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A preliminary fish survey of the estuaries on the south-east coast of South Africa, Kei Estuary to Mdumbi: A comparative study

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A preliminary ichthyofaunal and physico-chemical survey of estuaries on the south-east coast of South Africa from the Kei Estuary to the Mdumbi Estuary was undertaken between October and November 1997. Twenty-seven (27) estuaries were surveyed along this stretch of coastline and these were grouped into three estuary types: small (< 10 ha) predominantly closed estuaries, moderate to large (> 10 ha) predominantly closed estuaries and predominantly open estuaries. Multivariate analyses revealed significant differences between predominantly closed estuaries and predominantly open estuaries in terms of both their physico-chemical characteristics and their fish communities. There was no difference between small and moderate to large predominantly closed estuaries. A significant relationship was also observed between the physico-chemical characteristics of the estuaries and their fish communities. The estuaries in the study area fall within the warm-temperate biogeographic region; temperate species dominated the fish communities of all the estuaries. This survey represents one of the few fish surveys undertaken along this little-studied section of the coastline.

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INTRODUCTION

Research into fish communities in the Eastern Cape Province of South Africa has excluded to a large extent the former Transkei region of the province (Mbande et al., 2005), such that information on most systems along this coastline is classified as poor or non-existent (Whitfield and Baliwe, 2013). This paper focuses on the southern Transkei, which is regarded as falling within the warm-temperate biogeographic region; the boundary between the warm-temperate and subtropical regions is situated at the Mdumbi Estuary (Harrison, 2002). The fish species diversity in South African estuaries increases from west to east (Harrison, 2002) and, as such, the southern Transkei estuaries are expected to have more species than the estuaries further south/southwest (e.g. James and Harrison 2010a; 2010b; 2011; 2016). As the southern Transkei estuaries are situated south of the biogeographic boundary, estuaries in this region are likely dominated by temperate species with moderate numbers of tropical species.

The overall ecology, including the fish assemblage, of the large predominantly open Kei (Plumstead, 1984; Plumstead et al., 1985), Mbhashe (Plumstead, 1984b; Plumstead, 1990; Plumstead et al., 1989) and Mthatha (Plumstead, 1984; Plumstead et al., 1989) estuaries was studied in the 1970s and 1980s. Limited information has been published on the fish fauna of the temporarily open/closed Nqabara (Marais and Prinsloo, 1980), Ngoma/Kobule (Van der Elst, 1978) and Ngqusi/Inxaxo (Wasserman et al., 2010) estuaries. As part of a national assessment of South African estuaries, a fish survey was undertaken along the south-east coastline between the Kei Estuary and the Mdumbi Estuary; basic physico-chemical variables, fish community data and a comparative analysis are provided. Although this survey was conducted more than 20 years ago, this data provides useful baseline information on the fish fauna of this poorly studied region, particularly in the light of climate change related distribution shifts.

STUDY AREA

The section of coastline between the Kei Estuary and Mdumbi extends some 117 km and is intersected by 40 river outlets (Fig. 1). Along this section of the coastline, although rain falls all year, most falls in summer from November to January, with a minimum in July (Emmerson, 2005). Extreme rainfall events are common and are not only restricted to the summer rainfall season but may also occur in winter and early spring (Plumstead et al., 1985). The coastline is influenced by the south-flowing Agulhas Current (Shannon, 1989; Heydorn, 1991). Being tropical in origin, the waters of this current are relatively warm; however, as it flows south it tends to cool, with inshore water temperatures along the Eastern Cape coast varying between 17 and 20°C (Smit et al., 2013).

MATERIALS AND METHODS

The estuaries between the Kei and Mdumbi were sampled between October and November 1997. Each system was sampled once and took 1–3 days to survey, depending on the size of the system. Twenty-six of the forty estuaries were accessible for sampling.

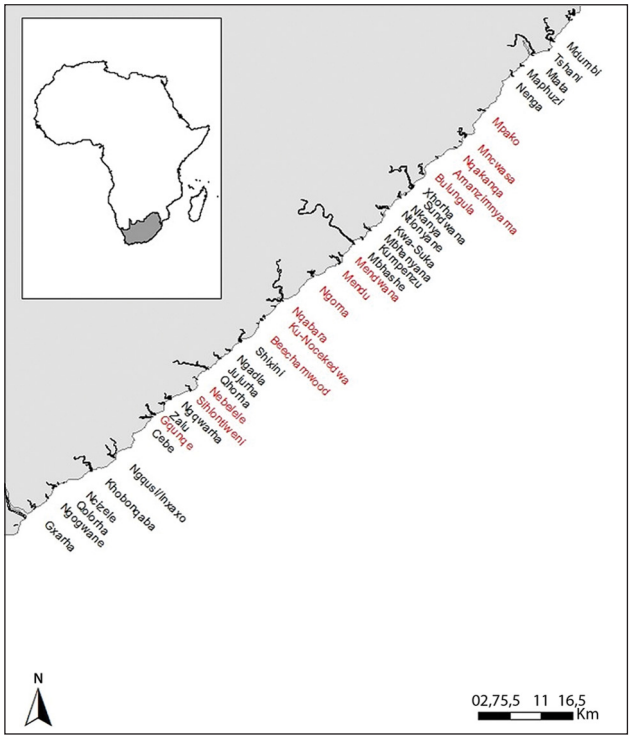

Figure 1. Coastal outlets between the Kei and Mdumbi estuaries. Estuaries in red were inaccessible for sampling.

Physico-chemical

During each survey, selected physico-chemical parameters were measured at various sites within each system, ranging from the mouth area (Site 1) upstream; the number of sites varied depending on the size of each system. Water depth and transparency were measured using a 20 cm diameter Secchi disc attached to a weighted shot line graduated at 10 cm intervals. Temperature (°C), salinity (psu), pH, dissolved oxygen (mg·L^{-1}), and turbidity (NTU) were measured using a Horiba U-10 Water Quality Checker. Where water depth permitted (usually >0.5 m), both surface and bottom waters were measured. The mouth state of each system at the time of sampling was also noted.

Ichthyofauna

The ichthyofauna of each estuary was sampled using a 30 m long x 1.7 m deep x 15 mm bar mesh seine net fitted with a 5 mm bar mesh purse, and a fleet of multi-mesh gill nets. The gill nets were either 10 m or 20 m in length and 1.7 m in depth and consisted of three equal sections of 45 mm, 75 mm and 100 mm stretch meshes. Seine netting was carried out during daylight hours in shallow (< 1.5 m deep), unobstructed areas with gently sloping banks. Fish caught were identified and measured to the nearest millimetre standard length (SL) before being released. Where large catches of a species were made, a sub-sample was kept and returned to the laboratory where the fish were identified, measured and weighed to the nearest 1.0 g; specimens that could not be identified in the field were also kept and processed in the laboratory. All fishes were identified by reference to Smith and Heemstra (1991) and Skelton (1993); taxonomic identities of certain species were adjusted using information provided in Whitfield (2019). The total fish species composition, by number and mass, was calculated for each system. The relative biomass contribution of each species was calculated using actual recorded masses as well as masses derived from length–mass relationships provided in Harrison (2001). Fishes were also classified according to their biogeographic affinity (endemic/temperate, temperate, tropical, widespread) and the contribution of each group calculated for each estuary based on the number of species, abundance, and biomass.

Estuary classification

Estuaries were divided into two main groups on the basis of predominant mouth condition, according to the classification given in Harrison and Whitfield (2006a). The two main groups were predominantly open estuaries and predominantly closed estuaries. Predominantly closed estuaries were further sub-divided into two groups based on surface area: small closed estuaries with a surface area below 10 ha and moderate to large closed estuaries with a surface area above 10 ha.

Multivariate analyses

Data were analysed using the Plymouth Routines in Multivariate Ecological Research (PRIMER) package (version 6.0) with PERMANOVA+ add-on (PRIMER-E, Plymouth Marine Laboratory, UK). A principal component analysis (PCA) was undertaken on the overall mean (surface and bottom) values of the physico-chemical variables recorded in each system. Each parameter was first examined for normality; turbidity, depth and dissolved oxygen required log-transformation ($\ln[1 + x]$). The data were also examined for any inter-correlations (Pearson r); pH exhibited significant correlations with both dissolved oxygen and salinity and was omitted from the analysis. Temperature and depth also showed a significant correlation; however, these parameters were retained in the analysis. A PCA was performed based on the following normalised parameters: depth, temperature, salinity, dissolved oxygen, and turbidity. An analysis of similarities (ANOSIM) was also undertaken (using the normalised Euclidean distance similarity measure) to test for significant differences between estuarine types.

Specimens not identified to species level (e.g. Mugilidae) as well as exotic species (e.g. *Micropterus* spp.) were excluded from the analysis. Abundance and biomass data were first standardised and then square-root transformed before calculating a Bray-Curtis similarity matrix. Standardisation removed the effect of variable sampling while transformation scales down the importance of dominant species (Field et al., 1982; Clarke and Warwick, 2001). A non-parametric multivariate analysis of variance (PERMANOVA) (Anderson, 2001) was applied to both the abundance and biomass data to examine differences in fish communities between estuary types. A similarity percentages analyses (SIMPER) was also undertaken to identify species that characterise estuary types as well as those that discriminate between estuary types. Relationships between physico-chemical and biotic resemblance matrices were also investigated using the RELATE routine; the measure of agreement is the Spearman rank correlation coefficient (Rho) between the corresponding elements of the two similarity matrices.

RESULTS

A total of 26 systems were sampled between Kei Estuary and the Mdumbi Estuary. Two systems, (Sundwana and Thsani) comprised small coastal streams and were not considered further. Of the remaining systems, 8 were predominantly open estuaries and 16 were predominantly closed estuaries. Of the predominantly closed estuaries, 12 were moderate to large (>10 ha) systems and 4 were small (<10 ha) systems.

Physico-chemical

Small predominantly closed estuaries

The four small predominantly closed systems were all closed at the time of sampling. All estuaries were relatively shallow, with average water depths generally not exceeding 1.4 m (Table 1). Mean water temperatures ranged between 20.2°C (Jujurha) and 22.7°C (Ncizele and Mbhanyana). Mean salinities were almost fresh (0.5) in the Mbhanyana and averaged from 16.3 (Kwa-Suka) to 27.2 in

the Ncizele. Salinities were fairly uniform throughout most of the systems with no clear horizontal or vertical gradients. Only the Jujurha exhibited a horizontal decrease in salinity from 27.9 in the lower reaches to 16.6 in the upper reaches. A vertical salinity and temperature gradient was also recorded in the Jujurha in a 3.5 m deep site in the otherwise very shallow system (Table 2). Average dissolved oxygen values ranged between 4.0 mg·L^{-1} (Kwa-Suka) and 7.7 mg·L^{-1} (Jujurha). Mean turbidity values were highly variable and ranged from 15.3 NTU (Jujurha) to 85 NTU (Mbhanyana). Average pH values were between 7.4 and 7.9 (Table 1).

Moderate to large predominantly closed estuaries

All 12 of the moderate to large predominantly closed estuaries were closed to the sea at the time of this survey. Mean water depths ranged from 0.5 m (Nenga) to 3.4 m (Qolorha) (Table 1). Water temperatures averaged between 20.2 (Kumpenzu) and 24.2°C (Cebe). Water temperatures increased from the lower to the upper reaches of the estuaries. Vertical temperature stratification, with a 1°C or more decrease in temperature from the surface to the bottom, was only evident in the Ngadla, Ntlonyane and Nkanya estuaries (Table 3). Mean salinities ranged from 16.5 (Qolorha) to 31.6 (Nkanya) (Table 1). A pronounced horizontal salinity gradient was present in the Qolorha, Ngqwara, Ngadla, Ntlonyane and Nenga estuaries, with salinities decreasing upstream from the mouth. These estuaries received marine water from overwash events. Pronounced vertical salinity stratification was observed in the Gxara, Qolorha, Ntlonyane, Nenga and Maphuzi estuaries (Table 3). Mean dissolved oxygen values ranged from 4.5 mg·L^{-1} (Qolorha) to 10.7 mg·L^{-1} (Mapuzi), with most values exceeding 5.0 mg·L^{-1}. The water column in these estuaries was clear (<10 NTU) to moderately turbid (<50 NTU). Mean pH values ranged from 7.6 (Ngogwane) to 8.1 (Maphuzi) (Table 1).

Predominantly open estuaries

The predominantly open estuaries were all open at the time of sampling. Mean water depths recorded in the eight predominantly open estuaries ranged from 1 m (Qhorha and Shixini) to 3.1 m (Mtata) (Table 1). Water temperatures averaged between 17.0°C (Qhorha) and 22.4°C (Xhorha). Water temperatures in most systems increased upstream of the mouth, except for the Inxaxo arm of the Ngqusi/Inxaxo Estuary, where water temperatures decreased upstream (Table 4). The Mbhashe and Mtata estuaries were freshwater-dominated with mean salinities of 14.6 and 12.6 recorded in these systems, respectively (Table 1). In these systems the surface water was predominantly fresh, with pronounced vertical salinity stratification (Table 4). In contrast, mean salinities in the other six predominantly open estuaries were all above 21 (Table 1) and very little vertical salinity stratification was evident (Table 4). Mean dissolved oxygen values ranged between 6.6 and 7.9 mg·L^{-1}. The Qhorha, Mbhashe and Mtata estuaries were very turbid (> 80 NTU), whereas the other estuaries were fairly clear (<23 NTU). The mean pH in all estuaries was similar to seawater (7.9–8.1) (Table 1).

Table 1. Mean physico-chemical parameters measured in estuaries between Kei Estuary and the Mdumbi Estuary on the south-east coast of South Africa, October–November 1997

Estuary	Mouth	Depth (m)	Temperature (°C)	Salinity	Dissolved oxygen (mg·L^{-1})	Turbidity (NTU)	pH
Small closed estuaries							
Ncizele	Closed	0.8	22.7	27.2	7.1	-	7.8
Jujurha	Closed	1.4	20.2	23.7	7.7	15.3	7.9
Mbhanyana	Closed	1.4	22.7	0.5	5.3	85.0	7.4
Kwa-Suka	Closed	1.1	27.1	16.3	4.0	23.7	7.5
Moderate to large closed estuaries							
Gxarha	Closed	1.3	21.4	19.0	5.7	16.5	7.7
Ngogwane	Closed	1.5	22.6	20.6	5.6	0.3	7.6
Qolorha	Closed	3.4	21.3	16.5	4.5	4.3	7.8
Cebe	Closed	1.2	24.2	25.7	6.7	11.3	7.9
Zalu	Closed	1.1	20.6	20.6	6.3	4.3	8.0
Ngqwarha	Closed	0.9	21.9	25.6	6.4	1.0	7.8
Ngadla	Closed	0.6	23.5	28.9	7.4	37.0	7.9
Kumpenzu	Closed	0.8	20.2	11.5	4.8	13.5	7.7
Ntlonyane	Closed	1.0	20.5	30.9	6.7	29.3	7.9
Nkanya	Closed	0.8	21.4	31.6	6.9	44.0	8.0
Nenga	Closed	0.5	23.02	16.7	2.1	19.3	7.9
Maphuzi	Closed	0.7	21.75	23.0	10.7	10.5	8.1
Predominantly open estuaries							
Khobonqaba	Open	1.5	20.4	28.4	7.1	5.5	8.0
Ngqusi/Inxaxo	Open	2.1	18.1	28.0	6.6	7.1	8.0
Qhorha	Open	1.0	17.0	23.4	7.9	83.3	7.9
Shixini	Open	1.0	18.8	30.9	7.8	14.3	8.1
Mbhashe	Open	2.8	20.2	14.6	7.4	163.0	8.0
Xhorha	Open	2.1	22.4	27.8	6.7	17.7	7.9
Mtata	Open	3.1	21.4	12.6	7.6	100.2	7.9
Mdumbi	Open	2.1	21.5	27.8	7.3	8.0	8.1

Table 2. Physico-chemical characteristics of small predominantly closed estuaries between the Kei Estuary and the Mdumbi Estuary on the south-east coast of South Africa, October–November 1997

System	Site	Depth (m)	Temperature		Salinity		Dissolved oxygen (mg·L^{-1})		Turbidity (NTU)		pH T	
			S	B	S	B	S	B	S	B	S	B
Ncizele	1	0.1	22.3	22.3	27.6	27.6	7.4	7.3			7.9	7.9
	2	0.8	22.5	22.5	27.3	27.4	7.5	7.3			7.2	8.0
	3	0.6	23.4	23.4	26.4	27.1	6.7	6.6			7.8	7.9
Jujurha	1	0.4	20.3		27.9		7.4		7		7.9	
	2	3.5	22.7	14.6	19	31.2	7.7	8.2	14	395	7.8	7.9
	3	0.4	23.3		16.6		7.6		25		7.8	
Mbhanyana	1	0.1	23.3	23.3	0.9	0.9	5.9	5.8	122	122	7.6	7.6
	2	1.9	23.8	21.9	0.6	0.4	5.4	1.0	85	45	7.4	7.0
	3	1.3	22	22	0.1	0.1	6.9	7.1	48	47	7.6	7.4
Kwa-Suka	1	0.1	26.4	26.2	16.5	18.5	4.9	3.6	33	18	7.7	7.6
	2	1.5	27.5	26.4	16.1	16.5	5.2	4	33	22	7.6	7.6
	3	0.9	28.2	27.7	14.9	15	3.2	3.2	5	5	7.3	7.3

Table 3. Physico-chemical characteristics of moderate to large predominantly closed estuaries between the Kei Estuary and the Mdumbi Estuary on the south-east coast of South Africa, October–November 1997

System	Site	Depth (m)	Temperature (°C)		Salinity		Dissolved oxygen (mg·L^{-1})		Turbidity (NTU)		pH	
			S	B	S	B	S	B	S	B	S	B
Gxarha	1	0.5	20.6	20.6	17.7	17.9	6.8	6.7			7.9	7.9
	2	1.6	21	21.5	17.1	25.1	7.0	3.2	23	44	7.8	7.6
	3	1.8	22.3	22.2	17.1	18.9	5.7	4.9	10	12	7.7	7.7
Ngogwane	1	1.5	21.7	21.7	20.4	20.5	6.5	6.3	0	0	7.8	7.8
	2	1.8	22.4	24.5	20.4	22.1	6.1	3.5	0	2	7.7	7.4
	3	1.1	22.7	22.7	19.9	20.2	5.6	5.8	1	1	7.6	7.6
Qolorha	1	2.7	20.8	21.5	11	21.7	7.6	0.7	7	20	8.1	7.3
	2	4.2	22.2	19.2	11.1	29.3	8.0	0.8	6	7	8.2	7.4
	3	3.3	21.6	22.4	1	25	8.0	2.1	0	1	8.4	7.2
Cebe	1	1.8	24.1	23.9	25.7	25.8	6.9	7.0	5	6	7.9	7.9
	2	0.6	24.6	24.6	25.5	25.5	6.6	6.6	20	24	7.8	7.8
	3	1.2	24.3	23.8	25.5	26	6.7	6.7	9	10	7.9	7.9
Zalu	1	0.6	20.4	20.5	20.8	20.8	6.3	6.1	0	3	8.0	8.0
	2	0.9	20.3	20.3	20.7	20.7	7.0	7.2	8	6	8.1	8.1
	3	1.8	21.3	20.7	20.1	20.6	6.1	5.0	5	5	8.0	7.9
Ngqwarha	1	0.6	22.7	20.7	26	26	7.4	7.4	1	1	8.0	8.0
	2	1.1	20.7	20.7	24.5	25.1	7.2	7.1	2	4	8.0	7.9
	3	1	23.3	23.3	25.9	26	4.8	4.7	0	0	7.5	7.5
Ngadla	1	0.5	24.1	18.6	31.6	32.3	7.0	7.7	37	37	7.9	8.0
	2	0.6	26.8	25.8	31.2	31.3	7.3	7.1	37	37	7.9	7.9
	3	0.8	27.2	18.5	15.3	31.8	7.8	7.6	37	37	7.8	8.0
Kumpenzu	1	0.7	19.8	20	11.6	11.7	5.0	4.8	2	2	7.7	7.7
	2	0.9	20.5	20.5	11.3	11.5	4.8	4.6	25	49	7.6	7.6
Ntlonyane	1	0.4	20.8	-	31.5	-	6.7	-	23	-	7.9	-
	2	1.5	22.2	17.4	30.2	32.5	6.2	7.3	32	70	7.9	8.0
	3	1	23.7	18.4	27.7	32.5	5.9	7.4	33	57	7.8	8.0
Nkanya	1	1	21.3	19.4	32.1	32.7	6.3	7.5	30	20	7.9	8.0
	2	0.6	24.6	20.3	29.2	32.3	6.9	7.1	58	60	7.9	8.1
Nenga	1	0.3	21.4		14.9		7.5	-	22	-	8.0	-
	2	0.5	22.3	22.5	23.5	25.9	6.6	6.8	19	14	8.0	8.1
	3	0.6	24.1	24.8	6.7	12.5	7.2	7.0	17	17	7.8	7.9
Maphuzi	1	0.6	22.2	22	23.1	24	9.7	9.3	10	6	8.1	8.1
	2	0.7	22.2	20.6	19.5	25.5	11.8	11.9	11	7	8.1	8.2

Table 4. Physico-chemical characteristics of predominantly open estuaries between the Kei Estuary and the Mdumbi Estuary on the south-east coast of South Africa, October–November 1997

System	Site	Depth (m)	Temperature		Salinity		Dissolved oxygen (mg·L^{-1})		Turbidity		pH	
			S	B	S	B	S	B	S	B	S	B
Khobonqaba	1	0.8	18.8	18.0	32.2	33.0	7.0	7.2	6	7	8.0	8.0
	2	1.6	22.1	16.6	28.9	33.6	7.2	6.9	7	23	7.9	8.0
	3	3.2	22.8	18.2	25.4	32.9	6.8	7.0	6	50	7.9	8.0
	4	0.5	23.3	23.2	12.3	28.6	7.6	6.8	3	2	8.0	7.9
Ngqusi/Inxaxo	1	1.2	17.5	17.6	34.4	34.4	7.5	7.6	1	1	8.1	8.1
Ngqusi	1	1.9	18.0	18.1	33.2	34.2	7.0	7.2	10	24	8.1	8.1
	2	1.8	16.7	18.4	26.1	34.3	7.1	5.6	11	47	8.0	8.0
	3	1.6	18.6	19.0	31.6	34.2	5.8	4.9	10	35	7.9	8.0
Inxaxo	1	1.8	18.4	18.0	32.7	34.0	6.8	6.5	10	26	8.1	8.1
	2	2.3	16.1	18.5	24.0	33.9	7.9	5.3	6	33	8.1	8.0
	3	4.4	17.8	20.1	2.0	3.4	7.7	4.9	2	1	8.0	7.9
Qhorha	1	1.3	15.0	14.3	28.2	32.6	8.0	8.1	188	231	7.9	8.0
	2	1.7	18.5	14.5	19.3	32.3	7.9	7.9	25	114	8.0	8.0
	3	1.8	20.3	16.0	8.4	25.5	8.1	8.0	45	93	7.9	7.9
	4	0.5	19.7	17.3	2.3	17.6	8.7	7.9	229	217	8.0	7.9
Qhorha arm	1	1.1	15.9	14.3	28.8	31.3	7.9	8.4	78	13	7.9	7.9
	2	1.2	18.5	16.8	16.3	30.7	8.1	7.7	41	59	7.9	7.9
	3	0.8	20.0	16.6	5.1	28.1	8.2	7.4	131	54	7.9	7.8
Shixini	1	1.7	17.3	17.2	31.6	31.7	8.0	7.8	10	10	8.1	8.1
	2	1.0	22.0	18.3	28.9	31.5	7.8	7.6	13	14	8.1	8.1
	3	0.4	19.4		30.6		8.0		20		8.0	
Mbhashe	1	2.3	21.3	17.8	8.5	32.0	7.9	7.9	12	59	8.1	8.1
	2	4.0	21.8	19.0	5.3	31.3	8.5	5.5	19	28	8.1	7.9
	3	4.3	21.3	18.6	1.9	23.5	8.4	4.8	102	62	8.1	7.4
	4	0.4	21.9		0.0		8.5		519		8.4	
Xhorha	1	1.0	20.9		32.7		7.6				8.0	
	2	2.8	22.1	21.3	30.3	32.5	7.4	7.4	20	4	8.0	8.0
	3	2.9	25.0	20.8	23.7	32.2	7.0	5.4	7	63	7.8	7.8
	4	1.7	25.4	21.5	13.5	30.0	7.6	4.4	26	15	7.7	7.6
Mtata	1	5.8	22.0	16.6	10.6	29.2	7.6	7.9	41	133	8.1	8.1
	2	1.3	23.6	18.0	9.0	21.0	7.5	7.3	53	28	8.1	8.2
	3	2.3	24.6	17.3	5.4	25.3	7.8	7.5	54	38	8.1	7.6
	4	4.1	24.8	18.7	0.7	24.7	7.8	7.0	177	305	7.9	7.6
	5	1.9	24.2	24.2	0.0	0.0	8.0	8.0	176	175	8.0	7.8
Mdumbi	1	0.9	20.9	21.0	32.0	32.0	7.2	7.3	10	9	8.2	8.2
	2	3.5	21.5	18.7	26.0	32.6	8.6	6.7	10	30	8.3	8.1
	3	3.0	23.2	19.0	25.6	32.4	7.6	5.8	8	14	8.2	8.0
	4	0.9	24.4	23.6	12.7	28.8	8.1	7.4	4	16	8.2	8.1

Multivariate analysis

The PCA classification (Fig. 2) divided the estuaries based on salinity (Axis 1) and depth, temperature and turbidity (Axis 2). The first two axes accounted for approximately 64% of the variation between the samples. Large predominantly open systems (Mbhashe, Mtata, Qhorha) were situated towards the upper right section of the plot associated with high turbidities, depth and dissolved oxygen (Fig. 2). The predominantly open Qhorha, Ngqusi/Inxaxo, Shixini, Khobonqaba, Xhorha and Mdumbi were situated towards the middle right associated with high salinities and low turbidities. The predominantly closed estuaries showed a gradation from estuaries with low salinities to estuaries with high salinities situated towards the right of the plot (Fig. 2). Although there was overlap between estuary types, the marine-dominated predominantly open estuaries were all situated towards the right of the plot. The ANOSIM test revealed a weak but significant difference between estuary types (Global R: 0.25; $p < 0.05$). Pairwise tests showed that there was no significant difference between small predominantly closed estuaries and moderate to large predominantly closed estuaries (R: 0.26; $p > 0.05$), however, significant differences were observed between predominantly open estuaries and both small and moderate to large predominantly closed estuaries (R: 0.24–0.35; $p > 0.05$).

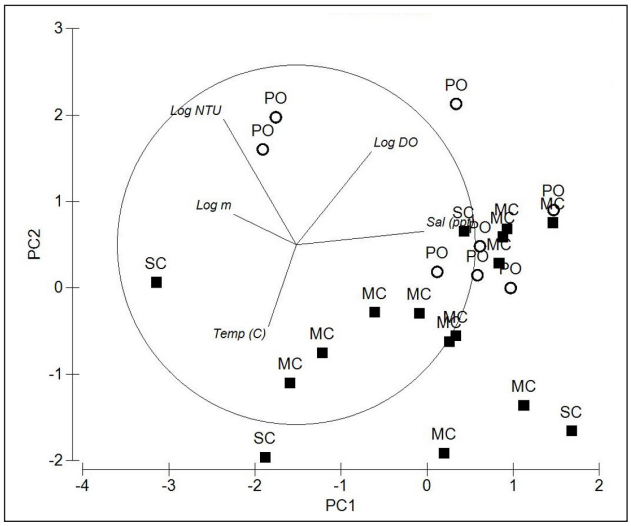

Figure 2. PCA ordination of physico-chemical variables measured between the Kei and Mdumbi estuaries. SC = small closed estuaries, MC = moderate to large closed estuaries, PO = predominantly open estuaries (■ = predominantly closed estuaries, ○ = predominantly open estuaries).

Fish communities

Small predominantly closed estuaries

A total of 28 species were captured in small predominantly closed estuaries with between 11 (Kwa-Suka) and 19 (Mbhanyana) species captured per estuary. Numerically important species captured within this group of estuaries were *Rhabdosargus holubi* (mean = 30.2%), *Gilchristella aestuaria* (mean = 24.7%), *Pseudomyxus capensis* (mean = 18.9%), *Atherina breviceps* (mean = 8.4%), *Glossogobius callidus* (mean = 3.2%), *Oreochromis mossambicus* (mean = 2.8%), *Mugil cephalus* (mean = 2.5%), and *Chelon dumerili* (mean = 1.5%) (Table 5). Estuarine-associated marine species (Category II) dominated catches, numerically comprising 59% of the catch, followed by estuarine species (Category I), comprising 38% of the catch, and freshwater species (Category IV – 3%). Numerical abundance per estuary is given in Table A1 (Appendix). In terms of biomass, important species included *Oreochromis mossambiccus* (mean = 18.8%), *R. holubi* (mean = 15.5%), *P. capensis* (mean = 12.9%), *Moolgarda buchanani* (mean = 9.4%), *Liza tricuspidens* (mean = 9.8%), *Argyrosomus japonicus* (mean = 8.2%), *M. cephalus* (mean = 6.2%), *Chelon richardsonii* (mean = 4.5%), *Pomadasys commersonii* (mean = 3.7%), *Planiliza macrolepis* (mean = 2.0%), and *Torpedo sinusperci* (mean = 1.6%) (Table 6). In terms of biomass, estuary-associated marine species comprised 79% of the catch, followed by freshwater species (19%) and estuarine species (2%). Biomass of fishes per estuary is given in Table A2 (Appendix). Endemic (temperate) and temperate species dominated the catches and accounted for 50.0% of the taxa, 65.6% of the biomass, and 93.3% of the overall abundance.

Moderate to large predominantly closed estuaries

A total of 41 species were captured in moderate to large predominantly closed estuaries, with between 10 (Ngogwane) and 29 (Qolora) species captured per estuary. The most abundant species within this group of estuaries overall were *R. holubi* (mean = 26.2%), *G. aestuaria* (mean = 19.8%), *P. capensis* (mean = 12.3%), *C. dumerili* (mean = 9.3%), *M. cephalus* (mean = 6.5%), *G. callidus* (mean = 5.8%), *Atherina breviceps* (mean = 4.7%), *Moolgarda robustus* (mean = 2.5%), *L. tricuspidens* (mean = 2.3%), and *O. mossambicus* (mean = 2.0%) (Table 5). Estuarine-associated marine species comprised 66% of the catch, followed by estuarine species (32%) and freshwater species (2%). Numerical abundances per estuary are given in Table A3 (Appendix). Dominant species overall in terms of biomass included *R. holubi* (mean = 14.9%), *C. richardsonii* (mean = 11.3%), *O. mossambicus* (mean = 10.5%), *L. tricuspidens* (mean = 10.4%), *A. japonicus* (mean = 10.3%), *P. capensis* (mean = 7.7%), *M. cephalus* (mean = 6.9%), *P. commersonnii* (mean = 4.9%), *C. dumerili* (mean = 4.1%), *Planiliza macrolepis* (mean = 3.8%), *Planiliza alata* (mean = 3.3%), *Moolgarda buchanani* (mean = 2.5) and *Elops machnata* (mean = 1.7%) (Table 6). In terms of biomass, estuary-associated marine species comprised 87% of the catch, followed by freshwater species (11%) and estuarine species (2%). Biomass of fishes per estuary is given in Table A4 (Appendix). Endemic (temperate) and temperate species dominated the catches both numerically (85.7%) and in terms of biomass (61.3%). In terms of taxa, tropical species comprised 48.8% of the overall catches and endemic (temperate) and temperate species comprised 43.9%.

Predominantly open estuaries

A total of 52 species were captured in the predominantly open estuaries, with between 22 (Shixini) and 31 (Ngqusi, Xhorha and Mtata) species captured per estuary. In terms of numbers, catches were dominated by *G. aestuaria* (mean = 44.6%), *R. holubi* (mean = 17.7%), *M. cephalus* (mean = 11.0%), *C. dumerili* (mean = 4.5%), *P. capensis* (mean = 4.2%), *G. callidus* (mean = 3.8%), *A. breviceps* (mean = 2.4%), *Caffrogobius gilchristi* (mean = 2.0%), *P. commersonnii* (mean = 1.9%), *C. richardsonii* (mean = 1.5%) and *A. japonicus* (mean = 1.1%) (Table 5). Estuarine species dominated catches numerically, comprising 54% of the catch, followed by estuarine-associated marine species (45%). Freshwater species and marine stragglers (Category III) together comprised 1% of the catch. Numerical abundances per estuary are given in Table A5 (Appendix). The fish species mass in predominantly open estuaries was dominated by *M. cephalus* (mean = 19.7%), *Elops machnata* (mean = 17.4%), *A. japonicus* (mean = 12.8%), *C. richardsonii* (mean = 8.4%), *P. commersonnii* (mean = 7.1%), *M. buchanani* (mean = 7.6%), *Lichia amia* (mean = 5.0%), *L. tricuspidens* (mean = 4.5%), *C. dumerili* (mean = 3.6%), *R. holubi* (mean = 3.2%), *G. aestuaria* (mean = 2.1%), *P. capensis* (mean = 1.9%) and *Galeichthys feliceps* (mean = 1.9%) (Table 6). In terms of biomass, estuary-associated marine species comprised 98% of the catch, followed by estuarine species (2%). Biomass of fishes per estuary is given in Table A6 (Appendix). Endemic (temperate) and temperate species dominated the catches numerically (82.8%); however, tropical species dominated in terms of biomass (48.8%) and taxa (57.7%).

Multivariate analyses

The nMDS plot based on abundance produced a pattern where predominantly open estuaries clustered together and separated from predominantly closed estuaries, which were situated to the left of the plot. There was no separation between small and moderate to large predominantly closed estuaries (Fig. 3a). In terms of biomass, the separation between predominantly closed and open systems was less distinct, with one medium to large predominantly open estuary (Ntlonyane) clustering together with the predominantly open estuaries (Fig. 3b). The PERMANOVA test based on abundance data revealed significant differences between predominantly closed and open estuaries (Pseudo F = 3.1048, p = 0.006). Biomass yielded similar results, with the two estuary types being significantly different (Pseudo F = 4.0978, p = 0.003).

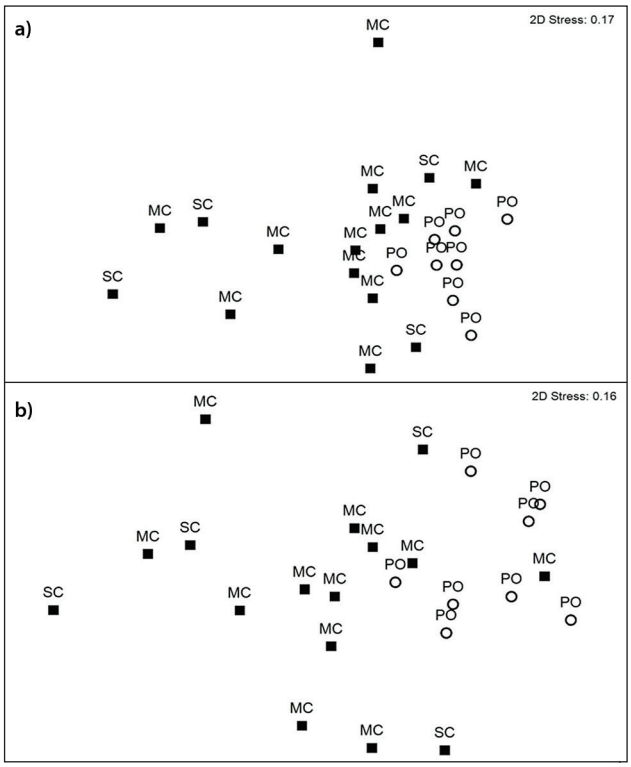

Figure 3. nMDS ordination of fish communities in estuaries between Kei Estuary and Mdumbi on the south-east coast of South Africa based on (a) abundance, and (b) biomass; SC = small closed estuaries, MC = moderate to large closed estuaries, PO = predominantly open estuaries (■ = predominantly closed estuaries, ○ = predominantly open estuaries)

Table 5. Mean numerical abundance (%) of fishes captured in small closed, moderate to large closed and predominantly open estuaries between Kei Estuary and the Mdumbi Estuary on the south-east coast of South Africa, October–November 1997, with an indication of biogeographic affinity (origin) for each species and estuarine association category (from Whitfield 2019).

Species	Estuary-association category	Origin	Small closed	Moderate to large closed	Predominately open
Acanthopagrus vagus	IIa	Tropical	0.02	0.02	0.01
Ambassis ambassis	I	Tropical			0.01
Ambassis dussumieri	I	Tropical		0.01	0.57
Ambassis natalensis	I	Tropical		0.01	0.01
Argyrosomus japonicus	IIa	Tropical	0.74	0.44	**1.11**
Atherina breviceps	I	Endemic (temperate)	**8.42**	**4.69**	**2.42**
Caffrogobius gilchristi	I	Endemic (temperate)	0.95	1.05	**1.97**
Caffrogobius natalensis	I	Endemic (temperate)		0.01	0.05
Caranx ignobilis	IIb	Tropical			0.00
Caranx sexfasciatus	IIb	Tropical		0.06	0.04
Chelon dumerilii	IIa	Endemic (temperate)	**1.46**	**9.33**	**4.45**
Chelon richardsonii	IIb	Endemic (temperate)	0.61	1.41	**1.46**
Clinus superciliosus	I	Temperate			0.00
Diplodus capensis	IIc	Temperate		0.03	0.02
Elops machnata	IIa	Tropical		0.06	0.42
Etrumeus whiteheadi	III	Endemic (temperate)		0.01	
Galeichthys feliceps	IIb	Endemic (temperate)	0.07		0.04
Genion honckenii	IIc	Tropical			0.03
Gerres methueni	IIb	Tropical		0.01	
Gilchristella aestuaria	I	Endemic (temperate)	**24.71**	**19.84**	**44.58**
Glossogobius callidus	I	Endemic (temperate)	**3.19**	**5.81**	**3.76**
Heteromycteris capensis	IIa	Endemic (temperate)		0.01	0.01
Hippichthys spicifer	I	Tropical			0.01
Leiognathus equula	IIb	Tropical			0.04
Lichia amia	IIa	Widespread		0.06	0.09
Lithognathus lithognathus	IIa	Endemic (temperate)	0.06	0.01	0.05
Liza tricuspidens	IIb	Endemic (temperate)	1.14	**2.28**	0.58
Lutjanus argentimaculatus	IIc	Tropical		0.01	0.01
Monodactylus falciformis	IIa	Tropical	0.30	1.12	0.33
Moolgarda buchanani	IIc	Tropical	0.48	0.13	0.24
Moolgarda cunnesius	IIa	Tropical	0.09	0.20	0.10
Moolgarda robustus	IIa	Tropical	0.73	**2.49**	0.35
Mugil cephalus	IIa	Widespread	**2.47**	**6.47**	**10.97**
Oligolepis acutipennis	I	Tropical			0.08
Oreochromis mossambicus	IV	Endemic (temperate)	**2.77**	**2.04**	0.01
Oxyurichthys keiensis	I	Tropical	0.02	0.12	0.23
Planiliza alata	IIa	Tropical	0.05	0.13	
Planiliza macrolepis	IIa	Tropical	0.35	1.36	0.20
Planiliza melinoptera	IIb	Tropical		0.02	
Platycephalus indicus	IIc	Tropical			0.01
Pomadasys commersonnii	IIa	Tropical	1.30	0.77	**1.92**
Pomadasys kaakan	IIc	Tropical			0.02
Pomadasys olivaceus	IIc	Tropical		0.46	
Pomatomus saltatrix	IIc	Widespread	0.02	0.02	0.22
Psammogobius knysnaensis	I	Endemic (temperate)	0.65	0.38	0.77
Pseudomyxus capensis	IIa	Endemic (temperate)	**18.90**	**12.30**	**4.17**
Rhabdosargus holubi	IIa	Endemic (temperate)	**30.15**	**26.16**	**17.67**
Rhabdosargus sarba	IIb	Tropical			0.01
Sardinops ocellatus	III	Temperate		0.02	0.09
Sarpa salpa	IIc	Tropical		0.01	0.01
Secutor ruconius	III	Tropical			0.01
Solea turbynei	IIa	Endemic (temperate)	0.25	0.27	0.67
Sphyraena jello	IIc	Tropical			0.02
Stolephorus holodon	IIc	Tropical			0.09
Terapon jarbua	IIa	Tropical	0.05	0.36	0.07
Torpedo fuscumaculata	IIc	Tropical			0.01
Torpedo sinusperci	IIc	Tropical	0.07		0.00
Number of species			28	41	52

Estuarine-association category: I = estuarine species, IIa = marine species with juveniles dependent on estuaries, IIb = marine species with juveniles mainly in estuaries, IIc = marine species with juveniles sometimes in estuaries, III = marine stragglers, IV = freshwater species. Numerically dominant species in each estuary category are highlighted in bold.

Table 6. Mean biomass (%) of fishes captured in small closed, moderate to large closed and predominantly open estuaries between Kei Estuary and the Mdumbi Estuary on the south-east coast of South Africa, October–November 1997, with an indication of biogeographic affinity (origin) for each species. and estuarine association category (from Whitfield 2019).

Species	Estuary-association category	Origin	Small closed	Moderate to large closed	Predominantly open
Acanthopagrus vagus	IIa	Tropical	0.28	0.18	0.11
Ambassis ambassis	I	Tropical			0.01
Ambassis dussumieri	I	Tropical		0.00	0.01
Ambassis natalensis	I	Tropical		0.00	0.00
Argyrosomus japonicus	IIa	Tropical	**8.15**	**10.34**	**12.77**
Atherina breviceps	I	Endemic (temperate)	0.17	0.19	0.03
Caffrogobius gilchristi	I	Endemic (temperate)	0.02	0.08	0.13
Caffrogobius natalensis	I	Endemic (temperate)		0.00	0.00
Caranx ignobilis	IIb	Tropical			0.00
Caranx sexfasciatus	IIb	Tropical		0.22	0.97
Chelon dumerilii	IIa	Endemic (temperate)	0.80	**4.08**	**3.59**
Chelon richardsonii	IIb	Endemic (temperate)	**4.45**	**11.33**	**8.43**
Clinus superciliosus	I	Temperate			0.00
Diplodus capensis	IIc	Temperate		0.00	0.00
Elops machnata	IIa	Tropical		**1.65**	**17.37**
Etrumeus whiteheadi	III	Endemic (temperate)		0.00	
Galeichthys feliceps	IIb	Endemic (temperate)	0.08		**1.86**
Geneion honckenii	IIc	Tropical			0.01
Gerres methueni	IIb	Tropical		0.03	
Gilchristella aestuaria	I	Endemic (temperate)	1.38	1.43	**2.07**
Glossogobius callidus	I	Endemic (temperate)	0.14	0.46	0.18
Heteromycteris capensis	IIa	Endemic (temperate)		0.00	0.00
Hippichthys spicifer	I	Tropical			0.00
Leiognathus equula	IIb	Tropical			0.12
Lichia amia	IIa	Widespread		1.32	**4.95**
Lithognathus lithognathus	IIa	Endemic (temperate)	1.37	0.06	0.46
Liza tricuspidens	IIb	Endemic (temperate)	**9.84**	**10.38**	**4.49**
Lutjanus argentimaculatus	IIc	Tropical		0.47	0.17
Monodactylus falciformis	IIa	Tropical	1.22	1.23	0.47
Moolgarda buchanani	IIc	Tropical	**9.37**	**2.54**	**7.59**
Moolgarda cunnesius	IIa	Tropical	0.15	0.16	0.03
Moolgarda robustus	IIa	Tropical	1.00	0.94	0.52
Mugil cephalus	IIa	Widespread	**6.19**	**6.88**	**19.74**
Oligolepis acutipennis	I	Tropical			0.00
Oreochromis mossambicus	IV	Endemic (temperate)	**18.84**	**10.49**	0.00
Oxyurichthys keiensis	I	Tropical	0.00	0.01	0.01
Planiliza alata	IIa	Tropical	0.34	**3.26**	
Planiliza macrolepis	IIa	Tropical	**1.95**	**3.82**	0.70
Planiliza melinoptera	IIb	Tropical		0.21	
Platycephalus indicus	IIc	Tropical			0.06
Pomadasys commersonnii	IIa	Tropical	**3.65**	**4.94**	**7.12**
Pomadasys kaakan	IIc	Tropical			0.01
Pomadasys olivaceus	IIc	Tropical		0.29	
Pomatomus saltatrix	IIc	Widespread	0.59	0.09	0.01
Psammogobius knysnaensis	I	Endemic (temperate)	0.03	0.04	0.01
Pseudomyxus capensis	IIa	Endemic (temperate)	**12.95**	**7.73**	**1.89**
Rhabdosargus holubi	IIa	Endemic (temperate)	**15.45**	**14.92**	**3.24**
Rhabdosargus sarba	IIb	Tropical			0.19
Sardinops ocellatus	III	Temperate		0.00	0.01
Sarpa salpa	IIc	Tropical		0.00	0.04
Secutor ruconius	III	Tropical			0.00
Solea bleekeri	IIa	Endemic (temperate)	0.04	0.10	0.03
Sphyraena jello	IIc	Tropical			0.31
Stolephorus holodon	IIc	Tropical			0.01
Terapon jarbua	IIa	Tropical	0.04	0.09	0.04
Torpedo fuscumaculata	IIc	Tropical			0.16
Torpedo sinusperci	IIc	Tropical	**1.55**		0.07
Number of species			28	41	52

Estuarine-association category: I = estuarine species, IIa = marine species with juveniles dependent on estuaries, IIb = marine species with juveniles mainly in estuaries, IIc = marine species with juveniles sometimes in estuaries, III = marine stragglers, IV = freshwater species. Dominant species in each estuary category are highlighted in bold.

SIMPER analysis based on abundance showed that predominantly closed and open estuaries had an average dissimilarity of 39.12%. Species such as *G.aestuaria, M. cephalus*, *C. dumerili, E. machnata, P. commersonnii* and *M. robustus*, which collectively accounted for 24.2% of the overall dissimilarity, were more abundant in predominantly open than closed estuaries. Species such as *R. holubi*, *M. capensis, G. callidus* and *O. mossambicus* (which collectively accounted for 12.1% of the overall dissimilarity) were more abundant in predominantly closed systems. In terms of biomass there was a 45.4% dissimilarity between predominantly open and closed estuaries. *Elops machnata, M. buchanani, L. amia, M. cephalus, C. richardsonii, P. commersonii* and *A. japonicus* comprised a greater proportion of the biomass in predominantly open estuaries (collectively comprised 34.8% of the dissimilarity). *Oreochromis mossambiccus* and *P. capensis* comprised a greater proportion of the biomass in predominantly closed estuaries (accounting for 9.3% of the dissimilarity). The results of the RELATE analysis revealed significant relationships between the physico-chemical similarity matrix and both the fish abundance and biomass similarity matrices (Rho > 0.30, $p < 0.05$).

DISCUSSION

This survey provides baseline information on the estuaries and fish assemblages found along a poorly studied section of the South African coastline. Of the 26 estuaries considered in this study, 8 were predominantly open estuaries and 16 predominantly closed estuaries. Only four of the predominantly closed estuaries were small systems. Multivariate analyses suggested that predominantly open and predominantly closed estuaries had distinctive physico-chemical characteristics. The eight predominately open systems comprised of two freshwater-dominated systems (Mbhashe and Mtata) characterised by high turbidities and relatively low salinities. The Mbhashe and Mtata estuaries are typically highly turbid systems, with the high turbidity of the Mbhashe attributed to highly erodible sediments present in the extensive catchment, which extends from the southern Drakensberg to the coast. Poor catchment management (e.g. overgrazing, bad farming practices) has further increased the rate of soil erosion, also resulting in elevated sediment to these estuaries (O'Keeffe, 1989; Plumstead, 1990; Le Roux et al., 2008). The other six predominantly open estuaries were characterised by high salinities and low to moderate turbidities.

The predominantly closed estuaries formed a gradation from small estuaries with low salinities to small to moderate and large closed estuaries with higher salinities. Closed estuaries usually breach during periods of high fluvial discharge, particularly after rainfall in the catchment (Perissinotto et al., 2000; Cowley and Whitfield, 2001). Although sampling was conducted during October and November, with November normally representing the onset of the high flow period (James et al., 2020), all the predominantly closed estuaries were closed at the time of sampling, following a period of low rainfall. Elevated salinities in many of these closed estuaries may be due to wave overwash events, which introduce seawater into these systems (Cowley and Whitfield, 2001).

Estuaries in this region are close to the warm-temperate/subtropical biogeographic boundary (Harrison, 2002). Transition zones are typically areas of rapid environmental variability (Attrill and Rundle, 2002) and species turnover, resulting in increased levels of species richness (Spector, 2002; Konar et al., 2010). Furthermore, many tropical and temperate species reach their southern and northern distributional limit, respectively, within South African estuaries in the subtropical/warm-temperate transition-zone (e.g. Maree et al., 2000; Harrison and Whitfield, 2006b). Indicative of the high species richness in this region was the fact that 28 species were recorded in the four small predominantly closed estuaries, 41 species in the moderate to large predominantly closed estuaries and 52 species in the predominantly open estuaries. A comparable survey along the East London and surrounding coastline documented 26, 34 and 44 fish species from small predominately closed, moderate to large predominantly closed and predominantly open estuaries, respectively (James and Harrison, 2016). Many of the species recorded in southern Transkei estuaries and not in previous studies of south-east coast estuaries (James and Harrison 2010a; 2010b; 2011; 2016) were tropical species that are mainly confined to subtropical estuaries and whose distribution is strongly linked to temperature (Harrison and Whitfield, 2006). The southern Transkei coastline is located south of the break between the warm-temperate and subtropical region (Harrison, 2002). Maree et al. (2000) suggested that the subtropical and warm-temperate transition-zone for estuaries incorporates an area where the contribution of tropical and temperate species is roughly equal, i.e., 50%. In this study tropical species comprised between 43 and 58% of the number of species recorded and temperate species (including endemic species) comprised 37–50% of the species. Temperate species dominated all estuaries numerically (>80%), while in terms of biomass, tropical species comprised 28–49% and temperate species composed 26–66%. These findings are indicative of the estuaries occurring within the subtropical/warm-temperate transition-zone.

The nMDS plot based on abundance and biomass showed that predominantly open estuaries clustered together and separated from predominantly closed estuaries, which were situated to the left of the plot. There was no separation between small and moderate to large predominantly closed estuaries. Overall, dominant species numerically in the predominantly closed estuaries were *Rhabdosargus holubi, Gilchristella aestuaria, Myxus capensis, Atherina breviceps, Chelon dumerili, Glossogobius callidus* and *Oreochromis mossambicus.* Dominant species by mass were *R. holubi*, *Argyrosomus japonicus, Pseudomyxus capensis, Mugil cephalus, Chelon richardsonii*, *Liza tricuspidens, Moolgarda buchanani, O. mossambicus* and *Pomadasys commersonii.* Although species assemblages were similar between small and moderate to large predominantly open estuaries, the number of species recorded in the moderate to large estuaries (41) was much greater than in the small estuaries (28 species). Species only recorded in moderate to large and not in small predominantly closed estuaries included *Ambassis ambassis, Ambassis natalensis, Caffrogobius natalensis, Caranx sexfasciatus, Diplodus capensis, Elops machnata, Etremeus whiteheadi, Gerres methueni, Heteromycteris capensis, Lichia amia, Planiliza melinoptera, Lutjanus argentimaculatus, Pomadasys olivaceus* and *Sardinops ocellatus*. Only two species, *Galeichthys feliceps* and *Torpedo sinusperci*, were only found in small predominantly closed estuaries and not in moderate to large predominantly closed estuaries.

The greatest species richness was recorded in the predominantly open estuaries. Species only recorded in predominantly open estuaries included *Ambassis dussumieri, Amblyrhynchotes honckenii, Anguila mossambica, Caffrogobius nudiceps, Caranx ignobilis, Clinus superciliosus, Hippichththys spicifer, Leiognathus equula, Oligolepis acutipennis, Platycephalus indicus, Pomadasys kaakan, Rhabdosargus sarba* and *Secutor ruconius*. Many of these species are stenohaline marine species that are not dependent on estuaries (marine stragglers) (Whitfield, 2019). An increase in the number of marine stragglers recorded in the lower reaches of predominantly open estuaries often accounts for the greater species richness in predominantly open estuaries compared to predominantly closed estuaries (e.g. Bennett, 1989; Whitfield and Kok, 1992; Vorwerk et al., 2003; James and Harrison, 2016). Dominant species numerically in the predominantly open estuaries were *G. aestuaria, R. holubi, Mugil cephalus, C. dumerili, P. capensis, G. callidus, A. breviceps, Caffrogobius gilchristi* and *P. commersonnii.* Dominant species by biomass were *M. cephalus*,

Elops machnata, A. japonicus, Chelon richardsonii, Moolgarda buchanani, Lichia amia, L. tricuspidens, C. dumerili, R. holubi, G. aestuaria, P. capensis and *Galeichthys feliceps*.

Although similar species were found to dominate catches in estuaries of East London and the surrounding coastline (James and Harrison, 2016), estuarine species such as *Atherina breviceps, Gilchristella aestuaria* and *Glossogobius callidus* comprised a greater proportion of the catch numerically in predominantly closed estuaries in the later study compared to this study. Overall, *G. aestuaria* and *A. breviceps* often represent a larger percentage of the catch, numerically, in predominantly closed estuaries than in predominantly open estuaries (James et al., 2007; Vorwerk et al., 2003; James and Harrison, 2016). The lower numbers of estuarine species recorded during this survey may be due to prolonged closed conditions. During extended closed periods fish populations in predominantly closed estuaries can decrease considerably due to predation (James et al., 2007).

This study found a significant link between estuary typology (and physico-chemical characteristics) and the fish communities present. Predominantly open estuaries have a near-permanent connection with the sea and are characterised by moderate to high salinities and high species richness. Predominantly closed systems have an intermittent connection with the sea and are characterised by shallow, warmer waters. Species richness in these systems is typically lower than predominantly open estuaries, although marine species may be introduced into these systems via barrier overwash. This study represents a unique survey of multiple estuaries along a little-studied section of the South African coastline.

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AUTHOR CONTRIBUTIONS

Conceptualisation, field work and sample analysis was done by TH. Interpretation of the results and writing of the first draft was done mainly by NJ.

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APPENDIX

Table A1. Numerical abundance of fishes captured in small closed estuaries between Kei Estuary and the Mdumbi Estuary on the south-east coast of South Africa, October–November 1997 (*n* = number; % = percentage contribution)

Species	Ncizele		Jujurha		Mbhanyana		Kwa-Suku	
	n	%	n	%	n	%	n	%
Acanthopagrus berda					1.0	0.1		
Argyrosomus japonicus			9.0	2.5	8.0	0.5		
Atherina breviceps	21.0	1.9	18.0	4.9	1.0	0.1	127.0	26.8
Caffrogobius gilchristi			13.0	3.6	4.0	0.2		
Galeichthys feliceps			1.0	0.3				
Gilchristella aestuaria	15.0	1.4	144.0	39.3	956.0	58.1		
Glossogobius callidus	6.0	0.5			38.0	2.3	47.0	9.9
Lithognathus lithognathus					4.0	0.2		
Liza alata							1.0	0.2
Liza dumerilii	2.0	0.2	20.0	5.5			1.0	0.2
Liza macrolepis					23.0	1.4		
Liza richardsonii	3.0	0.3	8.0	2.2				
Liza tricuspidens	13.0	1.2	7.0	1.9			7.0	1.5
Monodactylus falciformis	7.0	0.6	1.0	0.3	1.0	0.1	1.0	0.2
Mugil cephalus	61.0	5.6	12.0	3.3	17.0	1.0		
Myxus capensis	319.0	29.1			16.0	1.0	216.0	45.6
Oligolepis keiensis					1.0	0.1		
Oreochromis mossambicus	1.0	0.1					52.0	11.0
Pomadasys commersonnii			7.0	1.9	54.0	3.3		
Pomatomus saltatrix	1.0	0.1						
Psammogobius knysnaensis			4.0	1.1	21.0	1.3	1.0	0.2
Rhabdosargus holubi	649.0	59.1	105.0	28.7	474.0	28.8	19.0	4.0
Solea bleekeri			1.0	0.3	5.0	0.3	2.0	0.4
Terapon jarbua					3.0	0.2		
Torpedo sinusperci			1.0	0.3				
Valamugil buchanani			7.0	1.9				
Valamugil cunnesius					6.0	0.4		
Valamugil robustus			8.0	2.2	12.0	0.7		
Total individuals	1 098		366		1 645		474	
Total taxa	12		17		19		11	

Table A2. Biomass composition of fishes captured in small closed estuaries between Kei Estuary and the Mdumbi Estuary on the south-east coast of South Africa, October–November 1997 (*g* = mass; % = percentage contribution)

Species	Ncizele		Jujura		Mbhanyana		Kwa-Suku	
	g	%g	g	%g	g	%g	g	%g
Acanthopagrus vagus					206.4	1.1		
Argyrosomus japonicus			2 263.0	9.6	4 286.0	23.0		
Atherina breviceps	2.5	0.1	3.9	0.0	0.2	0.0	41.2	0.6
Caffrogobius gilchristi			7.5	0.0	5.8	0.0		
Chelon dumerilii	26.6	0.9	203.1	0.9			108.0	1.5
Chelon richardsonii	429.0	14.1	859.3	3.7				
Galeichthys feliceps			59.0	0.3				
Gilchristella aestuaria	23.5	0.8	109.6	0.5	796.5	4.3		
Glossogobius callidus	5.8	0.2			31.9	0.2	13.2	0.2
Lithognathus lithognathus					1 019.2	5.5		
Liza tricuspidens	221.7	7.3	5 408.2	23.0			661.5	9.1
Monodactylus falciformis	130.2	4.3	29.0	0.1	30.0	0.2	22.0	0.3
Moolgarda buchanani			8 824.0	37.5				
Moolgarda cunnesius					112.8	0.6		
Moolgarda robustus			16.6	0.1	731.6	3.9		
Mugil cephalus	239.3	7.9	1 206.3	5.1	2 189.8	11.7		
Oreochromis mossambicus	107.0	3.5					5 246.4	71.8
Oxyurichthys keiensis					1.7	0.0		
Planiliza alata							100.0	1.4
Planiliza macrolepis					1 458.1	7.8		
Pomadasys commersonnii			1 417.6	6.0	1 597.8	8.6		
Pomatomus saltatrix	72.0	2.4						
Psammogobius knysnaensis			2.3	0.0	21.4	0.1	2.2	0.0
Pseudomyxus capensis	1 117.8	36.9			143.1	0.8	1 034.1	14.2
Rhabdosargus holubi	657.0	21.7	1 665.9	7.1	5 989.7	32.1	69.3	0.9
Solea bleekeri			1.1	0.0	6.4	0.0	7.4	0.1
Terapon jarbua					27.3	0.1		
Torpedo sinusperci			1 461.1	6.2				
Total mass	3 032.23	100	23 537.36	100	18 655.66	100	7 305.43	100
Total taxa	12		17		19		11	

Table A3. Numerical abundance of fishes captured in moderate to large closed estuaries between Kei Estuary and the Mdumbi Estuary on the south-east coast of South Africa, October–November 1997 (*n* = number; % = percentage contribution)

Species	Gxara		Ngogwane		Qolora		Cebe		Zalu		Ngqwara		Ngadla		Ku-Mpenzu		Ntlonyane		Nkanya		Nenga		Mapuzi	
	n	%	n	%	n	%	n	%	n	%	n	%	n	%	n	%	n	%	n	%	n	%	n	%
Acanthopagrus vagus																	1.0	0.1	2.0	0.1				
Ambassis dussumieri																					1.0	0.1		
Ambassis natalensis																			2.0	0.1				
Argyrosomus japonicus	1.0	0.1			2.0	0.2	2.0	0.2			5.0	0.9	4.0	0.3	1.0	0.1	11.0	1.6	8.0	0.5	5.0	0.6	1.0	0.8
Atherina breviceps	17.0	1.0	9.0	2.3	38.0	3.1	17.0	1.8	133.0	14.6	77.0	13.7	103.0	8.3	43.0	5.2	6.0	0.9	62.0	3.6	1.0	0.1	2.0	1.5
Caffrogobius gilchristi	4.0	0.2			9.0	0.7	3.0	0.3	9.0	1.0	2.0	0.4	22.0	1.8			4.0	0.6	15.0	0.9	29.0	3.7	4.0	3.0
Caffrogobius natalensis	1.0	0.1			1.0	0.1																		
Caranx sexfasciatus																							1.0	0.8
Chelon dumerilii	33.0	1.9			109.0	8.9	102.0	11.0			29.0	5.2	19.0	1.5	1.0	0.1	407.0	60.7	6.0	0.4	102.0	13.1	12.0	9.1
Chelon richardsonii	3.0	0.2	6.0	1.6	14.0	1.1	9.0	1.0	1.0	0.1	45.0	8.0	12.0	1.0	1.0	0.1	1.0	0.1	12.0	0.7			4.0	3.0
Diplodus capensis	3.0	0.2									1.0	0.2												
Elops machnata	2.0	0.1					1.0	0.1									3.0	0.4						
Etrumeus whiteheadi													1.0	0.1										
Gerres methueni					1.0	0.1																		
Gilchristella aestuaria	964.0	55.4	41.0	10.7	367.0	30.1	213.0	23.0	302.0	33.1	136.0	24.2	53.0	4.3	24.0	2.9	13.0	1.9	845.0	49.4	25.0	3.2		
Glossogobius callidus	23.0	1.3	4.0	1.0	3.0	0.2	5.0	0.5	73.0	8.0	9.0	1.6	47.0	3.8	375.0	45.7	7.0	1.0	91.0	5.3	9.0	1.2		
Heteromycteris capensis					1.0	0.1																		
Lichia amia							1.0	0.1									4.0	0.6						
Lithognathus lithognathus											1.0	0.2												
Liza tricuspidens	84.0	4.8	6.0	1.6	2.0	0.2	5.0	0.5	7.0	0.8	28.0	5.0	14.0	1.1	2.0	0.2	66.0	9.9	2.0	0.1	1.0	0.1	4.0	3.0
Lutjanus argentimaculatus					1.0	0.1																		
Monodactylus falciformis	5.0	0.3	5.0	1.3	11.0	0.9	2.0	0.2	38.0	4.2	9.0	1.6			8.0	1.0			24.0	1.4	8.0	1.0	2.0	1.5
Moolgarda buchanani					1.0	0.1											10.0	1.5						
Moolgarda cunnesius					13.0	1.1									9.0	1.1			2.0	0.1	1.0	0.1		
Moolgarda robustus					7.0	0.6	10.0	1.1			1.0	0.2	1.0	0.1			7.0	1.0			9.0	1.2	34.0	25.8
Mugil cephalus	31.0	1.8	4.0	1.0	26.0	2.1			4.0	0.4	89.0	15.8	2.0	0.2	4.0	0.5	8.0	1.2	11.0	0.6	419.0	53.9		
Oreochromis mossambicus	5.0	0.3	8.0	2.1	8.0	0.7									167.0	20.3			3.0	0.2	7.0	0.9		
Oxyurichthys keiensis					2.0	0.2							13.0	1.1							2.0	0.3		
Planiliza alata					3.0	0.2									1.0	0.1					9.0	1.2		
Planiliza macrolepis	4.0	0.2			16.0	1.3					2.0	0.4	2.0	0.2	3.0	0.4	6.0	0.9	2.0	0.1	18.0	2.3	14.0	10.6
Planiliza melinoptera																					2.0	0.3		
Pomadasys commersonnii	7.0	0.4			12.0	1.0	3.0	0.3			2.0	0.4	23.0	1.9			11.0	1.6	7.0	0.4	8.0	1.0	3.0	2.3
Pomadasys olivaceus					1.0	0.1					1.0	0.2											7.0	5.3
Pomatomus saltatrix	1.0	0.1			2.0	0.2																		
Psammogobius knysnaensis	10.0	0.6			3.0	0.2	1.0	0.1	8.0	0.9	1.0	0.2	11.0	0.9	8.0	1.0	3.0	0.4	5.0	0.3				
Pseudomyxus capensis	143.0	8.2	294.0	76.8	170.0	13.9	33.0	3.6	48.0	5.3	1.0	0.2	2.0	0.2	106.0	12.9	3.0	0.4	36.0	2.1	28.0	3.6	27.0	20.5
Rhabdosargus holubi	397.0	22.8	6.0	1.6	388.0	31.8	514.0	55.4	283.0	31.0	122.0	21.7	898.0	72.8	67.0	8.2	94.0	14.0	553.0	32.3	92.0	11.8	14.0	10.6
Sardinops ocellatus													1.0	0.1					2.0	0.1				
Sarpa salpa											1.0	0.2												
Solea turbynei	1.0	0.1			5.0	0.4			7.0	0.8	1.0	0.2	5.0	0.4	1.0	0.1			20.0	1.2	1.0	0.1		
Terapon jarbua	1.0	0.1			4.0	0.3	7.0	0.8					1.0	0.1			5.0	0.7	1.0	0.1			3.0	2.3
Total individuals	1740		383		1220		928		913		563		1234		821		670		1711		777		132	
Total species	22		10		29		17		12		21		20		17		20		22		21		15	

Table A4. Biomass composition of fishes captured in moderate to large closed estuaries between Kei Estuary and the Mdumbi Estuary on the south-east coast of South Africa, October-November 1997 (*g* = mass; % = percentage contribution)

Species	Gxarha		Ngogwane		Qolorha		Cebe		Zalu		Ngqwarha		Ngadla		Kumpenzu		Ntlonyane		Nkanya		Nenga		Maphuzi	
	g	%g	g	%g	g	%g	g	%g	g	%g	g	%g	g	%g	g	%g	g	%g	g	%g	g	%g	g	%g
Acanthopagrus vagus																	377.8	1.1	199.7	1.1				
Ambassis dussumieri																					3.0	0.0		
Ambassis natalensis																			6.2	0.0				
Argyrosomus japonicus	714.0	3.7			411.0	1.5	2 122.4	13.7			5 860.0	26.8	1 553.0	10.3	1 867.0	13.3	6 307.3	18.4	4 344.4	23.0	335.3	3.6	442.0	9.9
Atherina breviceps	9.2	0.0	1.6	0.0	70.6	0.3	24.4	0.2	39.1	0.8	42.4	0.2	27.5	0.2	24.7	0.2	2.0	0.0	68.9	0.4	3.1	0.0	0.6	0.0
Caffrogobius gilchristi	9.4	0.0			12.9	0.0	4.2	0.0	4.7	0.1	4.5	0.0	45.3	0.3			3.4	0.0	24.8	0.1	21.5	0.2	3.8	0.1
Caffrogobius natalensis	1.6	0.0			7.4	0.0																		
Caranx sexfasciatus																							120.0	2.7
Chelon dumerilii	331.4	1.7			1 532.6	5.8	948.4	6.1			498.0	2.3	238.3	1.6	17.9	0.1	6 909.5	20.2	117.7	0.6	597.9	6.4	192.0	4.3
Chelon richardsonii	489.0	2.5	1308.4	20.2	1 370.2	5.1	1 889.2	12.2	219.0	4.3	7 940.5	36.3	2 666.5	17.7	131.0	0.9	142.4	0.4	4 208.8	22.3			625.0	13.9
Diplodus capensis	1.8	0.0									0.0	0.0												
Elops machnata	788.0	4.1					932.0	6.0									3 340.0	9.8						
Etrumeus whiteheadi													0.1	0.0										
Gerres methueni					92.0	0.3																		
Gilchristella aestuaria	686.1	3.5	15.6	0.2	322.2	1.2	111.1	0.7	381.4	7.5	97.4	0.4	47.1	0.3	16.0	0.1	6.7	0.0	521.3	2.8	30.2	0.3		
Glossogobius callidus	33.9	0.2	9.0	0.1	2.1	0.0	7.4	0.0	176.7	3.5	9.2	0.0	59.3	0.4	113.8	0.8	10.7	0.0	47.8	0.3	11.5	0.1		
Heteromycteris capensis					1.6	0.0																		
Lichia amia							1 101.0	7.1									2 982.0	8.7						
Lithognathus lithognathus											170.7	0.8												
Liza tricuspidens	1 687.8	8.7	353.7	5.5	1 526.0	5.7	1 100.6	7.1	2 647.0	52.3	3 848.4	17.6	2 799.5	18.6	434.0	3.1	1 383.1	4.0	76.1	0.4	14.6	0.2	63.8	1.4
Lutjanus argentimaculatus					1 515.0	5.7																		
Monodactylus falciformis	246.0	1.3	116.0	1.8	427.2	1.6	40.8	0.3	3.3	0.1	136.7	0.6			149.2	1.1			727.7	3.9	172.0	1.8	109.0	2.4
Moolgarda buchanani					554.0	2.1											9726.0	28.4						
Moolgarda cunnesius					176.8	0.7									140.1	1.0			38.6	0.2	7.1	0.1		
Moolgarda robustus					268.2	1.0	105.1	0.7			3.1	0.0	3.1	0.0			173.8	0.5			179.6	1.9	320.4	7.2
Mugil cephalus	3 484.5	18.0	364.2	5.6	4 501.9	16.9			11.4	0.2	1914.4	8.7	104.2	0.7	2 499.0	17.8	1 501.7	4.4	307.4	1.6	802.8	8.6		
Oreochromis mossambicus	2 995.0	15.5	2 828.0	43.7	2 670.6	10.0									5 044.5	35.9			1 006.8	5.3	1448.9	15.4		
Oxyurichthys keiensis					2.4	0.0							11.6	0.1							1.6	0.0		
Planiliza alata					855.0	3.2									113.0	0.8					3301.0	35.2		
Planiliza macrolepis	811.0	4.2			351.4	1.3					39.4	0.2	170.8	1.1	275.4	2.0	905.8	2.6	171.5	0.9	1477.1	15.7	796.8	17.8
Planiliza melinoptera																					231.9	2.5		
Pomadasys commersonnii	1 282.0	6.6			4 862.2	18.2	1 959.0	12.6			588.8	2.7	250.3	1.7			133.4	0.4	172.0	0.9	283.5	3.0	590.0	13.2
Pomadasys olivaceus					4.5	0.0					6.5	0.0											155.7	3.5
Pomatomus saltatrix	85.0	0.4			164.0	0.6																		
Psammogobius knysnaensis	15.5	0.1			3.4	0.0	0.9	0.0	11.9	0.2	1.1	0.0	12.5	0.1	8.5	0.1	0.9	0.0	4.0	0.0				
Pseudomyxus capensis	1 731.8	8.9	1 186.6	18.4	1 770.9	6.6	1 674.6	10.8	54.5	1.1	58.7	0.3	7.4	0.0	1 820.4	13.0	67.2	0.2	2 993.5	15.9	350.3	3.7	623.9	13.9
Rhabdosargus holubi	3 964.3	20.5	282.2	4.4	3 139.0	11.8	3 466.4	22.3	1 470.8	29.1	681.2	3.1	7 066.4	46.8	1 382.8	9.8	197.5	0.6	3 778.9	20.0	114.0	1.2	424.4	9.5
Sardinops ocellatus													1.6	0.0					1.1	0.0				
Sarpa salpa											0.2	0.0												
Solea turbynei	1.3	0.0			8.4	0.0			41.8	0.8	1.9	0.0	17.8	0.1	1.9	0.0			38.5	0.2	1.1	0.0		
Terapon jarbua	7.2	0.0			22.2	0.1	49.2	0.3					3.0	0.0			56.9	0.2	28.6	0.2			12.9	0.3
Total mass	19 375.8	100	6 465.18	100	26 645.6	100	15 536.6	100	5 061.59	100	21 902.9	100	15 085.1	100	14 039.3	100	34 227.8	100	18 884.2	100	9 387.91	100	4 480.32	100
Total taxa	22		10		29		17		12		21		20		17		20		22		21		15	

Table A5. Numerical abundance of fishes captured in predominantly open estuaries between Kei Estuary and the Mdumbi Estuary on the south-east coast of South Africa, October–November 1997 (*n* = number; % = percentage contribution)

Species	Kobonqaba		Ngqusi/Inxaxo		Qhora		Shixini		Mbashe		Xhora		Mtata		Mdumbi	
	n	%	n	%	n	%	n	%	n	%	n	%	n	%	n	%
Acanthopagrus vagus											1.0	0.1				
Ambassis ambassis									1.0	0.1						
Ambassis dussumieri					5.0	0.3							38.0	4.3		
Ambassis natalensis													1.0	0.1		
Argyrosomus japonicus	13.0	0.6	5.0	0.1	12.0	0.7	28.0	2.5	20.0	1.6	7.0	0.5	26.0	2.9	2.0	0.1
Atherina breviceps	3.0	0.1	40.0	0.9	12.0	0.7	24.0	2.2	23.0	1.8	138.0	8.9	11.0	1.2	107.0	3.6
Caffrogobius gilchristi	15.0	0.7	202.0	4.3	36.0	2.0	26.0	2.3	8.0	0.6	58.0	3.7	6.0	0.7	42.0	1.4
Caffrogobius natalensis	7.0	0.3									1.0	0.1				
Caranx ignobilis															1.0	0.0
Caranx sexfasciatus			1.0	0.0							2.0	0.1			6.0	0.2
Clinus superciliosus			1.0	0.0												
Diplodus capensis			7.0	0.1											1.0	0.0
Elops machnata	9.0	0.4	10.0	0.2	15.0	0.8	2.0	0.2	1.0	0.1	18.0	1.2	1.0	0.1	11.0	0.4
Galeichthys feliceps	4.0	0.2	7.0	0.1												
Geneion honckenii	1.0	0.0					2.0	0.2								
Gilchristella aestuaria	1 414.0	61.8	2 995.0	63.9	346.0	19.3	534.0	48.0	239.0	19.1	687.0	44.2	222.0	24.9	2 248.0	75.5
Glossogobius callidus	76.0	3.3	190.0	4.1	286.0	16.0	13.0	1.2	1.0	0.1	38.0	2.4			90.0	3.0
Heteromycteris capensis			3.0	0.1	1.0	0.1										
Hippichthys spicifer					1.0	0.1										
Leiognathus equula											4.0	0.3			1.0	0.0
Lichia amia	6.0	0.3	3.0	0.1							4.0	0.3	1.0	0.1	1.0	0.0
Lithognathus lithognathus			1.0	0.0			2.0	0.2	1.0	0.1	2.0	0.1				
Chelon dumerilii	17.0	0.7	241.0	5.1	20.0	1.1	61.0	5.5	100.0	8.0	158.0	10.2	11.0	1.2	111.0	3.7
Planiliza macrolepis	1.0	0.0	13.0	0.3	5.0	0.3	1.0	0.1	1.0	0.1	6.0	0.4	3.0	0.3	4.0	0.1
Chelon richardsonii	105.0	4.6	45.0	1.0	17.0	0.9	42.0	3.8	4.0	0.3	13.0	0.8	2.0	0.2		
Liza tricuspidens	14.0	0.6	2.0	0.0	16.0	0.9	5.0	0.4	4.0	0.3	8.0	0.5	2.0	0.2	46.0	1.5
Lutjanus argentimaculatus													1.0	0.1		
Monodactylus falciformis	4.0	0.2	19.0	0.4	12.0	0.7	2.0	0.2	12.0	1.0	2.0	0.1	1.0	0.1		
Mugil cephalus	155.0	6.8	340.0	7.2	108.0	6.0	16.0	1.4	558.0	44.6	81.0	5.2	144.0	16.1	8.0	0.3
Pseudomyxus capensis	1.0	0.0	93.0	2.0	44.0	2.5			57.0	4.6	12.0	0.8	207.0	23.2	10.0	0.3
Oligolepis acutipennis									1.0	0.1			5.0	0.6	1.0	0.0
Oxyurichthys keiensis			1.0	0.0	5.0	0.3	7.0	0.6			6.0	0.4	5.0	0.6		
Oreochromis mossambicus													1.0	0.1		
Platycephalus indicus							1.0	0.1								
Pomadasys commersonnii	20.0	0.9	5.0	0.1	57.0	3.2	15.0	1.3	45.0	3.6	15.0	1.0	46.0	5.2	3.0	0.1
Pomadasys kaakan											1.0	0.1	1.0	0.1		
Pomatomus saltatrix			1.0	0.0					1.0	0.1			12.0	1.3	3.0	0.1
Psammogobius knysnaensis	21.0	0.9	14.0	0.3	22.0	1.2	15.0	1.3			20.0	1.3	8.0	0.9	5.0	0.2
Rhabdosargus holubi	388.0	17.0	393.0	8.4	712.0	39.8	309.0	27.8	153.0	12.2	224.0	14.4	118.0	13.2	257.0	8.6
Rhabdosargus sarba	1.0	0.0														
Sardinops ocellatus	3.0	0.1	11.0	0.2			1.0	0.1			1.0	0.1	2.0	0.2		
Sarpa salpa	1.0	0.0														
Secutor ruconius									1.0	0.1						
Solea turbynei	8.0	0.3	32.0	0.7	38.0	2.1	6.0	0.5	7.0	0.6	7.0	0.5	5.0	0.6	3.0	0.1
Sphyraena jello															5.0	0.2
Stolephorus holodon			3.0	0.1					2.0	0.2	2.0	0.1	3.0	0.3	1.0	0.0
Terapon jarbua			10.0	0.2							1.0	0.1	2.0	0.2		
Torpedo fuscumaculata			1.0	0.0	1.0	0.1										
Torpedo sinusperci															1.0	0.0
Moolgarda buchanani	2.0	0.1							5.0	0.4	16.0	1.0	1.0	0.1	9.0	0.3
Moolgarda cunnesius									4.0	0.3	1.0	0.1	4.0	0.4		
Moolgarda robustus			1.0	0.0	19.0	1.1	1.0	0.1	1.0	0.1	19.0	1.2	2.0	0.2	2.0	0.1
Total individuals	2 289	100	4 690	100	1 790	100	1 113	100	1 250	100	1 553	100	892	100	2 979	
Total species	25		31		23		22		25		31		31		27	

Table A6. Biomass composition of fishes captured in predominantly open estuaries between Kei Estuary and the Mdumbi Estuary on the south-east coast of South Africa, October–November 1997 (*g* = mass; % = percentage contribution)

Species	Kobonqaba		Ngqusi/Inxaxo		Qora		Shixini		Mbashe		Xora		Mtata		Mdumbi	
	g	%g	g	%g	g	%g	G	%g	g	%g	G	%g	g	%g	g	%g
Acanthopagrus vagus											466.8	0.8				
Ambassis ambassis									57.2	0.1						
Ambassis dussumieri					10.5	0.0							49.9	0.1		
Ambassis natalensis													1.6	0.0		
Anguilla mossambica																
Argyrosomus japonicus	112 71.7	11.6	3 149.0	7.4	5 746.3	8.4	13 028.1	31.3	21 699.5	24.9	4 165.8	7.6	5 173.2	9.4	556.0	1.5
Atherina breviceps	0.4	0.0	6.0	0.0	4.0	0.0	6.5	0.0	5.6	0.0	68.4	0.1	2.2	0.0	22.2	0.1
Caffrogobius gilchristi	22.9	0.0	288.0	0.7	61.2	0.1	20.6	0.0	2.4	0.0	57.2	0.1	1.8	0.0	33.9	0.1
Caffrogobius natalensis	7.5	0.0									0.8	0.0				
Caffrogobius nudiceps																
Caranx ignobilis															3.4	0.0
Caranx sexfasciatus			181.0	0.4							128.1	0.2			2 732.7	7.1
Chelon dumerilii	1 042.5	1.1	4 050.5	9.6	1 291.6	1.9	2 199.5	5.3	2 212.2	2.5	1 744.6	3.2	474.7	0.9	1 654.3	4.3
Chelon richardsonii	23 265.4	24.0	3 345.4	7.9	7 245.5	10.5	8 301.9	20.0	547.2	0.6	2 105.7	3.8	315.8	0.6		
Clinus superciliosus			0.3	0.0												
Diplodus capensis			0.7	0.0											0.4	0.0
Elops machnata	11 832.0	12.2	10 793.0	25.5	18 565.0	27.0	2 033.0	4.9	2 021.0	2.3	18 539.0	33.6	939.0	1.7	12 151.0	31.7
Galeichthys feliceps	2 708.0	2.8	5 107.0	12.0												
Geneion honckenii	10.2	0.0					36.5	0.1								
Gilchristella aestuaria	1 187.2	1.2	3 006.5	7.1	453.6	0.7	531.8	1.3	313.9	0.4	477.9	0.9	196.4	0.4	1 799.6	4.7
Glossogobius callidus	63.0	0.1	171.8	0.4	401.4	0.6	23.5	0.1	1.6	0.0	52.1	0.1			77.3	0.2
Heteromycteris capensis			0.8	0.0	0.7	0.0										
Hippichthys spicifer					0.1	0.0										
Leiognathus equula											470.6	0.9			36.3	0.1
Lichia amia	18 510.0	19.1	2 465.0	5.8							3 871.0	7.0	2206.0	4.0	1 401.0	3.7
Lithognathus lithognathus			387.1	0.9			585.9	1.4	187.3	0.2	624.2	1.1				
Liza tricuspidens	9 323.9	9.6	1 214.0	2.9	10 543.0	15.3	518.7	1.2	2 510.6	2.9	87.4	0.2	550.1	1.0	1 083.7	2.8
Lutjanus argentimaculatus													732.0	1.3		
Monodactylus falciformis	265.0	0.3	831.2	2.0	620.7	0.9	219.0	0.5	2.2	0.0	59.2	0.1	0.3	0.0		
Moolgarda buchanani	2 339.0	2.4							6 028.0	6.9	14 109.4	25.6	1547.8	2.8	8 788.0	22.9
Moolgarda cunnesius									66.9	0.1	49.6	0.1	54.9	0.1		
Moolgarda robustus			9.4	0.0	210.2	0.3	1230.0	3.0	55.3	0.1	118.9	0.2	7.5	0.0	226.0	0.6
Mugil cephalus	1 043.1	1.1	1 244.6	2.9	6 636.5	9.7	892.7	2.1	48 297.7	55.5	3 136.1	5.7	39596.4	72.1	3 349.6	8.7
Oligolepis acutipennis									0.2	0.0			3.4	0.0	0.3	0.0
Oreochromis mossambicus													12.6	0.0		
Oxyurichthys keiensis			0.7	0.0	2.5	0.0	6.5	0.0			7.7	0.0	3.2	0.0		
Planiliza macrolepis	22.8	0.0	345.0	0.8	557.8	0.8	181.7	0.4	14.1	0.0	675.1	1.2	2.1	0.0	864.4	2.3
Platycephalus indicus							189.8	0.5								
Pomadasys commersonnii	9 252.5	9.6	1 540.1	3.6	8 629.5	12.6	9 497.0	22.8	1 488.0	1.7	1 478.5	2.7	1136.1	2.1	742.7	1.9
Pomadasys kaakan											27.6	0.1	22.1	0.0		
Pomatomus saltatrix			1.7	0.0					4.3	0.0			24.3	0.0	7.7	0.0
Psammogobius knysnaensis	7.4	0.0	12.3	0.0	8.2	0.0	4.7	0.0	0.0	0.0	12.6	0.0	2.5	0.0	1.4	0.0
Pseudomyxus capensis	0.9	0.0	1 957.5	4.6	1 559.1	2.3			1 352.9	1.6	1 323.2	2.4	1511.7	2.8	590.7	1.5
Rhabdosargus holubi	2 861.3	3.0	1 948.2	4.6	5 441.2	7.9	2 026.4	4.9	82.9	0.1	1 229.3	2.2	312.0	0.6	1032.0	2.7
Rhabdosargus sarba	1 506.0	1.6														
Sardinops sagax	0.7	0.0	6.7	0.0			42.5	0.1			0.4	0.0	0.2	0.0		
Sarpa salpa	292.0	0.3														
Secutor ruconius									10.6	0.0						
Solea bleekeri	16.2	0.0	72.0	0.2	18.7	0.0	2.8	0.0	4.7	0.0	4.8	0.0	2.9	0.0	1.6	0.0
Sphyraena jello															946.0	2.5
Stolephorus holodon			13.1	0.0					8.9	0.0	10.2	0.0	6.3	0.0	1.8	0.0
Terapon jarbua			136.0	0.3							1.2	0.0	12.9	0.0		
Torpedo fuscumaculata			100.0	0.2	700.0	1.0										
Torpedo sinusperci															200.0	0.5
Total mass	96 851.4	100.0	42 384.5	100.0	68 707.3	100.0	41 578.9	100.0	86 975.1	100.0	55 103.5	100.0	54 901.7	100.0	38 303.9	100.0
Total species	25		31		23		22		26		31		31		27	