Macrobenthic Communities in Selected River-Dominated Estuaries in KwaZulu-Natal, South Africa: Effects of Contrasting Environmental Variables and Seasonal Flow Changes

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Macrobenthic Communities in Selected River-Dominated Estuaries in KwaZulu-Natal, South Africa: Effects of Contrasting Environmental Variables and Seasonal Flow Changes

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ABSTRACT

Vezi, M.S.; Downs, C.T.; Wepener, V., and O'Brien, G., 2020. Macrobenthic communities in selected river-dominated estuaries in KwaZulu-Natal, South Africa: Effects of contrasting environmental variables and seasonal flow changes. *Journal of Coastal Research,* 36(5), 992–1004. Coconut Creek (Florida), ISSN 0749-0208.

Globally, estuaries are ecologically important, but many are threatened by anthropogenic activities. Macrozoobenthos organisms are suitable ecological indicators in estuaries because they can detect the effects of stress and pollution. Spatial and temporal composition of macrozoobenthos communities were quantified and compared within and between the three estuaries (uMvoti, Thukela, and aMatikulu estuaries) in KwaZulu-Natal, South Africa, with different levels of human pressure in their catchments. Macrozoobenthos of each estuary was also related to its respective environmental variables. The aMatikulu estuary was selected as a reference site because of its relatively good ecological condition. Sampling dates represented low flow (August and September) and high flow (March and April) from 2014 to 2016. Macrozoobenthos abundance expressed as individuals per square meter (ind·m^{-2}) was highest in aMatikulu estuary (39,167 ind·m^{-2}), followed by Thukela estuary (29,299 ind·m^{-2}) and then uMvoti estuary (10,336 ind·m^{-2}). Within estuaries, number of taxa and abundance between years were significantly different ($p < 0.05$), and number of taxa and species diversity between estuaries were also significantly different ($p < 0.05$). Coarse and very coarse sand were the important environmental determinants in structuring the macrozoobenthos community in the uMvoti estuary, whereas turbidity and water temperature were the important determinants in structuring the macrozoobenthos community in the Thukela estuary. Very fine sand, mud, and salinity were among the most important environmental variables in structuring macrozoobenthos communities in the aMatikulu estuary. Environmental variables differed between estuaries; consequently, macrozoobenthos communities differed between these three systems. Outcomes of the present study indicated that macrozoobenthos communities respond to changes in environmental variables. Results of this study showed that different levels of human pressure in the catchments of these three estuaries could explain variation in their environmental variables. Such variation could increase differences in taxon composition and abundances between the three estuaries, although they are from the same geographical region with similar river-dominated functions.

ADDITIONAL INDEX WORDS: *Macrozoobenthos, river inflow, human pressure, benthic habitat, ecological indicators, water quality.*

INTRODUCTION

Estuaries are among the most productive and dynamic ecosystems globally and have high ecological, economic, and social value (Vasconcelos *et al*., 2010). The ecological value of these systems includes the provision of nursery grounds for many marine species (Barbier *et al*., 2011). The distribution of fauna in estuaries is controlled primarily by salinity and secondarily by substrate, water temperature, dissolved oxygen, and anthropogenic pollution (Harrison and Whitfield, 2006; Schubert and Telesh, 2017; Teske and Wooldridge, 2003). Globally, the ecological health of many estuaries has deteriorated seriously as a result of anthropogenic activities, including excessive water abstraction, industrial effluents, and agricultural activities (Kennish, 2002; Liu *et al*., 2015; Quinton and Catt, 2007; Zhang *et al*., 2012). Most estuaries in the north coast of KwaZulu-Natal (KZN) Province, South Africa, are threatened by poor water quality, reduced flows, and habitat alterations originating from human pressures of different intensities (King and Pienaar, 2011). For example, the uMvoti estuary has been rated severely degraded in terms of sedimentology and is regarded as a polluted system (Wepener, 2007), whereas the ecological health of the Thukela estuary has deteriorated over the last few decades (DWAF, 2004). On the contrary, the aMatikulu/Nyoni estuary (hereafter referred to as the aMatikulu estuary) is in a relatively good ecological state, although siltation from the catchment is concerning (Whitfield, 2000). Consequently, the aMatikulu estuary was selected as the reference site for the present study.

Macrozoobenthos communities are regarded as principal components in the functioning of estuarine ecosystems because of their high contribution and importance in the structuring of estuarine food webs (Kang *et al*., 2015; Noh *et al*., 2019). These organisms support higher trophic levels in many estuaries and adjacent marine environments (Hossain, 2019), and this is one

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of the principal forces driving tidal migrations of fish into estuarine waters (Vinagre, Franca, and Cabral, 2006). Macrozoobenthos organisms are identified as suitable ecological indicators in estuaries because they can detect the effects of stress and pollution (Keeley *et al*., 2014; Tong *et al*., 2013), as well as water and sediment quality (Dauer, Weisberg, and Ranasinghe, 2000; Sarang and Sharma, 2009).

Estuarine benthic habitats are highly vulnerable to the effects of physical parameters such as reduced flows, sedimentation, erosion, altered water quality, and altered tidal regime (Adams, 2012; Van Colen, Vincx, and Degraer, 2006). Anthropogenic pressures such as overexploitation of water resources, dredging, pumping of organic waste, effluent discharge, and sand mining exacerbate environmental variability in estuarine systems (Cloern *et al*., 2015; Zhu *et al*., 2017). Such variations in environmental variables play a role in macrozoobenthos community structure, species distribution, species composition, abundance, and species richness (Guadayol *et al*., 2014; Sivadas, Ingole, and Fernandes, 2013). Although estuaries have high ecological and economical value, no studies have focused on the response of the macrozoobenthos to contrasting environmental variables and seasonal flow changes in the estuaries of KZN Province.

The aim of this study was to quantify and compare spatial and temporal composition of macrozoobenthos communities within and between the three estuaries (uMvoti, Thukela, and aMatikulu) with different ecological states and different levels of human pressure in their catchments. Additionally, effects of some environmental variables and seasonal flow patterns on macrozoobenthos community structuring were analyzed. The following questions were posed: (1) How does macrozoobenthos community structure change along the salinity gradient during high and low flow periods? (2) Which environmental variables were most important in structuring macrozoobenthos communities in the three estuaries studied? These estuarine systems are comparable in form and geographical area according to Harrison, Cooper, and Ramm (2000). Consequently, the hypothesis of this study was that macrozoobenthos abundances and taxon composition among the three estuaries would vary and that the differences would be associated with varying environmental variables in their catchments.

Study Area

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

uMvoti Estuary

The uMvoti estuary (29°23′ S, 31°20′ E) (Figure 1) is situated north of the coastal town of KwaDukuza (Stanger) and is considered a subtropical river mouth (Whitfield, 2000). This system has a shallow mean depth of 0.5 m and occupies an area of approximately 0.2 km^2 (Begg 1984). The catchment of the uMvoti River is subjected to agricultural activities, including sugar cane farming, commercial dry land agriculture, commercial forestry, and subsistence farming. The potential for significant tidal exchange is limited as a result of elevated rock outcrops in the mouth region of this system (Cooper, 1994; Wepener, 2007). Sea water can only penetrate up to 500 m upstream (Begg, 1978).

Thukela Estuary

The Thukela estuary (29°13′ S, 31°29′ E) (Figure 1) is a subtropical river mouth (Whitfield, 2000). The Thukela River has a catchment area of 29,000 km^2 and is the second largest river in South Africa (Whitfield and Harrison, 2003). The Thukela estuary has a relatively small surface area of approximately 0.6 km^2 with a depth of 1.5 m (Begg, 1978). The width of this estuary increases to 1000 m during floods, and the estuary extends out to sea, as no sea water can penetrate the estuary (Begg, 1978). Sea water penetration in this system is minimal as a result of large quantities of silt transported into the estuary, which has resulted in a vertical shelf (De Lecea and Cooper, 2016).

aMatikulu/Nyoni Estuary

The aMatikulu estuary (36°06′ S, 31°37′ E, Figure 1) is a subtropical, permanently open estuary that occupies a surface area of approximately 2.6 km^2 (Whitfield, 2000). The aMatikulu River connects with the Nyoni River and flows parallel to the Indian Ocean before it empties into this ocean approximately 105 km north of Durban. During the present study, the aMatikulu estuary was usually shallow, with a mean depth of 0.6 m. Upstream and in the lower reaches are sugarcane plantations, but the fauna generally remains in a good condition (Harrison, Cooper, and Ramm, 2000). This estuarine system has relatively good ichthyofauna in terms of diversity, good water quality, and good aesthetics (Harrison, Cooper, and Ramm, 2000). The aMatikulu and Nyoni systems share a common mouth and should be conserved as one estuarine system (Heydorn, 1986). The aMatikulu estuary lies within the aMatikulu Nature Reserve managed by Ezemvelo KwaZulu-Natal Wildlife Authority.

METHODS

Subtidal macrozoobenthos samples were collected in the uMvoti, Thukela, and aMatikulu estuaries during 2014 (August), 2015 (March and August), and 2016 (April and September) (Figure 1). Sampling dates were selected to represent low flow (August and September) and high flow (March and April), as referred to hereafter. Three sites were sampled in uMvoti and Thukela estuaries and four sites in aMatikulu estuary, which possesses greater length than the other two estuaries (Figure 1). Sites were selected to represent the upper, middle, and lower reaches of these three estuaries. For temporal comparisons, previously available macrozoobenthos data (March and August 2005 for uMvoti and aMatikulu estuaries and September 2013 for Thukela estuary) were included in the analysis of the present study. No sampling was performed in aMatikulu estuary during 2014.

During each survey *in situ* water quality data, including oxygen, pH, salinity, water temperature, and turbidity, were recorded in each site with a calibrated portable water meter (Eutech Lab Instruments CyberScan 600 Series, Thermo Fisher, Waltham, Massachusetts, U.S.A.). Three replicate biological samples comprising five grabs each were collected from the estuarine channels with a van Veen 12.110 grab (250 cm^2 area, 10 cm depth). All samples were preserved in 10% formalin

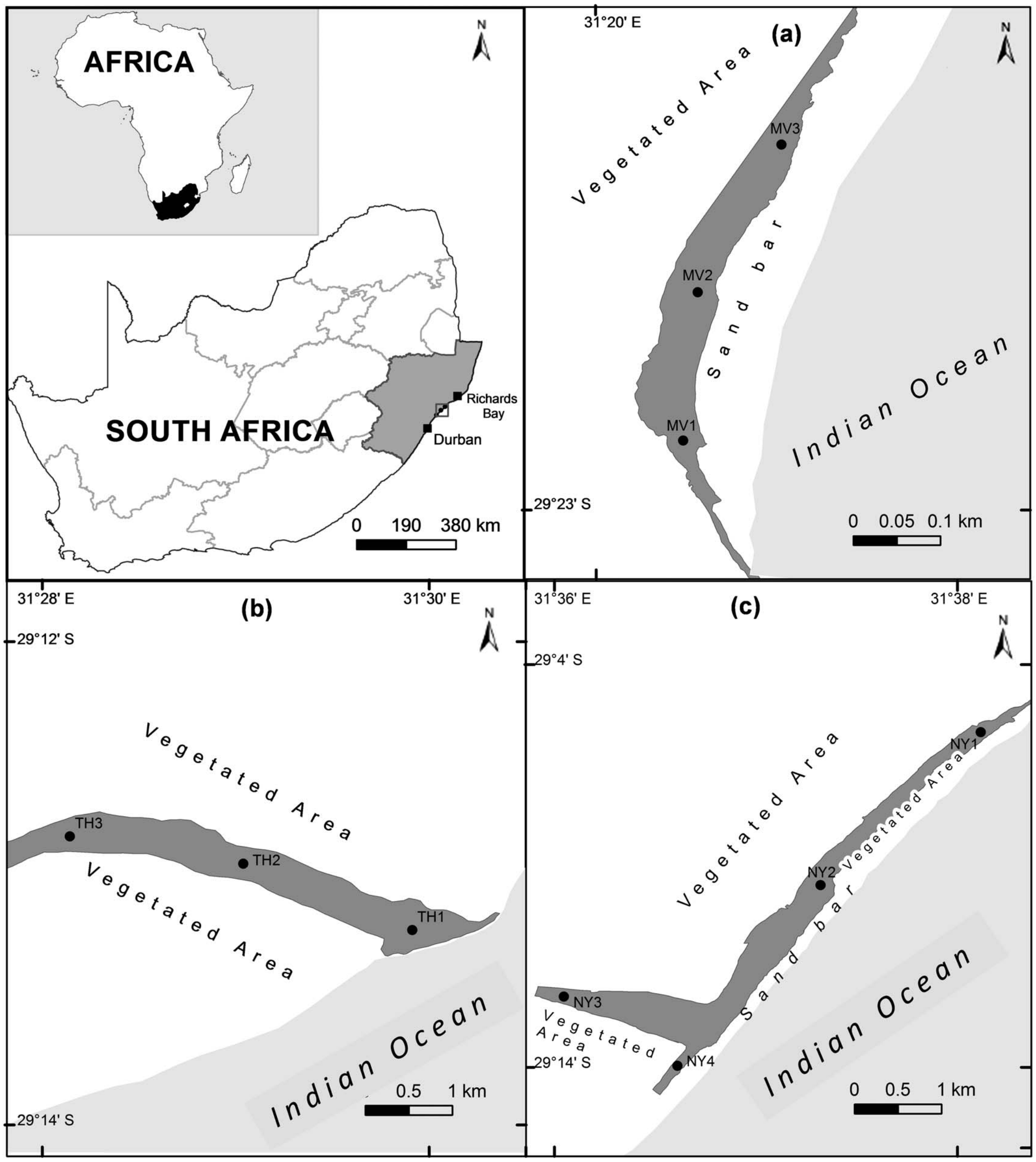

Figure 1. The uMvoti (a), Thukela (b), and aMatikulu (c) estuaries with sampling sites. MV1–3 = uMvoti estuary sites 1–3; TH1-3 = Thukela estuary sites 1–3; NY1–4 = aMatikulu estuary sites 1–4.

containing Rose Bengal dye to aid sorting in the laboratory. Additional sediment samples were collected at each site for particle size analyses and organic content. During March and August 2015, the high density of reeds and grass in the middle reaches of aMatikulu estuary (NY2 and NY3) prevented boat access. As a result, data from NY2 and NY3 in the aMatikulu estuary during March and August 2015 are absent.

In the laboratory, all macrozoobenthos organisms were sorted and identified to the lowest taxon possible and enumerated under a dissecting microscope. Most groups were identified to Family level because it is acknowledged that identification to Family level provides sufficient taxonomic resolution for detecting environmental change in strong environmental gradients (Warwick, 1988a,b). At each sampling site, final abundance was expressed as mean number of each taxon per square meter (ind. m^{-2}) of substratum. Sediment grain size composition was determined by the classical dry sieving method (Blair and McPherson, 1999). Dry sediment was run through a sieve stack of decreasing mesh sizes (between 2000 and 63 μm) and mechanically shaken for a standard duration of 10 minutes. The mass of sediment retained by each sieve was weighed and represented as a proportion of the total sediment. The dry sieving method with the Udden-Wentworth sedimentary grain scale was applied to get the cumulative percentage weights of gravel (>2 mm), very coarse sand (1–2 mm), coarse sand (0.5–1 mm), medium sand (0.25–0.5 mm), fine sand (0.125–0.25 mm), very fine sand (0.063–0.125 mm), and mud (<0.063 mm) sediment fractions (Wentworth, 1926). The percent organic content was determined by oven drying a sediment sample of approximately 5 g, which was then incinerated at 600°C for 6 hours (Gray, 1981). Previously available sediment samples for 2013 from uMvoti and Thukela estuaries were included in the sediment analysis. Although previously available biological and environmental data for 2005 were included in the uMvoti and aMatikulu estuary analyses, sediment data for this year were absent, as noted in Table 1.

Statistical Analyses

Factorial analysis of variance (ANOVA) by SPSS Statistics 25 was performed to test for significant differences in species richness, abundance, and Shannon-Wiener diversity index between sites, flows, years, and estuaries. Differences in community structure between and within estuaries were detected by multivariate analysis, which was performed by PRIMER statistical package (Clarke and Warwick, 2001). The PRIMER similarity percentages routine (SIMPER) was used to define the degree of similarity in community structures within estuaries, as well as dissimilarity between estuaries. Species that contributed the most within the group similarity were also examined by the SIMPER routine.

To determine the sets of environmental variables that could best explain the benthic community composition, redundancy analysis (RDA), a derivative of principal component analysis, was performed by the CANOCO version 4.5 software package (Ter Braak, 1994). To achieve this, the Monte Carlo permutation test was performed (999 unrestricted permutations) ($p < 0.05$). Only taxa with occurrences of >5% were included in the analyses to minimize the effects of rare species. Because macrozoobenthos abundance data were widely variable, data were transformed by a $\log(x + 2)$ transformation (Van den Brink, Van den Brink, and Ter Braak, 2003). A Monte Carlo permutation test was also performed to detect significant differences in macrozoobenthos community structure between sites and estuaries. Significant differences in macrozoobenthos community structures between flows and years were also evaluated by the Monte Carlo permutation test.

RESULTS

Abiotic data, including water quality variables, organic content, and sediment grain size, were compared along the salinity gradient and between flows, years, and estuaries. The macrozoobenthos community was characterized with species richness, abundance, and the Shannon-Wiener diversity index, which were compared along the estuarine salinity gradient and between flows, years, and estuaries.

Environmental Variables

Water temperature in the uMvoti (range = 17.0°C–29.6°C), Thukela (range = 17.5°C–30.6°C), and aMatikulu estuaries (range = 19.3°C–29.4°C) was lower during low flow, with lower values recorded near the mouth region (Table 1). Oxygen concentrations were higher in the aMatikulu estuary (range = 3.7–11.1 mg·L^{-1}) and Thukela estuary (range = 2.8–8.9 mg·L^{-1}) than in the uMvoti estuary (range = 1.8–6.5 mg·L^{-1}) (Table 1). Salinity values were lower in the uMvoti estuary (range = 0.2–2.6) and Thukela estuary (range = 0.2–16) than in the aMatikulu estuary (range = 1.4–35.0), with salinity values generally increasing from the upper to the lower reaches in all the three estuaries (Table 1). The pH values ranged from 6.8 to 7.9 in both the uMvoti and Thukela estuaries and from 6.8 to 8.9 in the aMatikulu estuary. Turbidity values (nephelometric turbidity units, NTU) were higher in the Thukela estuary (range = 28.3–874 NTU) than in the uMvoti (range = 3–14.6 NTU) and aMatikulu estuaries (range = 1.2–15 NTU) (Table 1).

Sediment organic content showed higher values in the aMatikulu estuary (range = 0.8%–12.5%) than in the uMvoti (range = 0.4%–3.9%) and Thukela estuaries (range = 0.6%–4.2%) (Table 1). Sediment grain size composition and distribution in all three estuaries studied are presented in Supplementary Figure S1. In the uMvoti estuary, sediment was dominated by coarse and very coarse sand, with coarse sand comprising more than 50%, whereas the percentage of mud, fine, and very fine sand was <1%. Sediment of the Thukela estuary was dominated by medium and coarse sand, with 60% medium sand. The sediment of the aMatikulu estuary was dominated by medium and fine sand, with >80% medium sand. In all the three estuaries, sediment composition was similar along the estuarine gradient (Supplementary Figure S1).

Species Composition, Abundance, and Diversity of Macrozoobenthos

Lists of macrozoobenthos taxa and abundance recorded in the uMvoti, Thukela, and aMatikulu estuaries during the present study are presented in Supplementary Tables S1, S2, and S3, respectively. Seventeen macrozoobenthos taxa were recorded in uMvoti, 31 in Thukela, and 35 in the aMatikulu estuaries. The highest mean abundance per site was 10,336 individuals·m^{-2} (ind·m^{-2}) in the uMvoti, 29,299 ind·m^{-2} in Thukela, and 39,167 ind·m^{-2} in the aMatikulu estuaries (Supplementary Tables S1–S3). The highest mean macrozoobenthos abundance per site was recorded in the upper reaches in the uMvoti (MV3) and Thukela (TH3) estuaries (Figure 2b). The range in number of taxa per site was 1–7, 1–20, and 2–12 in the uMvoti, Thukela, and aMatikulu estuaries, respectively (Supplementary Tables S1–S3). Species diversity values ranged from 0 to 1.3 in the uMvoti estuary, 0–1.9 in the Thukela estuary, and 0.7–1.8 in the aMatikulu estuary. Mean species diversity was highest in the lower reaches in all three estuaries (Figure 2c). Mean species diversity was higher in aMatikulu when compared with uMvoti and Thukela estuaries (Figure 2c).

Intraestuary variability analyses of the uMvoti estuary showed no significant differences between sampling sites with regard to number of taxa, abundance, and species diversity. However, number of taxa and abundance were significantly different between flows ($p < 0.05, F = 9.37$) and years ($p < 0.05, F = 3.9$) in this system. Number of taxa generally increased from the upper to the lower reaches in the uMvoti and Thukela estuaries, whereas the opposite pattern was observed in the aMatikulu estuary (Figure 2a). In the Thukela estuary, differences between sites were not significant regarding the

Table 1. *Selected environmental variables measured in the uMvoti, Thukela and aMatikulu estuaries during the current study.*

Estuary	Year-Flow[†]	Site	Temperature (°C)	Oxygen (mg/l)	Salinity	pH	Turbidity (NTU)	Organic Content (%)
uMvoti	2005-LF	MV1	17.0	4.5	0.8	7.9	5.7	—[‡]
		MV2	22.8	4.4	0.8	7.8	6.4	—[‡]
		MV3	23.6	1.9	1.0	7.6	7.5	—[‡]
	2005-HF	MV1	28.4	4.4	1.1	7.7	4.8	—[‡]
		MV2	28.9	3.7	1.0	7.9	3.0	—[‡]
		MV3	29.6	3.6	1.0	7.7	3.1	—[‡]
	2013-LF	MV1	24.8	3.0	0.5	7.1	4.7	1.4
		MV2	25.5	3.8	0.4	7.3	5.4	2.1
		MV3	26.0	2.4	0.3	7.2	6.5	0.5
	2014-LF	MV1	20.5	3.2	1.2	6.7	4.7	3.9
		MV2	21.3	3.3	1.2	6.8	5.4	0.0
		MV3	20.1	4.0	0.9	7.0	6.5	0.4
	2015-LF	MV1	20.8	2.5	0.5	6.7	11.1	3.9
		MV2	21.4	4.1	0.5	7.4	11.6	0.0
		MV3	22.1	6.5	0.5	7.5	14.6	0.4
	2015-HF	MV1	26.0	3.3	2.6	7.7	5.8	0.4
		MV2	25.0	3.4	0.4	7.9	4.0	1.0
		MV3	25.0	3.3	0.3	7.7	4.5	1.4
	2016-LF	MV1	25.8	1.8	0.9	7.0	9.1	1.4
		MV2	26.0	2.2	0.9	6.9	10.6	1.4
		MV3	26.4	2.3	0.9	6.9	13.6	0.4
	2016-HF	MV1	29.1	2.3	1.6	7.8	4.8	0.4
		MV2	25.4	1.8	1.4	7.6	4.0	1.0
		MV3	25.3	4.8	1.1	7.4	4.1	1.4
Thukela	2013-LF	TH1	23.6	6.4	5.2	7.7	51.6	1.5
		TH2	24.4	6.8	0.7	7.6	29.3	3.6
		TH3	24.0	6.8	0.3	7.6	37.0	0.6
	2014-LF	TH1	17.5	8.9	7.2	7.5	51.6	2.0
		TH2	17.7	8.6	0.2	7.3	29.3	2.2
		TH3	18.9	6.5	0.2	7.3	43.0	1.0
	2015-LF	TH1	20.3	5.7	16.0	7.6	50.6	2.0
		TH2	18.7	5.5	0.4	7.8	28.3	2.2
		TH3	21.4	7.7	0.4	7.9	38.0	1.0
	2015-HF	TH1	28.0	3.0	8.0	7.7	874.0	3.2
		TH2	30.6	2.8	0.6	7.9	703.0	4.2
		TH3	28.0	3.0	0.4	7.7	802.0	4.2
	2016-LF	TH1	24.0	5.0	8.5	7.4	65.0	4.2
		TH2	26.8	5.9	3.3	7.5	30.0	4.2
		TH3	26.9	3.7	2.7	7.4	40.0	4.2
	2016-HF	TH1	25.4	5.4	7.5	6.7	873.0	3.0
		TH2	26.5	7.2	4.0	6.8	708.0	2.5
		TH3	23.6	5.1	3.5	7.7	802.0	2.0
aMatikulu	2005-LF	NY1	19.6	5.5	34.4	8.2	6.0	—[‡]
		NY2	19.5	4.9	34.1	8.2	7.0	—[‡]
		NY3	19.3	4.4	33.1	8.1	6.0	—[‡]
		NY4	22.1	4.1	29.4	7.9	15.0	—[‡]
	2005-HF	NY1	25.7	5.9	31.1	8.4	7.0	—[‡]
		NY2	25.6	5.7	32.2	8.3	3.0	—[‡]
		NY3	25.3	5.5	31.3	8.4	4.0	—[‡]
		NY4	26.1	5.3	10.4	8.1	6.0	—[‡]
	2015-LF	NY1	20.7	8.7	7.2	8.2	6.6	5.2
		NY2	19.4	6.0	1.7	7.2	3.6	5.2
		NY3	20.7	6.2	1.4	7.4	3.7	9.7
		NY4	23.1	11.1	6.9	8.9	3.0	4.3
	2015-HF	NY1	27.3	3.8	33.0	8.4	1.2	1.9
		NY4	29.4	3.8	28.0	8.1	7.3	1.3
	2016-LF	NY1	24.5	9.8	35.0	8.1	7.0	1.9
		NY2	23.8	7.9	34.9	7.8	4.0	2.0
		NY3	25.9	8.5	27.3	7.1	4.0	1.0
		NY4	23.3	5.5	28.0	7.2	4.0	1.5
	2016-HF	NY1	25.7	6.2	33.6	8.0	6.0	1.9
		NY2	26.3	6.7	30.6	6.8	4.0	0.8
		NY3	27.9	5.7	28.7	7.3	5.0	12.5
		NY4	26.1	3.7	29.9	7.7	5.0	1.3

[†] *LF = low flow; HF = high flow*
[‡] *Absent organic matter values*

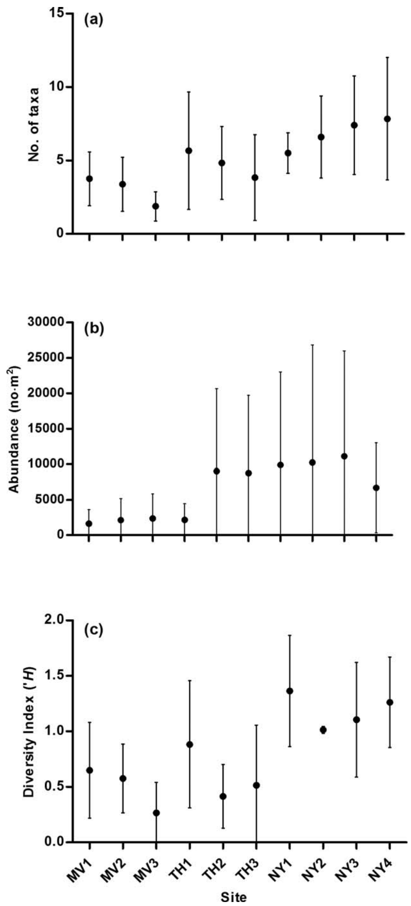

Figure 2. Mean (±SD) number of taxa, abundance, and Shannon-Weiner diversity recorded in the uMvoti (MV), Thukela (TH), and aMatikulu (NY) estuaries during the study period.

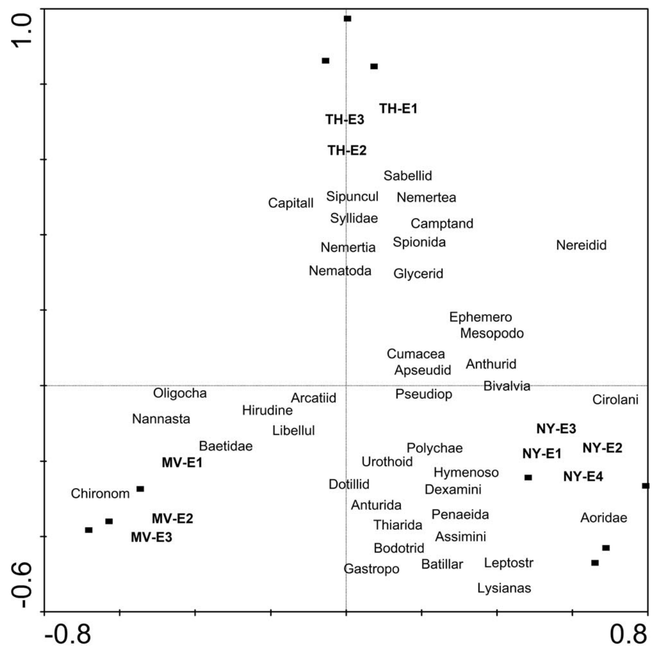

Figure 3. RDA triplots showing the relationship between benthic taxa and sampling sites. (MV-E1–3 = uMvoti estuary sites 1–3; TH-E1–3 = Thukela estuary sites 1–3, NY-E1–4 = aMatikulu estuary sites 1–4).

number of taxa, abundance, and species diversity. Additionally, no significant differences were observed between flows with regard to the number of taxa and species diversity in the Thukela estuary. However, differences between years were significant with regard to the number of taxa ($p < 0.05, F = 4.91$), abundance ($p < 0.05, F = 6.40$), and species diversity ($p < 0.05, F = 5.93$) in this estuary. In terms of intraestuary variability in the aMatikulu estuary, differences between sites and flows were not significant regarding number of taxa, abundance, and species diversity. However, significant differences between years regarding number of taxa ($p < 0.05, F = 7.99$) and abundance ($p < 0.05, F = 34.04$) were observed in this estuary.

The highest abundance was recorded during low flow periods in all the three estuaries. In terms of interestuarine variability, differences between estuaries were significant in number of taxa ($p < 0.05, F = 7.46$) and species diversity ($p < 0.05, F = 28.95$), although no significant differences in abundances between the estuaries were observed. Dominant macrozoobenthos groups in the uMvoti, Thukela, and aMatikulu estuaries are presented in Supplementary Figures S2, S3, and S4, respectively. The benthic community was dominated by Insecta and Oligochaeta in the uMvoti estuary. Polychaeta and Oligochaeta were the most dominant groups in the Thukela estuary. In the aMatikulu estuary, the benthic community was dominated by Polychaeta and Isopoda in 2005; Mysida, Tanaidacea, and Gastropoda in 2015; and Amphipoda, Polychaeta, and Malacostraca in 2016.

Changes in Benthic Community Structure

The RDA biplot constructed by log-transformed species data, separated macrozoobenthos data into three distinct faunal assemblages representing the three estuaries studied (Figure 3). The biplot explained 62.2% of variation in the data (47% on axis 1 and 15.2% on axis 2). The uMvoti estuary was mostly dominated by freshwater macrozoobenthos taxa, whereas the Thukela estuary was dominated by both the estuarine and freshwater macrozoobenthos taxa. The aMatikulu estuary was mainly dominated by macrozoobenthos taxa of marine and estuarine origin (Figure 3). From the SIMPER results, despite the few outliers, the three estuaries studied possessed unique assemblages that differed significantly from each other (Figure 4). Similarity in species composition within estuaries (regardless of site, years, and flows) was 42% in the uMvoti, 31% in the aMatikulu, and 29% in the Thukela estuaries, indicating relatively unstable benthic communities in these estuaries (Table 2). The Nereididae was the characteristic taxon in the Thukela and aMatikulu estuaries, whereas the Chironomidae was the characteristic taxon in the uMvoti estuary (Table 2).

Dissimilarity in terms of species composition was 79% between the aMatikulu and Thukela assemblages, and the characteristic discriminator taxon was the Aoridae. Dissimilarity was 84% between the uMvoti and Thukela macrozoobenthos assemblages, and the discriminator taxa were the Nereididae

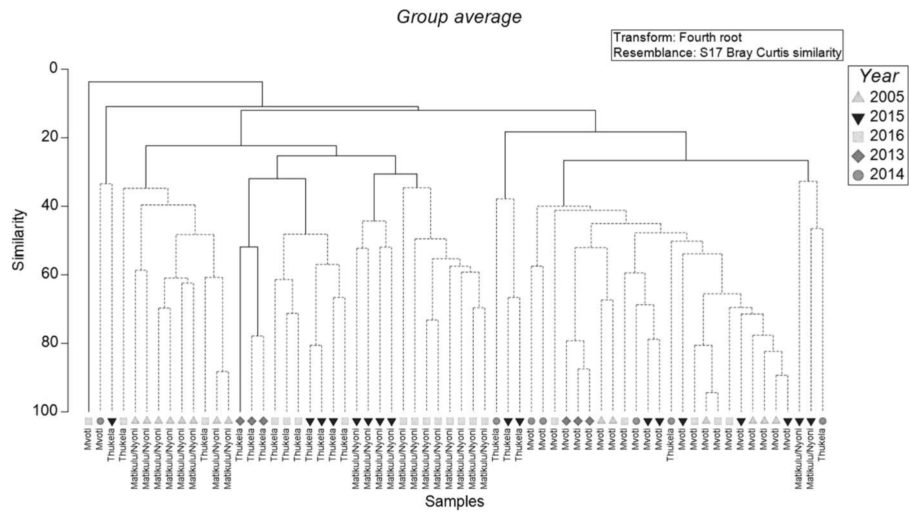

Figure 4. Classification constructed from Bray-Curtis similarities showing differences in the community structure between sites and years during the present study.

and Chironomidae. Dissimilarity between the aMatikulu and uMvoti assemblages was 90%, and the reliable discriminator taxa were the Nereididae and Aoridae. A multidimensional scaling plot for the aMatikulu estuary confirmed the separation of macrozoobenthos assemblages by year (Figure 5). From the SIMPER results, similarity in taxon composition in the aMatikulu estuary between years was 40% (2015), 49% (2005), and 51% (2016). This system was characterized by the Cirolanidae in 2005, and these were replaced by the Aoridae in 2015 and 2016. Benthic fauna of uMvoti and Thukela estuaries comprised homogeneous assemblages, although 2014 was an outlier sample in the uMvoti system (Figures 6 and 7). Results from a Monte Carlo test revealed significant differences in community structures between estuaries ($p < 0.05, F = 9.64$). Differences in macrozoobenthos community structures between flows were not significant ($p = 0.05, F = 1.79$), with either flows (low and high) having a more or less equal influence in the community structuring. The macrozoobenthos community structure differed significantly between years ($p < 0.05$, $F = 3.48$), with year 2013 having the highest contribution. Year 2016 and 2005 were the second most important years in structuring macrozoobenthos communities during the present study.

The macrozoobenthos was also examined separately for each estuary for the determination of the intraestuary variability of macrozoobenthos community structures by the Monte Carlo test. Within the uMvoti estuary, differences in community structure were not significant between sites ($p > 0.05, F = 0.91$) and flows ($p > 0.05$, $F = 0.19$); however, differences between years were significant ($p < 0.05$, $F = 7.24$). No significant differences in the macrozoobenthos community structure were observed between sites, years, and flows within the Thukela estuary. Within the aMatikulu estuary, although differences in community structure were not significant between sites ($p > 0.05, F = 0.71$), differences were significant between years ($p < 0.05, F = 5.61$) and flows ($p < 0.05, F = 1.87$).

Relationship between Macrozoobenthos Assemblages and Environmental Variables

Environmental variables responsible for structuring the macrozoobenthos community assemblages in the uMvoti,

Table 2. *Comparison of macrozoobenthos assemblages between estuaries by similarity percentage (SIMPER).*

	Contribution %			
Average Dissimilarity	Average Similarity (%)	uMvoti (42.4)	Thukela (28.7)	aMatikulu (30.6)
aMatikulu and uMvoti				
90.43	Nereididae		55.71	31.25
aMatikulu and Thukela				
79.12	Aoridae			23.46
uMvoti and Thukela				
83.5	Cirolanidae		15.61	22.28
	Lysianassidae			3.91
	Leptostraca			3.57
	Chironomidae	83.41	11.82	2.15
	Hymenosomatidae			2.00
	Spionidae		3.92	1.51
	Oligochaeta	13.00		
	Nematoda spp.		5.66	

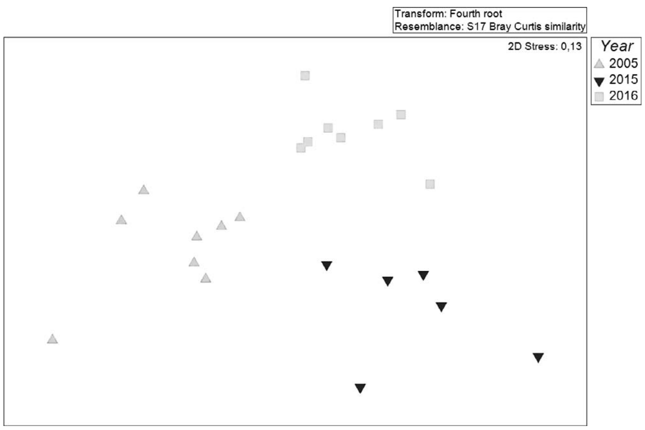

Figure 5. Multidimensional scaling ordination of macrozoobenthos data averaged over years in the aMatikulu estuary in the present study.

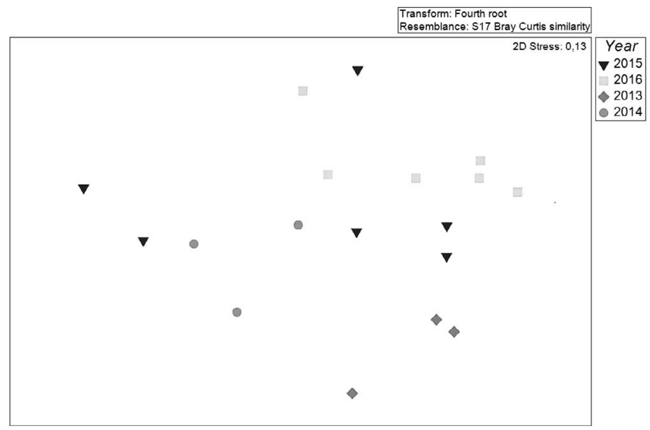

Figure 7. Multidimensional scaling ordination of macrozoobenthos data averaged over years in the Thukela estuary in the present study.

Thukela, and aMatikulu estuaries are shown in Figure 8. (Select examples of the macrozoobenthos are shown in Figure 9). The RDA triplot revealed that coarse and very coarse sand were the main drivers in structuring macrozoobenthos community in the uMvoti estuary. In the Thukela estuary the most important drivers in structuring macrozoobenthos community were turbidity and water temperature. Fine and very fine sand and salinity were the important drivers in structuring the macrozoobenthos communities in the aMatikulu estuary, followed by organic content, mud, and oxygen (Figure 8). The triplot explained 49.8% of the variation in the data (25.9% from axis 1 and 23.9% from axis 2). The influence of environmental variables in structuring the macrozoobenthos assemblages was significant ($p < 0.05$, $F = 11.34$).

DISCUSSION

In the present study, macrozoobenthos abundance, species richness, and diversity were compared along the salinity gradient between flows, years, and estuaries.

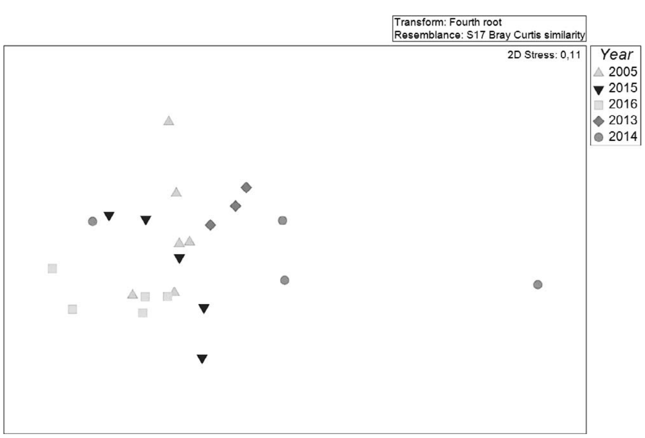

Figure 6. Multidimensional scaling ordination of macrozoobenthos data averaged over years in the uMvoti estuary in the present study.

Environmental Variables

Variability was high in some environmental variables between the three estuaries in the present study. Although the three estuaries lay in the same geographical area and are geomorphologically similar (Harrison, Cooper, and Ramm, 2000), the variability in environmental conditions could be attributed to different levels of human pressure in the catchments of these systems. Lower water temperatures recorded during low flow in the present study can be explained by the winter season of KZN, South Africa, where cold weather conditions are coupled with low rainfall. The aMatikulu

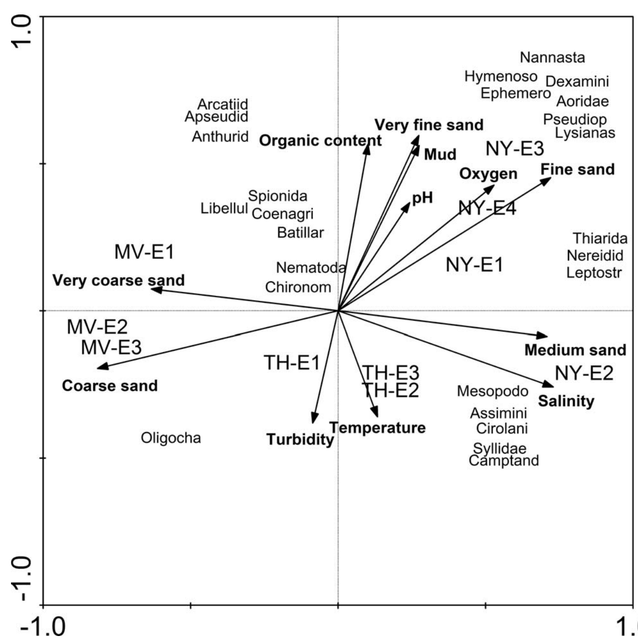

Figure 8. RDA triplots showing the relationship between benthic taxa and selected environmental variables. (MV-E1–3 = uMvoti estuary sites 1–3; TH-E1–3 = Thukela estuary sites 1–3; NY-E1–4 = aMatikulu estuary sites 1–4).

Figure 9. Selected examples of taxa found in the present study with examples of (a) the Cirolanidae, (b) the Spionidae, and (c) the Nereididae (WoRMS, 202).

estuary had higher oxygen levels than the uMvoti and Thukela estuaries. Anthropogenic activities associated with the catchment of the uMvoti include sugarcane agricultural activities, heavy industrial activities (*e.g*., sugar and paper mills, among others), informal settlements, rural communities with livestock, urban and peri-urban communities, wastewater treatment works, intensive irrigation, poor cultivation, sand mining, and water abstraction. Water quality of the uMvoti system was identified as highly polluted since 1964 (Begg, 1978). Water quality alteration has been previously reported in this system, including reduced oxygen and increased chemical oxygen demand (Malherbe, Wepener, and Van Vuren, 2010; Venter, 2013). Increased chemical oxygen demand may result from biodegradable wastes originating from sewage, chemical industries, and pulp and paper industries (Kanu and Achi, 2011). These industries operate in the catchment of the uMvoti system and could be altering water quality in the uMvoti estuary.

On the contrary, anthropogenic threats in the aMatikulu estuary are minimal, with sedimentation the primary concern (Whitfield, 2000). One sugar mill and associated agricultural activities upstream are the only sources of stressors in the aMatikulu system. Anthropogenic activities in the upper catchment of the Thukela estuary include industries (*e.g*., paper mill and other industrial complexes), mining, agricultural plantations, urban areas, and wastewater treatment works. Many of these ecosystem users extract water directly or indirectly (via municipal extraction works) from the Thukela River and its associated tributaries and release treated or partially treated effluent back into these systems (O'Brien and Venter, 2012). As such, the effects of the sources of stressors in the Thukela River persist into the Thukela estuary. Anthropogenic activities associated with the uMvoti and Thukela catchments might have resulted in reduced oxygen levels in these systems during the present study.

The sediments of the uMvoti and Thukela estuaries were well sorted, with coarse and very coarse sand dominating these systems, as opposed to the aMatikulu estuary, which was dominated by medium and fine sand. Human pressures such as sand mining, agricultural plantations, and poor irrigation practices in the catchments of the uMvoti and Thukela estuaries could result in changes in the sediment regime of these systems. Riparian vegetation has been removed from the banks of uMvoti River because of intensive irrigation and cultivation (Venter, 2013), resulting in excessive erosion of terrestrial sediment and causing the lower part of the river to be dominated by coarse sand. Such erosion effects persist downstream to the estuary, supported by the coarse and very coarse sand dominating the uMvoti estuary during the present study. Flow conditions of the uMvoti estuary have been altered as a result of excessive water extraction and a sand-dominated river channel (O'Brien and Venter, 2012). Habitat loss as a result of sugarcane plantations was reported for this system (Sukdeo, Pillay, and Bissessur, 2012).

The middle and lower reaches of the Thukela estuary were dominated by high loads of sediment, which could be a result of erosion in the catchment from commercial agricultural plantations. Such sediment accumulation in the estuary is exacerbated by reduced flows in the system, resulting in poor flushing of the sediment into the sea. Variability in salinity levels was high between the three estuaries. The river-dominated nature of the uMvoti and Thukela estuaries could explain the lower salinity values in these systems, which have very little marine tidal influence as a result of a high berm produced as a result of coarse-grained barrier sediment and relatively low wave energy (Harrison, Cooper, and Ramm, 2000). Additionally, the potential for significant tidal exchange in the uMvoti estuary is limited as a result of an elevated rock outcrop in the mouth region (Cooper, 1994; Wepener, 2007). The Thukela estuary only experiences effective sea water intrusion during spring high tide when river flow is low (Whitfield and Harrison, 2003). Salinities measured in the three estuaries during the present study were within the ranges of river-dominated estuaries in South Africa (Whitfield, 1992).

Turbidity values were highly variable between the three estuaries, with the lowest value recorded in the aMatikulu estuary and the highest in the Thukela estuary. Higher turbidity values were generally recorded during high flow, which can be associated with higher rainfall that disturbs sediments and thus increases levels of total suspended solids (Froneman, 2002). The structue and function of the Thukela system is facing pressure because of increasing anthropogenic demand for water resource services (King and Pienaar, 2011), as supported by the high loads of soft sediments accumulated in the estuary and poor flushing of this system as a result of reduced flows. The medium sand that dominated the Thukela estuary was always covered in soft silt on the surface during low flow periods. Although flow data were absent in the present study, historical flow data for the Thukela estuary was obtained from the National Department of Water and Sanitation and are presented in Supplementary Figure S5. Such data showed a decrease in flows since 2006, and such effects were generally prominent during high flow and were exacerbated during the present study (2014–2016). Consequently, extremely high turbidity levels in the Thukela estuary during the present study could be a result of the high amount of soft sediments accumulated in the estuary as a result of reduced flows.

Macrozoobenthos Communities

Information on macrozoobenthos communities in the uMvoti, Thukela, aMatikulu, and other river-dominated estuaries in South Africa is sparse. Macrozoobenthos abundance was higher during low flow when compared with high flow in all the three estuaries studied. A drop in salinity levels as a result of high river inflow can contribute to the reduction in macrozoobenthos abundances (Schlacher and Wooldridge, 1996). Similar to the present study, a reduction in macrozoobenthos abundance after high flow occurred in other South African permanently open estuaries (POEs; *e.g.*, Gamtoos and Great Berg estuaries; Schlacher and Wooldridge, 1996). A similar pattern was observed in the Schelde estuary, France (Ysebaert *et al.*, 1993). Macrozoobenthos abundance was lower near the mouth region in all the three estuaries studied. Highly fluctuating environmental variables such as water temperature and salinity near the mouth region may result in few organisms thriving in this region (Day, 1974).

Macrozoobenthos abundance and diversity were higher in the aMatikulu estuary when compared with the uMvoti and Thukela estuaries. Medium and fine sand together with high organic content in the aMatikulu estuary provided a favorable habitat in this system. Such favorable habitat together with good water quality and minimal human pressure in the catchment of the aMatikulu system could explain the higher abundance and diversity of the macrozoobenthos in this system when compared with the uMvoti and Thukela estuaries. The aMatikulu estuary is also more favorable because of a higher range of salinities, more extensive tidal prism, and more diverse substrate. Additionally, the aMatikulu system does not get flushed as frequently and is therefore a more stable environment. In the uMvoti and Thukela estuaries, the number of taxa increased from the upper to the lower reaches, a pattern previously reported in other South African POEs (*e.g.*, Branch and Grindley, 1979; Day, 1974; Schlacher and Wooldridge, 1996). The aMatikulu estuary showed an opposite trend with the number of taxa increasing from the lower to the upper reaches. This pattern might be attributed to the confluence of the Nyoni with the aMatikulu system in the upper reaches of this connected estuary. The Nyoni system might be contributing more macrozoobenthos taxa to this vicinity.

The Polychaeta was the most dominant group in terms of abundance in the Thukela and aMatikulu estuaries during the present study. However, in the aMatikulu estuary, this was replaced by the Mysida and Tanaidacea in March 2015 and August 2015, respectively. Such changes in dominant groups with river flow conditions has been reported in South African estuaries because of the dynamic nature of community change in the macrozoobenthos (Wooldridge and Deyzel, 2009b). Chironomids, which are mainly freshwater species, are indicative of organically polluted systems (Odume *et al.*, 2016; Rae, 1989). Water quality of the uMvoti system was described as grossly polluted since 1964 (Begg, 1978), which may explain the dominance of chironomids and oligochaetes in this system during the present study, because some water quality variables like oxygen were in a poor state. Chironomids and oligochaetes are good indicators of pollutants because they are resistant to higher levels of perturbation (Failla *et al.*, 2015; Lafont *et al.*, 2006). Similar to the uMvoti estuary, low species richness as a result of low oxygen levels was reported in the United States (Dauer, Rodi, and Ranasinghe, 1992; Muniz and Venturini, 2015; Shivarudrappa, Rakocinski, and Briggs, 2019). The uMvoti catchment is heavily affected by the anthropogenic water resource use activities as described above. The uMvoti riverine system has been modified completely, with nearly total loss of natural habitat and biota, as well as destruction of many basic ecosystem functions (Tharme, 1996). As a result, the uMvoti estuary is regarded as a degraded system that functions differently from the way it did in its former pristine state (MacKay, Weerts, and Cyrus, 2000).

Results of the present study showed that taxon richness and diversity were significantly different between the three estuaries. Although salinity varied between reaches in the aMatikulu estuary, the salinity gradient was less prominent in the uMvoti and Thukela estuaries because of the river-dominated nature of these systems and low sea water penetration. These factors can explain why the salinity was not important in structuring the macrozoobenthos community in the uMvoti system. Sediment grain size composition differed between the three estuaries. Dissimilarity in taxon composition and diversity between the three estuaries could be explained in part by these differences in salinity and sediment. In the present study, clustering with SIMPROF separated the macrozoobenthos of the aMatikulu estuary into distinct faunal assemblages; however, the uMvoti and Thukela estuaries comprised homogeneous assemblages. The poor quality of environmental variables in the uMvoti estuary could have an overriding effect in homogenizing the macrozoobenthos community in this system. The Thukela estuary is river dominated, and it is therefore possible that freshwater-related factors had an overriding effect in structuring a homogeneous macrozoobenthos community.

Canonical analyses of the present study showed that very fine sand, fine sand, and salinity had the highest influence in structuring the macrozoobenthos community in the aMatikulu estuary. Organic content, mud, and oxygen were the second most important variables that structured the macrozoobenthos community in this system. All these environmental variables were previously reported to support high abundances and diversities in the aMatikulu estuary when compared with the uMvoti estuary (Swemmer, 2009). Particle size and organic matter were also the important factors driving the benthic community structure in the Mfolozi-Msunduzi estuary (Ngqulana *et al*., 2010) and in other parts of the world (*e.g*., India, Japan and Europe; Denisenko, Denisenko, and Lehtonen, 2019; Kanaya, Uehara, and Kikuchi, 2016; Selleslagh, Lesourd, and Amara, 2012; van der Wal *et al*., 2017). Oxygen, salinity, and water temperature also played a role in structuring macrozoobenthos in South African estuaries and in other parts of the world, for example in the United States (Dauer, Weisberg, and Ranasinghe, 2000; Holland, Shaughnessy, and Hiegel, 1987), Denmark (Conley and Josefson, 2001), France (Selleslagh, Lesourd, and Amara, 2012), Finland (Laine *et al*., 2007), and Bangladesh (Matin *et al*., 2018).

The substrate of the Thukela and aMatikulu estuaries was dominated by medium, fine, and very fine sand, and the macrozoobenthos of these systems were dominated by polychaetes. Coarse and very coarse sand observed in the uMvoti estuary could explain very low numbers of polychaetes in this system. Such large particle sizes do not adequately support the burrowing species because of unstable, coarse sediment. Furthermore, the very low silt-clay fractions in the uMvoti estuary indicated a low amount of food for the deposit feeders. In the Thukela estuary, turbidity and water temperature were the most important environmental variables driving macrozoobenthos community. Water temperature was also an important variable in structuring macrozoobenthos communities in the Mfolozi-Msunduzi and Great Berg estuaries, and similarly, these systems were dominated by Polychaeta (Ngqulana *et al*., 2010; Wooldridge and Deyzel, 2009a). High sediment load in the Thukela estuary could negatively affect the abundance of macrozoobenthos in this system. Similarly, high sediment load associated with anthropogenic activities affected macrozoobenthos in several estuaries in Tasmania, Australia (Edgar and Barrett, 2000).

CONCLUSIONS

Macrozoobenthos abundance, species richness, and species diversity differed significantly between the three estuaries. Coarse and very coarse sand were the important environmental determinants in structuring the macrozoobenthos community in the uMvoti estuary, whereas turbidity and water temperature contributed to the macrozoobenthos community structuring in the Thukela estuary. Fine and very fine sand, mud, and salinity were among the most important drivers in macrozoobenthos community structuring in the aMatikulu estuary. Environmental variables differed between estuaries; consequently, macrozoobenthos communities differed between these three systems. Outcomes of the present study indicated that macrozoobenthos communities respond to changes in environmental variables. The conclusion is that environmental variability and seasonality in river flow are the important parameters influencing macrozoobenthos distribution, abundance, species richness, and taxon composition in the uMvoti, Thukela, and aMatikulu estuaries. Results of this study showed that different levels of human pressure in the catchments of these three estuaries could explain variation in their environmental variables. Such variation could increase differences in taxon composition and abundances between the three estuaries, although they are from the same geographical region with similar river-dominated function. Changes in the environmental variables (*e.g*., oxygen, turbidity, salinity, sediment composition, and flows) as a result of human pressure need to be monitored, and these anthropogenic activities need to be properly managed to reduce their effects on estuaries. With management of human activities, the response of macrozoobenthos to improving water quality and habitat is expected, and such response must also be monitored. Estuary Management Plans are urgently needed for the three estuaries studied, to establish protection, conservation, and management measures needed to reduce anthropogenic impacts. Water quality and aquatic habitats of the studied estuaries may be improved by restoring the riparian vegetation of these systems. Development of riparian buffers may be an important approach to reduce sediment loading and erosion into these affected estuaries.

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