Original Research Article

Response of zooplankton communities to altered water quality and seasonal flow changes in selected river dominated estuaries in KwaZulu-Natal, South Africa

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ABSTRACT

Globally, estuaries are among the most productive ecosystems with many threatened by anthropogenic activities. Zooplankton is a bioindicator of ecosystem integrity. The spatial and temporal composition of zooplankton communities were quantified and compared within and between three estuaries (uMvoti, Thukela and aMatikulu/Nyoni estuaries) with different levels of human pressure in KwaZulu-Natal, South Africa. Additional effects of some physico-chemical variables and seasonal flow patterns to zooplankton community structuring were analyzed. The aMatikulu/Nyoni Estuary was selected as a reference site due to its good ecological state. Sampling dates represented high flow (March and April) and low flow (August and September) from 2014 to 2016. Following aMatikulu/Nyoni, highest abundance was recorded in Thukela and then uMvoti Estuary with copepod *Pseudodiaptomus hessei* and *Acartia natalensis* dominating the three estuaries. Highest abundance was recorded during low flow in the uMvoti and Thukela estuaries. Redundancy analysis revealed higher salinity and oxygen as environmental determinants of zooplankton community structure in the aMatikulu/Nyoni while turbidity and pH were the determinants of zooplankton community structures in uMvoti and Thukela estuaries. Elevated concentrations of DIN in the Thukela Estuary during high flow identifies the Thukela River as an important source of nitrogen to this estuary. Our findings suggest that these estuaries be managed to ensure sufficient freshwater supply which controls primary production. Although the three estuaries were from the same biogeographical region with a similar river dominated function, high variability in their zooplankton communities could be explained by differing water quality due to differing human pressure in their catchments.

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1. Introduction

Estuaries provide nursery grounds for many marine species (Vasconcelos et al., 2010). There is spatial variation in zooplankton community structures in estuaries as a result of highly dynamic conditions experienced by organisms in these systems, such as salinity fluctuation and variation in water temperature (Allen et al., 2008; Barros et al., 2015).

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Zooplankton plays a significant role in energy transfer from primary producers to higher trophic levels (Degerman et al., 2018). Zooplankton also serves as a good indicator of biodiversity because of its high sensitivity to environmental change (Gorokhova et al., 2016). Zooplankton communities in South African permanently open estuaries (POE) are mostly dominated by copepods and mysids, with copepods making a substantial contribution to abundance (Wooldridge, 1999). As it is nutrient-rich from land drainage, river inflow is one of the drivers structuring estuarine zooplankton communities (Venkataramana et al., 2017).

Globally there has been a deterioration in the ecological health of many estuaries as a result of excessive anthropogenic water abstraction, agricultural activities and industrial effluents (Quinton and Catt, 2007; Zhang et al., 2012; Wang et al., 2014; Liu et al., 2015). Many estuaries along the north coast of the KwaZulu-Natal (KZN) Province, South Africa, are affected by the reduced flows, poor water quality, and habitat alterations originating from different levels of human pressure (King and Pienaar, 2011). The uMvoti Estuary is regarded as a polluted system (O'Brien et al., 2009). There has been a deterioration in the ecological health of the Thukela Estuary over the last few decades (Lamberth et al., 2009). The aMatikulu/Nyoni Estuary (hereafter referred to as aMatikulu Estuary) is in a good ecological condition although siltation from the catchment is of concern (Whitfield, 2000). As a consequence of its good condition, the aMatikulu Estuary was selected as the reference site for the present study.

Zooplankton is highly sensitive to environmental change and variation in their abundance, biomass and diversity depict that it is ecologically important (Gorokhova et al., 2016). However, zooplankton has been generally less considered when studying biological responses to changes in environment (Mialet et al., 2011; Gorokhova et al., 2016). The labour intensity needed to study zooplankton in generally turbid systems like estuaries is one reason for a low number of studies following response of zooplankton to environmental change (Mialet et al., 2011). Previous studies have reported negative effect on zooplankton as a result of hypoxic and anoxic conditions in polluted systems (e.g. Soetaert and Van Rijswijk, 1993; Albaina et al., 2009). However, in South Africa, studies on the response of zooplankton to altered water quality and quantity as a result of different levels of human pressure are scarce. There is a paucity of data on the zooplankton of KZN estuaries with only few systems investigated (e.g. Kibirige and Perissinotto, 2003; Jerling, 2005; Perissinotto et al., 2003; Montoya-Maya and Strydom, 2009), and there is hardly any seasonal flow studies.
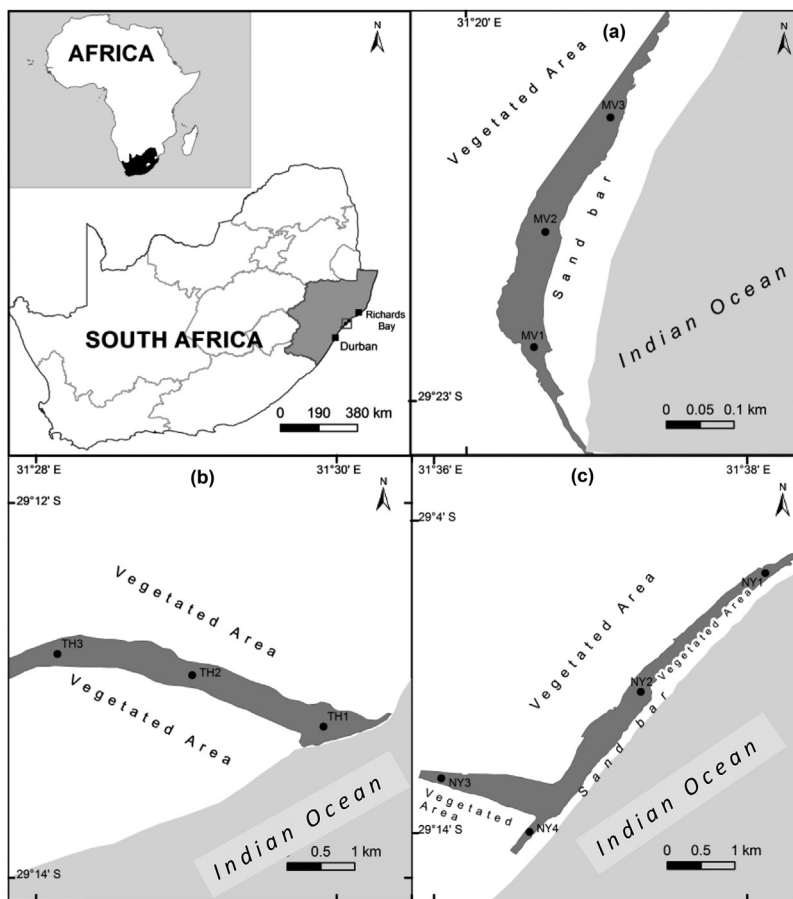

Fig. 1. The uMvoti (a), Thukela (b) and aMatikulu (c) estuaries with sampling sites occupied at each system during the study period. MV1-3 = uMvoti Estuary site 1–3; TH1-3 = Thukela Estuary sites 1–3, NY1-4 = aMatikulu Estuary sites 1–4.

The zooplankton of the uMvoti, Thukela and aMatikulu estuaries in KZN for the period of August 2014 to September 2016 was analyzed to determine the response of zooplankton to contrasting levels of water quality (e.g. oxygen, turbidity, nutrients and chl-a) as well as seasonal flow changes. We aimed to quantify and compare spatial and temporal composition of zooplankton communities within and between the three estuaries (uMvoti, Thukela and aMatikulu estuaries) in KZN with different ecological states and different levels of human pressure in their catchments. Additionally, effects of some physico-chemical variables and seasonal flow patterns to zooplankton community structuring were analyzed. We posed the following questions: (i) how zooplankton community structure changes along the salinity gradient during high and low flow periods, and (ii) which environmental variables were most important in structuring zooplankton communities in the three estuaries studied. These estuaries are similar in function and geographical area. We hypothesized that zooplankton abundances and taxa composition among the three estuaries would differ and that the differences would be related to varying water quality in their catchments.

2. Materials and methods

2.1. Study sites

Three estuaries (uMvoti (MV), Thukela (TH) and aMatikulu (NY) along the KZN north coast, South Africa (Fig. 1), were selected for this study. As a consequence of its relatively good ecological state, the aMatikulu system was selected as a reference site.

2.1.1. uMvoti Estuary

The uMvoti Estuary (29°23′ S, 31°20′ E) (Fig. 1) is a subtropical river mouth (Whitfield, 2000) situated north of the coastal town of KwaDukuza (Stanger). This Estuary occupies an area of approximately 0.2 km² with a shallow mean depth of less than 0.5 m (Begg, 1984). The uMvoti River catchment is subject to agricultural activities which include commercial forestry, sugar cane farming, commercial dry land agriculture and subsistence farming. The uMvoti Estuary has a limited potential for significant tidal exchange (Wepener, 2007). The seawater penetration is 500 m upstream (Begg, 1978).

2.1.2. Thukela Estuary

The Thukela Estuary (29°13′ S, 31°29′ E) (Fig. 1) is a subtropical river mouth (Whitfield, 2000). The Thukela River is the second largest river in South Africa with a catchment area of 29,000 km² (Whitfield and Harrison, 2003). The estuarine area is relatively small with a surface area of approximately 0.6 km² (Begg, 1978) and a depth of 1.5 m (Archibald, 1998). During floods the width of the Thukela Estuary increases to 1000 m and the estuary extends out to the sea as no sea water can penetrate the estuary (Begg, 1978). The large quantities of silt transported into the Thukela Estuary have resulted in a vertical shelf leading to minimal sea water penetration (De Lecea and Cooper, 2016).

2.1.3. aMatikulu/Nyoni Estuary

The aMatikulu Estuary (36°06′ S, 31°37′ E) (Fig. 1) is a subtropical permanently open estuary (Whitfield, 2000) with a surface area of approximately 2.6 km². The aMatikulu River joins the Nyoni River and flows parallel to the Indian Ocean before it empties into this ocean approximately 105 km north of Durban. The aMatikulu Estuary was usually shallow during the present study with a mean depth of 0.6 m. There are sugar cane plantations upstream of the aMatikulu River. In the lower reaches, the estuary is disturbed by agricultural activities but the fauna generally remains in good condition (Harrison et al., 2000). The aMatikulu Estuary has a good ichthyofauna, water quality and aesthetics (Harrison et al., 2000). This system is described as a system that shares a common mouth and should be conserved as an item (Heydorn, 1986). The aMatikulu Estuary forms part of the aMatikulu nature reserve, managed by the Ezemvelo KwaZulu-Natal Wildlife (EKZNW) Authority.

2.2. Sampling and laboratory analysis

Zooplankton samples were collected in the uMvoti, Thukela and aMatikulu Estuary during 2014 (15 August), 2015 (13 March and 17 August) and 2016 (18 April and 20 September). Sampling dates were selected for high flow (March and April) and low flow (August and September) as referred to hereafter. Three sites were sampled in uMvoti and Thukela estuaries and four sites in aMatikulu Estuary, which has a greater length than the other two estuaries (Fig. 1). During each sampling occasion, daytime sampling was conducted using a hyperbenthic zooplankton sled (mesh size = 200 μm, towing distance = 20 m, volume filtered = 1 m^{-3}) (Kibirige et al., 2006). In each estuary, three replicate samples were collected at each site during all sampling sessions. The zooplankton samples were preserved in 10% formalin containing Rose Bengal dye. In situ physico-chemical data including oxygen, salinity, temperature, pH and turbidity were recorded during each survey in each site using a calibrated portable metre (Eutech instruments CyberScan series 600, Thermo Fisher, USA). Water quality samples were collected from the water column using polyethylene bottles. These were thereafter sent to Umgeni Water Laboratory (an accredited laboratory with the South African National Accreditation System and the International Standard ISO/IEC 17025:2005) for nutrients (dissolved inorganic nitrogen (DIN) and dissolved inorganic phosphorus (DIP)) and chlorophyll a (chl-a). High reed density and grass in the middle reaches of aMatikulu Estuary (i.e. NY2 and NY3 during March 2015 and NY3 during August 2015) prevented boat access. As a result, some gaps in data from these two middle sites in the aMatikulu Estuary during this year occur. Some water quality data from the same sites and dates were obtained from the Department of Water and Sanitation, South Africa. Data for DIN, DIP and chl-a are absent for April 2016 in the uMvoti Estuary because of insufficient sample volume.

In the laboratory, zooplankton samples were diluted to 1–5 L solutions depending on the concentration of the sample. Organisms in each sample were kept in suspension
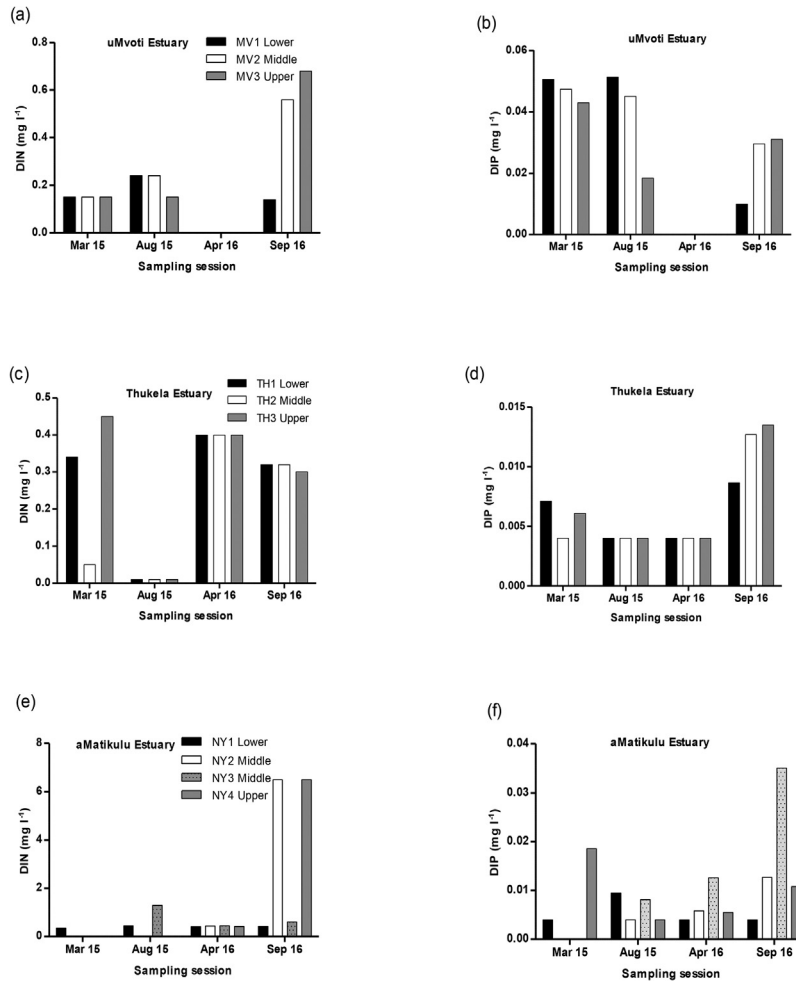
Fig. 2. Dissolved inorganic nitrogen (DIN) (a, c and e) and dissolved inorganic phosphorus (DIP) (b, d and f) measured in the uMvoti, Thukela and aMatikulu Estuary during the study period.

by thorough stirring of the sample and three sub samples for identification and enumeration withdrawn using a 20 ml scoop attached to a metal rod after penetrating the entire depth (Jerling and Wooldridge, 1995; Carrasco et al., 2010). The coefficient of variation between subsamples was below 10%. Organisms in each subsample were identified to the lowest taxa possible and enumerated using a dissecting microscope and zooplankton abundance for each main sample expressed as the number of individuals per cubic metre (ind. m^{-3}).

2.3. Statistical analysis

The CANOCO software package, version 4.5. (Ter Braak, 1994) was used. Ordination techniques were applied using the original zooplankton community data sets (main samples in each site) which allowed for intepretation of zooplankton community structures with regards to taxa recorded during the study (Van den Brink et al., 2003). These practises evaluated changes in zooplankton com-

munity structures and then tested the statistical signifi- cance of differences in communities after incorporated with Monte Carlo permutation testing (Ter Braak and Smillauer, 2004). Redundancy analysis (RDA) was adopted to accomplish this (Ter Braak, 1994). Because zooplankton abundance data were available, the data were transformed using a Log $X + 2$ – transformation (Van den Brink et al., 2003). Redundancy analyses were performed to detect if there were any significant differences in zooplankton community structures between sites, years and flows using Monte Carlo permutation tests (999 unrestricted permutations) ($p < 0.05$). Already available data for uMvoti and Thukela zooplankton collected in 2014 were incorporated to the data set. Sites and taxa were firstly presented as points at the location of the values in the diagram. After incorporating available environmental data, tri-plots were constructed. These tri-plots displayed arrows of environmental data which were directed to higher values where there was existence of correlations between sites and environmental variables (Van den Brink et al., 2003).

3. Results

3.1. Environmental variables

Measurements of the physico–chemical variables including temperature, dissolved oxygen, salinity, turbidity and chlorophyll a (chl-a) recorded in the uMvoti, Thukela and aMatikulu estuaries during the current study are presented in the supplementary material (Table S1). Concentrations of nutrients (DIN and DIP) measured in the three estuaries during the current study are presented in Fig. 2.

3.1.1. uMvoti estuary
Water temperature in the uMvoti Estuary exhibited lower values during low flows with the lower reaches exhibiting generally lower values. Dissolved oxygen concentrations increased from the lower to the upper reaches. Although there was a general increase in salinity values from the upper to the lower reaches, salinity values were the same throughout the estuary during August 2014 and March 2015. Turbidity levels showed no clear trend along the estuary. In Table S1 absent chl-a values in all the estuaries studied as a result of sample size are represented by (*) symbol. Maximum pelagic chl-a values in the uMvoti Estuary were measured during the low flow and the values ranged from a minimum of $0.3\ \mu g\,l^{-1}$ during 2016 to a maximum of $66.4\ \mu g\,l^{-1}$ during 2015. Dissolved inorganic nitrogen concentrations were higher during the low flow when compared with the high flow (Fig. 2). Concentrations of DIN ranged from $0.14\ mg\,l^{-1}$ during 2015 to $0.68\ mg\,l^{-1}$ during 2016. Highest DIP concentration ($0.05\ mg\,l^{-1}$) was recorded during 2015 while the lowest ($0.01\ mg\,l^{-1}$) was recorded during 2016 with a general decrease in values from lower to the upper reaches (Fig. 2).

3.1.2. Thukela Estuary
Water temperature in the Thukela Estuary exhibited lower values during low flows with generally lower values near the mouth region. There was no clear trend in oxygen concentrations and salinity values along the estuary. Higher turbidity levels were recorded during high flows with an increase from the upper to the lower reaches. Maximum chl-a values in the Thukela Estuary were measured during the low flow and the values ranged from $0.3\ \mu g\,l^{-1}$ during 2016 to $13\ \mu g\,l^{-1}$ during 2015. Concentrations of DIN were lower during low flow and ranged from $0.01\ mg\,l^{-1}$ during 2015 to $0.45\ mg\,l^{-1}$ during 2015 (Fig. 2). Concentrations of DIP showed no clear trend along the estuary and they ranged from $0.004\ mg\,l^{-1}$ during 2015 to $0.01\ mg\,l^{-1}$ during 2016 (Fig. 2).

3.1.3. aMatikulu/Nyoni Estuary
Similar to uMvoti and Thukela estuaries, water temperature in the aMatikulu Estuary exhibited lower values during the low flows and lower temperature values generally measured in the lower reaches. Contrary to the uMvoti Estuary, dissolved oxygen concentrations in the aMatikulu Estuary generally increased from the upper to the lower reaches. Salinity values increased from the upper to the lower reaches. Turbidity values showed no clear trend along the estuary. No clear pattern in chl-a values along the estuary was observed and values ranged from $0.3\ \mu g\,l^{-1}$ during 2016 to $15.8\ \mu g\,l^{-}$ during 2015. Concentrations of DIN ranged from $0.01\ mg\,l^{-1}$ during 2015 to $6.5\ mg\,l^{-1}$ during 2016 with higher concentrations recorded during low flow (Fig. 2). Highest DIP concentration ($0.03\ mg\,l^{-1}$) was recorded during 2016 while the lowest ($0.004\ mg\,l^{-1}$) was recorded during all the sampling sessions of the current study (Fig. 2).

3.2. Zooplankton

3.2.1. uMvoti Estuary
A total of six zooplankton taxa were recorded in the uMvoti Estuary during the present study (Table 1). Zooplankton abundances in this system were higher during the low flow with a maximum abundance ($456.5\ ind.\,m^{-3}$) recorded during 2014 (Fig. 3a). After *Pseudodiaptomus hessei, Acartia natalensis* and Chironomidae were the taxa more represented in terms of abundance (Fig. 3b). Combined the dominant zooplankton taxa accounted for 98% (Aug-14), 23% (Mar-15), 84% (Aug-15), 100% (Apr-16) and 61% (Sep-16) of the total zooplankton abundance in this system. Abundance for the most dominant zooplankton taxa reached a maximum of $145.3\ ind.\,m^{-3}$ (Fig. 3b).

3.2.2. Thukela Estuary
A total of nine zooplankton taxa were recorded in the Thukela Estuary out of a maximum zooplankton abundance of $955.3\ ind.\,m^{-3}$ (Table 2, Fig. 3c). Zooplankton abundances in this system were higher during the low flow when compared with the high flow. Following, *P. hessei, A. natalensis* and Nematoda were the most dominant taxa in terms of abundance (Fig. 3d). Combined, these zooplankton taxa accounted for 55% (Aug-14), 33% (Mar-15), 94% (Aug-15), 64% (Apr-16), and 48% (Sep-16) of the total zooplankton abundance. Abundance for the most dominant zooplankton taxa reached a maximum of $227.9\ ind.\,m^{-3}$ (Fig. 3d).

3.2.3. aMatikulu/Nyoni Estuary
A total of ten zooplankton taxa were recorded in the aMatikulu Estuary out of a maximum abundance of $15{,}086.9\ ind.\,m^{-3}$ (Table 3, Fig. 3e). After *A. natalensis, P. hessei* and *Mesopodopsis africana* were the taxa more represented in terms of abundance (Fig. 3f). Combined these zooplankton taxa accounted for 99% (Mar-15), 95% (Aug-15), 87% (Apr-16) and 45% (Sep-16) of the total zooplankton. Maximum abundance for the most dominant zooplankton taxa was $2049.3\ ind.\,m^{-3}$ (Fig. 3f).

3.2.4. Multivariate analyses
The RDA tri-plot which was constructed using log transformed species data, separated zooplankton data into three distinct faunal assemblages representing the three estuaries studied (Fig. 4a). The triplot explained 76.5% of variation in the data (65.7% on axis 1 and 10.8% on axis 2). There was a significant difference in zooplankton community structures between sampling sites ($p < 0.05$). Follow-

Table 1
Composition (mean ± SD) of zooplankton taxa (ind. m^{-3}) recorded in the uMvoti Estuary from August 2014 to September 2016. MV1-3 = uMvoti Estuary sites 1–3.

|	Aug-14			Mar-15			Aug-15			Apr-16			Sep-16		
	MV1	MV2	MV3	MV1	MV2	MV3	MV1	MV2	MV3	MV1	MV2	MV3	MV1	MV2	MV3
TAXA															
HEXANAUPLIA															
Acartiidae	45.6 ± 64.6	4.2 ± 0.0	264.2 ± 17.9	0.9 ± 1.6			44.3 ± 29.1								
Pseudodiaptomidae	376.3 ± 477.3	1.4 ± 1.9	55.3 ± 2.8				9.2 ± 16.0		5.5 ± 5.9	9.2 ± 16.0			15.2 ± 13.5	11.1 ± 2.8	0.9 ± 1.6
BRANCHIOPODA															
Cladocera sp.	17.9 ± 21.5		2.8 ± 0.0												
MALACOSTRACA															
Mysidae	1.4 ± 2.0			130.9 ± 226.8											
Cumacea sp.							2.8 ± 4.8								
OSTRACODA															
Ostracoda sp.					0.9 ± 1.6		2.8 ± 0.0						13.2 ± 18.4	4.6 ± 5.8	1.4 ± 2.4
INSECTA															
Chironomidae	15.2 ± 13.7		6.9 ± 1.4	1.8 ± 3.4	1.8 ± 1.6		47.9 ± 54.9	11.9 ± 4.2	108.2 ± 111.7	18.5 ± 32.0		9.2 ± 16.0	30.4 ± 25.4	24.9 ± 18.1	14.8 ± 13.6
Culicidae				0.9 ± 1.6											
Insecta sp.															5.5 ± 5.5
SCYPHOZOA															
Cyaneidae			1.4 ± 1.4										1.4 ± 1.6		
CLITELLATA															
Oligochaeta sp.							0.9 ± 1.6								
NEMATODA															
Nematoda sp.								1.8 ± 3.2	50.8 ± 71.9					12.9 ± 4.2	5.5 ± 5.5
TOTAL	456.4 ± 579.1	5.6 ± 1.9	330.6 ± 23.5	134.5 ± 233.4	2.7 ± 3.2	0.0	107.9 ± 106.4	13.7 ± 7.4	164.5 ± 189.5	27.7 ± 48.0	0.0	9.2 ± 16.0	60.2 ± 58.9	53.5 ± 30.9	28.1 ± 28.6
NO. OF TAXA	5	2	5	4	2	0	6	2	3	2	0	1	4	4	5
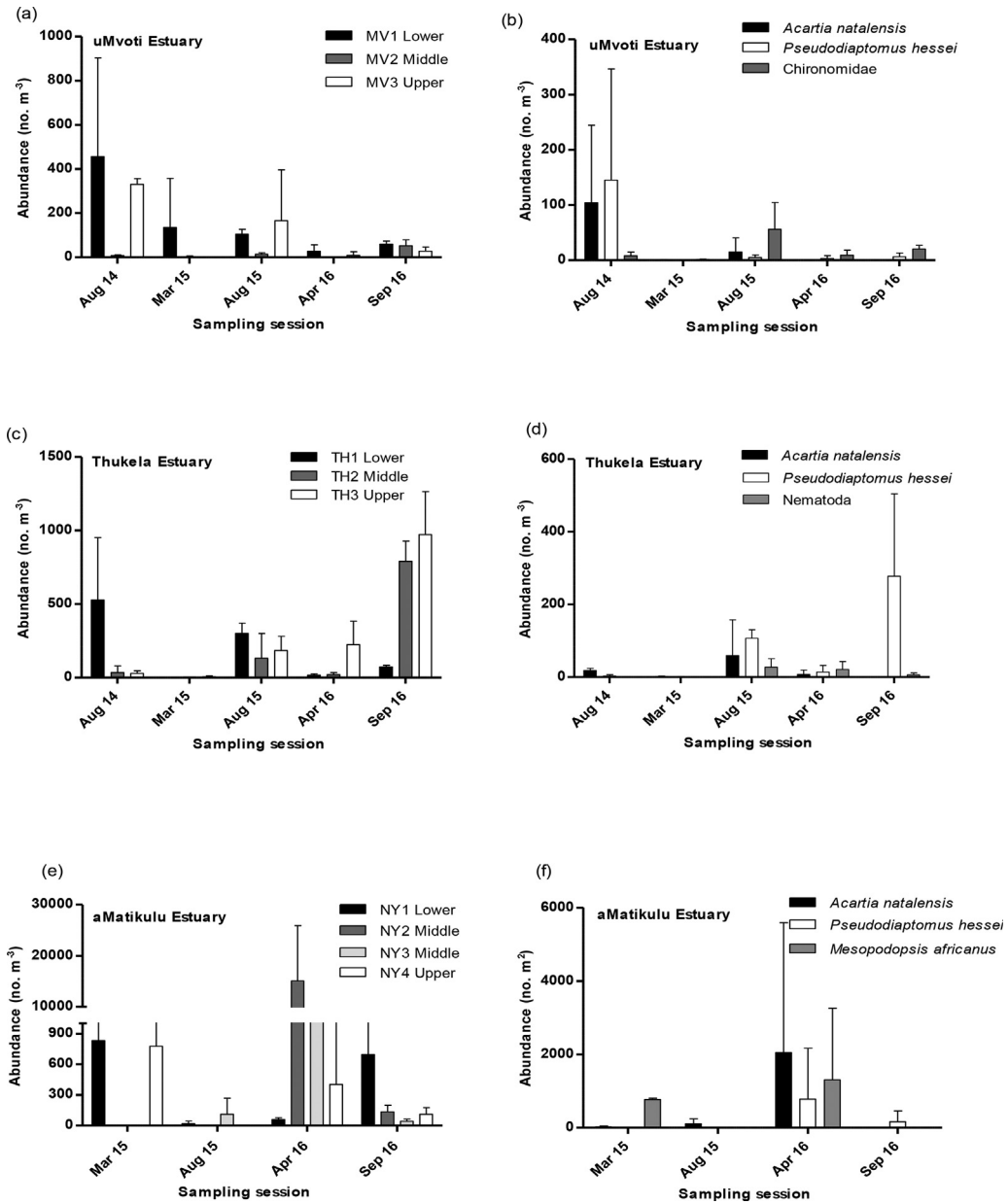
Fig. 3. Numerical abundance (mean ± SD, $n = 3$) of total zooplankton (a, c and e) and the three dominant species (b, d and f) in the uMvoti, Thukela and aMatikulu estuaries.

ing 2016, year 2014 and 2015 had highest influence in structuring zooplankton communities (Fig. 5b). This triplot explained 73.1% of variation in the data (51.4% on axis 1 and 21.7% on axis 2). There was a significant difference in zooplankton community structure between years ($p < 0.05$). There was also a significant difference between flows ($p < 0.05$), although with both flows having a more or less equal influence on the community structure (Fig. 5a). Water quality variables responsible for structuring the zooplankton community assemblages in the uMvoti,

Thukela and aMatikulu estuaries are shown in Fig. 4b. The RDA plot showed that higher salinity and oxygen contributed to the structuring of the zooplankton community in the aMatikulu Estuary while turbidity and pH contributed to the structuring of zooplankton community in the uMvoti and Thukela estuaries (Fig. 4b). The triplot explained 66% of variation in the data (42.2% on axis 1 and 23.8% on axis 2). The influence of water quality variables in structuring the zooplankton assemblages was significant ($p < 0.05$).

Table 2

Composition (mean ± SD) of zooplankton taxa (ind. m^{-3}) recorded in the Thukela Estuary from August 2014 to September 2016. TH1-3 = Thukela Estuary sites 1–3.

	Aug-14			Mar-15			Aug-15			Apr-16			Sep-16		
	TH1	TH2	TH3	TH1	TH2	TH3	TH1	TH2	TH3	TH1	TH2	TH3	TH1	TH2	TH3
TAXA															
HEXANAUPLIA															
Acartiidae	11.1 ± 11.7	22.1 ± 31.2	22.1 ± 19.6			2.8 ± 2.8	173.6 ± 42.5	1.8 ± 3.2	2.8 ± 4.8			21.2 ± 18.0			
Pseudodiaptomidae		6.9 ± 9.8	1.4 ± 2.0			0.9 ± 1.8	126.6 ± 93.9	81.2 ± 124.2	114.4 ± 71.1	9.2 ± 8.0		34.1 ± 37.8	21.2 ± 3.2	349.5 ± 227.9	459.3 ± 340.9
Copepod sp.								0.9 ± 1.6				0.9 ± 1.6			
Copepod nauplii	1.4 ± 2.0		1.4 ± 2.0									1.8 ± 3.2			
BRANCHIOPODA															
Cladocera sp.	513.2 ± 408.9	2.8 ± 3.9						0.9 ± 1.6							
MALACOSTRACA															
Mysidae											0.9 ± 1.6	106.9 ± 161.5			
Cumacea sp.															
Shrimp larvae				0.9 ± 1.6						0.9 ± 1.6					
Penaeidae						0.9 ± 1.6							0.9 ± 1.6	0.9 ± 1.6	
Luciferidae											0.9 ± 1.6				
Aoridae												2.8 ± 4.8			
Hymenosomidae												1.8 ± 3.2			
OSTRACODA															
Ostracoda sp.									28.6 ± 20.8						
INSECTA															
Chironomidae		4.2 ± 2.0		0.9 ± 1.6	0.9 ± 1.6								22.1 ± 4.8	374.4 ± 155.5	468.5 ± 73.5
Culicidae				0.9 ± 1.6											
Ectinosomatidae										0.9 ± 1.6					
Diptera sp.											0.9 ± 1.6				
Insect sp.														1.8 ± 1.6	
SCYPHOZOA															
Cyaneidae										0.9 ± 1.6					
CLITELLATA															
Oligochaeta sp.													0.9 ± 1.6	4.6 ± 8.0	
NEMATODA															
Nematoda sp.								45.2 ± 41.6	35.9 ± 36.0	0.9 ± 1.6	16.6 ± 14.4	45.2 ± 68.9	12.9 ± 8.4	46.0 ± 12.8	14.6 ± 6.4
LEPTOCARDII															
Branchiostomatidae			42.0 ± 2.0												
SAGITTOIDEA															
Sagittidae								1.8 ± 1.6	1.8 ± 3.2						
POLYCHAETA															
Nereididae											2.8 ± 2.8			3.7 ± 3.2	7.4 ± 3.2
Sabellidae											0.9 ± 1.6				
Phyllodocidae												1.8 ± 3.2			
GASTROPODA															
Gastropod sp.													0.9 ± 1.6		
TOTAL	527.7 ± 422.6	36.0 ± 46.9	66.9 ± 25.6	0	2.7 ± 4.8	5.5 ± 7.8	300.2 ± 136.4	131.8 ± 173.8	183.5 ± 135.9	16.5 ± 18.8	19.3 ± 19.2	216.5 ± 302.2	58.9 ± 21.2	780.9 ± 410.6	949.8 ± 424
NO. OF TAXA	3	4	4	0	3	4	2	6	5	7	4	9	6	7	4

Table 3

Composition (mean ± SD) of zooplankton taxa (ind. m^{-3}) recorded in the aMatikulu Estuary from March 2015 to September 2016. NY1-4 = aMatikulu Estuary sites 1–4.

|	Mar-15				Aug-15				Apr-16				Sep-16			
	NY1	NY2	NY3	NY4	NY1	NY2	NY3	NY4	NY1	NY2	NY3	NY4	NY1	NY2	NY3	NY4
TAXA																
HEXANAUPLIA																
Acartiidae	40.6 ± 70.3			11.1 ± 10.0			202.0 ± 116.6		20.3 ± 4.2	7349.3 ± 9230.0	489.9 ± 345.4	299.7 ± 444.9		12.9 ± 17.8	2.8 ± 8.9	11.0 ± 8.3
Pseudodiaptomidae				16.6 ± 28.8	15.7 ± 27.2		6.5 ± 11.2		18.4 ± 6.4	2865.8 ± 1902.9	143.3 ± 140.3	94.1 ± 158.1	603.1 ± 511.7	41.5 ± 10.0	10.1 ± 2.8	12.0 ± 4.2
MALACOSTRACA																
Mysidae	790.3 ± 684.6			747.2 ± 628.1					2.8 ± 2.8	4132.3 ± 1244.1	1100.1 ± 1040.5	2.8 ± 0.0				
Cumacea sp.										688.7 ± 427.9		1.8 ± 3.2				
Aoridae				0.9 ± 1.6	0.9 ± 1.6				2.8 ± 0.0	18.5 ± 32.0	4.6 ± 8.0		19.3 ± 33.5		22.1 ± 10.0	12.0 ± 8.5
Dexaminidae									0.9 ± 1.6							
Leptostraca sp.													56.0 ± 20.8	78.4 ± 46.3	2.8 ± 3.2	54.8 ± 28.8
Shrimp larvae													0.9 ± 1.6			0.9 ± 1.6
Mysid larvae	1.8 ± 3.2			3.7 ± 4.2												
Isopod sp.																0.9 ± 1.6
INSECTA																
Chironomidae					0.9 ± 1.6								5.5 ± 2.8	0.9 ± 1.6	0.9 ± 1.6	5.5 ± 7.3
NEMATODA																
Nematoda sp.									11.9 ± 13.6	27.7 ± 48.0			0.9 ± 1.6		0.9 ± 1.6	0.9 ± 1.6
POLYCHAETA																
Nereididae										4.6 ± 8.0			8.3 ± 12.1			7.4 ± 12.8
Spionidae												3.7 ± 6.4		0.9 ± 1.6		
Polychaete sp.												0.9 ± 1.6				
Phyllodosidae																2.8 ± 2.8
TOTAL	832.7 ± 722.1			779.5 ± 672.5	17.5 ± 30.4		208.5 ± 127.8		57.1 ± 28.6	4871.8 ± 1760.0	1737.9 ± 1534.2	403.0 ± 614.2	694.0 ± 584.1	134.6 ± 77.3	39.6 ± 28.1	108.2 ± 77.5
NO. OF TAXA	3			5	3		2		6	7	4	6	7	5	6	10
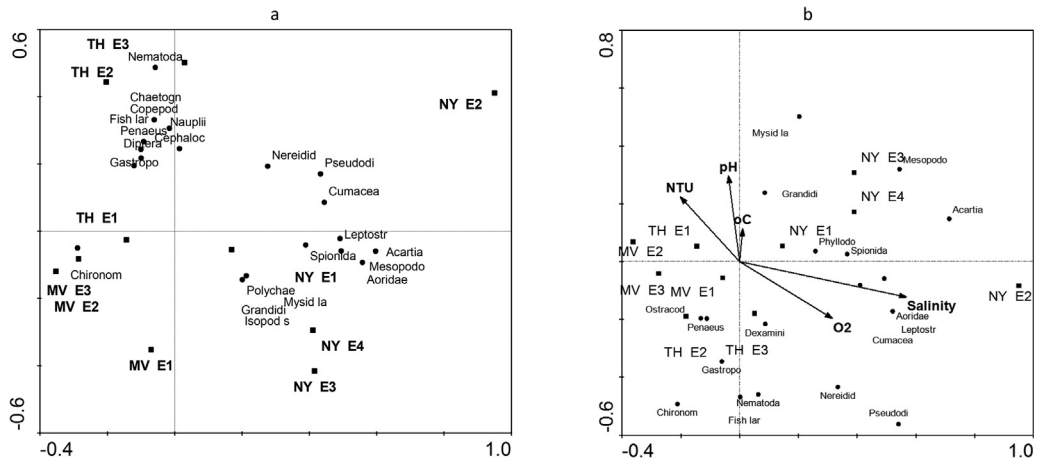
Fig. 4. RDA triplots showing the relationship between zooplankton species and (a) sampling sites and (b) selected water quality variables. (MV-E1-3 = uMvoti Estuary site 1–3; TH-E1-3 = Thukela Estuary sites 1–3, NY-E1-4 = aMatikulu Estuary sites 1–4).
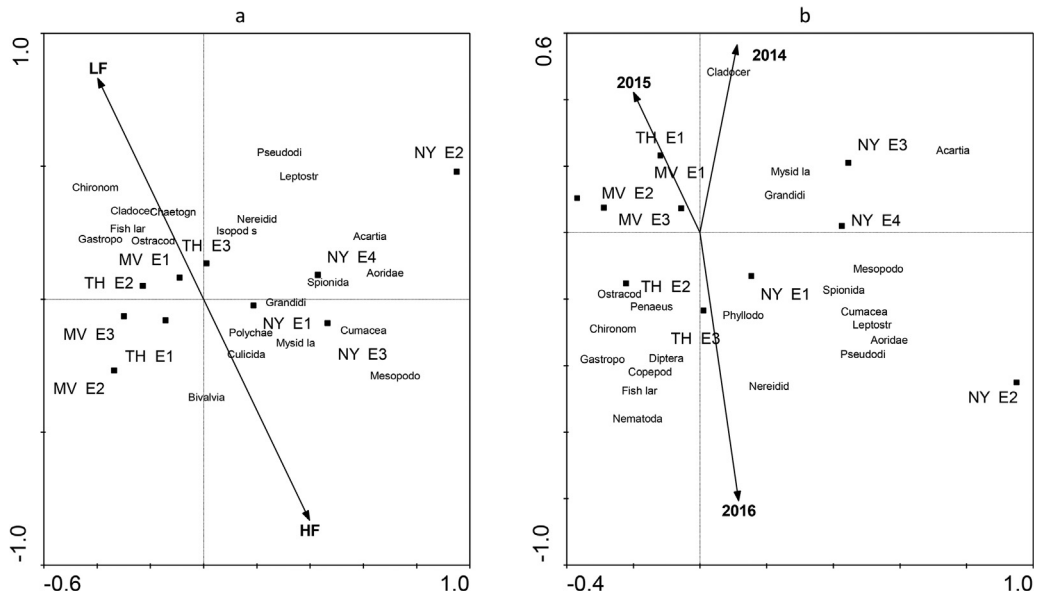

Fig. 5. RDA triplots showing the relationship between zooplankton species and (a) flows and (b) years. (MV-E1-3 = uMvoti Estuary site 1–3; TH-E1-3 = Thukela Estuary sites 1–3, NY-E1-4 = aMatikulu Estuary sites 1–4, HF = High flow, LF = low flow).

4. Discussion

4.1. Environmental variables

In the current study some physico-chemical parameters between the three estuaries were highly variable. Although the three estuaries studied occur in the same geographical area and are geomorphologically similar (Harrison et al., 2000), the variability in water quality conditions can be attributed to different levels of human pressure on these systems. Lower temperatures recorded during low flow were associated with the winter season of South Africa where there is low rainfall and cold weather conditions. The aMatikulu Estuary had the highest oxygen concentrations while the uMvoti Estuary displayed the lowest. Anthropogenic threats that might be affecting

oxygen concentrations in the aMatikulu Estuary are restricted to sedimentation and water quality alteration primarily. Sources of stressors in the aMatikulu system include one sugar mill and associated agricultural activities upstream.

The uMvoti River catchment in comparison is highly utilized and affected by multiple upstream sources including industries, waste water treatment works, agricultural activities, water abstraction and urban and peri-urban communities. Anthropogenic threats associated with these users might have resulted in reduction in oxygen levels in this system during the current study. The low to moderate oxygen levels in the Thukela Estuary may also be attributable to local catchment human pressure including industries, mining, agriculture, recreation, paper mill and waste water treatment works. Water quality of

uMvoti system has been identified as grossly polluted as early as 1964 (Begg, 1978). Other studies have also reported water quality alteration in this system including reduced oxygen and increased chemical oxygen demand (Malherbe et al., 2010, Venter, 2013). High chemical oxygen demand originates from biodegradable wastes such as those from sewage, pulp and paper industries, and chemical industry (Kanu and Achi, 2011). All these different anthropogenic pressures act in the upper catchment of the uMvoti Estuary thus affecting its water quality. High variability in salinity levels between the three estuaries studied was observed. The lower salinity values recorded from the Thukela and uMvoti systems are attributed to the river dominated nature of these systems. Marine water has a very little influence on these estuaries. The uMvoti Estuary has a limited potential for significant tidal exchange (Badenhorst, 1990). Furthermore, the sea water intrusion in the Thukela Estuary is only effective on spring high tide when the river flow is low (Whitfield and Harrison, 2003). Salinities recorded in the three estuaries were within the ranges of river dominated estuaries in South Africa (Whitfield, 1992).

Turbidity values varied largely between the three estuaries with the highest turbidity levels recorded from the Thukela and the lowest from the aMatikulu Estuary. Generally higher turbidity levels were recorded during high flow and this can be explained by associated higher rainfall which results in sediment disturbance increasing the levels of total suspended solids (Froneman, 2002). The Thukela system is facing pressure on its structure and function due to increasing anthropogenic demand for water resource services (King and Pienaar, 2011). This was evident in this study as high loads of soft sediments accumulated in the estuary accompanied by poor flushing of the river as a result of reduced flow. This sediment accumulation thus increased the turbidity levels on the Thukela Estuary.

The elevated concentrations of DIN during high flow in the Thukela Estuary were a result of higher rainfall and high flows leading to increased nutrient input from inland. The aMatikulu Estuary had higher DIN concentration when compared with the uMvoti and Thukela estuaries. Low concentrations of DIN in the uMvoti and Thukela estuaries can be attributed to the freshwater abstractions in the catchments of uMvoti and Thukela Rivers leading to limited nutrient input. The exhibition of elevated DIN concentrations in the Thukela Estuary when the river flow is high identifies Thukela River as a viable source of nitrogen to this estuary. Such flow dependent patterns highlight the importance of adequate release policy and adherence to this policy for this heavily utilized estuary. During high flow, dilution effect of DIN and DIP was evident in the aMatikulu and uMvoti estuaries. Dilution of nutrients during high flow has previously been reported in other South African POEs (MacKay, 1993; Scharler and Baird, 2003). Such fluctuations in nutrient concentrations in estuaries largely depend on the quality and quantity of freshwater inflow (Palmer et al., 2011). During low flow conditions, seepage from the agricultural land in the upper reaches generally becomes the primary source of nitrogen in estuaries (Snow et al., 2000). Higher nitrogen concen-

trations during low flow in uMvoti and aMatikulu are likely to have come from agricultural seepage associated with the agricultural activities upstream of these estuaries. Furthermore, higher primary productivity (high chl-a concentrations) was evident in the upper reaches of the uMvoti Estuary during 2016 low flow, highlighting sufficient nutrients for the primary producers in this region of the estuary.

Although some chl-a data for some sampling sessions are absent due to sample volume, chl-a values in the study area were expected to be low because these estuaries are river dominated with little resident time to allow for sufficient primary productivity. Available chl-a data support this expectation as most chl-a values were generally low in all estuaries although higher values were sometimes recorded during low flow. Higher concentrations of nutrients promote primary productivity in POEs (Perissinotto et al., 2003). While there was an increase in nutrient concentration in the uMvoti and aMatikulu estuaries during low flow, there was also an increase in chl-a concentrations.

A phytoplankton bloom is defined as chl-a concentration greater than $20 \mu g \, l^{-1}$ (Adams and Bate, 1999). Chlorophyll a concentrations measured in the uMvoti Estuary during 2015 low flow were greater than $20 \mu g \, l^{-1}$ and this depicts that this system experienced a phytoplankton bloom during this period. The current study suggests that the three estuaries studied have little potential for high primary production. The Thukela Estuary had the lowest chl-a values out of the three estuaries studied. Although both uMvoti and Thukela estuaries are impacted by water abstraction activities upstream, the lower phytoplankton biomass (chl-a) in the Thukela Estuary is likely to have been a result of higher turbidity levels in this system. Turbid waters of the Thukela Estuary may limit light penetration and this may prohibit primary productivity. In addition the Thukela Estuary is classified as River Mouth according to Whitfield (2000) and such systems have short residence time which limits phytoplankton accumulation. The significance of retention time on phytoplankton biomass has also been reported in other studies (Hilmer and Bate, 1990; Cromar and Fallowfield, 1997). Phosphate may be limiting to phytoplankton production in the Thukela Estuary, owing to its low concentrations during the current study. Reduced pelagic chl-a values in the three estuaries during high flow maybe due to strong river flow which might reduce water residence time essential for nutrient utilization by phytoplankton.

4.2. Zooplankton

Information on zooplankton communities in the uMvoti, Thukela and aMatikulu estuaries is sparse. Zooplankton abundances in the uMvoti and Thukela estuaries were higher during low flow as opposed to the aMatikulu Estuary which exhibited higher abundance during high flow. Freshwater flow is one of the main parameters controlling zooplankton seasonal variations in estuaries (Chicharo et al., 2006). Low abundance of zooplankton during high flow in the uMvoti and Thukela

estuaries could be a result of outflow of estuarine water flushing away the zooplankton into the adjacent sea. Throughout the study, calanoid copepods particularly *A. natalensis* and *P. hessei* remained the most dominant species in all the three estuaries studied. The next most abundant taxa during the present study were Chironomidae, Nematoda and *M. africana* in the uMvoti, Thukela and aMatikulu estuaries respectively. Dominance of copepods in these estuaries studied is a typical phenomenon for estuaries of South Africa (Jerling, 2005). The uMvoti and Thukela estuaries had salinities of less than 4 for most of the study period. This explained the relative dominance of freshwater taxa (Chironomidae and Nematoda) on these systems. As supported by previous reports, typical estuarine species dominate mesohaline waters while freshwater organisms dominate oligohaline and limnetic waters (Wooldridge and Bailey, 1982; Wooldridge, 1999). The mean zooplankton abundance recorded in the aMatikulu Estuary during the present study was higher than that previously recorded in other South African estuaries (Montoya-Maya and Strydom, 2009). Zooplankton abundances recorded in both uMvoti and Thukela were lower than those previously recorded in other South African estuaries (Montoya-Maya and Strydom, 2009; Vezi, 2013).

As observed in the aMatikulu Estuary during the current study, dissolved oxygen also controlled estuarine zooplankton community structure in other parts of the world e.g. Bilbao and Urdaibai (Albaina et al., 2009), Belgium (Mialet et al., 2011) and Brazil (Almeida et al., 2012). Higher zooplankton abundance and taxa composition in the aMatikulu Estuary could be attributed to higher oxygen levels in this system as opposed to uMvoti and Thukela estuaries which exhibited lower oxygen levels and lower abundances and diversities. Salinity was identified as the key environmental variable in structuring plankton communities in South African estuaries (Wooldridge, 1999). Similarly, salinity was one of the environmental parameters structuring zooplankton community in the aMatikulu Estuary during the current study. Turbidity and pH were determinants structuring zooplankton communities in the uMvoti and Thukela estuaries as determined by the RDA results of the present study. Similar to the current study, zooplankton community structures were controlled by pH, salinity, dissolved oxygen and turbidity in other parts of the world (Laprise and Dodson, 1994; Pandey and Verma, 2004; Tackx et al., 2004; Uriarte and Villate, 2004; David et al., 2005; Albaina et al., 2009; Mialet et al., 2011; Almeida et al., 2012; Farhadian and Pouladi, 2014).

Available chl-a data from the current study displayed relationship with the zooplankton abundance in the uMvoti and Thukela estuaries. Zooplankton abundance increased with phytoplankton biomass (chl-a) in the lower reaches of the uMvoti and Thukela estuaries during 2015 low flow. In these systems, zooplankton abundance decreased with decreasing chl-a concentrations during high flow. Such relationship between the zooplankton abundance and chl-a concentrations suggests the potential effect of phytoplankton availability on the zooplankton abundance. Such pattern was also reported in the Great Fish, Sundays and Kariega estuaries (Wooldridge and

Bailey, 1982; Jerling and Wooldridge, 1991; Grange et al., 2000) and in other parts of the world e.g. Scheldt Estuary in Belgium (Mialet et al., 2011) and Golden Horn Estuary in Turkey (Dorak and Albay, 2016). As zooplankton is a link between primary producers and larger organisms on the aquatic food chain, any negative impact on their abundance or community structure is expected to adversely affect higher trophic level taxa. No clear relationship was observed between zooplankton abundance and chl-a concentrations in the aMatikulu Estuary. This might suggest that the generally high chl-a concentration in this estuary was not a limiting factor to zooplankton abundance. This might also suggest that chl-a may be less important in controlling zooplankton abundance compared with water quality in this Estuary. A similar trend was reported in the Scheldt Estuary (Mialet et al., 2011). High turbidity levels in estuaries may affect zooplankton survival by restricting selective feeding and fecundity of these organisms (Sellner and Bundy, 1987; Gasparini and Castel, 1999). In addition sediments have high oxygen demand and have been reported to sequester as much as 16 times their volume of aerated water (Bruton, 1985; Donohue and Molinos, 2009). High turbidity levels in the Thukela Estuary might have resulted in the lower zooplankton abundance in this system when compared with the aMatikulu Estuary. Most estuaries in South Africa experience reduced zooplankton abundance during low flow, due to reduced nutrient input and reduced primary production (Wooldridge, 1999). Higher zooplankton abundance in the aMatikulu Estuary during high flow was consistent with this pattern. This pattern was similarly observed in other South African permanently open estuaries (Montoya-Maya and Strydom, 2009).

Although the uMvoti had higher chl-a concentrations when compared with the Thukela and aMatikulu estuaries, the lower zooplankton abundances in this system are likely attributable to the short residence time in this system together with low oxygen concentrations which reflected the higher degree of pollution in this system. Copepods which were the main dominant group in this system are known to have low tolerance to reduced oxygen levels (Roman et al., 1993), hence their low abundances when compared with the other two estuaries studied. Higher zooplankton abundance in the aMatikulu Estuary was likely to be attributed to the relatively higher phytoplankton biomass, higher nutrient levels, higher oxygen concentrations as well as sufficient residence time for both phytoplankton to utilize nutrients and zooplankton to utilize phytoplankton efficiently.

Numbers of *A. natalensis* in the aMatikulu Estuary were very low when compared with *P. hessei* and *M. africana*. Unlike vertically migrating species, *A. natalensis* is a permanent resident of the water column (Kibirige and Perissinotto, 2003). This may get these organisms washed to the sea during high flow. Salinity values recorded in the aMatikulu Estuary ranged from 1.4 to 53.9. Such variation in salinity may explain the low numbers of *A. natalensis* as these organisms are vulnerable to fluctuations in salinity as supported by Jerling and Cyrus (1999). The mysid *M. africana* displays an opportunistic behavioural response to low salinity as a result of freshwater inflow (Kibirige and

Perissinotto, 2003). Similarly, this species was recorded in high numbers during high flow in the aMatikulu Estuary during the current study. Mysids, particularly *Mesopodopsis* species were positively correlated with salinity in the Gironde Estuary (France) (David et al., 2005). Similarly this species is known to be controlled by salinity in other North European estuaries (Mees et al., 1993; Azeiteiro and Marques, 1999; Mouny et al., 2000).

5. Conclusions

The spatial variability in the zooplankton distribution, taxa composition and abundance can be explained by the horizontal salinity gradient in the three estuaries studied. The results of the current study showed that spatial and temporal variation in the water physico-chemical parameters of the three estuaries has an effect on the structure and abundance of zooplankton assemblages. We conclude that the environmental variability and seasonality in river inflow are the important factors influencing zooplankton distribution, taxa composition and abundance in the uMvoti, Thukela and aMatikulu estuaries. Changes in the environmental variables (e.g. oxygen, turbidity, nutrients and chl-a) as a result of human activities need to be monitored and these activities need to be properly managed to reduce their impacts on the estuarine systems. Following human activities management, response of zooplankton to improving water quality is expected and must also be monitored. Estuary Management Plans are urgently needed for these three estuaries so as to establish protection, conservation and management measures needed to minimize impacts. Restoration of riparian vegetation of these estuaries can aid in improving water quality and aquatic habitats of these systems. Development of riparian buffers may be another important strategy to reduce sediment loading and erosion into these impacted estuaries.

Conflict of interest

None declared.

Ethical statement

Authors state that the research was conducted according to ethical standards.

Acknowledgements

Appendix A. Supplementary data

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