A. natalensis* and *P. stuhlmanni* were in good agreement with the findings from the laboratory-based experiments. The population of *A. natalensis* underwent an immediate, and sharp decline, whereas that of *P. stuhlmanni* only declined in April 2014, after a month of surviving in highly turbid waters. However, *P. stuhlmanni* also took longer to recover, but this may be attributed to the attachment of parasitic epibiotic ciliates to this species. Therefore, although to different degrees, turbidity negatively impacted the dominant St Lucia zooplankton species. Through its observed positive correlation with the parasitic ciliates, turbidity further suppressed the abundance of the most turbid-water tolerant species, *P. stuhlmanni*. The importance of carefully managing sediment loading in St Lucia is stressed, as the effect of turbidity on zooplankton likely has food web-wide consequences.

PREFACE

The fieldwork described in this MSc dissertation was conducted in the iSimangaliso Wetland Park in KwaZulu-Natal, South Africa. Laboratory analyses and experimental work were carried out at the School of Life Sciences, University of KwaZulu-Natal, Westville Campus, from February 2014 to November October 2014, under the supervision of Prof. Renzo Perissinotto, Dr Nicola Carrasco and Dr Andre Vosloo.

These studies represent original work by the author and have not otherwise been submitted in any form for any degree or diploma to any tertiary institution. Where work of others has been used, this has been duly acknowledged in the text.

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Details of contribution to publications that form part and/or include research presented in this thesis (include publications in preparation, submitted, in press and published and give details of the contributions of each author to the experimental work and writing of each publication).

Publication 1

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Author Contributions:


Renzo Perissinotto conceived and designed the study with Salome Jones and Nicola K. Carrasco. Salome Jones carried out sample collections, laboratory processing, statistical analysis and wrote the manuscript. Renzo Perissinotto, Nicola K. Carrasco and Andre Vosloo contributed valuable comments to the manuscript.

Publication 2

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Author Contributions:

Salome Jones conceived and designed the study with Nicola K. Carrasco, Andre Vosloo and Renzo Perissinotto. Salome Jones carried out sample collections, laboratory processing, statistical analysis and wrote the manuscript. Nicola K. Carrasco, Andre Vosloo and Renzo Perissinotto contributed valuable comments to the manuscript.

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Author contribution: Salome Jones conceived and designed the study with Nicola K. Carrasco. Salome Jones performed the laboratory work, developed the presentation and presented the final product. Nicola K. Carrasco, Renzo Perissinotto and Andre Vosloo assisted in developing the presentation.

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Author contribution: Renzo Perissinotto conceived and designed the study with Salome Jones and Nicola K. Carrasco. Salome Jones performed the laboratory work, developed the presentation and presented the final product. Andre Vosloo and Nicola K. Carrasco assisted in developing the presentation.

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GENERAL INTRODUCTION

Rivers have suffered from intense and diverse stressors since the onset of the Anthropocene, primarily due to their inland location and accessibility to humans (Copeland, 1966; Eyre, 1998). The most common of these activities have altered the global land-to-ocean sediment flux (Walling, 2006). For instance, sediment trapping by dams has caused a reduction in the sediment load transferred to some estuaries and the ocean (Hay, 1994). Conversely, mining and agricultural activities have increased the rate of soil loss and sediment yields within many river catchments globally, and are credited as the most important causes of increased sediment loading in aquatic systems (Abernethy, 1990; Douglas, 1996; Walling, 2006).

The St Lucia Estuary is Africa's largest estuarine lake system and a Ramsar Wetland of International Importance (Fielding et al., 1991; Cyrus and Vivier, 2006; Whitfield et al., 2013). Lake St Lucia is known to experience cyclical wet and dry phases, which may last up to 10 years at a time (Bate and Taylor, 2008 and references therein). The more severe dry spells result in drastically reduced water levels, hypersalinity, and consequently, low species diversity (Begg, 1978; Carrasco and Perissinotto, 2010). Six rivers feed into Lake St Lucia, *viz.* Mpate, Nyalazi, Hluhluwe, Mzinene, Mkuze River, and Mfolozi (Whitfield and Taylor, 2009).

The Mfolozi River was historically the most important contributor, and inflow from this river performed the vital function of reducing drought symptoms during dry phases (Carrasco and Perissinotto, 2011; Whitfield et al., 2013). However, in the 1930s, the area in the vicinity of this river became the focal point of expanding sugarcane plantations (Whitfield and Taylor, 2009; Taylor, 2013). Due to flooding of the plantations during high rainfall periods, a canal was excavated to channel water away from the agricultural area (Begg, 1978). The Mfolozi floodplains, which historically filtered suspended particles before they flowed into St Lucia, subsequently became less effective at performing this function (Carrasco et al., 2007; Carrasco and Perissinotto, 2010). High sediment loads washed into St Lucia, reducing the water column clarity, and also accelerating sedimentation rates (Lindsay et al., 1996; Whitfield and Taylor, 2009; Jerling et al., 2010a; Whitfield et al., 2013). This problem culminated in the decision to alleviate the inflow of sediment-laden Mfolozi water into St Lucia, by diverting the river mouth away from the estuary in 1952 (Whitfield and Taylor, 2009; Cyrus et al., 2011; Whitfield et al., 2013).

However, this intervention was implemented without a full understanding of its ecological consequences (Bate and Taylor, 2008). Following isolation from its main freshwater source, and the frequent formation of a sand berm on the sea side, the St Lucia Estuary became prone to prolonged dry spells, accompanied by high rates of desiccation and hypersalinity (Carrasco and Perissinotto, 2011; Cyrus et al., 2011; Whitfield et al., 2013). Isolation of this important estuary from both the sea and the Mfolozi River meant the functional loss of the St Lucia Estuary as a nursery area for many estuarine dependent species (Whitfield et al., 2013 and references therein). Due to the geographic separation of estuaries in the northern KwaZulu-Natal region (Bate and Taylor, 2008), there is no alternative estuary for the recruitment of such species. Ecological studies conducted within Lake St Lucia over the years have revealed that the diversity of several important taxonomical groups has been greatly reduced due to this isolation (Forbes and Cyrus, 1991; Mann and Pradervand, 2007; Vivier and Cyrus, 2009).

There have been many attempts to combat the problems of low water levels and hypersalinity in the St Lucia Estuary, by artificial breaching of the sand berm, and by creating links between St Lucia and the Mfolozi River. Many of these were successful only in the short term, or, in the case of artificial breaching, often further exacerbated the problem of hypersalinity (Whitfield et al., 2013). There are presently more measures being taken to re-establish the link between the St Lucia Estuary and the Mfolozi River. A beach spillway connecting the St Lucia Estuary and the Mfolozi River mouths to each other, and to the Indian Ocean, became operational in 2012 (Carrasco et al., 2013; Whitfield et al., 2013). Although it closes during periods of low rainfall, the beach spillway has been shown to aid the recruitment and migration of marine, freshwater, and estuarine species through the three water bodies (van Elden et al., 2014). A narrow back-channel constructed in the 1960s in the Narrows region of Lake St Lucia has also been partially successful in channelling freshwater into the estuary (Taylor, 2013). However, this back-channel also carries high volumes of sediment-laden water during heavy flow events. The silt load of the Mfolozi River is currently regarded as among the highest in South African estuaries (Lindsay et al. 1996, Nhleko et al. 2012), with turbidity levels regularly exceeding 1000 NTUs after major rainfall events (Carrasco et al. 2007, Nhleko et al. 2012). Therefore, although there is merit behind the decision to re-connect the St Lucia-Mfolozi River system, sediment loading of the St Lucia Estuary remains a major ecological concern.

The effects that turbidity can have on biota are varied. Through light attenuation, turbidity reduces the volume of water supporting primary production (Whalen et al., 2006). This then decreases food availability for higher trophic level organisms. Turbidity may also reduce the field of vision, and therefore the reactive distance of visual predators (Gardner, 1981; Rowe and Dean, 1998), and in this way alter species interactions within aquatic systems. Therefore, through its modification of both top-down and bottom-up ecological processes, turbidity is known to alter energy flow pathways, often in a way that reduces the overall productivity of coastal systems (Donohue and Molinos, 2009).

Zooplankton play a pivotal role in the energy transfer of aquatic food webs (Jerling and Wooldridge, 1991; Hays et al., 2005; Guo et al., 2012). In St Lucia, there are four dominant species: the mysid *Mesopodopsis africana*, the calanoids *Acartiella natalensis* and *Pseudodiaptomus stuhlmanni*, and the cyclopoid *Oithona brevicornis*, which has only recently (2011— present) become numerically important with the onset of a wet phase. Various laboratory-based eco-physiological studies have tested the turbidity tolerance of *M. africana* and *A. natalensis* (Carrasco et al., 2007; Carrasco et al., 2013). The main findings are that turbidity reduces the feeding rate, and the survivorship of these two species. The turbidity tolerance of *P. stuhlmanni* and *O. brevicornis* has not as yet been documented.

Further, in March 2014, intense precipitation (~210 mm) in the northern KwaZulu-Natal region resulted in a flood event, during which sediment-laden Mfolozi water flowed from the back-channel into the Narrows region of St Lucia. Thereafter, a silt plume began to spread throughout the South Lake basins (Figure 1.1; Figure 2.1). This provided the ideal opportunity to determine the previously untested effects of turbidity on zooplankton community structure *in situ*. In addition, the observation of live and preserved St Lucia zooplankton specimens have led to the discovery of epibiotic peritrich ciliates. These epibionts were found in the highest densities following the March 2014 flood event. Epibionts are organisms that use the surface area of other organisms, termed the basibionts or hosts, as an attachment site (Green and Shiel, 2000; Dias et al., 2008). Epibiotic relationships may be either commensal or parasitic to the host (Utz, 2003). Most studies have revealed negative effects on zooplankton hosts, which range from inhibition of free movement, to competition for food resources (Utz and Coats, 2005; Visse, 2007; Souissi et al., 2013).

Many epibionts are host-specific (Utz and Coats, 2005; Ma and Overstreet, 2006), and at St Lucia it appears as though *P. stuhlmanni* is a preferred host. The negative impact epibionts

may have on their hosts may have community and food-web wide implications, as it may influence competitive interactions and alter grazing pressure. *Pseudodiaptomus stuhlmanni* is a key zooplankton species in Lake St Lucia, and is preyed upon by many important fish species (Nhleko et al., 2012; Peer et al., 2013; Dyer et al., 2015).

In summary, the purpose of this study was:

1. To determine the effect of turbidity on the feeding, respiration, and mortality rate of the copepod *P. stuhlmanni* (Chapter 1).
2. To determine the response of the dominant zooplankton species of the Narrows region of Lake St Lucia to the March 2014 flood event and silt plume; and to document the field prevalence of the epibiotic peritrich ciliates on the body of *P. stuhlmanni* (Chapter 2).

CHAPTER 1

**Turbidity effects on the feeding, respiration and mortality rate of the copepod
Pseudodiaptomus stuhlmanni in the St Lucia Estuary, South Africa**

ABSTRACT

The St Lucia Estuary is the largest estuarine lake in Africa and due to anthropogenic activities, it has since the 1950s been kept isolated from its main source of freshwater, the Mfolozi River. Stakeholders are increasingly calling for a full reconnection of the historical linkage in order to initiate system restoration. Studies conducted to test the effects of turbidity on the copepod *Acartiella natalensis* and the mysid *Mesopodopsis africana* have shown that turbidity reduces the fitness of these species. The turbidity tolerance of the dominant copepod *Pseudodiaptomus stuhlmanni* has not yet been documented. The aim of this study was to determine the effects of turbidity on the feeding, respiration and mortality rates of *P. stuhlmanni*. Although Chlorophyll consumption was negatively affected by inorganic silt, the use of natural silt resulted in more variable trends. In contrast, a positive relationship was found between total organic carbon (TOC) consumption and turbidity. The high ingestion rates in the highest turbidity treatments of the TOC experiments are attributed to loading of organically-enriched silt. High turbidity also resulted in increased respiration rates of *P. stuhlmanni*, highlighting the energetic demand of turbid environments. Compared with other previously studied St Lucia zooplankters, *P. stuhlmanni* appears to be relatively tolerant of high turbidity. However, as the overall effect on this species is also negative, it is concluded that the St Lucia Estuary needs to be protected from excessive silt inputs if its ecological integrity is to be sustained.

Keywords: turbidity, zooplankton, eco-physiology, *Pseudodiaptomus stuhlmanni*, St Lucia Estuary.

1.1. INTRODUCTION

The St Lucia estuarine lake of northern KwaZulu-Natal, South Africa, is the largest such system in Africa, covering an area of approximately 325 km² (Begg, 1978). This system is not only a Ramsar Wetland of International Importance, but it also forms part of the iSimangaliso Wetland Park, South Africa's first World Heritage Site (Whitfield et al., 2013). The primary source of freshwater for the St Lucia Estuary was historically the 10 645

km² large Mfolozi River system (Cyrus et al., 2011; Nhleko et al., 2012). Due to the scouring action characteristic of rivers and the high fetch exerted on large water bodies (Henley et al., 2000), the Mfolozi River is a naturally turbid system (Nhleko et al., 2012). Historically, the vast swamps of the Mfolozi River effectively filtered out suspended matter, so that by the time the water reached the St Lucia Estuary, it was relatively particle-free (Cyrus et al., 2010, Nhleko et al., 2012). However, in the early 1900s, expanding agricultural practices along the Mfolozi floodplains resulted in the degradation of the filtering services provided by these swamps (Carrasco and Perissinotto, 2011; Whitfield et al., 2013). As a result, much of the fine sediment originally trapped in the swamps washed into the St Lucia Estuary, drastically increasing the sediment load and turbidity within the estuary (Carrasco et al., 2007; Nhleko et al., 2012).

In a bid to stop the changes caused by the excessive sediment loading, stakeholders decided to physically separate the mouth of the Mfolozi River from that of the St Lucia Estuary in 1952, isolating the two systems (Bate and Taylor, 2008; Carrasco and Perissinotto, 2011; Cyrus et al., 2011). Following this, lake bed desiccation and hypersalinity became prominent features during dry phases (Carrasco et al., 2007; Jerling et al., 2010a and references therein). The services previously provided by the estuary became degraded, species were lost and the integrity of the estuary has since become compromised (Cyrus et al., 2011; Carrasco et al., 2013). St Lucia now maintains a connection with the Mfolozi River through a narrow back channel constructed in the late 1960s (Taylor, 2013). Further, there are currently system restoration measures being taken, to increase water inflow to the St Lucia Estuary.

A newly constructed beach spillway became operational in 2012, and although it is currently closed, it successfully channels fresh and marine water into the estuary when it is open (Whitfield et al., 2013). The opening of this channel also coincided with the beginning of a new wet phase, as the area started receiving above average rainfall from 2011 onwards (van Elden et al., 2014; Dyer et al., 2015). Since the Mfolozi floodplains are still being used for agricultural purposes, the problem of increased sediment loading is expected to re-emerge (Carrasco et al., 2013). In addition, a large portion of the St Lucia lakes is relatively shallow (less than one metre), and during windy conditions, organic and inorganic particles are readily re-suspended, increasing the turbidity of the water column.

Turbidity can play a structuring role in aquatic communities, as its effects have been shown to differ among taxa (Hart, 1988; Kirk and Gilbert, 1990; Kirk, 1991). While light attenuation

caused by turbidity decreases the level of primary production (Hart, 1988, 1992; Dejen et al., 2004), some secondary producers may utilise organically-enriched sediment as a supplementary source of food (Arruda et al., 1983). Furthermore, high-turbidity environments degrade the field of view of visual predators, thereby providing refuge to their prey (Vinyard and O'Brien, 1976; Henley et al., 2000; Lehtiniemi et al., 2005; Levine et al., 2005). The less discriminant negative effects of turbidity on aquatic biota include physical injury caused by abrasion, and malnutrition caused by gut loading of nutritionally-poor sediment (McCabe and O'Brien, 1983; Hart, 1988; Koenings et al., 1990). As a result, most literature on turbidity-effects report generally negative effects on aquatic biota (Hart, 1986; Koenings et al., 1990; Aka et al., 2000; Henley et al., 2000; Dejen et al., 2004; Carrasco et al., 2007, 2013).

The role that zooplankton play in the energy transfer of aquatic systems, combined with their quick turnover rate make them an important functional group in eco-physiology studies. At St Lucia, studies have been conducted to determine the effect of turbidity on the feeding and mortality of two dominant zooplankton species, the mysid *Mesopodopsis africana* and the calanoid copepod *Acartiella natalensis* (Carrasco et al., 2007, 2013). *Pseudodiaptomus stuhlmanni* is another abundant calanoid, which has been singled out as a key prey item for several fish species at St Lucia (Nhleko et al., 2012, Peer et al., 2013; Dyer et al., 2015). The present study aims to expand on the past studies, by investigating not only how turbidity affects mortality and feeding, but also the respiration rate of *P. stuhlmanni*.

1.2. MATERIALS AND METHODS

1.2.1. Sample collection

Sampling took place at Charter's Creek in South Lake (Figure 1.1) from April to June 2014. Daytime sampling was conducted on all occasions using a hyperbenthic sled with a mesh size of 100 μm to collect the copepods. Estuarine water and sediment were also collected at Charter's Creek. Experiments were conducted within three days of collection, and only healthy (i.e., active) adults were used.

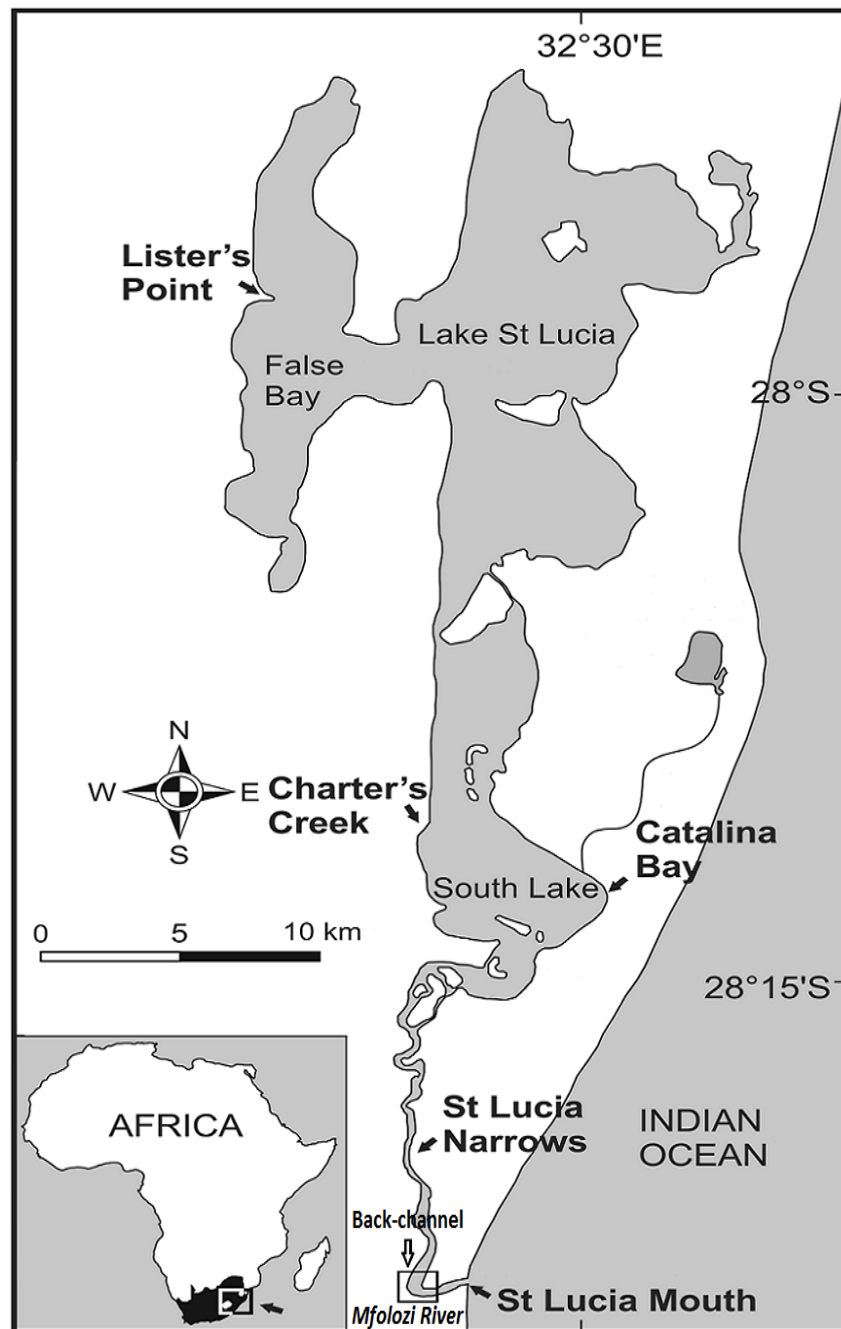


Figure 1.1: Map of the St Lucia estuarine lake, showing the main lake basins. Adapted with permission from Raw et al. (2013).

1.2.2. Experimental design

Five different types of *in vitro* experiments were conducted: two testing turbidity effects on the mortality and respiration rate of *P. stuhlmanni*, and the other three testing turbidity effects on the feeding rate of the copepods.

The experimental design used a range of six turbidity levels, between ~ eight Nephelometric Turbidity Units (NTU), consisting of estuarine water with no added silt and as such acting as the control; and 2500 NTU, which is the highest recorded value at the Mfolozi River. The intermediate turbidity levels were 500, 1000, 1500, and 2000 NTU. Silt-sized particles ($< 63\mu\text{m}$) were obtained by sieving the sediment collected at Charter's Creek through a $63\mu\text{m}$ mesh. The desired turbidity levels were achieved by adding silt to estuarine water and using a HACH 2100Qis instrument to measure turbidity. Prior to setting up the turbidity treatments, the estuarine water was filtered through a $55\mu\text{m}$ sieve to exclude other grazers.

To acquire inorganic silt, sediment was dried in an air circulating oven at $60\text{ }^{\circ}\text{C}$ for two days and thereafter placed in a muffle furnace at $450\text{ }^{\circ}\text{C}$ for 24 hours to burn off any organic matter. The sediment was then crushed for approximately three minutes using a grinder mill and only silt-sized ($< 63\mu\text{m}$) particles used. Both approaches were utilised to ascertain whether there was a positive effect associated with natural organic silt.

Adult *P. stuhlmanni* individuals were identified using a Kyowa SDZ dissecting microscope ($40\times$) and isolated with a Pasteur pipette. The copepods were then randomly assigned to the various turbidity levels.

Twenty-five mL vials were used in the mortality and feeding experiments, with five copepods incubated in each vial, while McCarthy vials (seven mL) were used in the respiration experiments, with three copepods incubated in each. There were three replicates of each type of experiment, and five replicate vials at each turbidity level. For the feeding and respiration experiments, there were three replicate blank treatment vials (without animals) at each turbidity level. All vials were attached to a laterally rotating plankton wheel (three rpm), in order to keep silt particles in suspension. Preliminary experiments showed that across the range of turbidities used, the copepods survived for at least 24 hours. Therefore, the copepods were left to feed and respire on the plankton wheel in a controlled temperature room ($21\pm 1\text{ }^{\circ}\text{C}$) for 24 hours under a natural day: night regime. For the mortality experiment, copepods were left under the same conditions as those above, but checked at 24hour intervals until 100% mortality across at least four levels was reached.

1.2.2.1. *In vitro* feeding rates

Pigment consumption, as chlorophyll *a* (chl *a*) and phaeopigment, was used as a proxy for ingestion rate in two feeding experiments (Carrasco et al., 2013). The difference between

these pigment consumption experiments is that one was set up using natural, therefore organically-enriched silt, whereas pre-combusted, inorganic silt was used in the other. The third feeding experiment investigated the total organic carbon (TOC) matter consumed across the turbidity gradient. The purpose of the TOC experiments was to determine how much organic matter *P. stuhlmanni* consumed, and if this changed along the turbidity gradient used. This information served as a test on the suitability of using pigment extraction methodologies in determining the feeding rate of this species. The complementary results obtained in all three feeding experiments should provide a more robust assessment of the relationship between turbidity and copepod feeding rates.

After the designated 24 hour feeding period, the copepods were removed from the incubation vials by pouring the contents through a 200 μ m sieve. For the feeding experiments that used pigment consumption as a proxy for ingestion rate, the contents of each 25 mL vial were filtered through Whatman GF/F filters at the end of the 24 hour period. In addition, prior to the start of the experiment, three replicate 25 mL sub-samples of each turbidity treatment were filtered, in order to calculate the initial phytoplankton biomass. In order to extract pigments, the filters were placed in test tubes containing six mL of 90% acetone and refrigerated in darkness for 48 hours. The phytoplankton biomass in each sample was thereafter measured using a Turner Designs 10-AU fluorometer. Equations for the estimation of ingestion rate were derived from Båmstedt et al. (2000) and results were expressed as ng pigm.ind⁻¹day⁻¹.

$$\text{Ingestion rate: } I = [V/(N.t)].[(C_o - C_{ta}) - (C_o - C_{tc})]$$

Where I is the ingestion rate; V = the container volume; N = the number of copepods per container; t = the duration of the experiment; C_o = the initial chlorophyll concentration (mg pigm.m⁻³); C_{ta} = the chlorophyll concentration at the end of the incubation period in the experimental treatments (with animals); and C_{tc} = the chlorophyll concentration at the end of the incubation period in the blank treatments (without animals).

For the TOC experiments, contents of all vials (i.e., three initials, three blanks and five treatment vials for each turbidity level) were filtered onto pre-combusted (eight hours, 450 °C) Whatman GF/F filters and oven-dried at 60°C for 48 hours. The filters were thereafter weighed using a Shimadzu AUW220D Uni Bloc balance to an accuracy of 0.1 mg to get a measure of the total suspended matter content. The filters and their contents were then placed in a muffle furnace (450°C) for eight hours, to burn the organic matter, after

which filters were re-weighed. The total organic carbon ($\mu\text{g C}\cdot\text{ind}^{-1}\cdot\text{day}^{-1}$) consumed was calculated by subtracting the organic matter values of the treatment vials from those of the initials, after taking into account the values of the blank vials.

1.2.2.2. Respiration rates

The general protocol used by Isla and Perissinotto (2004) was employed in this experiment. The 55 μm filtered estuarine water was further filtered through a 0.2 μm filter so as to exclude all other respiring organisms. The turbidity treatments were then set up using the filtered water and the inorganic silt.

In order to compensate for a possible decrease in dissolved oxygen content in the water after vacuum filtration, the water used in the incubations was aerated at the beginning of each experiment, *sensu* Ikeda et al. (2000). After the 24 hour incubation period, the copepods were removed from the bottles and the dissolved oxygen content of each incubation vial was immediately measured using a YSI 52 Dissolved Oxygen Meter. For each turbidity level, three replicates of initial dissolved oxygen content were measured. The amount of respired oxygen was thereafter calculated as the difference between the initial and final oxygen concentration, after taking the blank values into account. Specific respiratory rates were expressed as $\mu\text{g O}_2\cdot\text{ind}^{-1}\cdot\text{day}^{-1}$.

1.2.2.3. Mortality rates

At each 24 hour interval, the incubation vials were systematically removed from the plankton wheel and dead copepods were counted and removed. The general physical state of the copepods was also noted. Two litre buckets for each turbidity treatment were kept aerated throughout the duration of the experiment; after each time interval, live copepods were placed back into the 25mL bottles filled with fresh aerated medium. This served to eliminate oxygen and food deficiency effects. All three replicate mortality experiments ended at day eleven, as by then 100% mortality had occurred across the 1000— 2500 NTU levels.

1.2.3. Statistical analyses

Statistical analyses were conducted using IBM SPSS version 21 for Windows. One-way ANOVA was used to test the effects of turbidity on the feeding and respiration rate of *P. stuhlmanni*. The Kolmogorov-Smirnov One-sample test and the Levene's test were performed to test for normality and equal variance of residuals, respectively. Datasets which

did not satisfy either of the assumptions were $\log_{10}(x+1)$ transformed, and the assumptions tested again, to ensure that they were met before the use of the parametric test. To test the effect of turbidity on the mortality rate of *P. stuhlmanni*, a mixed-design repeated-measures ANOVA was carried out. Where the assumption of sphericity was violated, the Greenhouse–Geisser epsilon values were used instead. For all experiments, where significant effects were found, Tukey *post-hoc* tests were performed to identify the source of the difference.

1.3. RESULTS

1.3.1. Ingestion rates

1.3.1.1. Inorganic silt pigment experiments

Turbidity significantly affected ingestion rates (rep. 1: $p < 0.01$, $F_{1.6,0.3} = 5.3$; rep. 2: $p < 0.001$, $F_{0.019, 0.001} = 27.5$; rep. 3: $p < 0.001$, $F_{0.018, 0.0005} = 37.7$). There was a decrease in ingestion rate with an increase in turbidity across the full turbidity range (Figure 1.2a). In all three replicates, highest ingestion rates were recorded at the lowest turbidity level, and these were significantly different to all other turbidity levels (Tukey *post-hoc* test, $p < 0.05$ for all comparisons). Lowest ingestion rates were recorded at the highest turbidity levels (Figure 1.2a).

1.3.1.2. Natural silt pigment experiments

The use of natural organically-enriched silt resulted in more variable trends in copepod feeding. The trend was somewhat bell-shaped, with ingestion rates peaking at 500 NTU (Figure 1.2b). A significant difference was found in all three replicates (rep. 1: $p < 0.001$, $F_{0.068, 0.004} = 16.3$; rep. 2: $p < 0.001$, $F_{0.023, 0.003} = 6.8$; rep. 3: $p < 0.001$, $F_{0.03, 0.002} = 18.4$). In all replicates, there was no significant difference in feeding between the control and 2500 NTU treatment (Tukey *post-hoc* test, $p > 0.05$). Feeding at both these levels was significantly different to those at 500 and 1000 NTU ($p < 0.05$). In replicate two, there was large variability at 2000 NTU (Figure 1.2b), and this level did not significantly differ from any other level ($p > 0.05$). Overall, lowest ingestion rates were recorded in the control, respectively followed by 2500 NTU and 2000 NTU.

1.3.1.3. Total organic carbon experiments

A steady increase in total organic carbon consumption with an increase in turbidity was recorded (Figure 1.2c). In all three replicates, there was a significant increase in TOC consumption across the turbidity range (rep. 1: $p < 0.001$, $F_{371,6} = 64.8$; rep. 2: $p < 0.001$, $F_{363,24} = 15.2$; rep. 3: $p < 0.001$, $F_{359,8} = 44.6$). In all replicates, feeding in the 1000 and 1500 NTU levels did not significantly differ from each other (Tukey *post-hoc* test, $p > 0.05$). Feeding at 2500 NTU consistently differed from that at the control and at 500 NTU ($p < 0.05$). The control was further significantly different from all other levels in the first replicate, and from all but 500 NTU in the other two replicates.

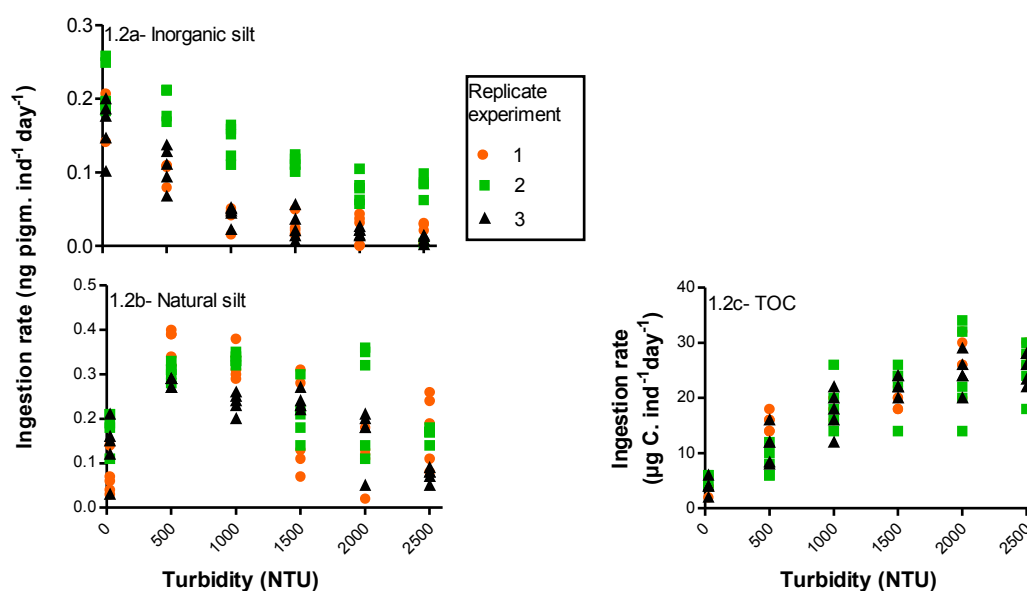


Figure 1.2: Ingestion rates of *Pseudodiaptomus stuhlmanni* in the various turbidity treatments. The inorganic silt pigment experiment, natural silt pigment experiment, and TOC experiment are represented by plots 1.2a, 1.2b and 1.2c, respectively.

1.3.2. Respiration rates

Because the copepods used in the respiration experiments exhibited uncontrolled and enhanced swimming activity at low and high turbidity levels, respectively, the metabolic rates may be defined as routine maximum as opposed to basal (see Ikeda et al. 2001). Turbidity significantly affected respiration (rep 1: $p < 0.01$, $F_{0.72,0.12} = 6.13$; rep 2: $p < 0.001$, $F_{2.23,0.24} =$

9.38; rep 3: $p < 0.001$, $F_{0.68,0.07} = 9.63$). Respiration rates in the control were responsible for most of the differences. In the first replicate, respiration rates in the control differed from those at 1000, 1500, and 2000 NTU. In the second and third replicate, control rates at the control differed from those of all other levels, and from all but 500 NTU. With the exception of the difference between 500 and 2000 NTU in the third replicate, in all replicates, respiration rates across 500—2500 NTU did not significantly differ from each other. Generally, respiration rates were lowest in the control, and plateaued from 500 to 2500 NTU (Figure 1.3).

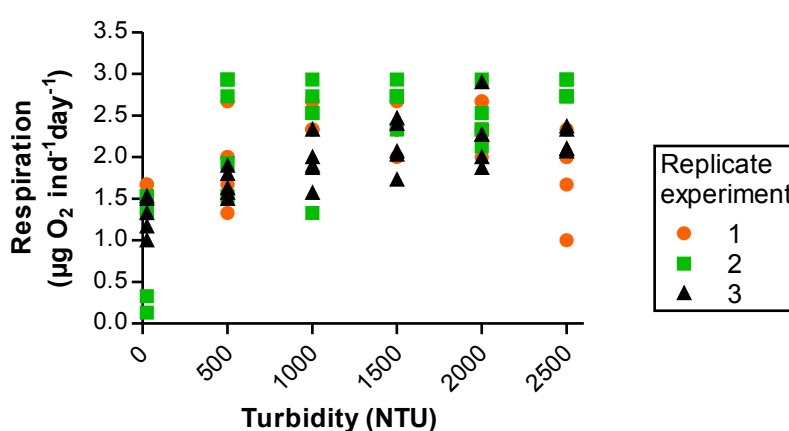


Figure 1.3: Respiration rate of *Pseudodiaptomus stuhlmanni* in the various turbidity treatments.

1.3.3. Mortality rates

The mortality experiments lasted for eleven days (264 hours, Figure 1.4), and in all three replicate experiments, turbidity significantly affected mortality (rep. 1: $p < 0.001$, $F_{64.7,0.38} = 170$; rep. 2: $p < 0.001$, $F_{63,0.34} = 187$; rep. 3: $p < 0.001$, $F_{72,0.42} = 173$). Results from all replicates were in good agreement (Figure 1.4; Figure 1.5). The highest survival at 96 hours was recorded at 500 NTU, wherein between 80 and 100% of the copepods were still alive. There was more variability in the survival of animals exposed to the control, 1000 and 1500 NTU. In the control, between 60 and 100 % survival was recorded in all replicates. Twenty to 60, and zero to 40% survival in 1000 and 1500 NTU was respectively recorded at 96 hours. Animals exposed to 2000 and 2500 NTU had a survival of zero (replicates one and three) and 20% (replicate two) after 96 hours (Figure 1.5).

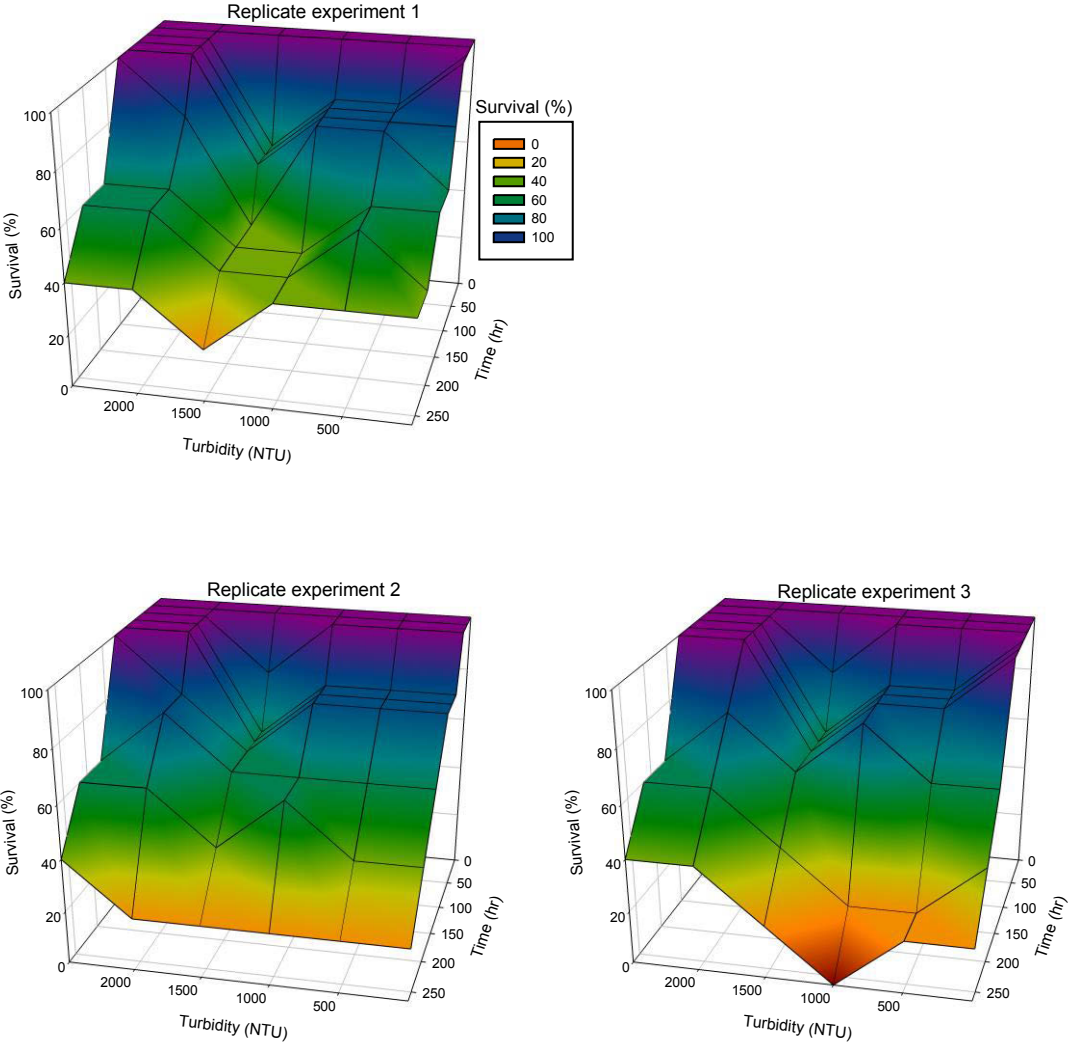


Figure 1.4: Survival rate of *Pseudodiaptomus stuhlmanni* in the various turbidity treatments over 11 days.

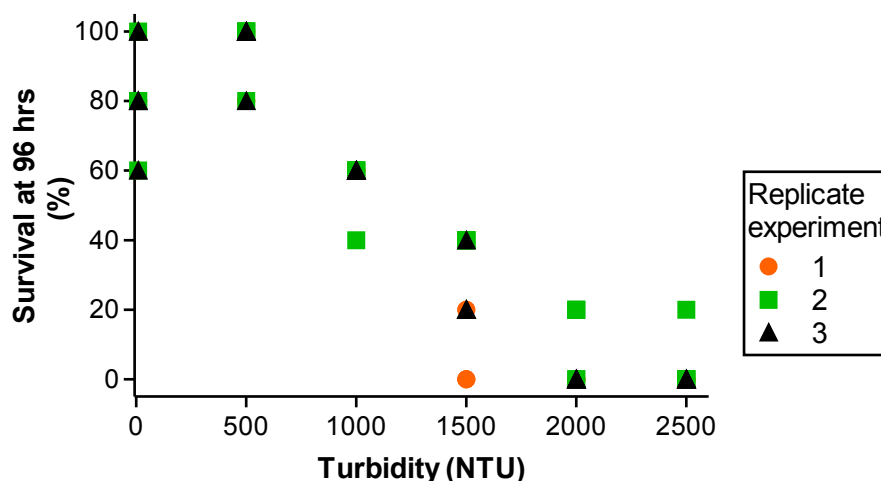


Figure 1.5: Survival rate of *Pseudodiaptomus stuhlmanni* in the various turbidity treatments at 96 hours.

Tukey *post-hoc* tests revealed that, for all replicates, survival between the 1000 and 1500 NTU did not differ significantly ($p > 0.05$) but differed from those at other levels ($p < 0.05$). The same was true for survival at 2000 and 2500 NTU, but only in replicates one and three. In replicate two, survival at 2000 differed to that at 2500 NTU ($p < 0.05$).

1.4. DISCUSSION

Although wind-induced turbidities at the St Lucia Estuary are seldom above 1200 NTU, turbidities in excess of 2500 NTU have been recorded in the Mfolozi River, and therefore pose a threat to the St Lucia biota should the two systems be reconnected. This study revealed a range of deleterious turbidity effects on *Pseudodiaptomus stuhlmanni*, particularly at the highest (1500—2500 NTU) levels. However, in the mortality experiments, this calanoid survived for much longer (eleven days) than was expected, particularly given results from similar studies (Carrasco et al., 2007, 2013). Further, the different trends of response observed in the feeding experiments show that it is both the proxy of ingestion (pigment versus TOC consumption), and the nature of silt used (organically enriched versus inorganic) that affect how turbidity may be perceived to affect this calanoid.

The TOC experiments revealed an increase in ingestion with increasing turbidity, implying beneficial turbidity effects. This, however, is likely not the case. Calanoid copepods are generally classified as selective feeders (Richman and Dodson, 1983; Kirk and Gilbert, 1990

and references therein; Koenings et al., 1990). However, it is possible that their ability to feed selectively at elevated turbidities becomes impaired. In this case, the copepods can be expected to indiscriminately ingest particles within their vicinity. It is, therefore, more likely that gut-loading of nutrient-rich silt occurred in the high-turbidity treatments. This assertion is supported by the mortality experiment, as the animals exposed to the high turbidities had a substantially higher mortality rate than those exposed to low turbidities.

Although both pigment feeding experiments showed an ultimately negative turbidity effect, the natural silt experiments produced a more variable trend, with the depression of ingestion only occurring from 1000 NTU. In contrast, the findings of the inorganic silt experiments revealed a consistently increasing negative effect across the full turbidity gradient. Previous studies (Carrasco et al., 2007, 2013) investigated the effect of inorganic turbidity on the feeding (pigment) of the other dominant St Lucia zooplankters, the calanoid *Acartiella natalensis* and the mysid *Mesopodopsis africana*. The *A. natalensis* findings were in complete agreement with those of the present study, as a reduction in feeding was observed across the control—2500 NTU gradient. This species also died within a week in mortality experiments conducted using natural silt. In contrast, the findings of the *M. africana* feeding study were more variable. In some cases, high inorganic turbidities depressed ingestion, whereas in others, either no relationship existed between ingestion rate and turbidity, or a positive correlation was recorded (Carrasco et al., 2007). The authors attributed the latter trends to a positive relationship between silt loading and mysid clearance rates (Carrasco et al., 2007). Carrasco et al. (2007) also found that mysids exposed to high turbidities had a significantly higher mortality rate than those exposed to low suspended silt loads. In the present study, mortality rates were also significantly higher at the higher turbidities. However, *P. stuhlmanni* survived for eleven days at the 500 NTU treatment, which is substantially longer than was observed with both *A. natalensis* and *M. africana* (Carrasco et al., 2007, 2013).

The findings of the respiration experiments served to corroborate those of the inorganic feeding experiments, by highlighting the energetic cost of living in a silt-laden, food-deprived environment. *Pseudodiaptomus stuhlmanni* was found to deplete significantly more oxygen with increasing turbidity. Richman and Dodson (1983) also found that the cladoceran *Daphnia pulex* respired more when exposed to low versus high quality food. The authors attributed this to the fact that the rejection of food boluses by *D. pulex* came with a metabolic cost, as the animals expended energy while using their labrum and abreptor. In the present

study, *P. stuhlmanni* likely had to expend more energy to prevent gut loading, and to expel any ingested inorganic silt. As adult copepods invest energy obtained from ingestion in reproduction among other metabolic costs, it is not only longevity, but secondary production of *P. stuhlmanni* that may be compromised by high, organically poor turbidities.

The negative effects of inorganic silt on the dominant St Lucia zooplankton species have high relevance. If a full reconnection of the Mfolozi River to the St Lucia Estuary were to result in added silt loading, the allochthonous silt would have a lower organic matter content than the autochthonous silt currently characterising St Lucia. This is because the quantity of organic matter is known to decrease during heavy flow pulses (e.g. Sluss et al., 2008). More importantly, Nqgulana et al. (2010) and Nhleko et al. (2012) reported the benthic fauna of the Mfolozi River as highly impoverished, whereas that of St Lucia was found to be diverse. Nqgulana et al. (2010) attributed this finding to periodic flooding and the unstable nature of the Mfolozi substrate. Nhleko et al. (2012) cited the strong scouring action within the Mfolozi River as the cause of the degraded benthic substrate. The organically poor nature of the scoured particles, combined with the loss of the Mfolozi swamps, has resulted in the high organically-poor turbidities associated with the Mfolozi River flows (Nhleko et al., 2012).

The turbidities currently characterising St Lucia are mainly as a result of silt and particulate organic matter re-suspended during windy conditions, which is why they are rich in organic matter. As shown by the natural silt experiments, at intermediate turbidities (500-1500 NTU) *P. stuhlmanni* is not as adversely affected by nutritious silt as it is by its inorganic counterpart. This may be due to the fact that nutritious silt is less abrasive, and can serve as a supplementary source of nutrition for zooplankton that are able to utilize the adsorbed carbon matter (Arruda et al., 1983, Koenings et al., 1990). Silt loading from the Mfolozi River would not only add to the already high *in situ* turbidities, it would also reduce the nutritional value and non-abrasive nature of the turbidities the St Lucia populations of *P. stuhlmanni* have to some degree adapted to.

In conclusion, this study revealed that *P. stuhlmanni* is not as susceptible to turbidity as the two other previously studied zooplankters (Carrasco et al., 2007, 2013). However, the overall effect of elevated turbidity on this species was also negative. Nutritionally poor silt had a particularly adverse effect. As such, a full Mfolozi-St Lucia reconnection would likely lead to a decline in the secondary production and abundance of all dominant St Lucia zooplankton species. *Pseudodiaptomus stuhlmanni* has been particularly singled out as a key prey item of

higher trophic-level species (Jerling et al., 2010a; Nhleko et al., 2012; Peer et al., 2013; Dyer et al., 2015). A population decline of this species might result in cascading effects on higher trophic levels (Cyrus et al., 2011). As such, reconnection of the St Lucia Estuary to the Mfolozi River should be accompanied by plans to reduce the threat of silt loading.

CHAPTER 2

Impact of a sediment-laden flood event on estuarine zooplankton in Lake St Lucia

ABSTRACT

The St Lucia Estuary has a history of excessive sediment loading. Previous laboratory-based studies revealed that the dominant zooplankton species *Mesopodopsis africana*, *Acartiella natalensis* and *Pseudodiaptomus stuhlmanni* are negatively affected by high turbidities. A flood event in March 2014 resulted in a silt plume spreading through part of this estuary. This provided an ideal opportunity to monitor the field response of zooplankton to high suspended silt loads. The Narrows region of St Lucia was sampled on a monthly basis from March to September 2014. For comparative purposes, data from samples collected during 2013, prior to the flood event, were included in the statistical analyses. ANOSIM revealed that the three months following the flood event, that is March— May 2014, were significantly different from the rest of the sampling occasions in terms of species abundance. This period was therefore termed “disturbed”, and the rest of the sampling occasions “undisturbed”. The abundance of the copepods *A. natalensis* and *Oithona brevicornis* was lowest during the disturbed March— May period, and highest in September 2014. The other, more turbid-water tolerant copepod, *P. stuhlmanni*, prevailed in March 2014, but declined markedly in April. As of September 2014, this copepod had yet to regain its pre-flood abundance. It is, however, possible that the potentially parasitic epibiotic peritrich ciliates, which were observed to preferentially attach to *P. stuhlmanni*, further depressed this population. The interpretation of these results is also complicated by the possible combined effect of physic-chemical variables such as salinity and dissolved oxygen content. However, there is stronger support for the conclusion that the high turbidities accompanied by the March 2014 flooding event are primarily responsible for the observed outcome.

Keywords: turbidity, zooplankton community structure, silt plume, epibiotic peritrich ciliates.

2.1. INTRODUCTION

Human-induced sediment loading and sedimentation are two of the most well-documented stressors of coastal ecosystems (Parkhill and Gulliver, 2002; Donohue and Molinos, 2009). During pulses of heavy flow, sediment-laden freshwater may discharge into estuaries, drastically increasing the sediment load, and in so doing, reducing the geological life of these systems (Whitfield et al., 2013). The finest sediment particles may persist in the water

column, resulting in high turbidities, which in turn affect, *inter alia*, the primary production and species interaction within affected estuaries (Tilzer, 1983; Cuker and Hudson, 1992; Cuker, 1993; Roach et al., 2014).

In northern KwaZulu-Natal, South Africa, the 1930s canalisation of the Mfolozi River for agricultural purposes resulted in sediment loading of the St Lucia Estuary, Africa's largest estuarine lake, and a Ramsar Wetland of International Importance (Bate and Taylor, 2008; Carrasco et al., 2007) (Figure 1.1). This problem accounted for the 1952 management decision to separate the then-common mouth of the two systems (Cyrus et al., 2011). Due to this isolation, other stressors, such as low water levels and hypersalinity during drought conditions, began to manifest (Jerling et al., 2010a). Early attempts at alleviating these latter stressors 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 1.1). There are currently other measures being taken to re-connect the Mfolozi River-St Lucia system (see Whitfield et al., 2013).

The crucial role of zooplankton in energy transfer up the trophic levels of aquatic systems, combined with their quick generational turnover rate (Hays et al., 2005; Guo et al., 2012; Deale et al., 2013;), make them important determinants of the general health status of aquatic systems. Although various laboratory-based eco-physiological experiments have improved understanding of the turbidity tolerance of the dominant St Lucia zooplankton (Carrasco et al., 2007; Carrasco et al., 2013; Chapter 1, Jones et al., in review), the *in situ* response of these species to turbid conditions has not been documented.

In March 2014, intense precipitation in the northern KwaZulu-Natal region resulted in a small flood (~210 mm rainfall) in the catchments of the St Lucia system. Sediment-laden water flowed from the Mfolozi River via the back-channel, as well as from the Mpathe River, a smaller freshwater source. Following the flood, a silt plume began to spread throughout the South Lake basins (Figure 2.1). This flooding event and resulting silt plume, which remained in place for approximately six weeks, provided the ideal opportunity to study the effect of turbidity on the ecology of the dominant zooplankton species, *in situ*. In addition, associated with this event was the discovery of epibiotic ciliates, which appeared to target and attach to the most turbid-water tolerant species, *Pseudodiaptomus stuhlmanni* (Figure 2.2).

Epibionts are organisms that use the exterior surface of other organisms (termed the hosts or basibionts) as an attachment substrate. They may have either a commensal or parasitic relationship with their hosts (Chatterjee et al., 2013; Utz and Coats, 2005). Many studies have described their attachment on crustaceans as parasitic (Bickel et al., 2012; Turner et al., 1979; Weissman et al., 1993). The zooplankton community structure of the Narrows region of Lake St Lucia was monitored on a monthly basis, from March to September 2014, with a two-fold aim:

- 1) To determine the density fluctuation of the dominant zooplankton taxa following the March 2014 flooding event and resulting silt plume;
- 2) To monitor the prevalence of epibiotic ciliates on the body of *P. stuhlmanni*, and the density fluctuations of *P. stuhlmanni* in response to this event.



Figure 2.1: The discoloured water at the Narrows region after the March 2014 flood event (photo: Caroline Fox, March 2014).

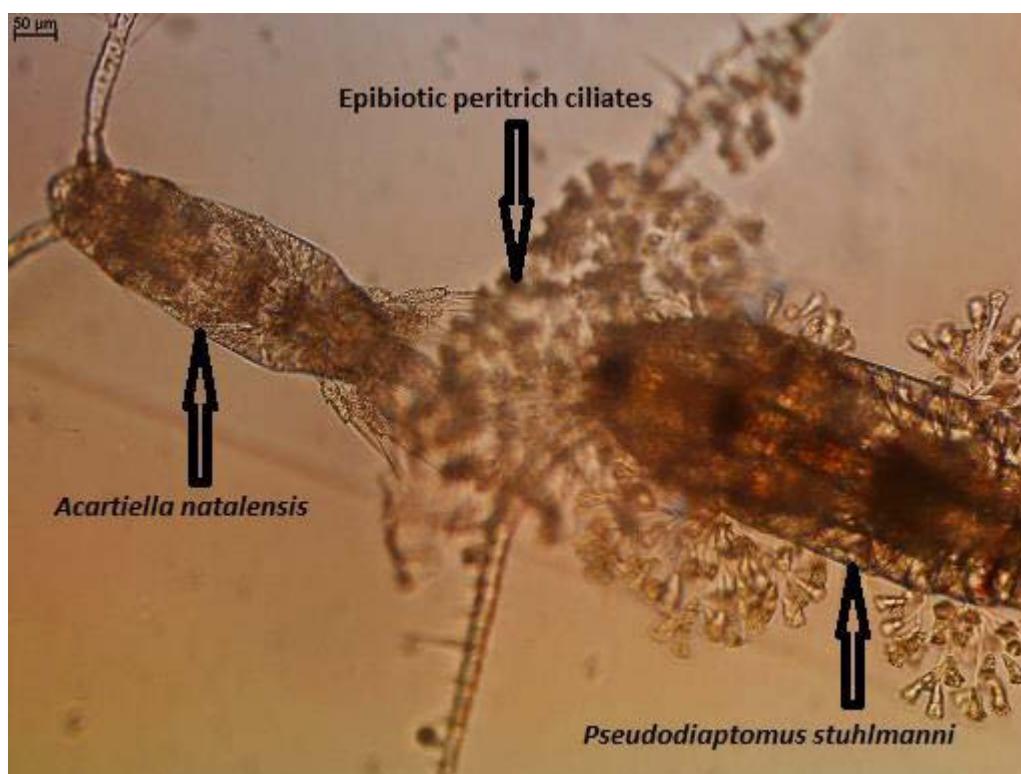


Figure 2.2: *Pseudodiaptomus stuhlmanni* individual heavily infested with epibiotic peritrich ciliates, next to a non-hosting calanoid, *Acartiella natalensis* (micrograph: Salome Jones, March 2014).

2.2. MATERIALS AND METHODS

2.2.1. Sample collection

Sampling was conducted at Esengeni in the Narrows region of the St Lucia estuarine lake (Figure 1.1). This region 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-disturbance” comparisons. Zooplankton, phytoplankton and microphytobenthic samples together with physico-chemical data were collected on each sampling occasion.

2.2.2. 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

[NTU]), dissolved oxygen (mg.L^{-1}), and salinity probes. Rainfall data was obtained from the Ezemvelo KwaZulu-Natal Wildlife conservation authority.

2.2.3. Microalgae, total suspended solids and particulate organic matter

Microphytobenthic cores (two cm internal diameter, depth= one cm) were collected and immediately transferred to 100 mL polyethylene bottles containing 30 mL 90% acetone for 48 hours cold-dark chlorophyll *a* (*chl 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 (~ three hours).

In the laboratory, 100 mL water subsamples were filtered through GF/F filters, which were then placed in six mL of 90 % acetone for 48 hours of cold-dark *chl a* and phaeopigment extraction. Phytoplankton (mg pigm.m^{-3}) and microphytobenthic (mg pigm.m^{-2}) biomass were determined fluorometrically, using a Turner Designs 10-A Unon-acidification system. 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 estuarine water through pre-combusted (6 hours, 420°C) Whatman GF/F filters. Once dried (48 hours, 60°C), the filters were weighed to 0.1 mg using a Shimadzu AUW220D Uni Bloc balance, combusted in a muffle furnace (six hours, 420°C) and then re-weighed so that TSS and POM could be calculated.

2.2.4. Zooplankton

Daytime zooplankton tows were taken off 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 raised 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 ($\approx 1.43 \text{ m}^3$). Two tows were taken per trip, and the samples collected in the cod end were each immediately emptied into a 500 mL polyethylene bottle containing five % phloxine-stained formalin.

In the laboratory, each sample was suspended in a one-five litre 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 and Wooldridge, 1989; Carrasco et al., 2009).

Zooplankton within the subsamples were identified and counted under a Kyowa SDZ

dissecting microscope (40 ×). Zooplankton density (ind.m⁻³) was then calculated. The epibiotic peritrich ciliate prevalence on *P. stuhlmanni* from March 2014 to September 2014 was also recorded.

To calculate 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 hours, 60°C). Biomass was estimated as the total dry weight (mg DW.m⁻³) of each sample.

2.2.5. Statistical analyses

Univariate statistical analyses were conducted with SPSS version 21 for Windows. All data met the assumptions of parametric testing (normality and even distribution of residuals). 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 regression analyses were used to test for relationships between environmental variables and total abundance, biomass and species richness.

Multivariate analysis was conducted using the PRIMER package (version 6.0). Abundance data were fourth-root transformed, in order to reduce the effect of the abundant species. Analysis of similarity (ANOSIM) was conducted to check for temporal differences in zooplankton community structure. A Bray-Curtis similarity matrix was then calculated for the different sampling periods. Cluster analysis (group averaged) and multidimensional scaling (MDS) plots were used to visually assess temporal differences in zooplankton community structure. Where differences were found, the similarity percentage (SIMPER) routine determined the magnitude of the difference between the sampling dates, and the different species' contribution to the community structure on the different sampling occasions. The BIOENV Harmonic Spearman Correlation function was used to relate environmental variables to the zooplankton assemblages.

2.3. RESULTS

2.3.1. Physico-chemical parameters

Water temperature ranged from 16.4 to 26.3 °C throughout the study period. Salinity was highest in November 2013 (21.6) and showed a sharp decline following the flood event, with

the lowest value (0.5) recorded in May 2014. Dissolved oxygen content was lowest in April 2014, at 5.23 mg.L⁻¹. Rainfall was highest in March 2014 (209.6 mm), and the water-column in the Narrows was two metres deep during the March–May 2014 period. Turbidity reached its peak following the flood event, with 962 NTU being recorded in March 2014 (Figure 2.3).

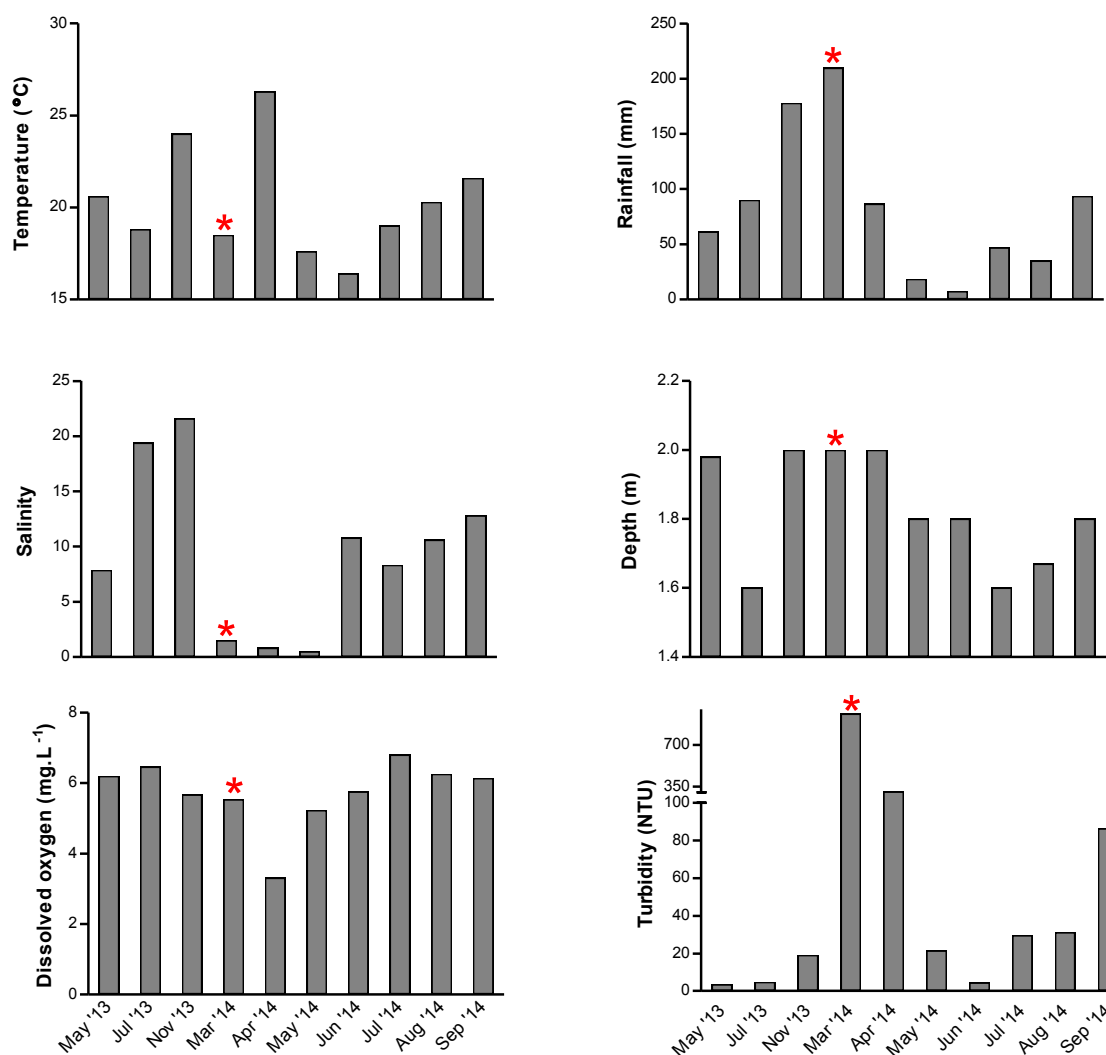


Figure 2.3: Environmental parameters measured in the Narrows region during each sampling occasion. The asterisk indicates the timing of the flood event.

2.3.2. Microalgae, total suspended solids and particulate organic matter

Highest phytoplankton biomass (22.9 mg.m⁻³) and lowest microphytobenthic biomass (1.45 mg.m⁻²) were recorded during March 2014, following the flood event (Figure 2.4). The highest TSS concentrations (426 mg.m⁻³) were also recorded after the flood. Percentage particulate organic matter content was highest in May 2013 (41%) (Figure 2.5).

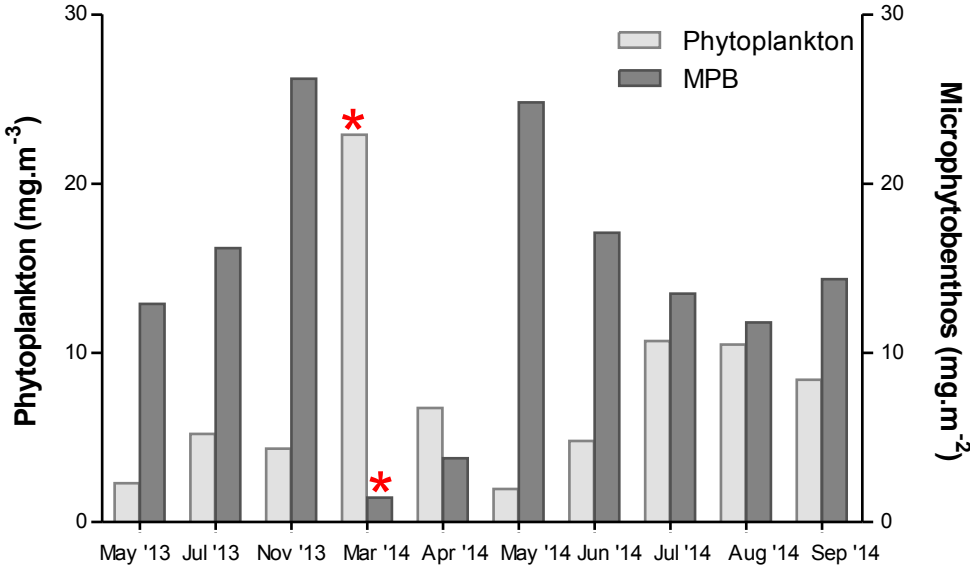


Figure 2.4: Phytoplankton and microphytobenthic biomass measured from water samples collected in the Narrows region after each sampling occasion. The asterisk indicates the timing of the flood event.

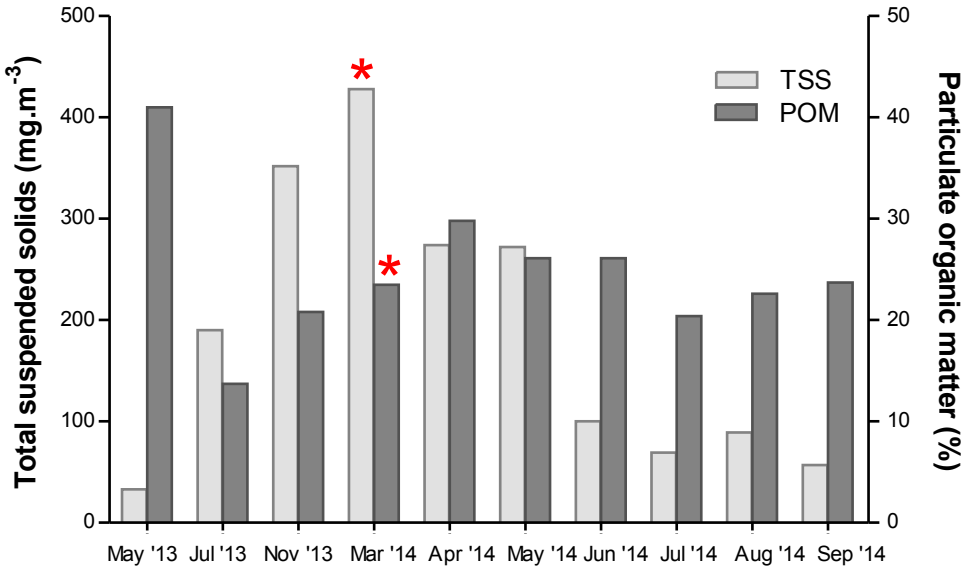


Figure 2.5: Total suspended solids (TSS) and the corresponding percentage particulate organic matter (POM) measured from water samples collected at the Narrows region after each sampling occasion. The asterisk indicates the timing of the flood event.

2.3.3. Zooplankton abundance, biomass and species richness

The total recorded zooplankton abundance ranged from 6.68×10^4 to 3.33×10^5 ind.m⁻³ throughout the study period. The lowest zooplankton densities coincided with the flood event in March 2014 (Figure 2.6). 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 ($p < 0.05$). In addition, the zooplankton abundance recorded during the March– May 2014 period was significantly different to those of all subsequent sampling occasions ($p < 0.05$).

Total zooplankton biomass ranged from 50.7 to 239 mg DW.m⁻³ (Figure 2.6). Biomass varied significantly between sampling occasions (ANOVA, $F_{9,10} = 179$, $p < 0.05$). The main month responsible for the difference was September 2014, which differed from all other months (Tukey *post-hoc* test, $p < 0.05$).

Species richness was greatest in March 2014, with 18 taxa recorded on this sampling occasion. The lowest species richness was recorded during July 2013 (Figure 2.6). There was a significant difference 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 from March, May, June and August 2014 (Tukey *post-hoc* test, $p < 0.05$).

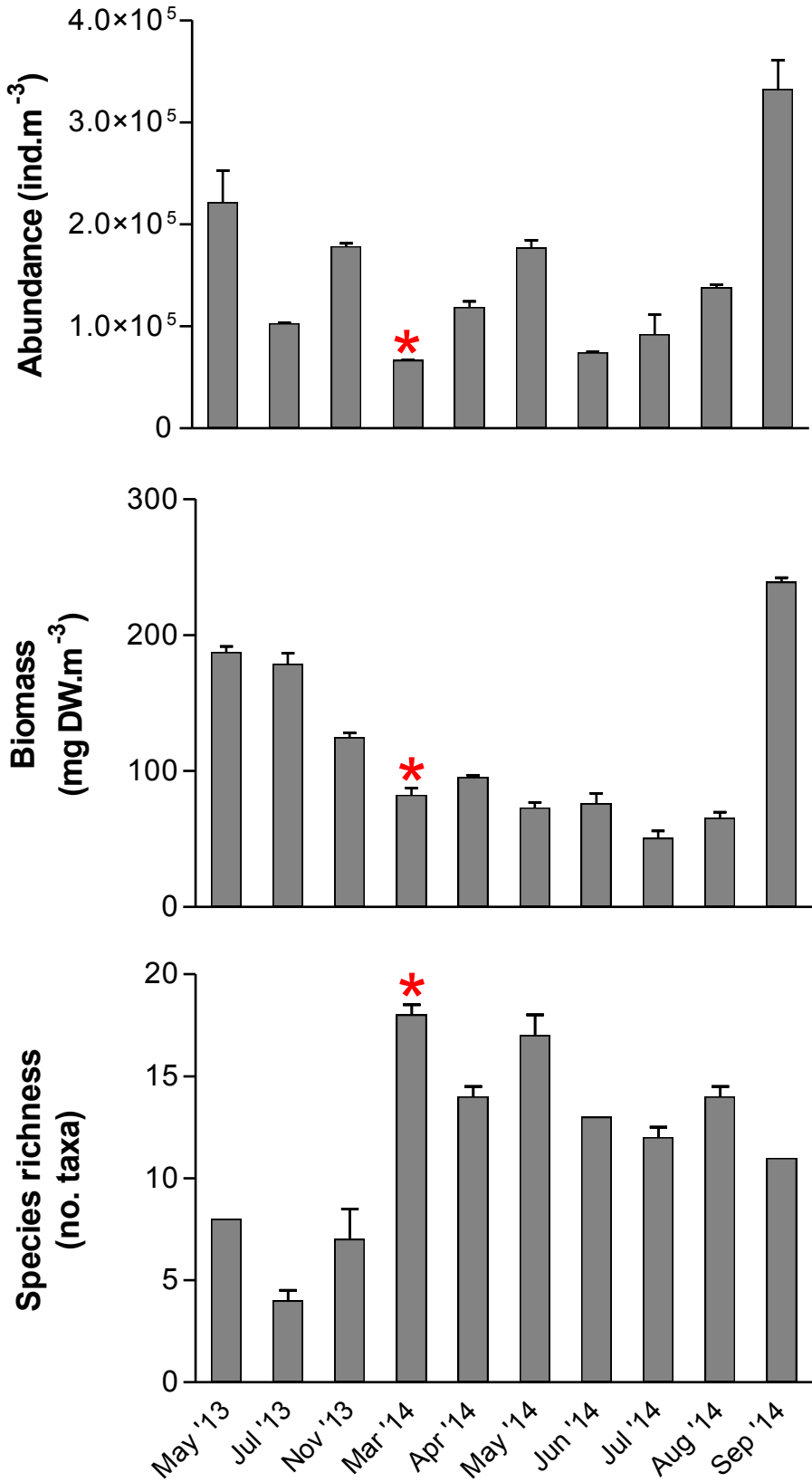


Figure 2.6: Mean (\pm SD) zooplankton abundance, biomass, and species richness recorded at each sampling occasion. The asterisk indicates the timing of the flood event.

Regression analyses revealed that neither total zooplankton abundance nor biomass were significantly correlated with any of the environmental parameters ($p > 0.05$). Species richness was significantly correlated only with salinity ($R = 0.8$; $p < 0.05$).

2.3.4. Zooplankton community structure

The abundance of *Pseudodiaptomus stuhlmanni* was highest in May 2013 (4.59×10^4 ind.m⁻³). Its lowest recorded abundance (1177 ind.m⁻³), and contribution (< 1 %) towards total abundance, were recorded during April 2014. Overall, *P. stuhlmanni* underwent a drastic population decline between March and April 2014, with about a third of the initial total abundance remaining after this period. This was not unique to this particular species, as the abundance of the other dominant St Lucia copepods, *Acartiella natalensis* and *Oithona brevicornis*, also decreased markedly from March to April 2014 (Figure 2.7).

Acartiella natalensis was present on all sampling occasions, with the exception of April 2014. The relative abundance of this species was significantly higher 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 2.71×10^4 ind.m⁻³ in September 2014 (Figure 2.7).

The cyclopoid copepod *O. brevicornis* occurred at densities of 3.12×10^4 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 2.3×10^5 ind.m⁻³ (Figure 2.7).

Only one exclusively freshwater species was recorded prior to the flood; the cladoceran *Moina cf. micrura* in July 2013 (74 ind.m⁻³) and November 2013 (172 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 the less than one % during the three pre-disturbance months. By April 2014, concurrent with the decline of 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 2.7).

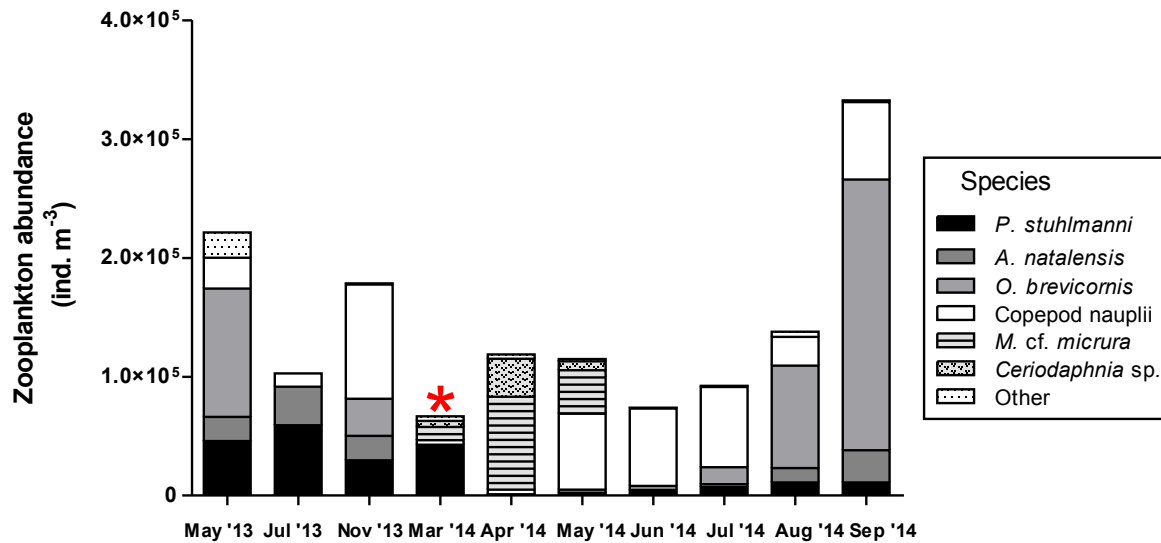


Figure 2.7: Abundance of zooplankton taxa recorded from May 2013 to September 2014 in the Narrows region of Lake St Lucia. The asterisk indicates the timing of the flood event.

Cluster analysis and MDS plots (Figure 2.8) showed that the zooplankton communities recorded in the three months following the disturbance, *viz.* March, April and May 2014 differed from those of the other months (Figure 2.8). These months were therefore termed “disturbed”, and the rest of the sampling occasions — “undisturbed”. ANOSIM revealed a significantly different community structure between the disturbed and undisturbed period ($R=0.92, p < 0.1$).

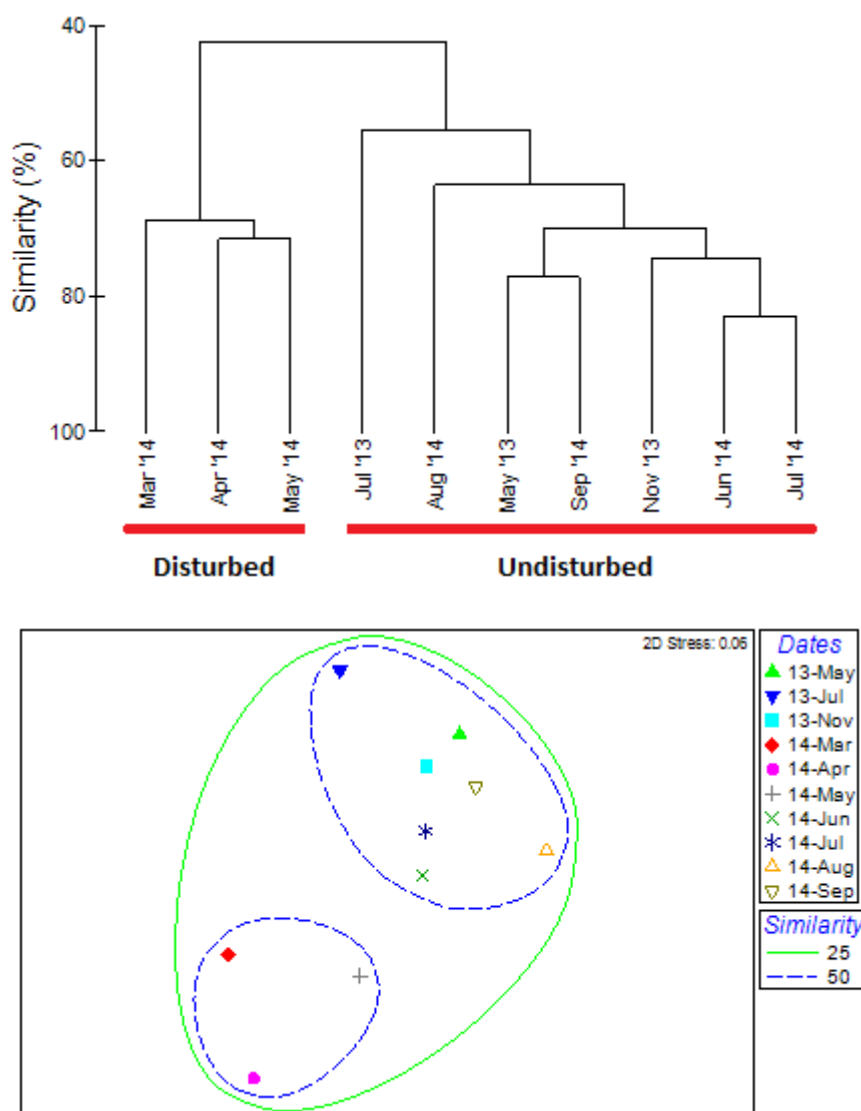


Figure 2.8: A Bray-Curtis similarity dendrogram and a multi-dimensional scaling (MDS) plot showing the grouping of zooplankton communities according to abundance in the Narrows region from May 2013 to September 2014.

SIMPER analysis revealed five taxa that accounted for ~ 90 % of the abundance in the undisturbed period. These were copepod nauplii, *P. stuhlmanni*, *A. natalensis*, *O. brevicornis* and the ostracod *Cyprideis torosa*. During the disturbed period, nine taxa accounted for ~ 90 % of the abundance. The most important of these were *M. cf. micrura*, *Ceriodaphnia* sp., copepod nauplii and *P. stuhlmanni* (Figure 2.7).

The species generally responsible for the dissimilarity between the 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 ($R=0.72$).

2.3.5. Epibiotic peritrich ciliate prevalence on *Pseudodiaptomus stuhlmanni*

Sixty-eight % of *P. stuhlmanni* individuals recorded in March 2014 harboured epibiotic ciliates. No epibionts were found on the specimens collected in April, but the epibionts re-emerged in May 2014, and were subsequently consistently found on *P. stuhlmanni*, although at a low prevalence (Figure 2.9).

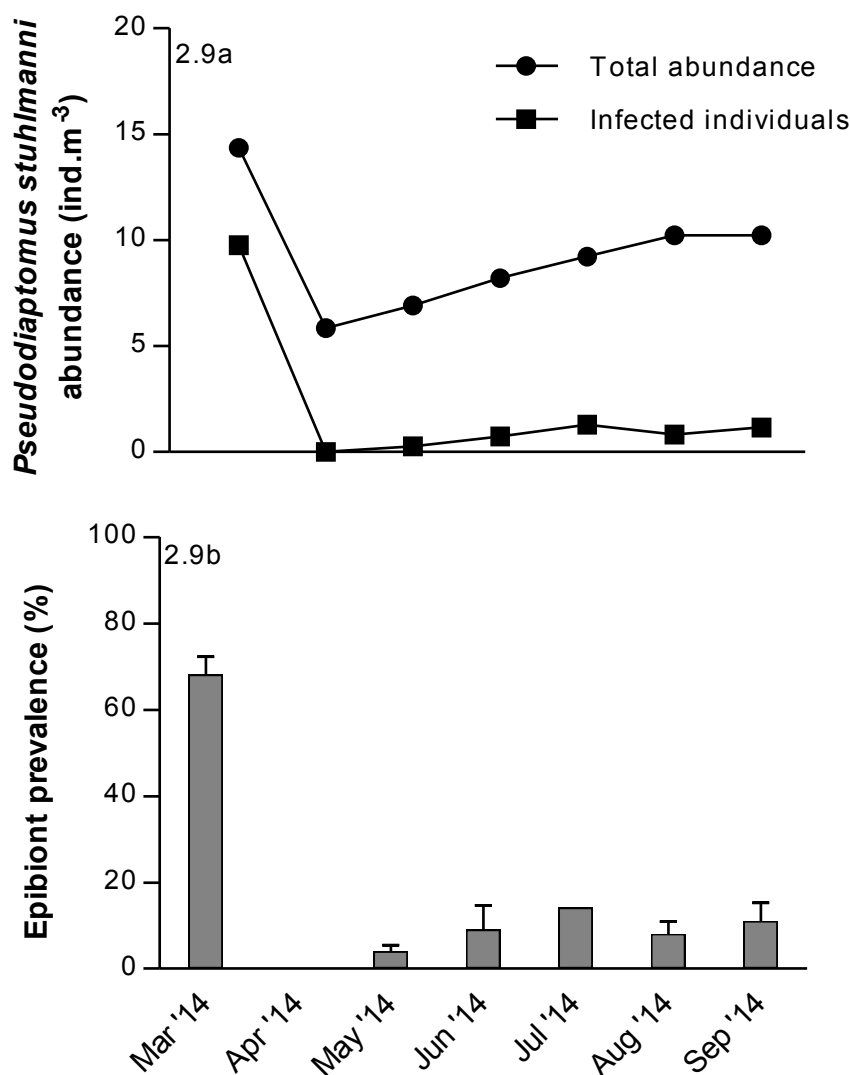


Figure 2.9: Epibiotic ciliate occurrence (2.9a), and epibiotic ciliate prevalence (2.9b) on *Pseudodiaptomus stuhlmanni* across the 2014 sampling dates. The data is fourth-root transformed.

2.4. DISCUSSION

Previous laboratory-based studies have revealed that turbidity has a negative effect on the eco-physiology of three of the dominant St Lucia zooplankters, *Mesopodopsis africana* (Carrasco et al., 2007), *Acartiella natalensis* (Carrasco et al., 2013), and *Pseudodiaptomus stuhlmanni* (Chapter 1, Jones et al., in review). However, the effect was not uniform among these species, as *P. stuhlmanni* appeared to be more turbidity tolerant than the other two species. The March 2014 flooding event and resulting silt plume were therefore expected to result in an uneven decline of estuarine species. As the mysid *M. africana* was virtually absent from the system before the disturbance, the attention was paid predominantly to the copepods. In the laboratory-based mortality experiments, *A. natalensis* was exposed to the 13.5—2500 NTU turbidity gradient, and by 96 hours, 100% mortality had occurred across this gradient. In a similar experiment run with *P. stuhlmanni*, there were still survivors across the eight—1500 NTU gradient after a week of exposure. The experiment was terminated at day eleven, when 100% mortality had occurred across the 1000—2500 NTU gradient. The findings of this *in situ* study therefore corroborate those obtained in laboratory studies, as the reaction of *A. natalensis* was an immediate population decline, whereas *P. stuhlmanni* remained abundant in March 2014, but eventually declined in April. However, at any given time, natural systems are impacted by an array of factors, which usually act in synergy to shape the prevailing community structure. Although turbidity was the main factor of interest in this study, other factors, namely salinity and dissolved oxygen content, also emerged as statistically significant drivers of the prevailing zooplankton assemblage.

As the silt-laden waters that caused high turbidity in March 2014 were of freshwater origin, it was expected that salinity would also play an important role in structuring the subsequent zooplankton assemblage of the Narrows region. The BIOENV analysis revealed that turbidity, dissolved oxygen and salinity were the main determinants of the Narrows community structure during “the disturbance”. The fact that regression analyses indicated that salinity was correlated with species richness, was therefore not surprising.

Low salinity prevailed for longer (March–May 2014) than high turbidities (March–April 2014). The low salinity regime was characterised 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 copepods *O. brevicornis* and *A. natalensis* were virtually absent. *Oithona brevicornis* has been variably abundant at St Lucia since the 2011 onset of

the wet phase. This cyclopoid mainly inhabits estuarine and marine environments (Boxshall et al., 2007). Therefore, both the low salinity and high turbidity could have been responsible for the decline of this species in March 2014. *Acartiella natalensis*, however, is able to withstand low salinity (freshwater to ~ 80) (Grindley, 1976, 1982), and is a dominant member of the Mfolozi River zooplankton community (Jerling et al., 2010b). Apart from salinity and turbidity, other factors, such as competition imposed by the cladocerans, may have also prevented this calanoid population from making a quicker recovery.

In contrast to *A. natalensis*, *P. stuhlmanni* was present in high densities in March 2014 following the flooding event. During the March sampling event, *P. stuhlmanni* was discovered grossly covered in parasitic epibiotic ciliates. Many studies have reported the parasitism of copepods by epibiotic ciliates (Weissman et al., 1993; Morado and Small, 1995; Visse, 2007; Bickel et al., 2012). These ciliates not only harm their hosts by inhibiting free movement (thus increasing predation risk, and reducing feeding efficiency), but also by competing for food resources (Souissi et al., 2013).

In the current study, 68% of *P. stuhlmanni* individuals were observed to host epibionts in the March 2014 samples. By April 2014, the *P. stuhlmanni* population had undergone a threefold decline in abundance. It was also noted during this time that the epibiotic ciliates were absent from the zooplankton samples. *Pseudodiaptomus stuhlmanni* re-emerged in May 2014, as did the epibionts, although with only a four % prevalence on *P. stuhlmanni* individuals. The field density of the epibionts has since been generally positively correlated with that of *P. stuhlmanni*. It is unclear whether the eventual demise of *P. stuhlmanni* in April-May 2014 was principally caused by the high turbidities, or the epibiotic ciliates. However, epibiotic ciliates have been found to be favoured by polluted environments, and have been associated with eutrophic conditions (Utz and Coats, 2005). Laboratory-based experiments have shown that turbidity facilitates the population growth of the St Lucia epibionts, as the epibiont prevalence on *P. stuhlmanni* individuals exposed to turbidities of 500 and 1000 NTU was found to be significantly higher than that on *P. stuhlmanni* exposed to lower (~0 and 12 NTU) turbidities (Jones et al., unpublished data). In addition, unaffected *P. stuhlmanni* individuals, and those with a low epibiont load, had a significantly lower mortality rate than their heavily infested counterparts (Jones et al., unpublished data). The decline of *P. stuhlmanni* may have therefore been caused by both the after-effects of high turbidity and the parasitic ciliates.

The freshwater cladocerans *M. cf. micrura* and *Ceriodaphnia* sp. were able to thrive during the time when *P. stuhlmanni* declined. Cladocerans are generally more sensitive to turbidity than copepods (Kirk and Gilbert, 1990; Koenings et al., 1990). Therefore, it is unlikely that the high turbidities of March favoured these cladocerans over the St Lucia copepods. The epibionts were microscopically observed to target only *P. stuhlmanni*, irrespective of the presence of the cladocerans and other zooplankton species (personal observation). The three-month persistence of the cladocerans may be attributed to both low salinity, 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 disturbance. *Oithona brevicornis* attained its peak densities in the last two months (August and September 2014) of this study. *Acartiella natalensis* also regained its pre-disturbance 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 epibiotic ciliates may be responsible for the continued suppression of this species. The quicker recovery of *O. brevicornis* and *A. natalensis* may also be attributable to their smaller body size at maturity, which might mean that they have a quicker regeneration time than the larger *P. stuhlmanni*. The findings of this study nonetheless exemplify the turbidity tolerance of *P. stuhlmanni* that was found through the laboratory experiments (Chapter 1, Jones et al., in review). In the laboratory experiments, *P. stuhlmanni* survived for up to 11 days, with the highest percentage survival recorded at a turbidity of 500 NTU. This species has now been found abundant in the field under turbidities in excess of 900 NTU, despite being parasitized by epibionts.

The March— May 2014 period was characterised 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 and Browder, 1998; Donohue and Molinos, 2009), and have been found to sequester as much as 16 times their volume of aerated water (Bruton, 1985). Therefore, high turbidities, such as those experienced at St Lucia during the March–April 2014 period, are generally accompanied by decreased oxygen content (Appleby and Scarratt, 1989; Donohue and Molinos, 2009). Further, there was generally a higher concentration of particulate organic matter in the Narrows in the four months following the disturbance. Large amounts of organic matter may result in a high ratio of water column community respiration: available

dissolved oxygen content. Studies on the effect of turbidity on the respiration of *P. stuhlmanni* have revealed that this species requires more oxygen at high versus low turbidities (Chapter 1, Jones et al., in review). Therefore, turbidity *per se* results in low physical oxygen availability, while simultaneously increasing the oxygen requirements of at least this species. In cases where oxygen is a limiting factor, attachment of epibiotic ciliates on *P. stuhlmanni* may not only elicit competition for food, but also for oxygen.

Other taxa of note during this study were various unidentified freshwater cyclopoids, which were mainly present in March 2014, and traditionally benthic taxa. The benthic taxa include the cosmopolitan ostracod *Cyprideis torosa*, and *Tenellia adspersa*, a small estuarine nudibranch previously unrecorded in Africa. A thorough discussion of the dynamics of these less abundant taxa is beyond the scope of this study. However, although species identification was not the purpose of this study, it is apparent that several potentially important zooplankton, particularly Mfolozi River cyclopoids, are in need of accurate identification.

The importance of the Mfolozi River as a source of freshwater for Lake St Lucia is well documented in the literature (Taylor, 2006; Cyrus et al., 2010, 2011; Carrasco and Perisinotto, 2011; Taylor, 2013; Whitfield et al., 2013). However, in the compromised current state of this river, the freshwater aid it provides during calm periods is to some degree offset by the sediment loads it discharges into St Lucia during heavy rainfall. The flooding event and resulting silt plume, although temporary (~ six weeks), has had a long-lasting effect on the community structure of the zooplankton of at least the Narrows region. Although literature pertaining to the Lake St Lucia-Mfolozi River system (Grindley, 1976, 1982; Jerling et al., 2010a, b) concur that the dominant St Lucia calanoids are euryhaline, it is difficult to isolate the effect of salinity from that of turbidity. However, recent eco-physiological experiments (Carrasco et al., 2013; Chapter 1, Jones et al., in review) suggest that turbidity may be primarily responsible for the community decline of the calanoid copepods *P. stuhlmanni* and *A. natalensis*.

Studies conducted in other parts of the world cite human-induced sediment loading of aquatic systems as one of the greatest threats to biodiversity and ecosystem service provision (Cooper, 1993; Wood and Armitage, 1997; Sklar and Browder, 1998; Gray et al., 2014;). One of the biggest biological impacts of this factor is on the food web structure of aquatic systems, and its effects on the feeding of fish have been well researched (Vinyard and O'Brien, 1976; McCabe and O'Brien, 1983; Bruton, 1985). The generally reported impacts

on the feeding of fish are a reduction in feeding efficiency due to field of view obstruction (Vinyard and O'Brien, 1976; Gardner, 1981), and a shift in prey items caused by their selective suppression by turbidity (Arruda et al., 1983; McCabe and O'Brien, 1983; Kirk and Gilbert, 1990; Dejen et al., 2004). At the St Lucia Estuary, stable isotope and gut content analyses of several dominant fish species have shown that *A. natalensis* and *P. stuhlmanni* are key dietary constituents (Nhleko et al., 2012; Peer et al., 2013; Dyer et al., 2014). Therefore, the decline of these copepods impacts important energy transfer pathways, which may affect the trophic functioning of Lake St Lucia as a whole.

Future turbidity effect studies should be conducted on *O. brevicornis*. This species has become important in St Lucia in terms of abundance, and the findings of this study revealed that it reacts similarly to *A. natalensis*; its density declined dramatically following the March 2014 flood event. There are currently on-going laboratory experiments to test the effect of turbidity on the feeding, oxygen depletion, ammonia excretion, and mortality of this cyclopoid copepod.

CONCLUSIONS AND RECOMMENDATIONS FOR FUTURE WORK

Sediment loading has been described as a primary and global threat to the functioning of coastal ecosystems (Ryan, 1991; Parkhill and Gulliver, 2002, Donohue and Molinos, 2009). Despite this, there has been a relatively small body of work dedicated to understanding the biological impacts of sediment loading on lake systems (Donohue and Molinos, 2009). This is especially true for African water bodies (but see Hart, 1986, 1988, 1992; Dejen et al., 2012, and Carrasco et al., 2007, 2013). Findings of this study are therefore of importance not only for the conservation of St Lucia, but for that of other similarly challenged systems.

At St Lucia, the effects of turbidity are important to understand for two reasons. Firstly, a large proportion of this estuary is shallow, and during windy conditions, organic and inorganic particles are readily re-suspended. Secondly, its connection to the Mfolozi River subjects it to excessive sediment loading, as exemplified by the March 2014 flood event. Therefore, with the current measures to establish more links between the St Lucia Estuary and the Mfolozi River, the St Lucia zooplankton, as well as other functional groups, will be subjected to more frequent turbidity spells, resulting from both wind-induced particle re-suspension, and silt loading from the Mfolozi River.

Through laboratory experiments and ecosystem monitoring, this study has confirmed that turbidity exerts a negative impact on all dominant St Lucia zooplankters. The feeding rates of the mysid *Mesopodopsis africana* (Carrasco et al., 2007), and the calanoids *Acartiella natalensis* (Carrasco et al., 2013) and *Pseudodiaptomus stuhlmanni* (Chapter 1, Jones et al., in review), are reduced at high turbidity. Turbidity also exerts added metabolic costs on *P. stuhlmanni*, as this copepod was found to deplete significantly more oxygen at high versus low turbidities. High turbidity ultimately reduces the fitness of all three dominant St Lucia zooplankton species, as it results in premature mortality. However, this study has also highlighted the differential impact of turbidity on different species, as *P. stuhlmanni* has been found to be substantially more tolerant than *M. africana* and *A. natalensis*.

The finding of the first chapter might therefore lead to the prediction that with more frequent turbidity spells, *P. stuhlmanni* will cope better than the other currently co-dominant zooplankton species. However, on-going laboratory experiments have revealed that nutrient-rich turbidity also provide ideal conditions for the proliferation of the epibiotic

peritrich ciliates (Jones et al., unpublished data). Chapter 2 revealed that once the population of *P. stuhlmanni* declines, it takes a relatively long time (> five months) for this species to recover. Therefore, the less detrimental effects of turbidity on *P. stuhlmanni* become more pronounced through its facilitation of the epibionts, which act to ensure the suppression of *P. stuhlmanni*.

The Mfolozi River flows are generally associated with organically poor particles (Nqgulana et al., 2010, Nhleko et al., 2012; Chapter 1, Jones et al., in review). Given the fact that the highest epibiont densities were observed in the Narrows region following discharge of Mfolozi River water (Chapter 2), the findings of this study might seem contradictory. However, as this was a flood event, other factors, such as terrestrial runoff, and re-suspension of settled organic particles at St Lucia, may have contributed towards making this water more organically-rich than would regular inflow of sediment-laden Mfolozi River water.

The findings of this study have major implications for the food web of Lake St Lucia. The shorter life span of *M. africana*, *A. natalensis*, and *P. stuhlmanni* during turbid conditions has the effect of reducing the egg production rate of these dominant species. Stable isotope and gut content analyses studies have identified *P. stuhlmanni* and *A. natalensis* as primary prey items of the dominant fish species at St Lucia (Nhleko et al., 2012; Peer et al., 2013; Dyer et al., 2014). Although the Mfolozi River flows carry a high sediment load, inflow into St Lucia is accompanied by freshwater zooplankton, particularly cladocerans, which the planktivorous fish might temporarily prey upon in the absence of the dominant St Lucia species. Wind-induced turbidity associated with epibiont proliferation, on the other hand, can be expected to result in a population decline of the St Lucia zooplankton, and therefore a reduction of prey items for planktivorous species.

Wind-induced turbidity might intuitively be expected to be a comparatively smaller threat, due to its short-lived nature, and the fact that it is characterised by autochthonous particles. However, on one occasion at Charter's Creek (Figure 1.1) in 2013, intense wind action resulted in turbidities in excess of 1200 NTU, and zooplankton samples collected during this period revealed a low abundance (personal observation). Additionally, *P. stuhlmanni* was covered in the then-unidentified peritrich ciliates. In light of these findings, it is even more important that the inflow of Mfolozi River sediments be controlled. Through increasing the sedimentation rate, allochthonous sediment further reduces the depth of the lake basins,

which results in increased concentrations of suspended silt during wind-induced turbidities (Whitfield et al., 2013).

RECOMMENDATIONS FOR FUTURE WORK

There are currently on-going laboratory experiments, aimed at determining how turbidity affects the feeding, respiration, and mortality rate of the cyclopoid copepod *Oithona brevicornis*, which has gained prominence since the 2011 onset of the wet phase. Other on-going studies have also confirmed that the turbid-water associated epibiotic peritrich ciliates recently discovered at St Lucia are specific for *P. stuhlmanni*. At high densities, these epibionts also parasitize *P. stuhlmanni*, ultimately reducing survivorship. Future studies should aim at quantifying the food web effects of turbidity, as well as those of the epibiotic peritrich ciliates, which are currently being identified to species level. Sediment control measures, and a better understanding of the ecological role of the epibiotic peritrich ciliates, may be vital in maintaining the ecological functioning of the St Lucia Estuary.

REFERENCES

- Abernethy, C., 1990. The use of river and reservoir sediment data for the study of regional soil erosion rates and trends. International Symposium on Water Erosion, Sedimentation and Resource Conservation, Dehradun, India, October, 1990.
- Aka, M., Pagano, M., Saint-Jean, L., Arfi, R., Bouvy, M., Cecchi, P., Thomas, S., 2000. Zooplankton variability in 49 shallow tropical reservoirs of Ivory Coast (West Africa). *International Review of Hydrobiology* 85 (4), 491-502.
- Appleby, J., Scarratt, D. J., 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 Science* 1681, 37-38.
- Arruda, J. A., Marzolf, G. R., Faulk, R. T., 1983. The role of suspended sediments in the nutrition of zooplankton in turbid reservoirs. *Ecology* 64, 1225-1233.
- Båmstedt, U., Gifford, D.T., Irigoien, X., Atkinson, A., Roman, M., 2000. Feeding. *in*: R., Harris, P. H., Wiebe, J., Lenz, H. R., Skjoldal, M., Huntley, editors. *ICES Zooplankton Methodology Manual*. Academic Press, pp. 297-377.
- Bate, G., Taylor, R., 2008. Sediment salt-load in the St Lucia Estuary during the severe drought of 2002–2006. *Environmental Geology* 55, 1089-1098.
- Begg, G.W., 1978. The estuaries of Natal. Report no. 41, Natal Town and Regional Planning Commission, Pietermaritzburg, pp. 1-657.
- Bickel, S. L., Tang, K. W., Grossart, H. P., 2012. Ciliate epibionts associated with crustacean zooplankton in German lakes: distribution, motility, and bacterivory. *Frontiers in Microbiology* 3 (243), 1-10.
- Boxshall, G., Boero, F., Olenin, S. 2007. Establishment of *Oithona brevicornis* Giesbrecht, 1892 (Copepoda: Cyclopoida) in the Black Sea. *Aquatic Invasions*, 2 (4), 407-410.
- Bruton, M., 1985. The effects of suspensoids on fish. *Hydrobiologia* 125, 221-241.
- Carrasco, N. K., Perissinotto, R., Miranda, N. A., 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, 152-164.
- Carrasco, N. K., Perissinotto, R., Pillay, D., 2009. Zooplankton of the St. Lucia Estuary during the current drought cycle: a comparison between open-and closed-mouth conditions. *Marine Ecology Progress Series* 399, 157-160.

- Carrasco, N.K., Perissinotto, R., 2010. Spatial and temporal variations in the diet of the mysid *Mesopodopsis africana* in the St Lucia Estuary (South Africa). *Marine Ecology Progress Series* 417, 127-135.
- Carrasco, N.K., 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, 93-100.
- Carrasco, N. K., 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, A. A., Fernández-Leborans, G., 2013. A checklist of epibiotic ciliates (Peritrichia and Suctorina) on the cladoceran crustaceans. *Biologia* 68, 439-447.
- Copeland, B., 1966. Effects of decreased river flow on estuarine ecology. *Water Pollution Control Federation* 38 (11), 1831-1839.
- Cooper, C., 1993. Biological effects of agriculturally derived surface water pollutants on aquatic systems: a review. *Journal of Environmental Quality* 22, 402-408.
- Cuker, B. E., 1993. Suspended clays alter trophic interactions in the plankton. *Ecology* 74 (3), 944-953.
- Cuker, B. E., Hudson, L., 1992. Type of suspended clay influences zooplankton response to phosphorus loading. *Limnology and Oceanography* 37, 566-576.
- Cyrus, D., Vivier, L., 2006. Status of the estuarine fish fauna in the St Lucia Estuarine System, South Africa, after 30 months of mouth closure. *African Journal of Aquatic Science* 31, 71-81.
- Cyrus, D. P., Vivier, L., Owen, R. K., Jerling, H. L., 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), 109-116,
- 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, 1-13.
- Deale, M., Perissinotto, R., Carrasco, N., 2013. Recovery dynamics of zooplankton following mouth-breaching in the temporarily open/closed Mdloti Estuary, South Africa. *African Journal of Aquatic Science* 38, 67-78.

- Dejen, E., Vijverberg, J., Nagelkerke, L. A. J., Sibbing, F. A., 2004. Temporal and spatial distribution of microzooplankton crustacean in relation to turbidity and other environmental factors in a large tropical reservoir (L. Tana, Ethiopia). *Hydrobiologia* 513, 39-49.
- Dias, R. J. P., Avila, S. D., Agosto, M. D., 2008. First record of epibiont peritrichids and suctorians (Protozoa, Ciliophora) on *Pomacea lineate* (Spix, 1827). *Brazilian Archives of Biology and Technology* 49 (5), 808-809.
- Douglas, I., 1996. The impact of land-use changes, especially logging, shifting cultivation, mining and urbanization on sediment yields in humid tropical Southeast Asia: a review with special reference to Borneo. *in*: D. E. Walling, B. W., Webb, (eds.), *Erosion and Sediment Yield: Global and Regional Perspectives*. Proceedings of the Exeter Symposium, July 1996, IAHS Publication, vol. 236. IAHS Press, Wallingford, UK, pp. 463-471.
- Donohue, I., Molinos, J. G., 2009. Impacts of increased sediment loads on the ecology of lakes. *Biological Reviews* 84, 517-531.
- Dyer, D. C., Perissinotto, R., Carrasco, N. K., 2015. Temporal and spatial dietary dynamics of the Longspine Glassy (*Ambassis ambassis*) in the St Lucia Estuary, iSimangaliso Wetland Park. *Water SA*, 41 (1), 95–97.
- Eyre, B., 1998. Transport, retention and transformation of material in Australian estuaries. *Estuaries* 21, 540-551.
- Fielding, P. J., Forbes, A. T., Demetriades, N. T., 1991. Chlorophyll concentrations and suspended particulate loads in St Lucia, a turbid estuary on the east coast of South Africa, *South African Journal of Marine Science* 11(1), 492-496.
- Forbes, A. T., Cyrus, D. P., 1991. Recruitment and origin of penaeid prawn post-larvae in two south-east African estuaries. *Estuarine and Coastal Shelf Science* 33, 281-289.
- Gardner, M. B., 1981. Mechanisms of size selectivity by planktivorous fish: a test of hypotheses. *Ecology* 62, 571-578.
- Gray, S. M., Bieber, F. M. E., Mandrak, N. E., 2014. Experimental evidence for species-specific response to turbidity in imperilled fishes. *Aquatic Conservation: Marine and Freshwater Ecosystems* 24 (4), 3-11.
- Green, J. D., Shiel, R. J., 2000. Mobilineperitrich riders on Australian calanoid copepods. *Hydrobiologia* 437, 203-212.

- Grindley, J. R., 1976. Zooplankton of St Lucia. *in*: A. E. F., Heydorn, editor. St Lucia Scientific Advisory Council Workshop meeting, Charter's Creek 15-17 February 1976. Paper 12. Natal Parks Board, Pietermaritzburg.
- Grindley, J. R., 1982. The role of zooplankton in the St Lucia estuary system. *in*: R. H., Taylor, editor. St Lucia Research Review. Natal Sharks Board, Pietermaritzburg, pp. 88-107.
- Guo, Z., Liu, S., Hu, S., Li, T., Huang, Y., Liu, G., Zhang, H., Lin, S., 2012. Prevalent ciliate symbiosis on copepods: high genetic diversity and wide distribution detected using small subunit ribosomal RNA gene. *PloS one* 7 (4), 48-47.
- Hart, R.C., 1986. Zooplankton abundance, community structure and dynamics in relation to inorganic turbidity, and their implications for a potential fishery in subtropical Lake le Roux, South Africa. *Freshwater Biology* 16 (3), 351-367.
- Hart, R.C., 1988. Zooplankton feeding rates in relation to suspended sediment content: potential influences on community structure in a turbid reservoir. *Freshwater Biology* 19, 123-139.
- Hart, R.C., 1992. Experimental studies of food and suspended sediment effects on growth and reproduction of six planktonic cladocerans. *Journal of Plankton Research* 14, 1425-1442.
- Hay, B.J., 1994. Sediment and water discharge rates of Turkish Black Sea rivers before and after hydropower dam construction. *Environmental Geology* 23, 276-281.
- Hays, G. C., Richardson, A. J., Robinson, C., 2005. Climate change and marine plankton. *Trends in Ecology and Evolution* 20, 337-344.
- Henley, W.F., Patterson, M.A., Neves, R.J., Lemly, A.D., 2000. Effects of sedimentation and turbidity on lotic food webs: a concise review for natural resource managers. *Review of Fisheries Science* 8(2), 125-137.
- Ikeda, T., Kanno, Y., Ozaki, K., Shinada, A., 2001. Metabolic rates of epipelagic marine copepods as a function of body mass and temperature. *Marine Biology* 139(3), 587-596.
- Ikeda, T., Torres, J.J., Hernandez-Leon, S., Geiger, S.P., 2000. Metabolism. *in*: R., Harris, P. H., Wiebe, J., Lenz, H. R., Skjoldal, M., Huntley, editors. ICES Zooplankton Methodology Manual. Academic Press, London, pp. 455-530.
- Isla, J.A., Perissinotto, R., 2004. Effects of temperature, salinity and sex on the basal metabolic rate of the estuarine copepod *Pseudodiaptomus hessei*. *Journal of Plankton Research* 26 (5), 579-583.

- Jerling, H. L., Vivier, L., Cyrus, D.P., 2010a. Response of the mesozooplankton community of the St Lucia Estuary, South Africa, to a mouth-opening event during an extended drought. *Estuarine Coastal Shelf Science* 86, 543-552.
- Jerling, H. L., 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, 117-122.
- Jerling, H.L., Wooldridge, T.H., 1991. Population dynamics and estimates of production for the calanoid copepod *Pseudodiaptomus hessei* in a warm temperate estuary. *Estuarine Coastal Shelf Science* 33, 121-135.
- Jones, S., Carrasco, N. K., Perissinotto, R. (In review) 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*.
- Kirk, K. L., Gilbert, J. J., 1990. Suspended clay and the population dynamics of planktonic rotifers and cladocerans. *Ecology* 71 (5), 1741-1755.
- Kirk, K.L., 1991. Inorganic particles alter competition in grazing plankton: the role of selective feeding. *Ecology* 72 (3), 915-919.
- Koenings, J., Burkett, R. D., Edmundson, J. M., 1990. The exclusion of limnetic cladocera from turbid glacier-meltwater lakes. *Ecology* 71 (1), 57-67.
- Lehtiniemi, M., Engström-Öst, J., Viitasalo, M., 2005. Turbidity decreases anti-predator behaviour in pike larvae, *Esox lucius*. *Environmental Biology of Fishes* 73 (1), 1-6.
- Levine, S.N., Zehrer, R.F., Burns, C.W., 2005. Impact of re-suspended sediment on zooplankton feeding in Lake Waiholo, New Zealand. *Freshwater Biology* 50, 1515-1534.
- Lindsay, P., Mason, T. R., Pillay, S., Wright, C. I., 1996. Suspended particulate matter and dynamics of the Mfolozi Estuary, KwaZulu-Natal: implications for environmental management. *Environmental Geology* 28, 40-51.
- Mann, B.Q., 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, 133-138.
- Ma, H., Overstreet, R. M., 2006. Two new species of *Epistylis* (Ciliophora: Peritrichida) on the lue crab (*Callinectes sapidus*) in the Gulf of Mexico. *Journal of Eukaryotic Microbiology* 53 (2), 85-93.

- McCabe, G.B., O'Brien, W.J., 1983. The effects of suspended silt on feeding and reproduction of *Daphnia pulex*. *American Midland Naturalist* 110, 324–337.
- Morado, J. F., and E. B. Small. 1995. Ciliate parasites and related diseases of Crustacea: a review. *Reviews in Fisheries Science* 3, 275-354.
- Nhleko, J.B.B., Cyrus, D.P., Vivier, L., 2012. Diet of the demersal feeding *Leiognathus equula* in the Mfolozi–Msunduzi estuarine system, South Africa, in response to an impoverished macrobenthic invertebrate community. *African Journal of Aquatic Science* 37 (2), 175-180.
- Ngqulana, S.G., Owen, R.K., Vivier, L., Cyrus, D.P., 2010. Benthic faunal distribution and abundance in the Mfolozi–Msunduzi estuarine system, KwaZulu-Natal, South Africa. *African Journal of Aquatic Science* 35(2), 123-129.
- Parkhill, K. L., and J. S. Gulliver., 2002. Effect of inorganic sediment on whole-stream productivity. *Hydrobiologia* 472, 5-17.
- Peer, N., Carrasco, N.K., Perissinotto, R. du Plooy, S.J., 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), 341-347.
- Parkhill, K. L., Gulliver, J. S., 2002. Effect of inorganic sediment on whole-stream productivity. *Hydrobiologia* 472, 5-17.
- 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, 205-219.
- Raw, J. L., Miranda, N. A. F., Perissinotto, R., 2013. Chemical cues released by an alien invasive aquatic gastropod drive its invasion success. *PLoS ONE* 8 (5), 2-2.
- Richman, S., Dodson, S. I., 1983. The effect of food quality on feeding and respiration by *Daphnia* and *Diaptomus*. *Limnology and Oceanography* 28 (5), 948-956.
- Roach, K. A., Winemiller, K. O., Davis, S. E., 2014. Autochthonous production in shallow littoral zones of five floodplain rivers: effects of flow, turbidity and nutrients. *Freshwater Biology* 59, 1278-1293.
- Rowe, D. K., Dean, T. L., 1998. Effects of turbidity on the feeding ability of the juvenile migrant stage of six New Zealand freshwater fish species. *New Zealand Journal of Marine and Freshwater Research* 32, 21-29.
- Ryan, P. A. (1991). Environmental effects of sediment on New Zealand streams: a review. *New Zealand Journal of Marine and Freshwater Research* 25, 207–215.

- Sklar, F. H., Browder, J. A., 1998. Coastal environmental impacts brought about by alterations to freshwater flow in the Gulf of Mexico. *Environmental Management* 22, 547-562.
- Sluss, T. D., Cobbs, G.A., Thorp, J.H., 2008. Impact of turbulence on riverine zooplankton: a mesocosm experiment. *Freshwater Biology* 53, 1999-2006.
- Souissi, A., Souissi, S., Hwang, J.-S., 2013. The effect of epibiont ciliates on the behavior and mating success of the copepod *Eurytemora affinis*. *Journal of Experimental Marine Biology and Ecology* 445, 38-43.
- Taylor, R. H., 2006. Ecological responses to changes in the physical environment of the St Lucia Estuary. Ph. D. Thesis, Department of Plant and Environmental Sciences, Norwegian University of Life Sciences.
- Taylor, R. H., 2013. Management history. Pages 21-45 *in*: R., Perissinotto, D., Stretch, and R., Taylor, editors. *Ecology and Conservation of Estuarine Ecosystems: Lake St Lucia as a Global Model*. Cambridge University Press, USA.
- Tilzer, M. M., 1983. The importance of fractional light absorption by photosynthetic pigments for phytoplankton productivity in Lake Constance. *Limnology and oceanography* 28, 833-846.
- Turner, J. T., Postek, M. T., Collard, S. B., 1979. Infestation of the estuarine copepod *Acartia tonsa* with the ciliate *Epistylis*. *Transactions of the American Microscopical Society* 98 (1), 136-138.
- Utz, L., 2003. Identification, life history, and ecology of peritrich ciliates as epibionts on Calanoid copepods in the Chesapeake Bay. Ph. D. Thesis, Smithsonian Environmental Research Center.
- Utz, L., Coats, D., 2005. Spatial and temporal patterns in the occurrence of peritrich ciliates as epibionts on calanoid copepods in the Chesapeake Bay, USA. *The Journal of Eukaryotic Microbiology* 52, 236-244.
- van Elden, S., Dyer, M. J., Carrasco, N. K., Perissinotto, R., 2014. Meso-zooplankton movement through the newly constructed Mfolozi channel into and out of the St Lucia Estuary, South Africa: short communication. *African Zoology* 49, 317-325.
- Vinyard, G. L., O'Brien, W. J., 1976. Effects of light and turbidity on the reactive distance of bluegill (*Lepomis macrochirus*). *Canadian Journal of Fishery and Aquatic Science* 33, 2845-2849.

- 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, 173-178.
- Vivier, L., Cyrus, D. P., 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, 118-125.
- Walling, D. E., 2006. Human impact on land–ocean sediment transfer by the world's rivers. Geomorphology 79, 196-213.
- Weissman, P., Lonsdale, D. J., Yen, J., 1993. The effect of peritrich ciliates on the production of *Acartia hudsonica* in Long Island Sound. Limnological Oceanography 38, 613-622.
- Whalen, S. C., Chalfant, B. B., Fischer, E. N., Fortino, K. A. Hershey, A. E., 2006. Comparative influence of resuspended glacial sediment on physicochemical characteristics and primary production in two arctic lakes. Aquatic Sciences 68, 65-77.
- Whitfield, A. K., Bate, G. C., Forbes, T., Taylor, R. H., 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, 104-110.
- Whitfield, A.K., Taylor, R.H., 2009. A review of the importance of freshwater inflow to the future conservation of Lake St Lucia. Aquatic Conservation 19, 838-848.
- Wood, P. J., Armitage, P. D., 1997. Biological effects of fine sediment in the lotic environment. Environmental Management 21, 203-217.

