

# A preliminary fish survey of the estuaries on the east coast of South Africa, Mpande to Mtentwana: a comparative study

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A preliminary ichthyofaunal and physico-chemical survey of estuaries on the east coast of South Africa from the Mpande Estuary to the Mtentwana Estuary was undertaken between November 1997 and January 1998. Sixteen 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 the three groups in terms of both their physico-chemical characteristics (small predominantly closed estuaries were different from predominantly open estuaries) and their fish communities (all three estuary types were significantly different). The estuaries in the study area fall within the subtropical/warm-temperate transition-zone and north of the subtropical/warm-temperate biogeographic break; tropical species dominated the fish communities of all the estuaries in terms of numbers of species and biomass. This survey represents one of the few fish surveys undertaken along this little-studied section of the coastline.

## INTRODUCTION

Research into fish communities in the Eastern Cape Province of South Africa has excluded to a large extent the former Transkei region (Great Kei to Mtamvuna) of the province (Mbande et al., 2005), such that information on most of the smaller systems along this coastline is classified as poor or non-existent (Whitfield and Baliwe, 2013). This paper focuses on the northern Transkei, which is regarded as a transition zone between the warm-temperate and subtropical biogeographic regions, with the boundary between the warm-temperate and subtropical regions occurring at the Mdumbi Estuary in the southern Transkei (Harrison, 2002). The fish species diversity in South African estuaries decreases from east to west (Harrison, 2002) and, as such, the northern Transkei estuaries are expected to have more species than the estuaries further south (e.g. James and Harrison 2010a; 2010b; 2011; 2016; 2020). As the northern Transkei estuaries are situated north of the biogeographic boundary, estuaries in this region are likely dominated by tropical species with moderate numbers of temperate species.

The fish assemblages of the Mngazana and Mngazi estuaries have been studied seasonally in the 2000s (Mbande et al., 2005). Limited information has been published on the physico-chemical properties of the Msikaba Estuary (Blaber et al. 1973) and the fish fauna of the Msikaba, Mtentu (Blaber, 1977), Mntafufu (Plumstead, 1984; Plumstead et al., 1991) and Mzamba (Plumstead, 1984; Plumstead et al., 1991) estuaries. As part of a national assessment of South African estuaries, a fish survey was undertaken along the east coast between the Mpande and Mtentwana estuaries; 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 from the Mpande Estuary to the Mtentwana Estuary extends some 114 km and is intersected by 32 river outlets (Fig. 1). The coastline is situated within the subtropical region of the Eastern Cape, and is comprised of steep valleys and gorges (Colloty et al., 2002). Average summer temperatures are around 23°C (Hoppe-Speer et al., 2015) and most of the rainfall is recorded in summer (Landman et al., 2005). 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 from the Mpande to the Mtentwana were sampled between November 1997 and January 1998. Each system was sampled once and took 1–3 days to survey, depending on the size of the system. Eighteen of the 32 estuaries were accessible 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

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### DATES

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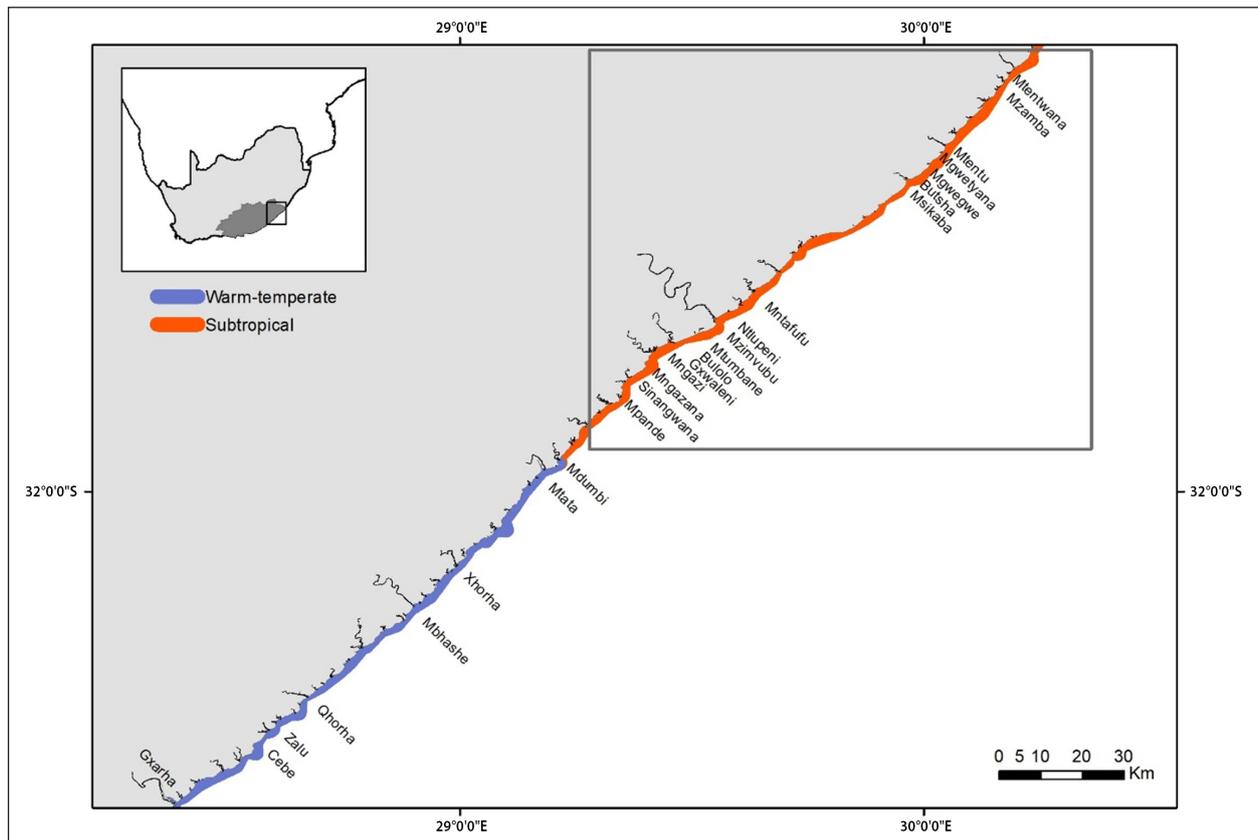
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### KEYWORDS

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**Figure 1.** Coastal outlets sampled from the Mpande to the Mtentwana estuaries on the east coast of South Africa

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 ( $^{\circ}\text{C}$ ), salinity (psu), pH, dissolved oxygen ( $\text{mg}\cdot\text{L}^{-1}$ ), 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) (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 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). An analysis of similarities (ANOSIM) was undertaken (using the Bray-Curtis similarity measure) to test for significant differences between estuarine 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.

## RESULTS

A total of 18 systems were sampled from the Mpande to the Mtentwana estuaries. Two systems, (Gxwaleni and Nkodusweni) comprised small coastal streams and were not considered further. Of the remaining systems, eight were predominantly open estuaries and eight were predominantly closed estuaries. Of the predominantly closed estuaries, four (Mpande, Bulolo, Mtumbane and Mtentwana) were moderate to large (>10 ha) systems and four (Ntlupeni, Butsha, Mgwegwe and Mgwetyana) were small (<10 ha) systems.

### Physico-chemical

#### Small predominantly closed estuaries

The small predominantly closed systems were open at the time of sampling, with the exception of the Butsha estuary. All estuaries were relatively shallow, with average water depths not exceeding 1.4 m (Table 1). Mean water temperatures were high in the four small predominantly closed estuaries and ranged between 27.5°C (Ntlupeni) and 30.4°C (Mgwegwe). Mean salinities were almost fresh (0.7–1.0) in the small Butsha and Ntlupeni estuaries and 10.9 in the Mgwegwe and 18.7 in the Mgwetyana. Salinities were fairly uniform throughout most of the systems with no clear horizontal gradients. The Mgwetyana, however, exhibited a reverse salinity gradient, with surface salinity increasing from 11.0 in the lower reaches to 14.0 in the upper reaches. A vertical salinity gradient was evident in the Mgwegwe and Mgwetyana estuaries. Average dissolved oxygen values ranged between 5.3 mg·L<sup>-1</sup> (Butsha) and 8.6 mg·L<sup>-1</sup> (Ntlupeni). The small predominantly closed estuaries

were fairly clear systems, with mean turbidity <34.0 NTU. Average pH values were between 7.6 and 8.0 (Table 1). Physico-chemical parameters by site are given in Table 2.

#### Moderate to large predominantly closed estuaries

The moderate to large predominantly closed systems were open at the time of sampling, with the exception of the Mtentwana estuary. All estuaries were relatively shallow, with average water depths not exceeding 1.8 m (Table 1). Mean water temperatures measured between 24.2°C (Mpande) and 26.9°C (Mtumbane). Mean salinities ranged from 6.0 (Mtumbane) to 29.2 (Bulolo). Clear horizontal and vertical salinity gradients were evident in all four estuaries, with surface and bottom salinities increasing upstream of the mouth. Average dissolved oxygen values ranged between 5.3 mg·L<sup>-1</sup> (Mpande) and 7.4 mg·L<sup>-1</sup> (Mtentwana). The estuaries were moderately clear systems, with a mean turbidity of between 12.0 and 31.7 NTU. Average pH values were between 7.6 and 8.0 (Table 1). Physico-chemical parameters by site are given in Table 2.

#### Predominantly open estuaries

Mean water depths recorded in the eight predominantly open estuaries ranged from 1.0 m (Sinangwana) to 4.1 m (Msikaba) (Table 1). Water temperatures averaged between 23.5°C (Mngazana) and 26.8°C (Mzamba). Water temperatures in most estuaries were highest in the middle reaches (Table 3). The Msimvubu Estuary was sampled during a period of high rainfall and runoff and this is reflected in the salinities recorded; freshwater extended throughout the system with a mean salinity of 0.9 (Table 1). Mean salinities in the other systems ranged between 17.0 (Msikaba) and 30.3 (Sinangwana). Vertical and horizontal salinity stratification was also pronounced in these systems (Table 3). Mean dissolved oxygen values ranged between 5.9 (Mngazana and Mngazi) and 7.4 mg·L<sup>-1</sup> (Mtentwana). The Mzimvubu was very turbid (> 484.1 NTU), whereas the other estuaries were moderately turbid (10.8–56.0 NTU). The mean pH in all estuaries ranged between 7.4 and 8.2 (Table 1). Physico-chemical parameters by site are given in Table 3.

**Table 1.** Mean physico-chemical parameters measured in estuaries from the Mpande to the Mtentwana on the east coast of South Africa, November 1997 to January 1998

Estuary	Mouth	Depth (m)	Temperature (°C)	Salinity	Dissolved oxygen (mg·L <sup>-1</sup> )	Turbidity (NTU)	pH
<b>PREDOMINANTLY CLOSED ESTUARIES</b>							
<b>Small</b>							
Ntlupeni	Open	0.7	27.5	1.0	8.6	33.4	7.8
Butsha	Closed	1.4	29.0	0.7	5.3	16.8	7.6
Mgwegwe	Open	1.2	30.4	10.9	6.6	11.8	8.0
Mgwetyana	Open	0.6	28.9	18.7	5.6	1.3	8.0
<b>Moderate to large</b>							
Mpande	Open	1.4	24.2	10.1	5.3	14.3	7.8
Bulolo	Open	0.8	26.1	29.2	6.6	31.7	8.0
Mtumbane	Open	0.8	26.9	5.9	6.5	23.6	7.6
Mtentwana	Closed	1.8	28.3	14.8	7.4	12.0	7.8
<b>PREDOMINANTLY OPEN ESTUARIES</b>							
Mngazana	Open	2.3	23.5	28.5	5.9	16.3	8.1
Mngazi	Open	2.1	24.1	19.3	5.9	56.0	7.8
Mzimvubu	Open	2.7	25.5	0.9	7.9	484.1	7.4
Mntafufu	Open	3.2	24.8	20.3	6.9	27.0	8.1
Msikaba	Open	4.1	25.8	17.0	7.3	22.5	8.1
Mtentu	Open	3.9	25.6	18.9	7.4	13.9	8.2
Mzamba	Open	2.3	26.8	23.9	7.0	12.5	8.2
Sinangwana	Open	1.0	26.6	30.0	6.5	10.8	8.1

**Table 2.** Physico-chemical characteristics of predominantly closed estuaries from the Mpande to the Mtentwana estuaries on the east coast of South Africa, November 1997 to January 1998

System	Site	Depth (m)	Temperature		Salinity		Dissolved oxygen (mg·L <sup>-1</sup> )		Turbidity (NTU)		pH	
			S	B	S	B	S	B	S	B	S	B
<b>Small predominantly closed</b>												
Ntlupeni	1	0.5	28.7	29.0	1.2	1.3	8.6	8.8	46	47	8.0	8.0
	2	1.3	27.8	25.0	0.5	2.0	8.4	7.4	25	25	7.6	7.4
	3	0.3	26.8		0.2		9.7		24		8.1	
Butsha	1	0.6	29.2	28.8	0.7	0.7	5.5	5.3	6	8	7.5	7.7
	2	2.1	30.9	26.9	0.7	0.8	6.3	4.1	3	50	7.6	7.4
Mgwegwe	1	1.1	29.1	31.3	5.9	15.0	7.2	6.3	3	9	7.8	8.5
	2	1.2	28.9	32.1	5.5	17.1	7.3	5.6	20	15	7.8	7.7
Mgwetyana	1	0.5	26.6	30.3	11.0	23.5	6.9	5.2	2	2	8.1	8.0
	2	0.7	27.4	31.4	14.0	26.2	6.8	3.5	1	0	8.1	7.9
<b>Moderate to large predominantly closed</b>												
Mpande	1	0.7	24.2	24.3	8.0	10.6	5.7	6.0	9	9	7.8	8.0
	2	2.9	24.7	22.0	7.7	23.9	6.5	2.3	18	19	8.0	7.5
	3	0.7	24.9	25.1	3.0	7.2	6.2	4.9	18	13	7.7	7.6
Bulolo	1	0.5	27.1	26.4	26.8	28.0	6.8	6.8	19	27	7.9	8.1
	2	0.7	27.3	25.8	27.4	32.1	6.2	8.0	16	62	8.0	8.2
	3	1.2	25.6	24.4	29.7	30.9	5.5	6.3	16	50	8.0	8.1
Mtumbane	1	0.4	28.0		4.2		6.3		11		7.9	
	2	1.1	27.2	26.8	5.2	5.8	7.7	6.9	25	25	7.6	7.6
	3	0.9	26.5	25.8	5.9	8.5	6.9	4.9	23	34	7.4	7.4
Mtentwana	1	1.1	28.1	26.9	12.8	13.1	8.4	8.9	10	8	8.0	8.1
	2	1.5	28.7	26.4	12.8	13.2	7.6	6.3	8	7	7.9	7.8
	3	2.8	29.2	29	11.1	22.2	7.7	5.8	15	24	7.7	7.4

**Table 3.** Physico-chemical characteristics of predominantly open estuaries from the Mpande to the Mtentwana estuaries on the east coast of South Africa, November 1997 to January 1998

System	Site	Depth (m)	Temperature (°C)		Salinity		Dissolved oxygen (mg·L <sup>-1</sup> )		Turbidity (NTU)		pH	
			S	B	S	B	S	B	S	B	S	B
Mngazana	1	3.1	23.7	23.5	33.4	33.5	6.6	6.8	0	0	8.3	8.3
	2	3.2	22.3	23.2	30.3	33.5	6.9	6.7	11	4	8.2	8.3
	3	2.5	22.4	23.1	27.7	33	7.3	5.5	16	32	8.2	8.2
	4	2.1	23.0	22.9	24.8	32.6	6.9	3.7	15	33	8.2	8.0
	5	1.6	24.7	25.1	28.5	31	5.4	3.6	16	30	7.9	7.8
	6	1.5	21.3	26.5	5.8	27.7	8.3	3.1	17	21	8.2	7.5
Mngazi	1	1.2	23.8	23.5	22.8	32.1	6.4	6.3	45	29	8.0	8.1
	2	2	24.7	23.3	21.6	33.1	5.5	6.8	52	19	8.0	8.2
	3	4.2	25.3	23.3	2.3	32.7	7.2	4.2	101	22	7.6	8.0
	4	1.7	24.5	23.9	1.4	31.4	7.1	3.6	113	23	7.5	7.9
	5	1.3	24.2	24.5	0.0	15.1	7.4	4.3	120	36	7.4	7.2
Mzimvubu	1	2.6	25.3	25.3	0.0	0.3	7.8	7.9	434	400	7.5	7.5
	2	3.5	25.4	25.4	0.0	9	7.9	7.3	432	428	7.5	7.1
	3	2.8	25.4	25.6	0.0	0	7.8	8.0	505	500	7.6	7.3
	4	2	25.4	25.6	0.0	0	8.0	8.1	520	526	7.5	7.3
	5	2.4	25.5	25.7	0.0	0	8.1	8.1	545	551	7.4	7.4
Mntafufu	1	2	24.6	23.9	21.7	29.8	7.6	7.5	19	28	8.1	8.2
	2	1.3	26.5	23.0	6.7	32	8.6	6.4	18	48	8.2	8.2
	3	2.9	26.4	23.4	6.1	31.2	8.1	4.9	18	33	8.1	8.0
	4	6.5	25.5	24.8	4.1	30.8	8.6	3.1	23	29	8.0	7.8
Msikaba	1	3.3	28.0	23.5	8.7	32.2	8.4	7.6	8	109	8.2	7.7
	2	5.5	27.7	23.3	6.9	32.4	8.6	4.5	10	17	8.3	8.0
	3	5.3	27.4	24.5	4.3	27.3	8.8	6.2	11	7	8.3	7.8
	4	2.2	27.0	25.3	0.5	23.7	8.5	6.0	12	6	8.4	8.0
Mtentu	1	2.9	26.0	23.5	21.5	32.9	7.9	7.4	7	25	8.3	8.2
	2	4.3	27.2	23.3	11.7	32.7	8.7	5.7	5	60	8.4	8.1
	3	1.2	26.9	26.7	5.9	11.7	8.0	7.9	2	4	8.2	8.2
	4	7	26.3	24.9	3.7	31.1	8.3	5.7	4	4	8.2	8.0
Mzamba	1	1.2	26.2	25.7	30.6	32.6	7.2	7.1	13	4	8.2	8.3
	2	3.3	29.1	25.4	16.3	31.1	8.2	6.5	17	16	8.2	8.1
	3	2.4	28.5	25.6	1.2	31.8	8.6	4.5	10	15	8.3	8.0

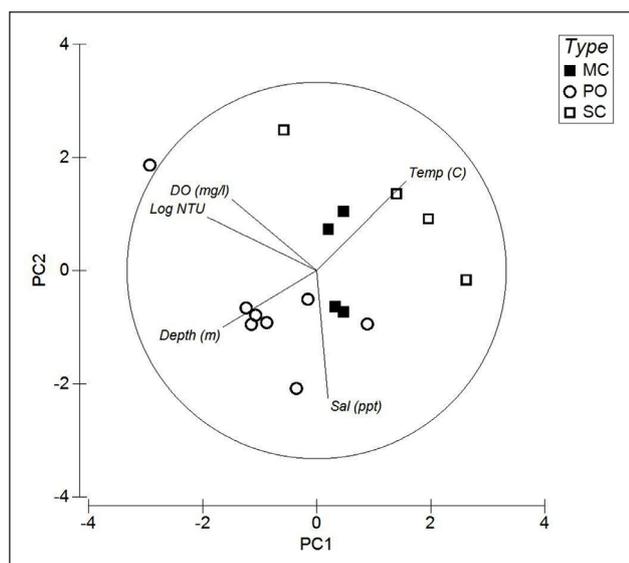
## Multivariate analysis

The PCA classification (Fig. 2) divided the estuaries based on turbidity and depth (Axis 1) and salinity and temperature (Axis 2). The first two axes accounted for approximately 68% of the variation between the samples. Most predominantly open estuaries were situated towards the bottom right of the plot associated with depth (deep) and high salinities, with the exception of the Mzimvubu, which was situated at the top right associated with high turbidity and low salinity. Most small predominantly closed estuaries were situated towards the left of the plot and were associated with high temperatures and depth (shallow), with the exception of the Ntlupeni situated towards the top and associated with low salinity. The moderate to large predominantly closed estuaries were situated towards the middle of the plot (and intermediate conditions) (Fig. 2). Although there was some overlap between estuary types, the ANOSIM test revealed a weak but significant difference between estuary types (Global R: 0.34;  $p < 0.05$ ). Pairwise tests showed that there was no significant difference between small predominantly closed estuaries and moderate to large predominantly closed estuaries (R: 0.22;  $p > 0.05$ ); however, significant differences were observed between predominantly open estuaries and small predominantly closed estuaries (R: 0.60;  $p > 0.05$ ).

## Fish communities

### Small predominantly closed estuaries

A total of 27 species were captured in small predominantly closed estuaries, with between 14 (Mgwetyana) and 17 (Ntlupeni) species captured per estuary. Numerically important species captured within this group of estuaries were *Moolgarda robustus* (mean = 19.6%), *Rhabdosargus holubi* (mean = 17.9%), *Pseudomyxus capensis* (mean = 15.3%), *Chelon dumerilii* (mean = 11.2%), *Planiliza macrolepis* (mean = 8.8%), *Terapon jarbua* (mean = 6.6%), *Mugil cephalus* (mean = 5.7%), *Liza tricuspidens* (mean = 3.8%), *Oreochromis mossambicus* (2.4%), *Monodactylus falciformis* (2.1%) and *Ambassis ambassis* (1.1%) (Table 4). Estuarine-associated marine species (Category II) dominated catches numerically comprising 94% of the catch, followed by estuarine species (Category I), comprising 3% of the catch and freshwater species (Category IV – 2.4%). Numerical abundance per estuary are given in Table A1 (Appendix).



**Figure 2.** PCA ordination of physico-chemical variables measured from the Mpande to the Mtentwana estuaries. □ = small closed estuaries, ■ = moderate to large closed estuaries, ○ = predominantly open estuaries.

In terms of biomass, important species included *P. macrolepis* (mean = 19.0%) and *Planiliza alata* (mean = 18.2%), *O. mossambicus* (mean = 12.6%), *M. robustus* (mean = 12.3%), *C. dumerili* (mean = 10.1%), *M. cephalus* (mean = 5.6%), *R. holubi* (mean = 5.1%), *Moolgarda buchmanani* (mean = 4.6%), *P. capensis* (mean = 3.8%), *Gerres methueni* (mean = 2.4%), *Argyrosomus japonicus* (mean = 1.5%), *M. falciformis* (mean = 1.3%) and *T. jarbua* (mean = 1.0%) (Table 5). In terms of biomass, estuary-associated marine species comprised 86.5% of the catch, followed by freshwater species (12.6%), estuarine (0.7%) and marine (0.4%) species. Biomass of fishes per estuary are given in Table A2 (Appendix). Tropical species accounted for 59% of the taxa, but temperate species accounted for 50.1% of the overall abundance. In terms of biomass, tropical species dominated and comprised 72% of the catch.

### Moderate to large predominantly closed estuaries

A total of 32 species were captured in moderate to large predominantly closed estuaries with between 14 (Mtentwana) and 26 (Bulolo) species captured per estuary. The most abundant species within this group of estuaries overall were *Gilchristella aestuaria* (mean = 22.6%), *P. capensis* (mean = 22.3%), *R. holubi* (mean = 13%), *O. mossambicus* (mean = 9.0%), *C. dumerili* (mean = 8.6%), *Glossogobius callidus* (mean = 7.8%), *M. cephalus* (mean = 7.2%), *P. macrolepis* (mean = 2.5%), *M. falciformis* (mean = 1.4%) and *L. tricuspidens* (mean = 1.1%) (Table 4). Estuarine-associated marine species comprised 59% of the catch, followed by estuarine species (32%) and freshwater species (9%). Numerical abundance per estuary is given in Table A3 (Appendix).

Dominant species overall in terms of biomass included *O. mossambicus* (mean = 21.9%), *M. cephalus* (mean = 15.8%), *P. capensis* (mean = 14.2%), *P. alata* (mean = 12.3%), *P. macrolepis* (mean = 12.1%), *R. holubi* (mean = 5.1%), *C. dumerili* (mean = 4.8%), *Leiognathus equula* (mean = 2.6%), *M. robustus* (mean = 2.0%), *Pomadasy commersonnii* (mean = 1.9%), *M. falciformis* (mean = 1.7%) and *G. aestuaria* (mean = 1.5%) (Table 5). In terms of biomass, estuary-associated marine species comprised 75% of the catch, followed by freshwater species (22%) and estuarine species (3%). Biomass of fishes per estuary are given in Table A4 (Appendix). In terms of taxa, tropical species comprised 62.5% of the overall catches. Endemic (temperate) and temperate species dominated the catches numerically (76.4%), while tropical species dominated the biomass (57%).

### Predominantly open estuaries

A total of 58 species were captured in the predominantly open estuaries with between 11 (Gxwaleni) and 38 (Mngazana) species captured per estuary. In terms of numbers, catches were dominated by *G. aestuaria* (mean = 24.4%), *C. dumerili* (mean = 16.5%), *R. holubi* (mean = 10.8%), *P. macrolepis* (mean = 6.6%), *P. commersonnii* (mean = 5.6%), *M. cephalus* (mean = 4.3%), *G. callidus* (mean = 3.1%), *Caranx sexfasciatus* (mean = 2.2%), and *Caffrogobius gilchristi* (mean = 1.9%) (Table 4). Estuarine-associated marine species numerically dominated and comprised 64% of the catch, followed by estuarine species (35%). Freshwater species and marine stragglers (category III) together comprised 1% of the catch. Numerical abundance per estuary is given in Table A5 (Appendix).

The biomass in predominantly open estuaries was dominated by *M. cephalus* (mean = 16.8%), *Argyrosomus japonicus* (mean = 12.7%), *P. alata* (mean = 12.6%), *Elops machnata* (mean = 11.9%), *M. buchmanani* (mean = 10.6%), *C. sexfasciatus* (mean = 4.4%), *C. dumerili* (mean = 4.0%), *Hilsa kelee* (mean = 3.6%), *P. macrolepis* (mean = 2.8%), *Lutjanus argentimaculatus* (mean = 2.7%), *O. mossambicus* (mean = 2.3%), *P. commersonnii* (mean = 2.2%) and *P. capensis* (mean = 2.0%) (Table 5). In terms of biomass,

**Table 4.** Mean numerical abundance (%) of fishes captured in small predominantly closed estuaries (small closed), moderate to large predominantly closed estuaries (moderate closed) and predominantly open estuaries (open) from the Mpande to the Mtentwane estuaries on the east coast of South Africa, November 1997 – January 1998. Biogeographic affinity (origin) and estuarine association category (from Whitfield 2019) are also provided for each species. 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.

Species	Estuary-association category	Origin	Small closed	Moderate closed	Open
<i>Acanthopagrus vagus</i>	IIa	Tropical	0.07	0.04	0.73
<i>Ambassis ambassis</i>	I	Tropical	<b>1.06</b>	0.09	0.05
<i>Ambassis dussumieri</i>	I	Tropical			<b>1.81</b>
<i>Ambassis natalensis</i>	I	Tropical	0.24	0.05	<b>1.19</b>
<i>Argyrosomus japonicus</i>	IIa	Tropical	0.09		<b>1.26</b>
<i>Atherina breviceps</i>	I	Endemic (temperate)			0.76
<i>Caffrogobius gilchristi</i>	I	Endemic (temperate)	0.28	0.19	<b>1.98</b>
<i>Caffrogobius natalensis</i>	I	Endemic (temperate)			0.04
<i>Caranx heberi</i>	III	Tropical			0.00
<i>Caranx ignobilis</i>	IIb	Tropical		0.03	<b>1.80</b>
<i>Caranx papuensis</i>	IIc	Tropical			0.03
<i>Caranx sexfasciatus</i>	IIb	Tropical	0.24	0.08	<b>2.15</b>
<i>Chelon dumerilii</i>	IIa	Endemic (temperate)	<b>11.22</b>	<b>8.58</b>	<b>16.52</b>
<i>Chelon richardsonii</i>	IIb	Endemic (temperate)		0.04	
<i>Chelonodon laticeps</i>	III	Tropical			0.04
<i>Crenimugil crenilabis</i>	III	Tropical	0.17		
<i>Elops machnata</i>	IIa	Tropical			0.74
<i>Epinephelus malabaricus</i>	III	Tropical			0.02
<i>Favonigobius reichei</i>	I	Tropical			0.02
<i>Genion honckenii</i>	IIc	Tropical			<b>1.17</b>
<i>Gerres methueni</i>	IIb	Endemic	0.54		0.09
<i>Gilchristella aestuaria</i>	I	Endemic	0.21	<b>22.57</b>	<b>24.43</b>
<i>Glossogobius callidus</i>	I	Endemic	0.92	<b>7.81</b>	<b>3.13</b>
<i>Glossogobius giuris</i>	I	Tropical		0.04	0.01
<i>Hilsa kelee</i>	IIb	Tropical			0.49
<i>Hippichthys spicifer</i>	I	Tropical		0.03	0.01
<i>Leiognathus equula</i>	IIb	Tropical		0.44	0.23
<i>Lichia amia</i>	IIa	Temperate		0.05	0.02
<i>Lithognathus lithognathus</i>	IIa	Endemic			0.00
<i>Liza tricuspidens</i>	IIb	Endemic	<b>3.76</b>	<b>1.10</b>	0.89
<i>Lutjanus argentimaculatus</i>	IIc	Tropical			0.05
<i>Megalops cyprinoides</i>	IIa	Tropical			0.06
<i>Monodactylus argenteus</i>	IIa	Tropical		0.05	
<i>Monodactylus falciformis</i>	IIa	Tropical	<b>2.07</b>	<b>1.38</b>	0.09
<i>Moolgarda buchmanii</i>	IIc	Tropical	0.09		1.20
<i>Moolgarda cunnesius</i>	IIa	Tropical	0.66	0.60	0.54
<i>Moolgarda robustus</i>	IIa	Tropical	<b>19.64</b>	0.81	<b>1.12</b>
<i>Moolgarda seheli</i>	III	Tropical	0.32		0.09
<i>Mugil cephalus</i>	IIa	Widespread	<b>5.67</b>	<b>7.21</b>	<b>4.29</b>
<i>Oligolepis acutipennis</i>	I	Tropical		0.05	0.65
<i>Oreochromis mossambicus</i>	IV	Tropical	<b>2.36</b>	<b>8.97</b>	0.67
<i>Oxyurichthys keiensis</i>	I	Tropical		0.23	0.46
<i>Planiliza alata</i>	IIa	Tropical	0.71	0.42	0.99
<i>Planiliza macrolepis</i>	IIa	Tropical	<b>8.80</b>	<b>2.51</b>	<b>6.55</b>
<i>Platycephalus indicus</i>	IIc	Tropical			0.01
<i>Polydactylus plebeius</i>	III	Tropical			0.00
<i>Pomadasys commersonii</i>	IIa	Tropical	0.54	0.25	<b>5.60</b>
<i>Pomadasys kaakan</i>	IIc	Tropical			0.00
<i>Pomatomus saltatrix</i>	IIc	Widespread			0.03
<i>Psammogobius biocellatus</i>	I	Tropical			0.02
<i>Psammogobius knysnaensis</i>	I	Endemic (temperate)	0.37	0.52	0.42
<i>Pseudomyxus capensis</i>	IIa	Endemic (temperate)	<b>15.27</b>	<b>22.28</b>	<b>1.11</b>
<i>Rhabdosargus holubi</i>	IIa	Endemic (temperate)	<b>17.89</b>	<b>13.01</b>	<b>10.78</b>
<i>Rhabdosargus sarba</i>	IIb	Tropical			0.06
<i>Scomberoides lysan</i>	IIc	Tropical		0.03	<b>1.80</b>
<i>Solea turbynei</i>	IIa	Endemic (temperate)	0.21	0.25	0.91
<i>Sphyræna jello</i>	IIc	Tropical			0.03
<i>Stolephorus holodon</i>	IIc	Endemic			0.79
<i>Terapon jarbua</i>	IIa	Tropical	<b>6.62</b>	0.27	<b>1.58</b>
<i>Thryssa vitrirostris</i>	IIb	Tropical			0.33
<i>Upeneus vittatus</i>	III	Tropical			0.12
Number of species			27	32	58

**Table 5.** Mean biomass (%) of fishes captured in small predominantly closed estuaries (small closed), moderate to large predominantly closed estuaries (moderate closed) and predominantly open estuaries (open) from the Mpande to the Mtentwane estuaries on the east coast of South Africa, November 1997 – January 1998. Biogeographic affinity (origin) and estuarine association category (from Whitfield 2019) are also provided for each species. 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.

Species	Estuary-association category	Origin	Small closed	Moderate closed	Open
<i>Acanthopagrus vagus</i>	IIa	Tropical	0.11	0.73	<b>1.43</b>
<i>Ambassis ambassis</i>	I	Tropical	0.57	0.15	0.02
<i>Ambassis dussumieri</i>	I	Tropical			0.17
<i>Ambassis natalensis</i>	I	Tropical	0.03	0.01	0.02
<i>Argyrosomus japonicus</i>	IIa	Tropical	<b>1.47</b>		<b>12.72</b>
<i>Arothron immaculatus</i>	IIc	Tropical			
<i>Atherina breviceps</i>	I	Endemic (temperate)			0.02
<i>Caffrogobius gilchristi</i>	I	Endemic (temperate)	0.04	0.02	0.04
<i>Caffrogobius natalensis</i>	I	Endemic (temperate)			0.00
<i>Caranx heberi</i>	III	Tropical			0.00
<i>Caranx ignobilis</i>	IIb	Tropical		0.02	<b>1.24</b>
<i>Caranx papuensis</i>	IIc	Tropical			0.23
<i>Caranx sexfasciatus</i>	IIb	Tropical	0.11	0.12	<b>4.44</b>
<i>Chelon dumerilii</i>	IIa	Endemic (temperate)	<b>10.14</b>	<b>4.79</b>	<b>4.00</b>
<i>Chelon richardsonii</i>	IIb	Endemic (temperate)		0.09	
<i>Chelonodon laticeps</i>	III	Tropical			0.00
<i>Crenimugil crenilabis</i>	III	Tropical	0.02		
<i>Elops machnata</i>	IIa	Tropical			<b>11.92</b>
<i>Epinephelus malabaricus</i>	III	Tropical			0.00
<i>Favonigobius reichei</i>	I	Tropical			0.00
<i>Genion honckenii</i>	IIc	Tropical			0.07
<i>Gerres methueni</i>	IIb	Endemic	<b>2.37</b>		0.00
<i>Gilchristella aestuaria</i>	I	Endemic	0.02	<b>1.53</b>	0.88
<i>Glossogobius callidus</i>	I	Endemic	0.03	0.81	0.05
<i>Glossogobius giurus</i>	I	Tropical		0.00	0.00
<i>Hilsa kelee</i>	IIb	Tropical			<b>3.56</b>
<i>Hippichthys spicifer</i>	I	Tropical		0.00	0.00
<i>Leiognathus equula</i>	IIb	Tropical		<b>2.62</b>	0.27
<i>Lichia amia</i>	IIa	Temperate		0.04	<b>1.29</b>
<i>Lithognathus lithognathus</i>	IIa	Endemic			0.07
<i>Liza tricuspidens</i>	IIb	Endemic	0.24	0.13	0.61
<i>Lutjanus argentimaculatus</i>	IIc	Tropical			<b>2.75</b>
<i>Megalops cyprinoides</i>	IIa	Tropical			0.17
<i>Monodactylus argenteus</i>	IIa	Tropical		0.19	
<i>Monodactylus falciformis</i>	IIa	Tropical	<b>1.29</b>	<b>1.67</b>	0.03
<i>Moolgarda buehanani</i>	IIc	Tropical	<b>4.63</b>		<b>10.62</b>
<i>Moolgarda cunnesius</i>	IIa	Tropical	0.73	<b>1.16</b>	0.95
<i>Moolgarda robustus</i>	IIa	Tropical	<b>12.26</b>	2.02	0.85
<i>Moolgarda seheli</i>	III	Tropical	0.12		0.02
<i>Mugil cephalus</i>	IIa	Widespread	<b>5.57</b>	<b>15.80</b>	<b>16.84</b>
<i>Oligolepis acutipennis</i>	I	Tropical		0.01	0.03
<i>Oreochromis mossambicus</i>	IV	Tropical	<b>12.64</b>	<b>21.91</b>	<b>2.34</b>
<i>Oxyurichthys keiensis</i>	I	Tropical		0.03	0.01
<i>Planiliza alata</i>	IIa	Tropical	<b>18.25</b>	<b>12.28</b>	<b>12.61</b>
<i>Planiliza macrolepis</i>	IIa	Tropical	<b>18.96</b>	<b>12.06</b>	<b>2.79</b>
<i>Platycephalus indicus</i>	IIc	Tropical			0.02
<i>Polydactylus plebeius</i>	III	Tropical			0.03
<i>Pomadasys commersonnii</i>	IIa	Tropical	0.43	<b>1.91</b>	<b>2.22</b>
<i>Pomadasys kaakan</i>	IIc	Tropical			0.00
<i>Pomatomus saltatrix</i>	IIc	Widespread			0.00
<i>Psammogobius biocellatus</i>	I	Tropical			0.00
<i>Psammogobius knysnaensis</i>	I	Endemic (temperate)	0.00	0.05	0.00
<i>Pseudomyxus capensis</i>	IIa	Endemic (temperate)	<b>3.83</b>	<b>14.23</b>	<b>1.99</b>
<i>Rhabdosargus holubi</i>	IIa	Endemic (temperate)	<b>5.09</b>	<b>5.05</b>	<b>1.28</b>
<i>Rhabdosargus sarba</i>	IIb	Tropical			0.15
<i>Scomberoides lysan</i>	IIc	Tropical		0.00	0.02
<i>Solea turbynei</i>	IIa	Endemic (temperate)	0.02	0.03	0.03
<i>Sphyræna jello</i>	IIc	Tropical			0.24
<i>Stolephorus holodon</i>	IIc	Endemic			0.01
<i>Terapon jarbua</i>	IIa	Tropical	<b>1.03</b>	0.51	0.12
<i>Thryssa vitrirostris</i>	IIb	Tropical			0.81
<i>Upeneus vittatus</i>	III	Tropical			0.01
Number of species			27	32	58

estuary-associated marine species comprised 96% of the catch followed by freshwater (2%) and estuarine species (1%). Biomass of fishes per estuary are given in Table A6 (Appendix). Tropical species dominated the catches (71%) in terms of taxa, while endemic (temperate) and temperate species dominated the catches numerically (62%). Tropical species also dominated in terms of biomass (73%).

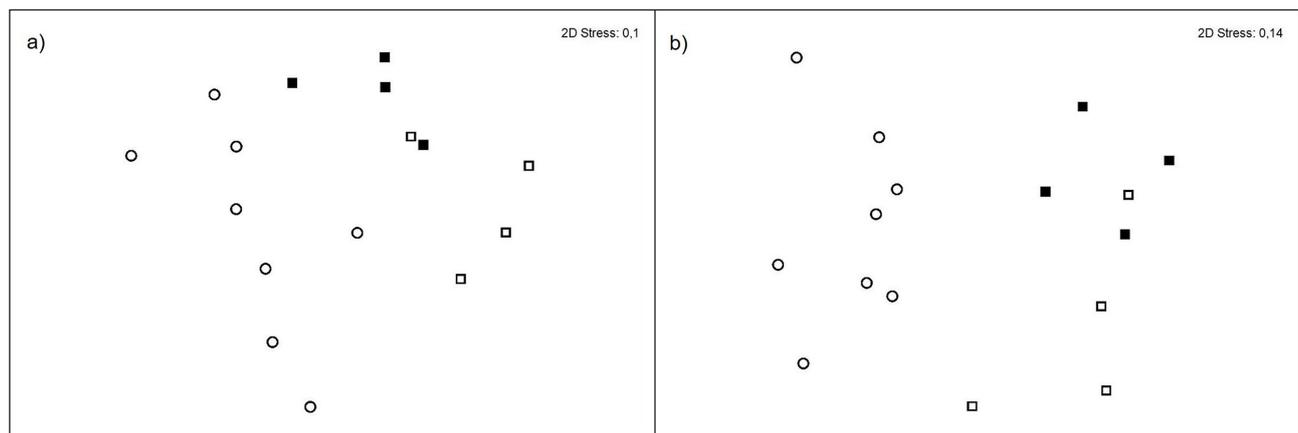
### Multivariate analyses

The nMDS plots based on abundance and biomass produced a pattern where predominantly open estuaries separated from predominantly closed estuaries, which were situated to the right of the plot. The small and moderate to large predominantly closed estuaries also separated, although one small predominantly closed estuary (Ntlupeni) clustered with the large to moderate predominantly closed estuaries (Fig. 3). The ANOSIM test based on abundance data revealed significant differences between estuaries based on type ( $R = 0.55$ ). Biomass yielded similar results, with the three estuary types being significantly different ( $R = 0.69$ ).

SIMPER analysis based on abundance showed that small predominantly closed and moderately to large predominantly closed estuaries had an average dissimilarity of 45.7%. Species such as *M. robustus*, *C. dumerili* and *P. macrolepis*, which collectively accounted for 21.5% of the overall dissimilarity, were more

abundant in small predominantly closed estuaries. Species such as *G. aestuaria*, *P. capensis*, *O. mossambicus* and *G. callidus* (which collectively accounted for 33.4% of the overall dissimilarity) were more abundant in moderate to large predominantly closed systems. These species, along with *R. holubi*, also accounted for differences between small and moderate to large predominantly closed estuaries and predominantly open estuaries (Table 6), with catches in predominantly open estuaries dominated by *G. aestuaria*, *C. dumerili* and *R. holubi* (Table 4). There was a 58.8% dissimilarity between small closed estuaries and open estuaries and a 53.8% dissimilarity between moderate to large closed estuaries and open estuaries (Table 6).

In terms of biomass, there was a 50.3% dissimilarity between small and moderate to large predominantly closed estuaries. *Planiliza alata*, *P. macrolepis*, *M. robustus*, *C. dumerili*, *M. buchani* and *G. methueni*, which contributed 40.6% of the dissimilarity between small and moderate to large predominantly closed estuaries (Table 7), were more abundant in small predominantly closed estuaries (Table 5). *Oreochromis mossambicus*, *P. capensis*, *M. cephalus* and *P. commersonii*, which contributed 28.9% to the dissimilarity (Table 7), were more abundant in terms of biomass in the moderate to large predominantly closed estuaries (Table 5). In terms of biomass, there was a 63.5% dissimilarity between small predominantly closed estuaries and predominantly open estuaries and a 63.9% dissimilarity between moderate to large predominantly



**Figure 3.** nMDS ordination of fish communities in estuaries from the Mpande to the Mtentwana estuaries on the east coast of South Africa based a) on abundance and b) biomass; □ = small closed estuaries, ■ = moderate to large closed estuaries, ○ = predominantly open estuaries.

**Table 6.** SIMPER analysis for fish species (based on abundance) contributing the most to dissimilarities among estuary types (D% = percentage contribution to total dissimilarity)

Small closed vs moderate to large closed		Small closed vs predominantly open		Moderate to large closed vs predominantly open	
Species	D%	Species	D%	Species	D%
<i>Gilchristella aestuaria</i>	14.31	<i>Gilchristella aestuaria</i>	9.53	<i>Pseudomyxus capensis</i>	9.6
<i>Moolgarda robustus</i>	10.1	<i>Moolgarda robustus</i>	7.62	<i>Gilchristella aestuaria</i>	7.49
<i>Glossogobius callidus</i>	7.83	<i>Pseudomyxus capensis</i>	6.25	<i>Oreochromis mossambicus</i>	6.04
<i>Pseudomyxus capensis</i>	6.74	<i>Chelon dumerili</i>	4.4	<i>Chelon dumerili</i>	5.32
<i>Terapon jarbua</i>	6.54	<i>Rhabdosargus holubi</i>	3.98	<i>Pomadasys commersonii</i>	4.47
<i>Chelon dumerili</i>	6.02	<i>Planiliza macrolepis</i>	3.82	<i>Planiliza macrolepis</i>	3.84
<i>Planiliza macrolepis</i>	5.37	<i>Pomadasys commersonii</i>	3.72	<i>Rhabdosargus holubi</i>	3.62
<i>Liza tricuspidens</i>	4.72	<i>Terapon jarbua</i>	3.4	<i>Glossogobius callidus</i>	3.59
<i>Oreochromis mossambicus</i>	4.57	<i>Glossogobius callidus</i>	3.27	<i>Mugil cephalus</i>	3.24
<i>Mugil cephalus</i>	3.76	<i>Liza tricuspidens</i>	3.27	<i>Caranx sexfasciatus</i>	3.02
Average dissimilarity = 45.71		Average dissimilarity = 58.75		Average dissimilarity = 53.83	

**Table 7.** SIMPER analysis for fish species (based on biomass) contributing the most to dissimilarities among estuary types (D% = percentage contribution to total dissimilarity)

Small vs moderate to large closed		Small closed vs predominantly open		Moderate to large closed vs predominantly open	
Species	D%	Species	D%	Species	D%
<i>Oreochromis mossambicus</i>	11.75	<i>Planiliza alata</i>	7.57	<i>Oreochromis mossambicus</i>	9.69
<i>Planiliza alata</i>	10.72	<i>Elops machnata</i>	7.41	<i>Argyrosomus japonicus</i>	7.59
<i>Planiliza macrolepis</i>	9.21	<i>Argyrosomus japonicus</i>	6.85	<i>Elops machnata</i>	7.22
<i>Moolgarda robustus</i>	7.65	<i>Moolgarda robustus</i>	6.55	<i>Planiliza alata</i>	6.79
<i>Pseudomyxus capensis</i>	7.44	<i>Liza macrolepis</i>	6.36	<i>Pseudomyxus capensis</i>	6.11
<i>Mugil cephalus</i>	6.61	<i>Moolgarda buchanani</i>	6.05	<i>Moolgarda buchanani</i>	5.97
<i>Chelon dumerili</i>	5.88	<i>Oreochromis mossambicus</i>	5.74	<i>Planiliza macrolepis</i>	5.36
<i>Moolgarda buchanani</i>	3.57	<i>Mugil cephalus</i>	4.96	<i>Mugil cephalus</i>	4.99
<i>Gerres methueni</i>	3.53	<i>Chelon dumerili</i>	4.26	<i>Caranx sexfasciatus</i>	3.63
<i>Pomadasys commersonnii</i>	3.09	<i>Caranx sexfasciatus</i>	3.7	<i>Hilsa kelee</i>	3.57
Average dissimilarity = 50.29%		Average dissimilarity = 63.54		Average dissimilarity = 63.94	

closed estuaries and predominantly open estuaries. Species such as *P. alata*, *M. robustus*, *P. capensis*, *C. dumerili* and *G. methueni*, which collectively accounted for 30.5% of the overall dissimilarity between small predominantly closed and predominantly open estuaries (Table 7), contributed more to the biomass in small predominantly closed estuaries (Table 5). *Elops machnata*, *A. japonicus*, *M. cephalus*, *M. buchanani* and *P. commersonnii* (29.0% of overall dissimilarity) contributed more to the biomass of predominantly open estuaries (Table 5). *Oreochromis mossambicus*, *P. capensis* and *P. macrolepis*, which collectively accounted for 47.9% of the overall dissimilarity between moderate to large predominantly closed estuaries and predominantly open estuaries, were more important, in terms of biomass, in the moderate to large predominantly closed estuaries. *Argyrosomus japonicus*, *E. machnata*, *M. buchanani*, *C. sexfasciatus* and *H. kelee* (collectively accounted for 28.0% of the dissimilarity) were more important in the predominantly open estuaries (Table 5).

## DISCUSSION

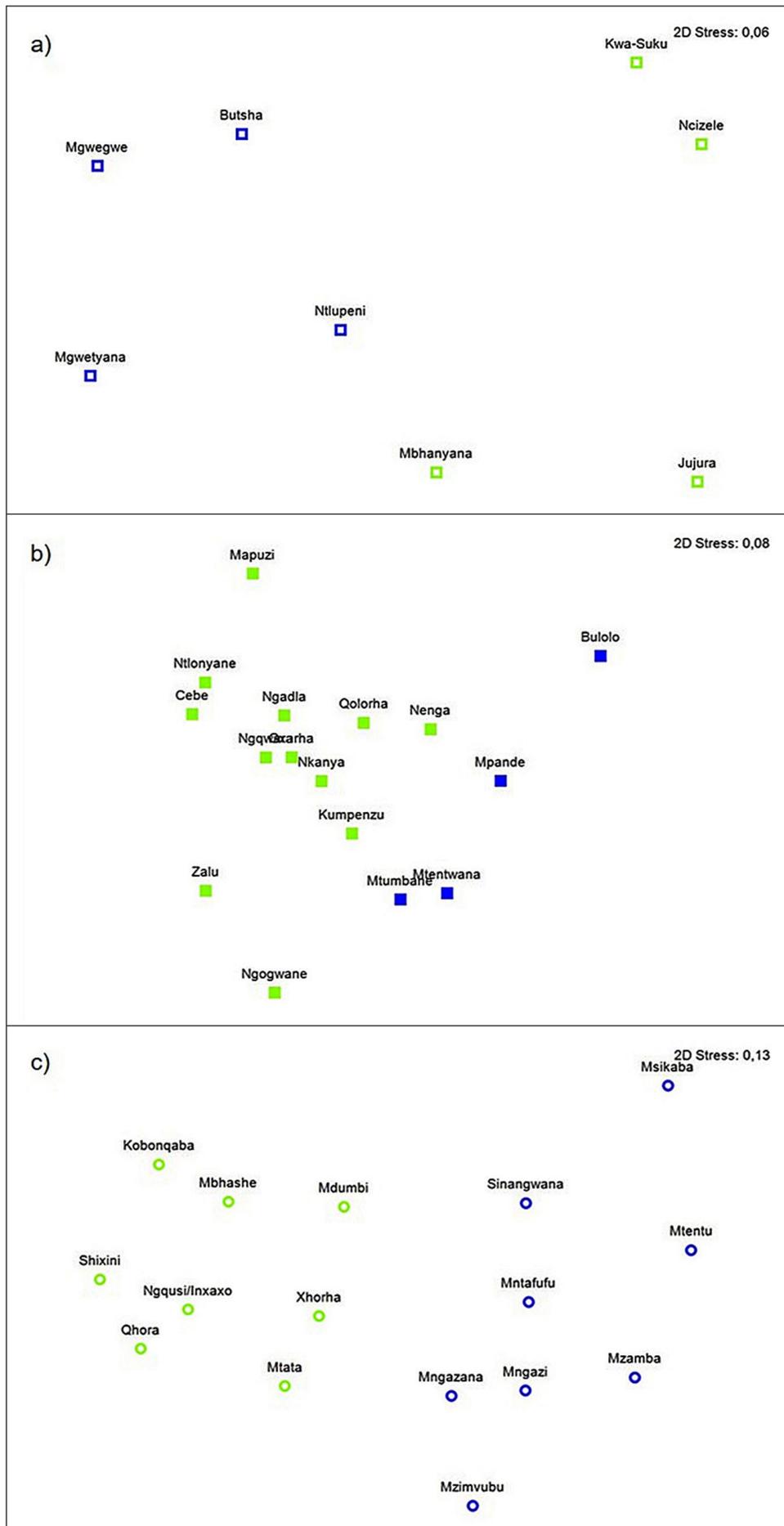
This survey provides important baseline information on the fish assemblages of estuaries found along a poorly studied section of the South African coastline. Of the sixteen estuaries included in this analysis, eight were classified as predominantly closed estuaries and eight as predominantly open estuaries. The predominantly closed estuaries were further divided into four small and four moderate to large predominantly closed estuaries. In terms of physico-chemical parameters, the predominantly open estuaries clustered separately from the predominantly closed estuaries and were all fairly deep systems (1–4 m average depth), mostly characterized by high salinities (19–30). The Mzimvuba was, however, sampled following heavy rainfall and was fresh at the time of sampling, with very high turbidities (average turbidity = 481 NTU). Sampling was conducted during October and November, with November normally representing the onset of the high-flow period (James et al., 2020). The small predominantly closed estuaries were mostly shallow systems characterized by high temperatures. The moderate to large predominantly closed estuaries were characterized by intermediate physico-chemical conditions.

Estuaries in this region are within the warm-temperate/subtropical biogeographic transition zone, with the warm-temperate region extending to just south of Port St Johns and the subtropical zone extending northwards of the Mdumbi Estuary near Port St Johns (Harrison, 2002). Transition zones are typically areas of high 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 61 species were recorded in estuaries in the region (Table 8), with 27 species recorded in the four small predominantly closed estuaries, 32 species in the moderate to large predominantly closed estuaries and 58 species in the predominantly open estuaries. A comparable survey along the southern Transkei coast, which lies to the south of the biogeographic break, documented 57 species in total (Table 8) with 28, 41 and 52 fish species from small predominantly closed, moderate to large predominantly closed and predominantly open estuaries, respectively (James and Harrison, 2020).

When combining data for the whole of the transition zone (James and Harrison, 2020 and this study) fish communities in small (Fig 4a) and moderate to large (Fig 4b) predominantly closed and predominantly open estuaries (Fig. 4c) clustered into two distinct groups based on whether they occurred in estuaries to the south of the break (southern Transkei) or to the north of the break (northern Transkei). This was most evident and significant (ANOSIM  $R = 0.807$ ) in predominantly open estuaries. Endemic species such as *Gilchristella aestuaria*, *Rhabdosargus holubi*, *Glossogobius callidus*, *Atherina breviceps*, *Caffrogobius gilchristi* and *Chelon richardsonii*, which collectively accounted for 41.3% of the overall dissimilarity (SIMPER analysis) between southern and northern predominantly open estuaries, contributed more to the abundance in southern Transkei estuaries. Both warm-water and cool-water endemic species, although present in estuaries throughout South Africa, are most common in warm-temperate estuaries, where they dominate the fish community (Harrison and Whitfield, 2006b). Tropical species, including *Planiliza macrolepis*, *Pomadasys commersonnii*, *Ambassis dussumieri* and *Terapon jarbua*, which accounted for 10% of the dissimilarity between northern and southern predominantly open estuaries, contributed more to the abundance in northern Transkei estuaries. These species typically comprise a major component of the fish community in subtropical estuaries (Harrison and Whitfield, 2006b).

Many of the species recorded in northern Transkei estuaries (Table 8) and not in previous studies of south-east and east coast estuaries (James and Harrison, 2010a; 2010b; 2011; 2016; 2020) were tropical species that are mainly confined to subtropical estuaries and whose distribution is strongly linked to temperature (Harrison and Whitfield, 2006b). In estuaries north



**Figure 4.** nMDS ordination of fish communities (presence/absence) in (a) small closed estuaries, (b) moderate to large closed estuaries and (c) predominantly open estuaries between the Kei and the Mntwana estuaries on the east coast of South Africa; blue = northern Transkei estuaries and green = southern Transkei estuaries.

**Table 8.** Abundance (%n) and biomass (%g) of species caught in estuaries south and north of the biogeographic break between the Kei to the Mntentwana estuaries on the east coast of South Africa. 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.

Species	Estuary-association category	Origin	South		North	
			%n	%g	%n	%g
<i>Atherina breviceps</i>	Ib	Endemic	3.3	0.1	1.0	0.0
<i>Caffrogobius gilchristi</i>	Ib	Endemic	1.6	0.1	2.0	0.0
<i>Caffrogobius natalensis</i>	Ib	Endemic	0.0	0.0	0.0	0.0
<i>Chelon richardsonii</i>	IIc	Endemic	1.1	9.3	0.0	0.0
<i>Clinus superciliosus</i>	Ib	Endemic	0.0	0.0		
<i>Etrumeus whiteheadi</i>	III	Endemic	0.0	0.0		
<i>Galeichthys feliceps</i>	IIb	Endemic	0.0	1.1		
<i>Gerres methueni</i>	IIb	Endemic	0.0	0.0	0.1	0.3
<i>Gilchristella aestuaria</i>	Ia	Endemic	40.9	1.5	33.2	1.0
<i>Glossogobius callidus</i>	Ib	Endemic	4.6	0.2	4.1	0.1
<i>Heteromycteris capensis</i>	IIb	Endemic	0.0	0.0		
<i>Lithognathus lithognathus</i>	IIa	Endemic	0.0	0.4	0.0	0.1
<i>Liza dumerilii</i>	IIb	Endemic	5.0	3.6	10.9	4.1
<i>Liza tricuspidens</i>	IIb	Endemic	1.1	6.6	1.2	0.5
<i>Moolgarda robustus</i>	IIa	Endemic	0.4	0.5	2.7	2.2
<i>Psammogobius knysnaensis</i>	Ib	Endemic	0.6	0.0	0.3	0.0
<i>Pseudomyxus capensis</i>	V	Endemic	6.0	3.1	6.1	3.3
<i>Rhabdosargus holubi</i>	IIa	Endemic	23.1	6.8	11.5	1.9
<i>Solea bleekeri</i>	IIb	Endemic	0.5	0.0	0.7	0.0
<i>Stolephorus holodon</i>	IIc	Endemic	0.0	0.0	0.3	0.0
<i>Diplodus capensis</i>	IIc	Temperate	0.0	0.0		
<i>Lichia amia</i>	IIa	Temperate	0.1	4.5	0.1	1.6
<i>Sardinops sagax</i>	III	Temperate	0.1	0.0		
<i>Sarpa salpa</i>	IIc	Temperate	0.0	0.0		
<i>Acanthopagrus vagus</i>	IIa	Tropical	0.0	0.2	0.3	1.1
<i>Ambassis ambassis</i>	Ia	Tropical	0.0	0.0	0.2	0.1
<i>Ambassis dussumieri</i>	Ib	Tropical	0.1	0.0	1.7	0.1
<i>Ambassis natalensis</i>	Ib	Tropical	0.0	0.0	0.6	0.0
<i>Amblyrhynchotes honckenii</i>	III	Tropical	0.0	0.0	0.5	0.1
<i>Argyrosomus japonicus</i>	IIa	Tropical	0.5	13.1	0.7	10.5
<i>Caranx heberi</i>	III	Tropical			0.0	0.0
<i>Caranx ignobilis</i>	IIb	Tropical	0.0	0.0	0.9	0.9
<i>Caranx papuensis</i>	IIc	Tropical			0.0	0.3
<i>Caranx sexfasciatus</i>	IIb	Tropical	0.0	0.4	1.1	3.4
<i>Chelonodon laticeps</i>	III	Tropical			0.0	0.0
<i>Crenimugil crenilabis</i>	IIb	Tropical			0.0	0.0
<i>Elops machnata</i>	IIa	Tropical	0.2	11.2	0.4	10.4
<i>Epinephelus malabaricus</i>	III	Tropical			0.0	0.0
<i>Favonigobius reichei</i>	Ib	Tropical			0.0	0.0
<i>Glossogobius giuris</i>	IV	Tropical			0.0	0.0
<i>Hilsa kelee</i>	IIc	Tropical			0.3	3.3
<i>Hippichthys spicifer</i>	Ib	Tropical	0.0	0.0	0.0	0.0
<i>Leiognathus equula</i>	IIb	Tropical	0.0	0.1	0.4	0.5
<i>Lutjanus argentimaculatus</i>	IIc	Tropical	0.0	0.3	0.0	2.3
<i>Megalops cyprinoides</i>	V	Tropical			0.0	0.1
<i>Monodactylus argenteus</i>	IIb	Tropical			0.0	0.0
<i>Monodactylus falciformis</i>	IIa	Tropical	0.6	0.6	0.5	0.3
<i>Moolgarda buchanani</i>	IIc	Tropical	0.2	7.1	0.5	9.8
<i>Moolgarda cunnesius</i>	IIa	Tropical	0.1	0.1	0.5	1.0
<i>Moolgarda seheli</i>	IIc	Tropical			0.1	0.0
<i>Oligolepis acutipennis</i>	Ia	Tropical	0.0	0.0	0.4	0.0
<i>Oreochromis mossambicus</i>	IV	Tropical	0.8	2.9	1.4	4.3
<i>Oxyurichthys keiensis</i>	Ia	Tropical	0.1	0.0	0.4	0.0
<i>Planiliza alata</i>	IIb	Tropical	0.0	0.6	0.6	14.9
<i>Planiliza macrolepis</i>	IIa	Tropical	0.4	1.3	4.4	5.4
<i>Planiliza melinoptera</i>	IIb	Tropical	0.0	0.0		
<i>Platycephalus indicus</i>	IIc	Tropical	0.0	0.0	0.0	0.0
<i>Polydactylus plebeius</i>	III	Tropical			0.0	0.0
<i>Pomadasys commersonnii</i>	IIa	Tropical	1.1	6.4	3.5	1.9
<i>Pomadasys kaakan</i>	IIc	Tropical	0.0	0.0	0.0	0.0
<i>Pomadasys olivaceum</i>	III	Tropical	0.0	0.0		
<i>Psammogobius biocellatus</i>	Ia	Tropical			0.0	0.0
<i>Rhabdosargus sarba</i>	IIb	Tropical	0.0	0.2	0.0	0.1
<i>Scomberoides lysan</i>	IIb	Tropical			0.7	0.0
<i>Secutor ruconius</i>	III	Tropical	0.0	0.0		
<i>Sphyræna jello</i>	IIc	Tropical	0.0	0.1	0.0	0.2
<i>Terapon jarbua</i>	IIa	Tropical	0.1	0.0	1.5	0.2
<i>Thryssa vitrostris</i>	IIb	Tropical			0.4	1.0
<i>Torpedo fuscumaculata</i>	IIc	Tropical	0.0	0.1		
<i>Torpedo sinuspersi</i>	IIc	Tropical	0.0	0.2		
<i>Upeneus vittatus</i>	III	Tropical			0.0	0.0
<i>Mugil cephalus</i>	IIa	Widespread	6.7	16.9	3.7	12.4
<i>Pomatomus saltatrix</i>	IIc	Widespread	0.1	0.0	0.1	0.0

of the biogeographic break, tropical species comprised 69% of the number of species recorded, which was greater than in the southern Transkei estuaries where tropical species comprised 54% of the species (Table 8). Endemic and temperate species dominated all estuaries numerically (74%), while in terms of biomass, tropical species dominated catches and comprised 72% of the catch. In the southern Transkei, overall endemic and temperate species comprised 89% of the catch numerically and 38% of the biomass (with tropical species comprising 45% of the biomass). These findings are indicative of all estuaries in the Transkei occurring within a biogeographic transition zone and northern Transkei estuaries occurring north of the subtropical/warm-temperate break.

The nMDS plots based on abundance and biomass showed that predominantly open estuaries clustered together and separated significantly from predominantly closed estuaries, which were situated to the right of the plots. Small and moderate to large predominantly closed estuaries also had significantly different fish assemblages. Overall, dominant species in the small predominantly closed estuaries included *Pseudomyxus capensis*, *Planaliza alata*, *Planaliza macrolepis*, *Moolgarda robustus*, *Chelon dumerili*, *Moolgarda buehanani*, *Gerres methueni* and *Rhadosargus holubi*. Dominant species in moderate to large predominantly closed estuaries included *Gilchristella aestuaria*, *R. holubi*, *P. capensis*, *Oreochromis mossambicus*, *Glossogobius callidus*, *Mugil cephalus* and *Pomadasys commersonii*. Predominantly open estuaries, in terms of abundance and biomass, were dominated by *G. aestuaria*, *C. dumerillii*, *R. holubi*, *Argyrosomus japonicus*, *Elops machnata*, *Moolgarda buehanani*, *Caranx sexfasciatus* and *Hilsa keele*.

Only one of the 27 species, namely *Crenimugil crenilabis*, recorded in the small predominantly closed estuaries, was only found in this estuary type. Two (*Chelon richardonii* and *Monodactylus argenteus*) of the 32 species recorded in moderate to large predominantly closed estuaries were only recorded in this estuary type. As in other regions surveyed (e.g. James and Harrison, 2020), species richness was much higher in predominantly open estuaries, with 58 species recorded. Twenty-two species were only recorded in predominantly open estuaries and these were *Ambassis dussumieri*, *Atherina breviceps*, *Caffrogobius natalensis*, *Caranx heberi*, *Chelonodon laticeps*, *Elops machnata*, *Epinephelus malabaricus*, *Favanigobius reichei*, *Genion honckenii*, *Hilsa keele*, *Lithognathus lithognathus*, *Lutjanus argentimaculatus*, *Megalops cyprinoides*, *Polydactylus plebius*, *Pomadasys kaakan*, *Pomatomus saltatrix*, *Psammogobius biocellatus*, *Rhabdosargus sarba*, *Sphyræna jello*, *Stolephorus holodon*, *Thryssa vitriostriis* and *Upeneus vittatus*. Six of these species are stenohaline marine stragglers not dependent on estuaries. 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; James and Harrison, 2020). 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.

## CONCLUSION

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%. This study, which represents a unique survey of multiple estuaries along a little-studied section of the South African coastline, shows that although all estuaries in both

the southern and northern Transkei fall within a transition zone, predominantly open estuaries to the north of the Sinangwana Estuary are more subtropical in nature. This was evidenced by the increase in the number and abundance of tropical species recorded in these estuaries (and the clustering of fish communities in the northern Transkei into a significantly distinct group).

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## APPENDIX

**Table A1.** Numerical abundance of fishes captured in small predominantly closed estuaries from the Mpande to the Mtentwana on the east coast of South Africa, November 1997 to January 1998 (n = number; % = percentage contribution)

Species	Ntlupeni		Butsha		Mgwegwe		Mgwetyana	
	n	% n	n	% n	n	% n	n	% n
<i>Acanthopagrus vagus</i>	1	0.3				0.0		
<i>Ambassis ambassis</i>	1	0.3	12	3.6	1	0.4		
<i>Ambassis natalensis</i>			2	0.6	1	0.4		
<i>Argyrosomus japonicus</i>					1	0.4		
<i>Caffrogobius gilchristi</i>	4	1.1						
<i>Caranx sexfasciatus</i>							3	0.9
<i>Chelon dumerilii</i>	77	21.7	2	0.6	41	15.3	23	7.3
<i>Crenimugil crenilabis</i>					1	0.4	1	0.3
<i>Gerres methueni</i>			6	1.8	1	0.4		
<i>Gilchristella aestuaria</i>	3	0.8						
<i>Glossogobius callidus</i>	13	3.7						
<i>Liza tricuspidens</i>			25	7.4			24	7.6
<i>Monodactylus falciformis</i>	13	3.7	13	3.9	2	0.7		
<i>Moolgarda buchanani</i>					1	0.4		
<i>Moolgarda cunnesius</i>	4	1.1	3	0.9			2	0.6
<i>Moolgarda robustus</i>	1	0.3	123	36.6	104	38.8	9	2.8
<i>Moolgarda seheli</i>							4	1.3
<i>Mugil cephalus</i>	13	3.7	17	5.1	6	2.2	37	11.7
<i>Oreochromis mossambicus</i>	15	4.2	3	0.9	9	3.4	3	0.9
<i>Planiliza alata</i>			7	2.1	2	0.7		
<i>Planiliza macrolepis</i>	6	1.7	15	4.5	10	3.7	80	25.3
<i>Pomadasys commersonii</i>	2	0.6					5	1.6
<i>Psammogobius knysnaensis</i>			5	1.5				
<i>Pseudomyxus capensis</i>	132	37.2	50	14.9	8	3.0	19	6.0
<i>Rhabdosargus holubi</i>	63	17.7	48	14.3	61	22.8	53	16.8
<i>Solea turbynei</i>	3	0.8						
<i>Terapon jarbua</i>	4	1.1	5	1.5	19	7.1	53	16.8
<b>Total individuals</b>	<b>355</b>		<b>336</b>		<b>268</b>		<b>316</b>	
<b>Total taxa</b>	<b>17</b>		<b>16</b>		<b>16</b>		<b>14</b>	

**Table A2.** Biomass composition of fishes captured in small predominantly closed estuaries from the Mpande to the Mtentwana on the east coast of South Africa, November 1997 to January 1998 (g = mass; % = percentage contribution)

Species	Ntlupeni		Butsha		Mgwegwe		Mgwetyana	
	g	% g	g	% g	g	% g	g	% g
<i>Acanthopagrus vagus</i>	31.0	0.5		0.0		0.0		
<i>Ambassis ambassis</i>	37.0	0.5	194.0	1.6	14.4	0.2		
<i>Ambassis natalensis</i>			14.9	0.1	0.4	0.0		
<i>Argyrosomis japonicus</i>					504.0	5.9		
<i>Caffrogobius gilchristi</i>	10.2	0.2						
<i>Caranx sexfasciatus</i>							14.8	0.4
<i>Chelon dumerilii</i>	1 042.9	15.3	48.4	0.4	519.9	6.0	634.6	18.8
<i>Crenimugil crenilabis</i>		0.0		0.0	1.2	0.0	2.0	0.1
<i>Gerres methueni</i>		0.0	854.0	6.8	226.0	2.6		
<i>Gilchristella aestuaria</i>	4.6	0.1						
<i>Glossogobius callidus</i>	8.0	0.1						
<i>Liza tricuspidens</i>			50.7	0.4			18.6	0.6
<i>Monodactylus falciformis</i>	281.0	4.1	82.2	0.7	32.8	0.4		
<i>Moolgarda buchanani</i>					1 593.0	18.5		
<i>Moolgarda cunnesius</i>	142.3	2.1	95.3	0.8		0.0	2.1	0.1
<i>Moolgarda robustus</i>	23.2	0.3	1 989.2	16.0	2 018.2	23.5	313.5	9.3
<i>Moolgarda seheli</i>							15.8	0.5
<i>Mugil cephalus</i>	431.0	6.3	445.1	3.6	71.5	0.8	389.5	11.5
<i>Oreochromis mossambicus</i>	3 158.4	46.4	513.5	4.1	2.8	0.0	0.2	0.0
<i>Planiliza alata</i>		0.0	6 050.0	48.5	2 103.0	24.5		
<i>Planiliza macrolepis</i>	556.0	8.2	1 163.1	9.3	761.0	8.9	1 670.4	49.5
<i>Pomadasys commersonii</i>	56.5	0.8					30.3	0.9
<i>Psammogobius knysnaensis</i>		0.0	1.7	0.0				
<i>Pseudomyxus capensis</i>	709.3	10.4	575.9	4.6	3.3	0.0	8.6	0.3
<i>Rhabdosargus holubi</i>	286.1	4.2	234.1	1.9	535.8	6.2	271.3	8.0
<i>Solea turbynei</i>	4.5	0.1						
<i>Terapon jarbua</i>	22.7	0.3	155.3	1.2	209.8	2.4	3.4	0.1
Total mass	6 806.0		12 467.2		8 597.0		3 375.1	100.0
Total taxa	17		16		16		14	

**Table A3.** Numerical abundance of fishes captured in medium to large predominantly closed estuaries from the Mpande to the Mtentwana on the east coast of South Africa, November 1997 to January 1998 (n = number; % = percentage contribution)

Species	Mpande		Bulolo		Mtumbane		Mtentwana	
	n	% n	n	% n	n	% n	n	% n
<i>Acanthopagrus vagus</i>	1	0.2						
<i>Ambassis ambassis</i>	2	0.4						
<i>Ambassis natalensis</i>			2	0.2				
<i>Caffrogobius gilchristi</i>			7	0.8				
<i>Caranx ignobilis</i>			1	0.1				
<i>Caranx sexfasciatus</i>			3	0.3				
<i>Chelon dumerilii</i>	2	0.4	39	4.2	15	7.7	77	22.0
<i>Gilchristella aestuaria</i>	140	24.6	438	47.7	27	13.9	14	4.0
<i>Glossogobius callidus</i>	10	1.8	101	11.0	22	11.3	25	7.1
<i>Glossogobius giuris</i>	1	0.2						
<i>Hippichthys spicifer</i>			1	0.1				
<i>Leiognathus equula</i>			16	1.7				
<i>Lichia amia</i>			2	0.2				
<i>Liza richardsonii</i>	1	0.2						
<i>Liza tricuspidens</i>	10	1.8			4	2.1	2	0.6
<i>Monodactylus argenteus</i>			2	0.2				
<i>Monodactylus falciformis</i>	8	1.4	2	0.2	2	1.0	10	2.9
<i>Moolgarda cunnesius</i>	1	0.2	3	0.3	2	1.0	3	0.9
<i>Moolgarda robustus</i>	2	0.4	9	1.0	2	1.0	3	0.9
<i>Mugil cephalus</i>	110	19.4	14	1.5	6	3.1	17	4.9
<i>Oligolepis acutipennis</i>			2	0.2				
<i>Oligolepis keiensis</i>	1	0.2	7	0.8				
<i>Oreochromis mossambicus</i>	20	3.5	33	3.6	53	27.3	5	1.4
<i>Planiliza alata</i>	9	1.6	1	0.1				
<i>Planiliza macrolepis</i>	26	4.6	8	0.9			16	4.6
<i>Pomadasys commersonnii</i>	5	0.9	1	0.1				
<i>Psammogobius knysnaensis</i>					4	2.1		
<i>Pseudomyxus capensis</i>	161	28.3	73	8.0	36	18.6	120	34.3
<i>Rhabdosargus holubi</i>	57	10.0	149	16.2	19	9.8	56	16.0
<i>Scomberoides lysan</i>			1	0.1				
<i>Solea turbynei</i>	1	0.2	3	0.3	1	0.5		
<i>Terapon jarbua</i>					1	0.5	2	0.6
Total individuals	568		918		194		350	
Total species	20		25		14		13	

**Table A4.** Biomass composition of fishes captured in moderate to large predominantly closed estuaries from the Mpande to the Mtentwana on the east coast of South Africa, November 1997 to January 1998 (g = mass; % = percentage contribution)

Species	Mpande		Bulolo		Mtumbane		Mtentwane	
	g	% g	g	% g	g	% g	g	% g
<i>Acanthopagrus vagus</i>	400.0	2 898.6		0.0				
<i>Ambassis ambassis</i>	80.0	579.7		0.0				
<i>Ambassis natalensis</i>			3.7	1.5				
<i>Caffrogobius gilchristi</i>			6.4	2.5				
<i>Caranx ignobilis</i>			6.2	2.5				
<i>Caranx sexfasciatus</i>			34.0	13.5				
<i>Chelon dumerilii</i>	15.7	114.1	145.4	57.6	240.5	194.5	755.3	181.2
<i>Gilchristella aestuaria</i>	16.3	118.3	393.3	155.7	13.1	10.6	0.0	0.0
<i>Glossogobius callidus</i>	9.4	67.9	166.0	65.7	20.7	16.8	9.6	2.3
<i>Glossogobius giurus</i>	0.1	1.0						
<i>Hippichthys spicifer</i>			0.2	0.1				
<i>Leiognathus equula</i>			742.5	293.9				
<i>Lichia amia</i>			11.8	4.7				
<i>Liza richardsonii</i>	46.6	337.4						
<i>Liza tricuspidens</i>	47.4	343.7			3.3	2.6	6.4	1.5
<i>Monodactylus argenteus</i>			54.0	21.4				
<i>Monodactylus falciformis</i>	124.5	902.4	7.9	3.1	88.0	71.2	226.2	54.3
<i>Moolgarda cunnesius</i>	4.4	31.5	4.4	1.7	106.0	85.7	70.8	17.0
<i>Moolgarda robustus</i>	9.5	68.5	248.3	98.3	17.7	14.3	346.0	83.0
<i>Mugil cephalus</i>	743.8	5 390.0	218.0	86.3	955.5	772.7	1 853.4	444.7
<i>Oligolepis acutipennis</i>			3.5	1.4				
<i>Oligolepis keiensis</i>	1.3	9.6	8.6	3.4				
<i>Oreochromis mossambicus</i>	1 526.1	11 058.7	1 579.8	625.4	1023.4	827.5	1 598.5	383.6
<i>Planiliza alata</i>	5 740.0	41 594.2	502.1	198.8				
<i>Planiliza macrolepis</i>	2 450.2	17 755.1	99.4	39.4			2 564.9	615.4
<i>Pomadasys commersonii</i>	986.5	7 148.6	28.7	11.4				
<i>Psammogobius knysnaensis</i>					5.6	4.5		
<i>Pseudomyxus capensis</i>	1 108.4	8 032.1	2 101.7	832.0	190.2	153.8	1 103.4	264.8
<i>Rhabdosargus holubi</i>	333.9	2 419.7	719.1	284.7	105.4	85.2	346.7	83.2
<i>Scomberoides lysan</i>			1.4	0.6				
<i>Solea turbynei</i>	4.8	34.4	5.1	2.0	0.5	0.4		
<i>Terapon jarbua</i>					57.0	46.1	2.3	0.5
<b>Total mass</b>	13.8		252.61		123.67		416.77	
<b>Total taxa</b>	20		25		14		13	

**Table A5.** Numerical abundance of fishes captured in predominantly open estuaries from the Mpande to the Mtentwana on the east coast of South Africa, November 1997 to January 1998 (n = number; % = percentage contribution)

Species	Sinangwana		Mngazana		Mngazi		Mzimvubu		Mntafufu		Msikaba		Mtentu		Mzamba	
	n	% n	n	% n	n	% n	n	% n	n	% n	n	% n	n	% n	n	% n
<i>Acanthopagrus vagus</i>	2	0.9	1	0.0	2	0.1	11	1.2	2	0.1			9	1.7	9	1.7
<i>Ambassis ambassis</i>															2	0.4
<i>Ambassis dussumieri</i>			8	0.3	51	3.7	10	1.1	126	9.4						
<i>Ambassis natalensis</i>			1	0.0			31	3.4			10	1.9	5	1.0	11	2.1
<i>Amblyrhynchotes honckenii</i>								0.0	9	0.7	18	3.5	25	4.8	2	0.4
<i>Argyrosomus japonicus</i>	10	4.7	10	0.4	32	2.3	11	1.2	5	0.4	1	0.2	4	0.8	1	0.2
<i>Atherina breviceps</i>			63	2.5	50	3.6										
<i>Caffrogobius gilchristi</i>			14	0.5	63	4.5	4	0.4	133	10.0	1	0.2	1	0.2		
<i>Caffrogobius natalensis</i>							1	0.1			1	0.2				
<i>Caranx ignobilis</i>	3	1.4	2	0.1	5	0.4	6	0.7	39	2.9	18	3.5	22	4.3	7	1.3
<i>Caranx papuensis</i>			2	0.1							1	0.2				
<i>Caranx sem</i>			1	0.0												
<i>Caranx sexfasciatus</i>	1	0.5	6	0.2	3	0.2	10	1.1	25	1.9	23	4.5	24	4.6	23	4.3
<i>Chelon dumerilii</i>	29	13.7	115	4.5	134	9.6	11	1.2	211	15.8	198	38.4	155	30.0	103	19.4
<i>Chelonodon laticeps</i>					1	0.1		0.0	1	0.1					1	0.2
<i>Elops machnata</i>	4	1.9	18	0.7	2	0.1	7	0.8	4	0.3	3	0.6	2	0.4	6	1.1
<i>Epinephelus malabaricus</i>													1	0.2		
<i>Favonigobius reichei</i>															1	0.2
<i>Gilchristella aestuaria</i>	9	4.2	1834	72.0	412	29.5	415	45.0	367	27.5					92	17.3
<i>Glossogobius callidus</i>	2	0.9	22	0.9	159	11.4	13	1.4	61	4.6	3	0.6	16	3.1	12	2.3
<i>Glossogobius giuris</i>			2	0.1												
<i>Hilsa kelee</i>	2	0.9	15	0.6	1	0.1			3	0.2			7	1.4	4	0.8
<i>Hippichthys spicifer</i>									1	0.1						
<i>Leiognathus equula</i>			7	0.3	15	1.1			2	0.1			1	0.2	1	0.2
<i>Lichia amia</i>			3	0.1					1	0.1				0.0		
<i>Lithognathus lithognathus</i>			1	0.0										0.0		
<i>Liza macrolepis</i>	7	3.3	32	1.3	37	2.7			36	2.7	119	23.1	34	6.6	69	13.0
<i>Liza tricuspidens</i>	9	4.2	52	2.0					1	0.1	3	0.6	1	0.2		
<i>Lutjanus argentimaculatus</i>			1	0.0					2	0.1					1	0.2
<i>Megalops cyprinoides</i>	1	0.5														
<i>Monodactylus falciformis</i>			1	0.0	1	0.1	2	0.2							2	0.4
<i>Moolgarda buchanani</i>	2	0.9	11	0.4				0.0	4	0.3	26	5.0	9	1.7	6	1.1
<i>Moolgarda cunnesius</i>	1	0.5	8	0.3	2	0.1	9	1.0	7	0.5	3	0.6	4	0.8	3	0.6
<i>Moolgarda robustus</i>	13	6.1	26	1.0					2	0.1			3	0.6	6	1.1
<i>Moolgarda seheli</i>					1	0.1			1	0.1	2	0.4	1	0.2		
<i>Mugil cephalus</i>	25	11.8	15	0.6	28	2.0	37	4.0	12	0.9	44	8.5	25	4.8	9	1.7
<i>Oligolepis acutipennis</i>					3	0.2	29	3.1	2	0.1			6	1.2	3	0.6
<i>Oligolepis keiensis</i>			2	0.1	1	0.1	24	2.6	10	0.7					1	0.2
<i>Oreochromis mossambicus</i>	11	5.2			1	0.1	1	0.1								
<i>Planiliza alata</i>	7	3.3	3	0.1	26	1.9			4	0.3	8	1.6	3	0.6	1	0.2
<i>Platycephalus indicus</i>							1	0.1								
<i>Polydactylus plebeius</i>			1	0.0												
<i>Pomadasys commersonii</i>	3	1.4	14	0.5	36	2.6	215	23.3	45	3.4	7	1.4	50	9.7	14	2.6
<i>Pomadasys kaakan</i>			1	0.0												
<i>Pomatomus saltatrix</i>			6	0.2												
<i>Psammogobius biocellatus</i>																
<i>Psammogobius knysnaensis</i>	3	1.4	1	0.0	12	0.9	8	0.9	2	0.1						
<i>Pseudomyxus capensis</i>	2	0.9	25	1.0	7	0.5	32	3.5	7	0.5			5	1.0	8	1.5
<i>Rhabdosargus holubi</i>	60	28.3	181	7.1	273	19.6	10	1.1	186	13.9	3	0.6	41	7.9	42	7.9
<i>Rhabdosargus sarba</i>	1	0.5														
<i>Scomberoides lysan</i>					1	0.1			1	0.1	6	1.2	4	0.8	66	12.4
<i>Solea bleekeri</i>	3	1.4			30	2.1	23	2.5	9	0.7					3	0.6
<i>Sphyræna jello</i>					3	0.2										
<i>Stolephorus holodon</i>													32	6.2	1	0.2
<i>Terapon jarbua</i>	2	0.9	9	0.4	4	0.3	1	0.1	14	1.0	17	3.3	17	3.3	18	3.4
<i>Thryssa vitrirostris</i>			33	1.3									7	1.4		
<i>Upeneus vittatus</i>				0.0									2	0.4	3	0.6
Total individuals	212		2547		1396		922		1335		515		517		531	
Total species	25		38		31		25		34		22		31		33	

**Table A6.** Biomass composition of fishes captured in predominantly open estuaries from the Mpande to the Mtentwana on the east coast of South Africa, November 1997 to January 1998 (g = mass; % = percentage contribution)

Species	Sinangwana		Mngazana		Mngazi		Mzimvubu		Mntafufu		Msikaba		Mtentu		Mzamba	
	g	% g	g	% g	g	% g	g	% g	g	% g	g	% g	g	% g	g	% g
<i>Acanthopagrus vagus</i>	761.0	3.1	516.0	0.9	185.6	0.5	794.3	4.2	616.1	1.9	0.0	0.0	46.6	0.1	141.9	0.6
<i>Ambassis ambassis</i>															47.4	0.2
<i>Ambassis dussumieri</i>			11.9	0.0	130.2	0.3	5.0	0.0	321.3	1.0						
<i>Ambassis natalensis</i>			0.2	0.0			12.0	0.1			3.5	0.0	2.3	0.0	18.7	0.1
<i>Amblyrhynchotes honckenii</i>									25.6	0.1	64.4	0.2	92.2	0.3	5.5	0.0
<i>Argyrosomus japonicus</i>	4 263.5	17.5	6 339.0	11.1	14 886.6	38.6	4 312.1	23.1	1 837.1	5.8	386.0	1.1	1 282.0	4.1	132.0	0.5
<i>Atherina breviceps</i>			14.3	0.0	55.1	0.1										
<i>Caffrogobius gilchristi</i>			4.0	0.0	32.3	0.1	3.3	0.0	69.8	0.2	0.8	0.0	1.2	0.0		
<i>Caffrogobius natalensis</i>							5.9	0.0			0.3	0.0				
<i>Caranx ignobilis</i>	660.0	2.7	7.2	0.0	30.9	0.1	69.0	0.4	176.0	0.6	74.6	0.2	1 856.5	5.9	10.4	0.0
<i>Caranx papuensis</i>			604.0	1.1							257.0	0.7				
<i>Caranx sem</i>			6.5	0.0												
<i>Caranx sexfasciatus</i>	174.0	0.7	958.0	1.7	7.8	0.0	27.4	0.1	81.4	0.3	3 074.5	8.9	3 127.3	10.0	3 396.0	13.8
<i>Chelon dumerilii</i>	408.8	1.7	1 316.4	2.3	648.2	1.7	27.0	0.1	1 421.8	4.5	2 012.0	5.8	1 321.1	4.2	2 871.9	11.7
<i>Chelonodon laticeps</i>					0.2	0.0	0.0	0.0	0.2	0.0					0.2	0.0
<i>Elops machnata</i>	3 592.0	14.8	13 907.9	24.4	16.9	0.0	628.7	3.4	4 761.0	14.9	4 350.8	12.6	998.0	3.2	5 423.0	22.0
<i>Epinephelus malabaricus</i>													0.2	0.0		
<i>Favonigobius rechei</i>															1.7	0.0
<i>Gilchristella aestuaria</i>	9.8	0.0	1 815.7	3.2	408.5	1.1	357.2	1.9	205.9	0.6					47.5	0.2
<i>Glossogobius callidus</i>	1.4	0.0	12.2	0.0	67.1	0.2	5.0	0.0	25.4	0.1	1.2	0.0	9.3	0.0	5.0	0.0
<i>Glossogobius giuris</i>			1.2	0.0												
<i>Hilsa kelee</i>	887.0	3.6	5 394.0	9.5	533.0	1.4			1 354.0	4.2			1 373.0	4.4	1 310.0	5.3
<i>Hippichthys spicifer</i>									0.2	0.0						
<i>Leiognathus equula</i>			450.8	0.8	379.4	1.0			72.1	0.2			7.8	0.0	31.1	0.1
<i>Lichia amia</i>			4 158.0	7.3					955.0	3.0						
<i>Lithognathus lithognathus</i>			334.2	0.6												
<i>Liza macrolepis</i>	502.9	2.1	3 252.0	5.7	1 226.7	3.2			1 382.5	4.3	474.9	1.4	471.8	1.5	1 017.6	4.1
<i>Liza tricuspidens</i>	885.2	3.6	440.9	0.8					21.5	0.1	4.3	0.0	126.0	0.4		
<i>Lutjanus argentimaculatus</i>			1 168.0	2.1					5 404.0	16.9					741.0	3.0
<i>Megalops cyprinoides</i>	325.0	1.3														
<i>Monodactylus falciformis</i>		0.0	0.1	0.0	0.2	0.0	1.3	0.0							61.3	0.2
<i>Moolgarda buchani</i>	1 135.5	4.7	8 115.0	14.3					136.9	0.4	11 349.3	33.0	7 429.5	23.7	2 191.0	8.9
<i>Moolgarda cunnesius</i>	225.0	0.9	1 102.0	1.9	57.4	0.1	74.1	0.4	608.9	1.9	4.1	0.0	216.3	0.7	398.1	1.6
<i>Moolgarda robustus</i>	365.5	1.5	668.0	1.2					14.0	0.0			501.0	1.6	606.7	2.5
<i>Moolgarda seheli</i>					11.7	0.0			12.3	0.0	11.5	0.0	12.8	0.0		
<i>Mugil cephalus</i>	544.7	2.2	1 105.4	1.9	3 427.6	8.9	11 094.8	59.3	5 320.0	16.7	4 411.8	12.8	5 708.3	18.2	3 594.1	14.6
<i>Oligolepis acutipennis</i>		0.0			4.7	0.0	31.7	0.2	3.6	0.0			7.3	0.0	2.5	0.0
<i>Oreochromis mossambicus</i>	4 426.5	18.2			183.7	0.5	6.5	0.0								
<i>Oxyurichthys keiensis</i>			1.6	0.0	0.2	0.0	7.1	0.0	4.2	0.0					0.2	0.0
<i>Planiliza alata</i>	3 131.1	12.9	320.7	0.6	14 810.0	38.4			3 361.0	10.5	7 863.0	22.9	3 338.0	10.7	1 251.7	5.1
<i>Platycephalus indicus</i>							33.8	0.2								
<i>Polydactylus plebeius</i>			150.0	0.3												
<i>Pomadasys commersonnii</i>	937.1	3.8	1 129.4	2.0	66.9	0.2	1 006.7	5.4	692.5	2.2	19.5	0.1	648.0	2.1	519.1	2.1
<i>Pomadasys kaakan</i>			19.1	0.0												
<i>Pomatomus saltatrix</i>			12.7	0.0												
<i>Psammogobius biocellatus</i>													2.3	0.0		
<i>Psammogobius knysnaensis</i>	1.8	0.0	0.2	0.0	3.1	0.0	3.0	0.0	0.4	0.0						
<i>Pseudomyxus capensis</i>	97.2	0.4	259.0	0.5	10.1	0.0	85.5	0.5	2 016.7	6.3			1 895.0	6.1	547.3	2.2
<i>Rhabdosargus holubi</i>	693.5	2.8	510.8	0.9	627.6	1.6	84.6	0.5	1 000.1	3.1	19.0	0.1	189.4	0.6	153.4	0.6
<i>Rhabdosargus sarba</i>	292.0	1.2														
<i>Scomberoides lysan</i>					0.4	0.0			0.3	0.0	6.1	0.0	3.8	0.0	32.6	0.1
<i>Solea turbynei</i>	1.5	0.0			16.8	0.0	24.9	0.1	6.9	0.0					1.8	0.0
<i>Sphyaena jello</i>					731.1	1.9										
<i>Stolephorus holodon</i>													21.5	0.1	0.4	0.0
<i>Terapon jarbua</i>	25.5	0.1	50.4	0.1	47.0	0.1	0.1	0.0	23.4	0.1	19.8	0.1	97.1	0.3	47.2	0.2
<i>Thryssa vitrirostris</i>			2 734.0	4.8									512.0	1.6		
<i>Upeneus vittatus</i>													6.8	0.0	10.3	
Total mass	24 347.4		56 890.8		38 607.1		18 700.8		31 932.1		34 408.3		31 304.5		24 618.5	
Number of species	25		38		31		25		34		22		31		33	