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Preliminary assessment of the biogeography of fishes in South African estuaries

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Abstract. The biogeography of the fishes of 42 South African estuaries was investigated using an extensive synoptic dataset collected over the period 1993–99. Fish species richness was low on the west (Atlantic Ocean) coast and high in estuaries on the east (Indian Ocean) coast. Endemic species dominated the systems on the west and south coasts, whereas species of tropical origin dominated estuaries on the east coast. Multivariate analyses indicated that those estuaries on the west and south-west coast were distinct from the remaining systems, which showed a gradation from estuaries on the south coast to those on the north-east coast. An analysis of similarities showed that three biogeographic regions could be delineated. A cool-temperate region extended from the Orange River, down the west coast and along the south-west coast to Cape Agulhas; a warm-temperate zone stretched from Cape Agulhas to just south of Port St Johns; and a subtropical region extended up the east coast from approximately Port St Johns.

Introduction

The South African coastline stretches for ~3000 km from the Orange River mouth (28°38′S,16°27′E) on the west (Atlantic Ocean) coast to Kosi Bay (26°54′S,32°48′E) on the east (Indian Ocean) coast (Fig. 1). This region covers a wide range of climatic and oceanic conditions and hence supports a great diversity of plants and animals.

Stephenson and Stephenson (1972) examined the distribution of rocky-shore biota and defined three biogeographic provinces: a West Coast Province down the west coast to Cape Point, characterized by cold-water forms; a warm-temperate South Coast Province, with mainly cooler-water species, from approximately Cape Point to Port St Johns; and a subtropical East Coast Province, characterized by warm-water species, from approximately Port St Johns to Mozambique.

Emanuel *et al.* (1992), on the basis of an analysis of marine invertebrates, divided the South African coast into three zoogeographic regions: a cool-temperate Namaqua Province from Lüderitz (Namibia) to Cape Point; a warm-temperate Agulhas Province from Cape Point eastward to East London; and a subtropical Natal Province from East London north to Mozambique, comprising two sub-provinces, one from Durban southward and the other from Durban northward.

Analyses of rocky-shore biota also yielded three biogeographic groupings (Bustamante 1994): the west-coast Namaqua Province between Lüderitz and Cape Columbine; a south-coast Agulhas Province from Cape Infanta to approximately the Mbashe estuary; and an east-coast Natal Province from Ballito Bay (just north of Durban) to Inhaca Island in Mozambique.

Analyses of intertidal fishes yielded four major biogeographic regions (Prochazka 1994): a Namaqua Province, extending from Lüderitz at least to Koppie Alleen, east of Cape Agulhas; the warm-temperate Agulhas Province between Tsitsikamma and Port Alfred; and two east-coast Natal Provinces, one from Pennington (just south of Durban) to Durban and the other from Durban northward to Kosi Bay.

From the distribution and ordination of shelf-associated fish species, Turpie *et al.* (2000) identified three biogeographic regions: a cool-temperate region along the west coast from the Orange River to Cape Point; a warm-temperate region from Cape Point to approximately Port Edward; and a subtropical region from Port Edward north to Kosi Bay.

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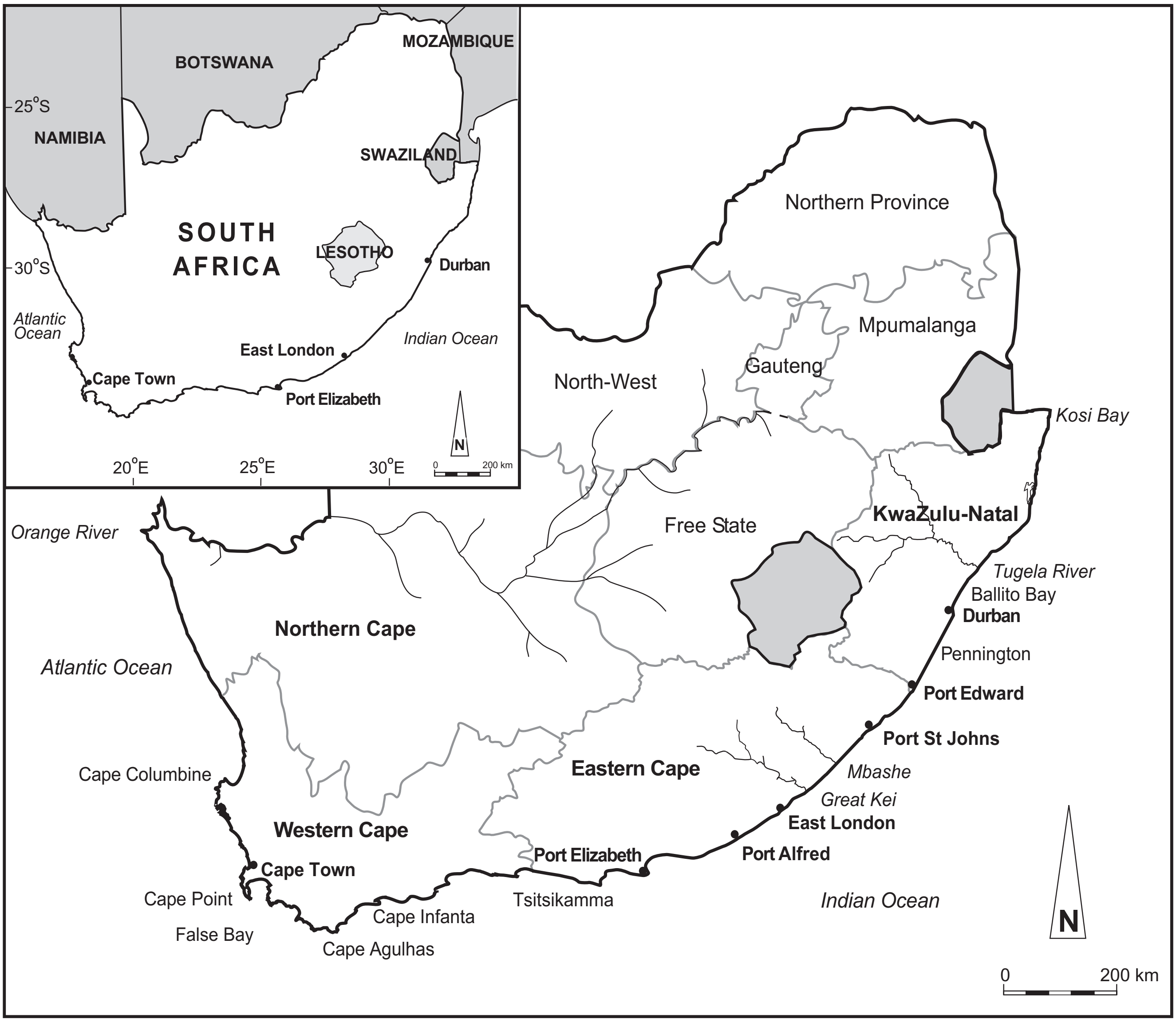

Fig. 1. Locality map of South Africa indicating place names and estuaries mentioned in the text.

In terms of estuaries, Day (1981) identified three main provinces based mainly on water temperature, rainfall and river flow. Cold-temperate estuaries included those on the west (Atlantic) coast between the Orange River and Cape Point; this area has very low rainfall and high evaporation (Day 1981). Estuaries from Cape Point to the Great Kei were characterized as warm-temperate; these systems have minimum winter temperatures of 12–14°C and experience variable rainfall. The estuaries from the Great Kei system to southern Mozambique were classified as subtropical; these systems are characterized by warm waters (>16°C) and a good summer rainfall and river discharge. These three coincided with three faunistic provinces based on estuarine fishes (Day *et al.* 1981).

On the basis of marine biota, Potter *et al.* (1990) described three biotic provinces for southern African estuaries: a cold-temperate west-coast region, from beyond Walvis Bay (Namibia) to Cape Point; a warm-temperate region from Cape Point to 31°S on the east coast (approximately Port Edward); and a subtropical region along the east coast from 31°S northwards to 26°S.

Whitfield (1994*a*) suggested that the cold-temperate region be referred to as cool-temperate since estuarine water temperatures in this region are always above 10°C. He also suggested that the division between the warm-temperate and subtropical regions be placed at the Mbashe estuary. This boundary coincides with the presence of a strong, inshore subsurface temperature front, which maintains a fixed

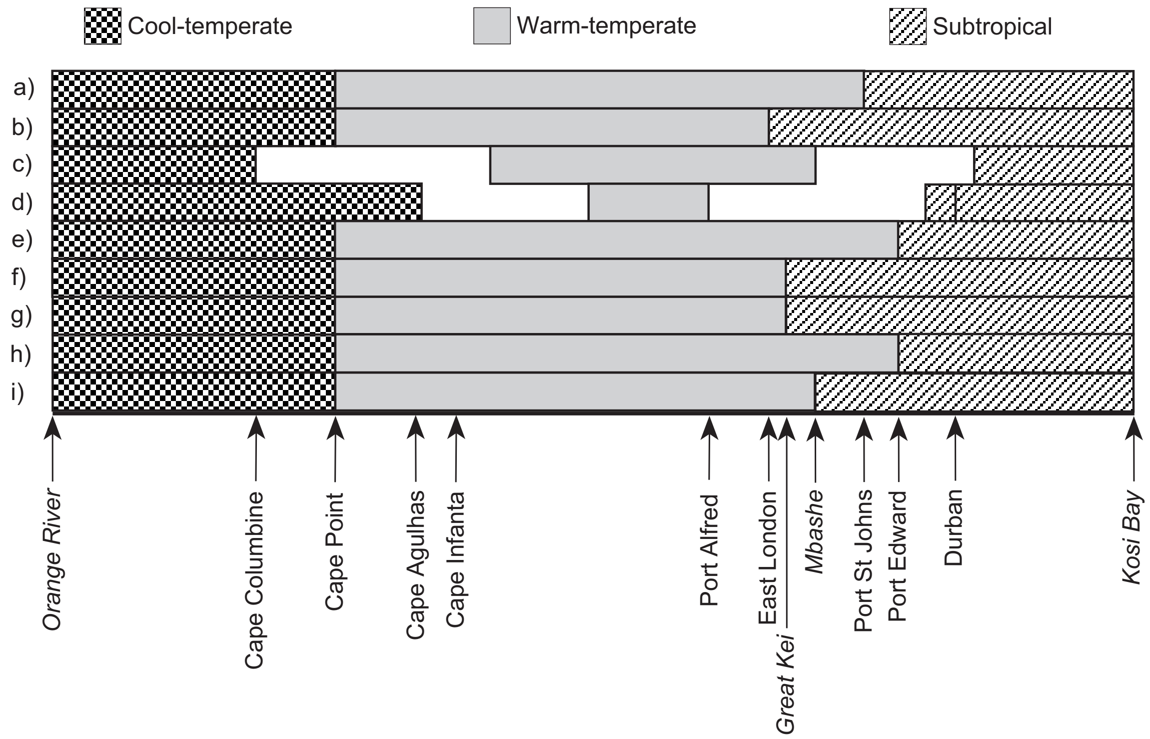

Fig. 2. Summary diagram indicating South African marine biogeographic provinces after: *(a)* Stephenson and Stephenson (1972); *(b)* Emanuel *et al.* (1992); *(c)* Bustamante (1994); *(d)* Prochazka (1994); *(e)* Turpie *et al.* (2000); *(f)* Day (1981); *(g)* Day *et al.* (1981); *(h)* Potter *et al.* (1990); *(i)* Whitfield (1994*a*).

location in the vicinity of the Mbashe estuary (Beckley and van Ballegooyen 1992). The transitional nature of the Mbashe was also exemplified by the presence of both saltmarshes that are normally associated with temperate systems and mangroves that favour subtropical conditions (Whitfield 1994*a*).

In terms of freshwater fishes, a west-coast region characterized by a temperate (Karroid) fauna was found to extend from the Orange River to Cape Columbine while a temperate endemic (Cape) fauna occurred along the south-west and southern coast to approximately Port Elizabeth (Skelton 1993). The south-east coast to approximately the Tugela River comprises a mixture of tropical (Zambezian) and temperate (Karroid) fauna. A tropical Zambezian fauna extends from the Tugela River northwards.

Hence, although there is broad agreement that the South African coast covers at least three biogeographical regions, there is still some question regarding the boundaries of these faunistic provinces (Fig. 2). Furthermore, many of the studies outlined above have relied on a combination of limited field collections, historical data, and existing distribution records. A recent study on the state of South African estuaries (Harrison *et al.* 2000) has produced a synoptic dataset of fishes in these systems and this presents an opportunity to study the biogeography of the fishes of South African estuaries. The aim of this paper is to examine whether estuarine fish communities conform to current zoogeographic zones identified for the coastal environment and to delineate the boundaries between these zones.

Materials and methods

Study area

The ~300 coastal outlets intersecting the South African coastline range from relatively large, permanently open estuaries to very small coastal streams. These systems also occur in a wide range of climatic conditions from semi-arid conditions in the west, to a Mediterranean climate in the south and subtropical in the east.

The region to the north of Cape Columbine has an arid climate and rainfall is usually <300 mm year^{-1}, and the Western Cape between Cape Columbine and Cape Agulhas receives between 400 and 700 mm year^{-1}, predominantly in winter (Heydorn and Tinley 1980; Day 1981). From Cape Agulhas to East London, rainfall decreases to ~500 mm per year and is either bimodal or occurs almost equally in all seasons (Heydorn and Tinley 1980). The Tsitsikamma sector (west of Port Elizabeth), however, comprises a discrete sub-region and experiences good year-round rainfall of 700–1000 mm year^{-1}. The Eastern Cape region, from the Great Kei River to Port Edward receives predominantly summer rainfall that varies from ~800 to 1250 mm year^{-1}. The province of KwaZulu-Natal, from Port Edward to Kosi Bay, receives >1000 mm year^{-1}, most of which falls in summer (Day 1981).

The coastal waters of southern Africa are influenced by two major current systems. The west (Atlantic) coast is influenced by the cold Benguela system of upwelled inshore waters. The surface water temperatures of the Benguela system average between 13° and 15°C with a pronounced upwelling 'season' during the summer (September–March) (Shannon 1989). The east coast, which borders the Indian Ocean, is influenced by the south-flowing Agulhas Current. Being tropical in origin, the waters of the Agulhas Current are relatively warm; however, as this water flows south it tends to cool. Inshore temperatures north of Port St Johns in the Eastern Cape normally vary seasonally between 25° and 18°C and seldom fall below 16°C (Day 1981). Further to the south where wind-induced upwelling may occur (Shannon 1989), temperatures are lower and more variable. Between East London and Cape Agulhas inshore temperatures vary from 11° to 25°C (Day 1981).

Field and laboratory

The ichthyofauna of some 250 coastal outlets between the Orange River and Kosi Bay were sampled over the period 1993 to 1999. Each system was sampled once during spring/summer (usually September–November) with a seine net (30 m × 1.7 m × 15 mm bar mesh; 5 mm bar mesh purse). In some estuaries, gill-nets were also used; each gill-net comprised three monofilament panels (45 mm, 75 mm and 100 mm stretch mesh) and was 10 m or 20 m in length and 1.7 m deep. The use of two sampling methods (seine netting and gill-netting) was an attempt to obtain as representative a sample as possible (Harrison and Whitfield 1995) of the overall fish community in each estuary.

Seine netting was carried out during daylight hours and was limited to shallow (<1.5 m), unobstructed areas with gently sloping banks. Gill-netting was generally carried out in deep (>1.0 m) open, mid-channel waters with the nets being deployed in the evening and lifted the following morning. In most cases only the larger, deeper estuaries were sampled with gill-nets. Netting was generally carried out until no new species were collected and/or until all habitats within each estuary had been sampled.

Specimens collected by seine netting were, where possible, identified in the field, measured to the nearest millimetre standard length (SL), and returned alive to the system. At least 25 specimens of the abundant species as well as those specimens that could not be identified in the field were placed in labelled plastic bags and preserved in 4% formaldehyde for transport to the laboratory. Specimens collected in the gill-nets were identified, measured (mm SL) and weighed (g wet mass). Specimens that could not be identified in the field were placed in labelled plastic bags and preserved in 4% formaldehyde for later processing in the laboratory.

In the laboratory, preserved specimens were identified by reference to Smith and Heemstra (1995) and Skelton (1993). At least 25 specimens of the abundant species were measured (mm SL) and weighed to the nearest 0.01 g; the remaining specimens were counted and batch weighed.

The total species composition, both by number and by mass, for each estuary was then calculated. The relative biomass contribution of each species was established by reference to actual recorded masses and masses derived from length–weight relationships presented in Harrison (2001).

Data analyses

The occurrence and diversity of fishes in South African estuaries essentially varies according to two broad parameters: latitude (biogeography) and the individual characteristics of each estuary (estuary type) (Blaber 1985). In order to remove the effect of the latter, representative estuaries were selected according to a broad agreement between two physical/morphological classification schemes. Whitfield (1992, 2000) identified and classified South Africa's estuaries into five broad types based on a combination of physiography, hydrography and salinity whereas Harrison *et al.* (2000) classified South Africa's estuaries into six categories based on the main forms of morphological variability among these systems along the coast. In total, 42 estuaries were selected for analysis; these comprised representatives of large open estuaries (Harrison *et al.* 2000) and permanently open estuaries (Whitfield 1992, 2000).

Species richness and distribution

In each of the selected estuaries, the taxa were grouped into one of the following four categories based on their origin and distribution.

Tropical species: tropical Indian Ocean and Indo-Pacific species.

Temperate species: temperate East Atlantic species.

Endemic species: species with a distribution limited to southern Africa (south of 20°S).

Cosmopolitan species: species with a worldwide distribution.

Information on species origin and distribution was derived from Smith (1950), Wallace (1975), Day *et al.* (1981), van der Elst (1988), Potter *et al.* (1990), Skelton (1993), Smith and Heemstra (1995) and Whitfield (1998) as well as from data from this study. All exotic species were omitted from the analysis, and translocated indigenous taxa (e.g. *Oreochromis mossambicus*) were adjusted by removal of occurrences outside their natural range.

The total number of species and relative (%) contribution of each category to the ichthyofauna of each estuary was then calculated in terms of number of taxa, abundance and biomass.

Multivariate analysis

The selected estuaries were also subject to multivariate statistical analyses using the Plymouth Routines in Multivariate Ecological Research package (PRIMER) (Clarke and Warwick 1994). The ichthyofaunal composition of each estuary was compared in terms of the Bray–Curtis similarity coefficient calculated for presence/absence, abundance and biomass data. Abundance and biomass data were first standardized by computing the relative (%) contribution of each species within each estuary, and were then 4th-root transformed. Standardization removes the effect of variable sampling effort while transformation scales down the importance of dominant species (Field *et al.* 1982; Clarke and Warwick 1994). The estuaries were then analysed by use of a combination of hierarchical agglomerative clustering and non-metric multi-dimensional scaling (MDS). For the results of the multivariate analyses, the estuaries were labelled according to their geographic position (Fig. 3).

Results

Species richness and distribution

The number of taxa recorded in each estuary ranged between 4 and 55 (Fig. 4). A moderate increase in the number of taxa occurred between the Uilkraals and Heuningnes estuaries at Cape Agulhas. Between the Heuningnes and Mkomazi estuaries the number of species recorded was somewhat variable. A notable increase occurred between the Mkomazi and Matigulu/Nyoni estuaries (on the north-east coast).

No tropical species were captured on the west and south-west coast. From the Heuningnes estuary near Cape Agulhas, the proportion of tropical species increased toward the north-east coast (Fig. 5*a*). South of the Mngazana estuary (east coast), tropical species generally comprised <40% of the taxa while from the Mngazana estuary northward, the proportion of tropical species usually exceeded 60%. The proportion of endemic species showed the opposite trend and decreased from the west coast toward the north-east coast. South of the Mdumbi estuary (east coast), this group of

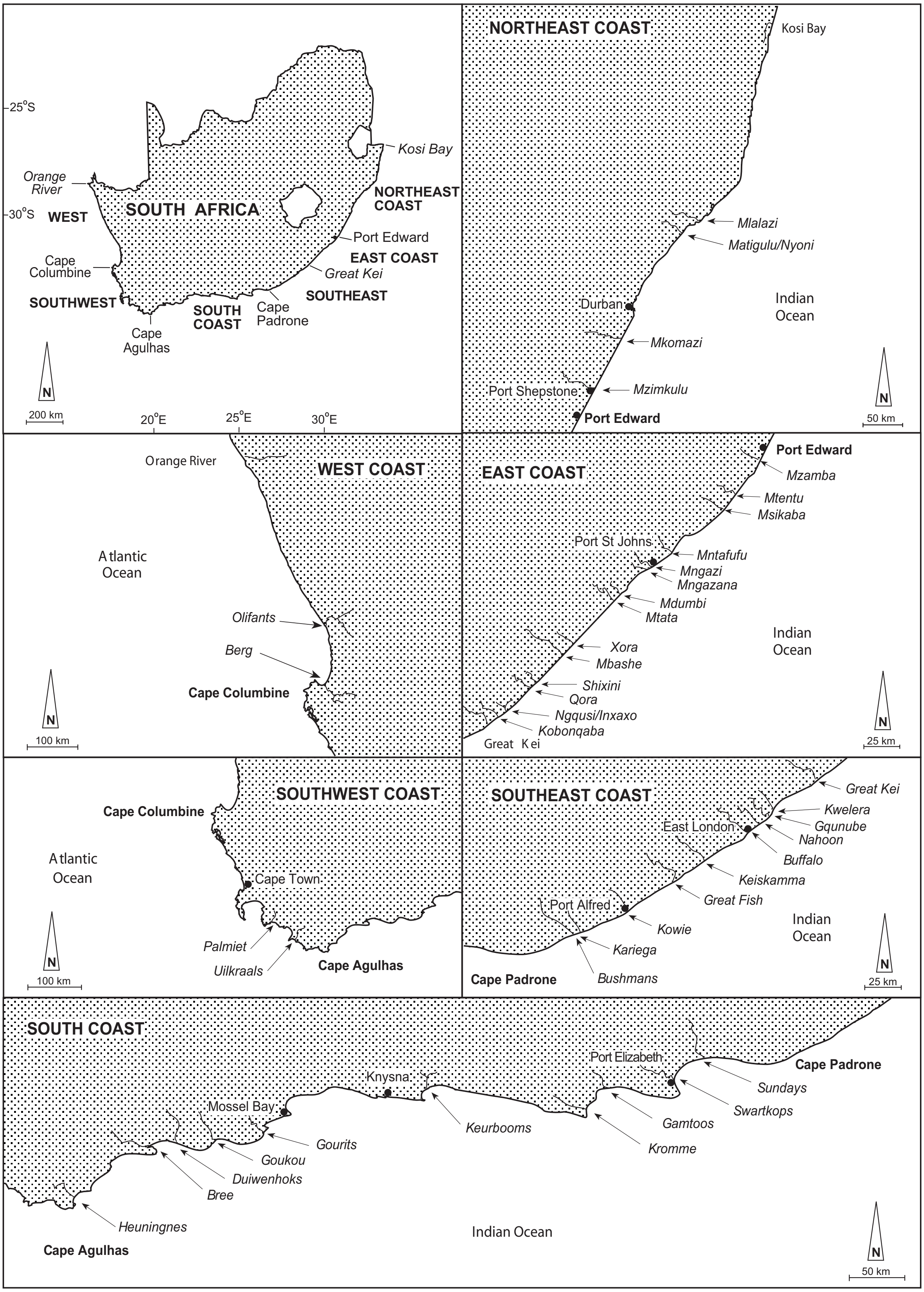

Fig. 3. South African coastline divided into geographic regions and showing the estuaries included in the study.

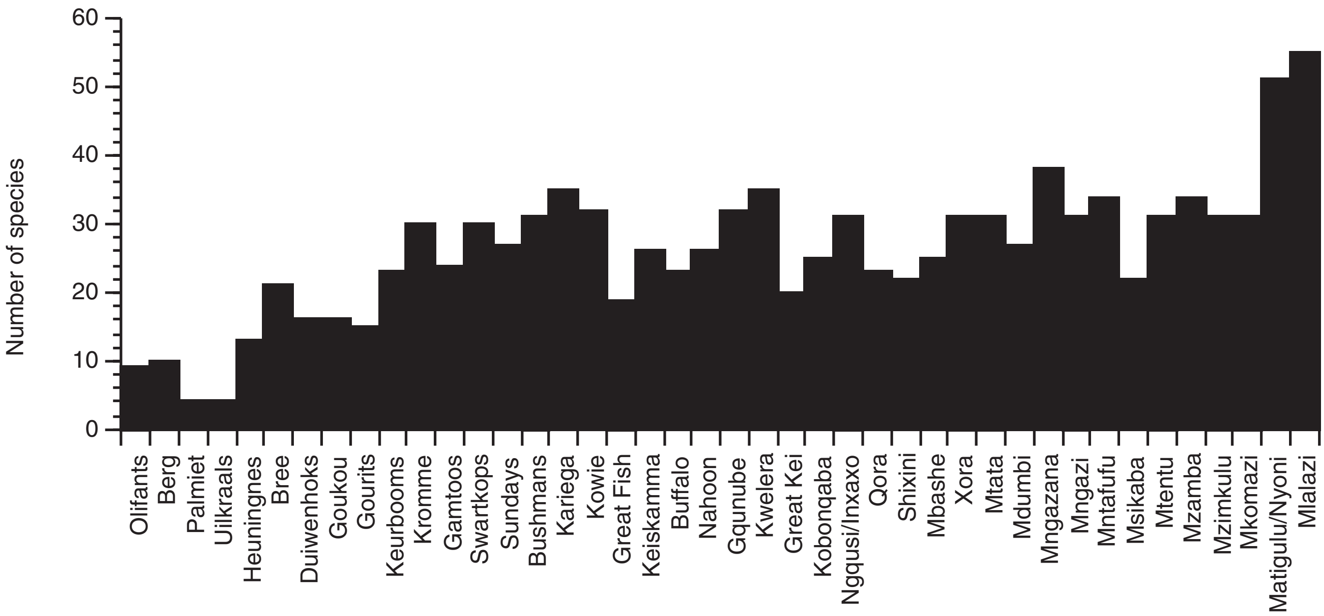

Fig. 4. Number of fish taxa recorded in selected South African estuaries.

fishes generally comprised >50% of the taxa recorded whereas north of the Mdumbi they comprised <30% of the species. The proportion of temperate species showed a similar trend with a notable decline occurring between the Mdumbi and Mngazana systems (east coast). Apart from the estuaries on the west and south-west coast such as the Olifants, Palmiet and Uilkraals systems, the proportion of cosmopolitan species remained fairly constant and generally comprised <10% of the taxa recorded (Fig. 5*a*).

In terms of relative abundance, the contribution of tropical species was usually <10% south of the Mngazi estuary (east coast); from the Mgazi system northward, the contribution of this group increased to over 88% in the Mlalazi estuary (north-east coast) (Fig. 5*b*). Endemic species dominated the fish fauna of the estuaries between the Olifants estuary (west coast) and the Mntafufu system (east coast) and generally comprised >70% of the catch. North of the Mntafufu estuary the contribution of this group was typically <50%. Apart from the Keurbooms and Bushmans estuaries (south and south-east coast) the contribution of temperate species was generally low (mostly <1%). With the exception of a few estuaries (e.g. Goukou, Keurbooms, Bushmans, Nahoon, Mtata), the contribution of cosmopolitan species usually did not exceed 10% (Fig. 5*b*).

Apart from a few south-east coast systems (Kariega, Great Fish, Nahoon), the relative biomass contribution of tropical species typically comprised <50% of the catch south of the Xora estuary (east coast); north of the Xora system this group generally exceeded 70% of the biomass (Fig. 5*c*). The biomass composition of endemic species comprised over 70 % of the catch in systems south of the Keurbooms estuary (south coast). From the Keurbooms system northward to the Mbashe estuary (east coast) this group generally comprised between 30 and 60% of the biomass, but north of the Mbashe estuary did not comprise >20% of the catch. The biomass contribution of temperate species was variable but generally did not comprise >1% of the catch in estuaries north of the Mntafufu (east coast). The biomass contribution of cosmopolitan species was also somewhat variable and comprised a major proportion of the catch in the Great Kei, Mbashe and Mtata estuaries (east coast) (Fig. 5*c*).

Multivariate analyses

From the cluster analyses based on presence/absence of fish species (Fig. 6), relative abundance (Fig. 7) and biomass (Fig. 8), estuaries on the west and south-west coast separated from the remaining estuaries at ~20% similarity. The remaining estuaries formed two groups at just over 40% similarity; one group comprised a mixture of estuaries from the east and north-east coasts, while the other group consisted of estuaries mainly from the south, south-east and east coast regions. In the ordination of the presence/absence data, estuaries on the west and south-west coast were situated to the left of each plot while the remaining systems formed a gradation from those on the south and south-east coasts to estuaries on the east and north-east coasts.

Discussion

Species richness and distribution

Along the South African coast there is an increase in taxonomic richness from the temperate west (Atlantic

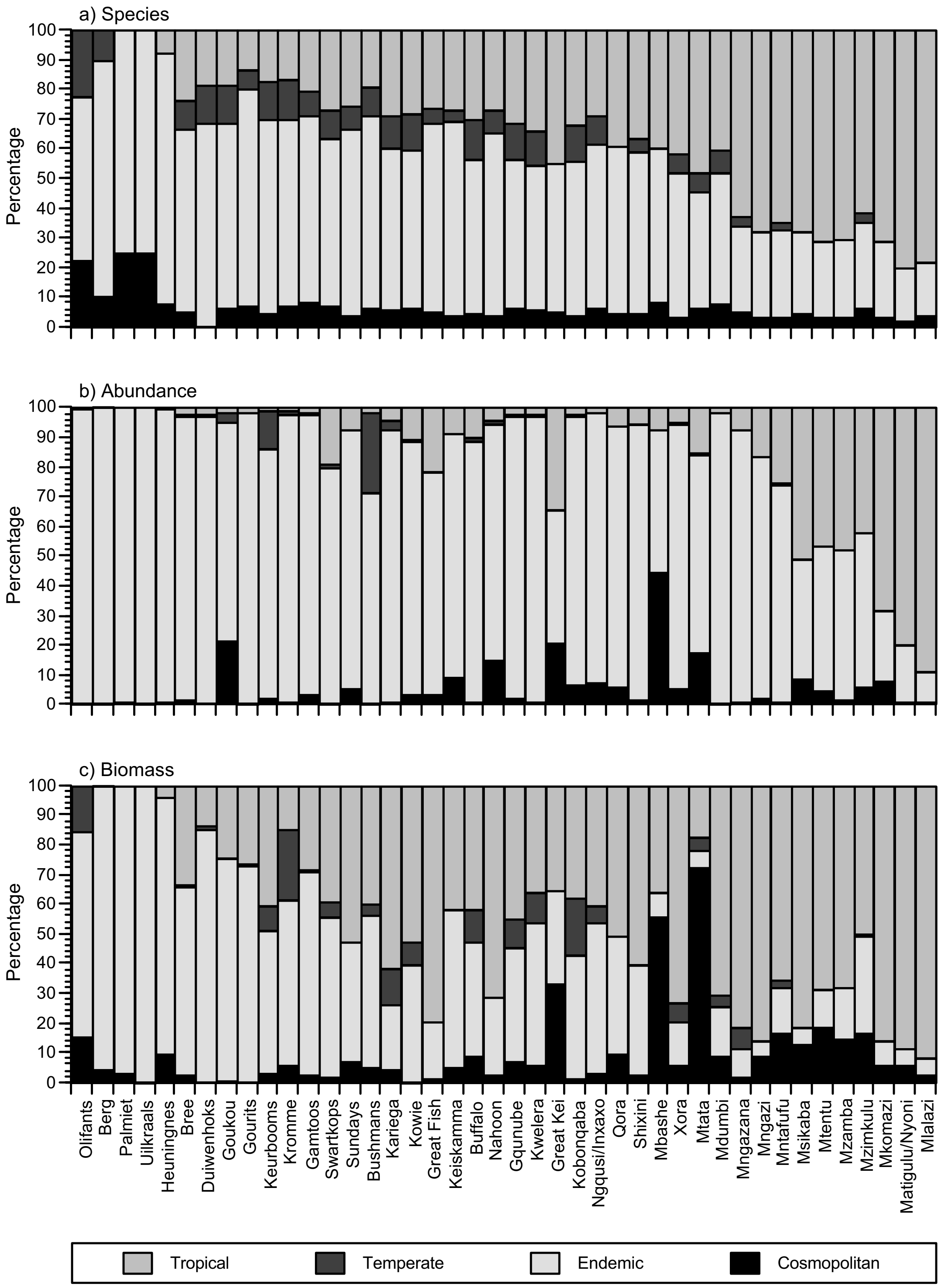

Fig. 5. Relative contribution of tropical, temperate, endemic and cosmopolitan species to the ichthyofauna of selected South African estuaries by *(a)* species, *(b)* abundance, and *(c)* biomass.

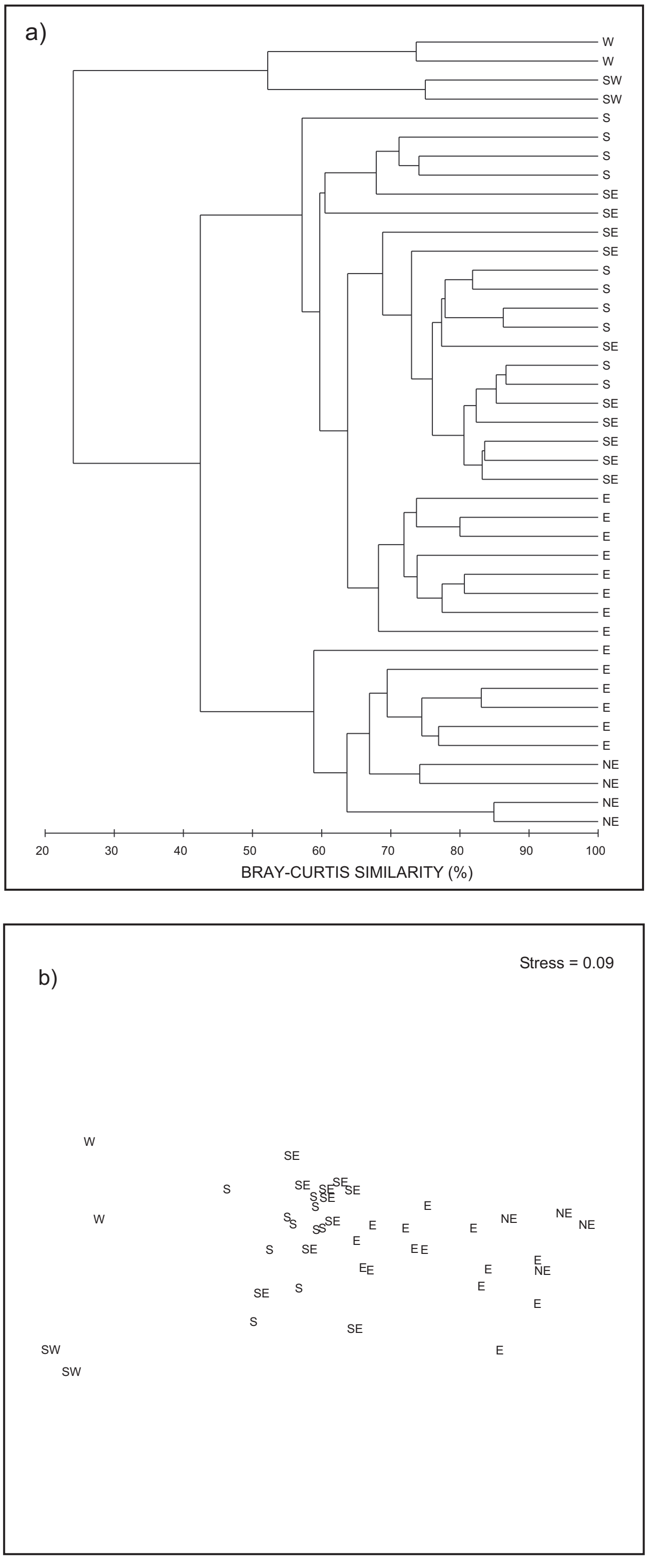

Fig. 6. Results of *(a)* cluster analysis and *(b)* MDS ordination of selected South African estuaries based on presence/absence data. See Fig. 3 for boundaries of regions.

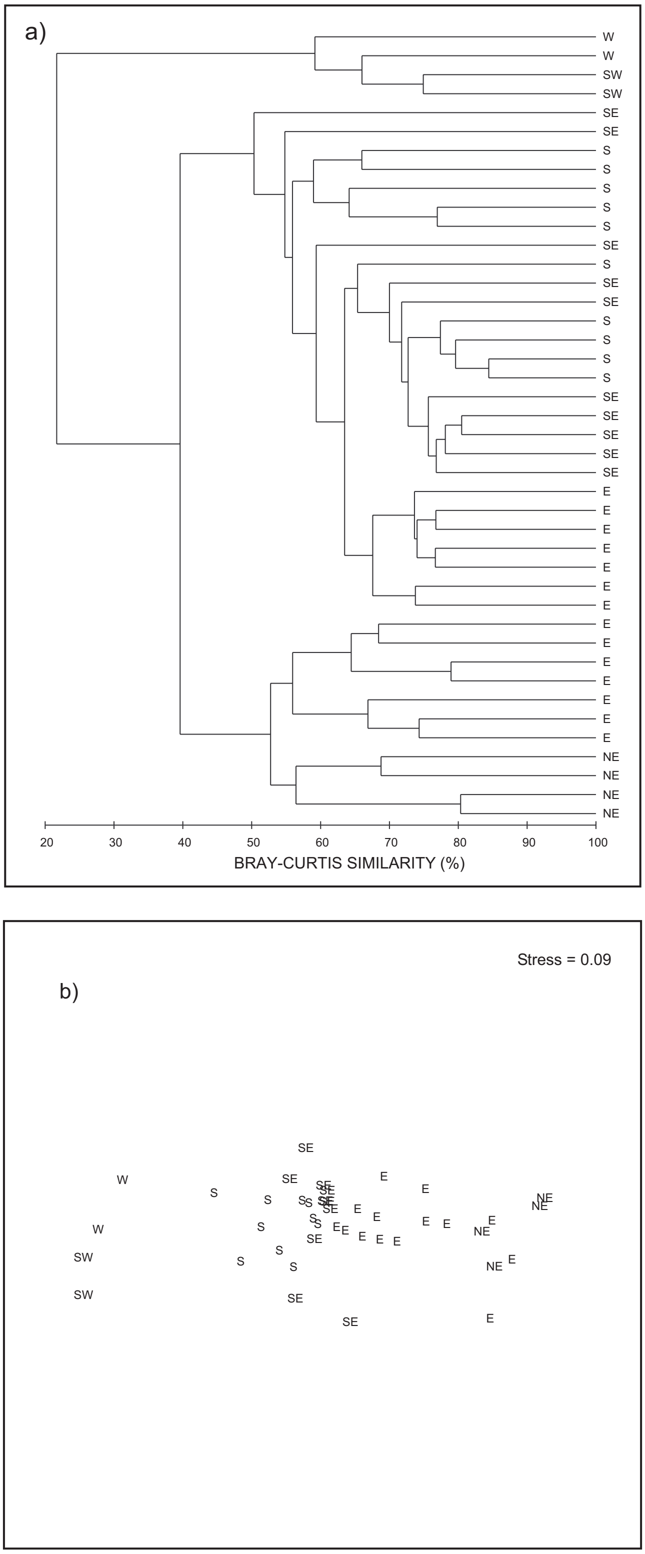

Fig. 7. Results of *(a)* cluster analysis and *(b)* MDS ordination of selected South African estuaries based on abundance data. See Fig. 3 for boundaries of regions.

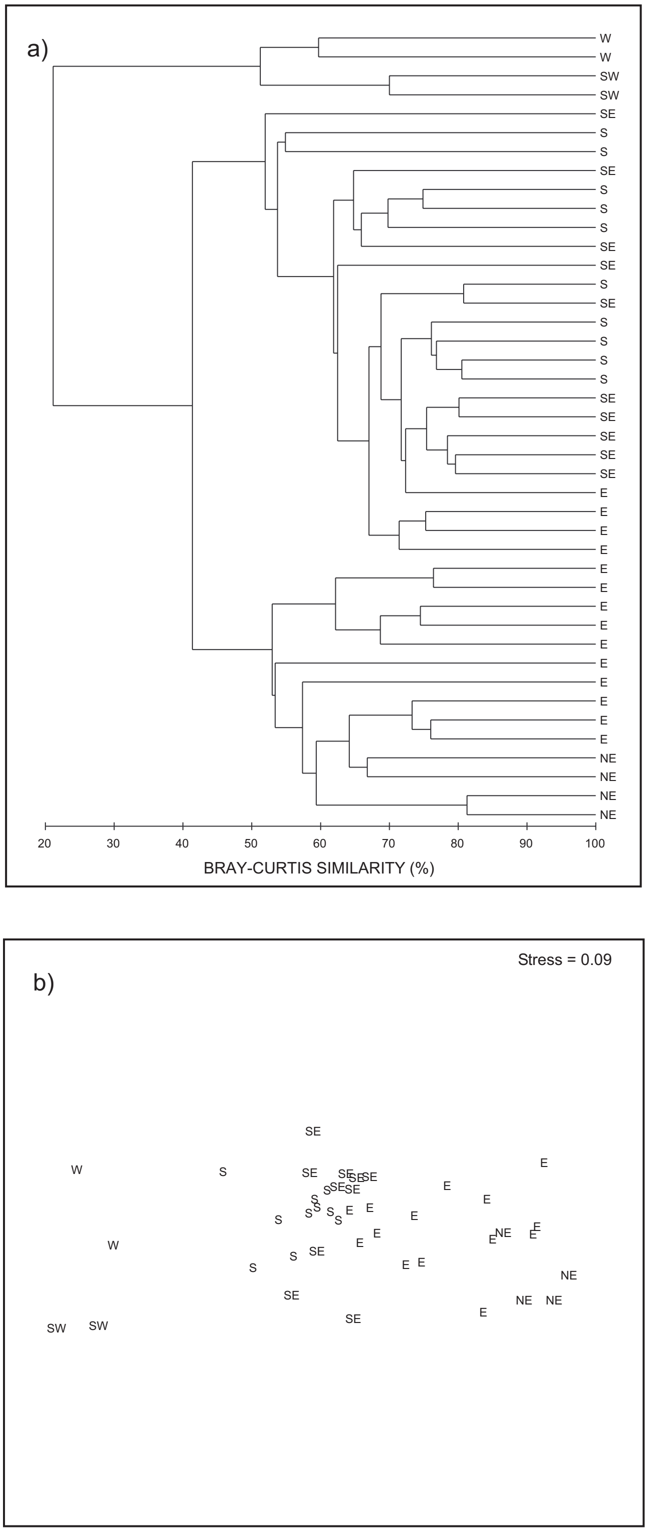

Fig. 8. Results of *(a)* cluster analysis and *(b)* MDS ordination of selected South African estuaries based on biomass data. See Fig. 3 for boundaries of regions.

Ocean) toward the subtropical north-east (Indian Ocean) coast. This trend has been observed for a number of coastal and marine taxa including rocky shore plants and animals (Stephenson and Stephenson 1972), marine intertidal and subtidal invertebrates (Emanuel *et al.* 1992), marine molluscs (Kilburn and Rippey 1982), rocky intertidal fish species (Burger 1990; Prochazka 1994), rock pool fishes (Hockey and Buxton 1991), and shelf-inhabiting fishes (Turpie *et al.* 2000). The diversity of southern African indigenous freshwater fishes also decreases from north to south, with most southern (Cape) rivers having only a few indigenous freshwater species (O'Keeffe *et al.* 1991; Skelton 1993). In addition, Siegfried (1981) found that the percentage of resident bird species was relatively low in west coast estuaries but increased in east coast systems toward the Mozambique border.

An increase in estuarine fish diversity was also reported from the west coast around the south and south-east coast to the north-east coast (Day 1974; Wallace and van der Elst 1975; Whitfield *et al.* 1989; Whitfield 1994*a*, 1994*b*, 1998; Maree *et al.* 2000). This is a result of the addition of tropical marine species (which comprise the bulk of the estuary-associated ichthyofauna) and is linked to the Agulhas Current through its influence on sea temperatures and the dispersal of these fishes in a southerly direction (Wallace and van der Elst 1975; Blaber 1981; Day *et al.* 1981; Whitfield *et al.* 1989; Whitfield 1998, 1999). Along the west coast, the cold upwelled waters associated with the Benguela Current system probably act as a barrier to the distribution of tropical and subtropical taxa from both the west and east African coasts and thus accounts for the low species richness in the region (Whitfield 1983, 1996, 1999).

In this study, low numbers of species were captured in estuaries on the west coast and south-west coast, with higher numbers of species reported from north-east coast estuaries; the number of species in the intermediate area, however, was somewhat variable. This is largely a result of a combination of the distribution of tropical and endemic taxa. As the numbers of tropical species increased from the west coast towards the north-east coast, this was accompanied by an decrease in the numbers of endemic species.

Both Day *et al.* (1981) and Whitfield *et al.* (1989) reported a similar increase in the percentage of tropical fish species from west coast estuaries toward those on the north-east coast. The percentage endemicity was also found to decrease from west to north-east (Whitfield 1994*a*, 1994*b*, 1998).

A similar pattern has been described for other marine organisms, with a rapid increase in the proportion of warm-water rocky-shore taxa north of Port St Johns (Stephenson and Stephenson 1972), and a major change in sandy beach macrofaunal composition between the Great Kei estuary and Port St Johns where temperate species are replaced by a subtropical fauna (Wooldridge *et al.* 1981). Kilburn and

Rippey (1982) found that endemic species dominate the mollusc fauna of the west (Atlantic) coast but that these species decline up the east coast with a corresponding increase in tropical taxa.

High proportions of endemic species have also been found to occur on the west and south coasts for marine intertidal fishes (Penrith 1970; Burger 1990; Prochazka 1994), rock pool fishes (Hockey and Buxton 1991), and shelf-associated fishes (Turpie *et al.* 2000); up the east coast, the proportion of endemic taxa declined with a corresponding increase in tropical species.

Multivariate analyses

In terms of their fish communities, estuaries on the west and south-west coasts were distinct from other South African systems. The remaining estuaries appeared to form a gradation from systems on the south coast to those on the south-east, east and north-east coasts. A similar pattern was obtained for shelf-associated fish species with a clear ordination break at Cape Point, and, to the east of Cape Point, a gradual turnover of species (Turpie *et al.* 2000).

However, Marais (1988) noted that geographical affinity had a strong influence on the clustering of 14 estuaries between the Kromme, on the south coast, and the Mtata, on the east coast; east coast estuaries (north of the Great Kei) grouped separately from those to the south. Maree *et al.* (2000) obtained similar results among eight permanently open estuaries between the Kromme and the Mntafufu (east coast), with the ichthyofaunal communities of estuaries north of the Great Kei differing from those to the south.

The east coast, between Port St Johns and the Great Kei estuary, is generally regarded as a zone of overlap between the warm-temperate and subtropical regions. Changes in communities, from tropical to temperate/endemic groups have been observed in this region for rock pool fishes (Hockey and Buxton 1991), rocky shore biota (Stephenson and Stephenson 1972), beach macrofauna (Wooldridge *et al.* 1981), marine molluscs (Kilburn and Rippey 1982), estuarine vegetation (Colloty 2000), shelf-associated fishes (Turpie *et al.* 2000), estuarine fishes (Day *et al.* 1981) and even freshwater fishes (Skelton 1993).

The area between Cape Point and Cape Agulhas has also been shown to represent a zone of overlap between the cool-temperate and warm-temperate faunal provinces (Penrith 1970; Stephenson and Stephenson 1972; Day *et al.* 1981; McLachlan *et al.* 1981; Kilburn and Rippey 1982; Emanuel *et al.* 1992; Prochazka 1994; Turpie *et al.* 2000).

To determine if any clear boundary between the various biogeographic regions could be established from this study, an analysis of similarities (ANOSIM) was performed on the data; this uses the (rank) similarity matrix underlying the clustering/ordination procedure and tests for differences between and within *a priori* groupings (Clarke and Warwick 1994). A test statistic (R) is computed, which reflects the observed differences between groupings, contrasted with differences within groupings. The R statistic usually falls between 0 and 1: if $R = 1$ then all sites within a group are more similar to each other than any sites from different groups, and if $R = 0$ then the similarities between and within groups are the same on average (Clarke and Warwick 1994).

For the cool-temperate/warm-temperate region, the ANOSIM test was performed on estuaries between the Orange River and the Great Kei estuary using Cape Point and Cape Agulhas as the potential biogeographic boundaries respectively. For the warm-temperate/subtropical region, the test was performed on estuaries between Cape Agulhas and Kosi Bay using the Great Kei, Mbashe, Mdumbi, Mngazi, and Mzamba estuaries (east coast) as potential boundaries. The test used presence/absence, abundance and biomass data.

The result of the ANOSIM test suggests that the break between the cool-temperate and warm-temperate zones occurred at Cape Agulhas (Table 1). This division is slightly east of Cape Point, the cool-temperate/warm-temperate division suggested by Day (1981) and Whitfield (1994*a*) for South African estuaries. The break between the warm-temperate and subtropical zones also differed from those proposed by Day (1981) and Whitfield (1994*a*) and lay further north, in the region of the Mdumbi estuary, just south of Port St Johns (Table 2). However, no estuaries were sampled between the Mdumbi system and Port St Johns, and it is possible that this boundary may lie further north, extending even to Port St Johns as suggested by the abundance data (Table 2).

Table 1. Test statistic (*R*) (and significance) of the ANOSIM test applied to presence/absence, abundance and biomass data using Cape Point and Cape Agulhas as the cool-temperate/warm-temperate biogeographic break

	Cape Point	Cape Agulhas
Presence/absence	0.679 ($P = 0.022$)	0.998 ($P < 0.001$)
Abundance	0.655 ($P = 0.018$)	0.983 ($P = 0.001$)
Biomass	0.717 ($P = 0.018$)	0.996 ($P < 0.001$)

Table 2. Test statistic (*R*) (and significance) of the ANOSIM test applied to presence/absence, abundance and biomass data in open estuaries using Great Kei, Mbashe, Mdumbi and Mngazi as the warm-temperate/subtropical biogeographic break
$P < 0.001$ in all cases

	Great Kei	Mbashe	Mdumbi	Mngazi	Mzamba
Presence/absence	0.638	0.812	0.874	0.795	0.617
Abundance	0.517	0.698	0.837	0.850	0.699
Biomass	0.541	0.807	0.881	0.783	0.616

Conclusions

On the basis of their fish communities, three biogeographic provinces are identified for South African estuaries. A cool-temperate region extends along the west and south-west coasts from the Orange River to Cape Agulhas; a warm-temperate region stretches from Cape Agulhas along the south, south-east and east coasts to just south of Port St Johns; and a subtropical region extends along the east coast from approximately Port St Johns northwards to Kosi Bay. Branch and Grindley (1979) have reported that the fish fauna in the Mngazana estuary (near Port St Johns) exhibit a seasonal variation, with many tropical species occurring only in summer and those with southern affinities appearing most often in winter. Recent studies, however, have shown that the fish fauna of the system is dominated by tropical taxa both in summer and in winter, suggesting that it lies well within the subtropical region (Whitfield, personal communication). It is possible that the bio-geographic boundaries may shift seasonally.

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