# SMITHIANA

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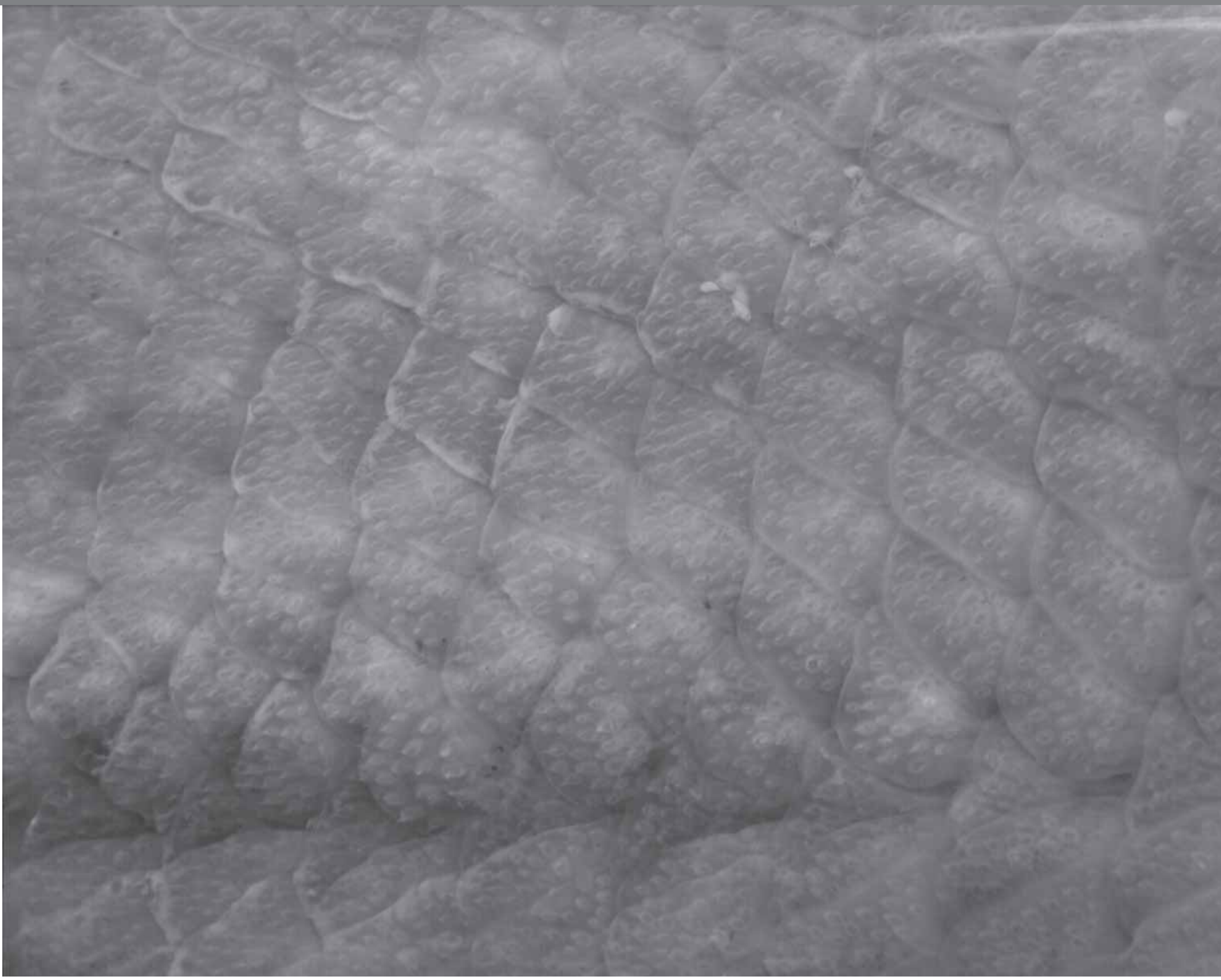

## Ichthyofauna of South African estuaries in relation to the zoogeography of the region

T. D. Harrison

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SAIAB

Margaret Mary Smith (1916 - 1987),
James Leonard Brierley Smith (1897 - 1968)
with their dog Marlin

The publication series (Monographs, Bulletins & Special Publications) of the SAIAB (formerly the JLB Smith Institute of Ichthyology), in its new format honors James Leonard Brierley Smith and Margaret Mary Smith with the name *Smithiana*, in recognition of their many years of devoted service to African aquatic biology. Their life's work, a team effort, established modern ichthyology in southern Africa and laid the groundwork for the expansion of aquatic biology throughout the region.

# Ichthyofauna of South African estuaries in relation to the zoogeography of the region

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**ABSTRACT**

The fish fauna of South African estuaries are described and compared in relation to the zoogeography of the region. Estuaries within each biogeographic region were found to contain fairly distinctive fish communities. Subtropical estuaries are characterised by species of tropical origin that prefer warmer waters. South coast endemic taxa that enter warmer waters are also important, although these species seem to have a preference for warm-temperate systems. In the warm-temperate region, the fauna generally comprises endemic taxa as well as some eurythermal tropical species. The estuaries of the cool-temperate region do not contain any unique taxa, but rather comprise those south coast endemic species that are able to extend their range westwards.

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# Ichthyofauna of South African estuaries in relation to the zoogeography of the region

T.D. Harrison

## INTRODUCTION

The South African coast, which extends for some 3400 km from the Orange River mouth (28° 38S; 16° 27E) on the west coast to Kosi Bay (26° 54S; 32° 48E) on the east coast, is intersected by numerous outlets ranging from relatively large, permanently open estuaries to small coastal streams. Since estuaries are formed where rivers meet the sea, they are affected by variations in both climatic and marine conditions (Day, 1981; Cooper, 2001). The South African coastline spans a range of climatic and oceanographic conditions and as a result, estuarine environments and their associated ichthyofauna are not uniformly distributed along the coast; many estuarine fish species are confined to specific geographic regions, or even to estuaries within these regions (Whitfield, 1994).

A great deal of estuarine fish research has been conducted across the South African region. Such studies have included basic ecological surveys within estuaries around the country (e.g. Branch & Grindley, 1979; Branch & Day, 1984; Plumstead *et al*., 1985; 1989a; 1989b; 1991; Ter Morshuizen *et al*., 1996a; Cowley & Whitfield, 2001). The seasonal abundance and distribution of fishes in selected estuaries has also been investigated (e.g. Marais & Baird, 1980; Marais, 1981; 1983a), with particular emphasis on the larger size classes of marine species found in these systems. Some studies (e.g. Marais, 1983b; Bennett, 1994; Ter Morshuizen *et al*., 1996b) considered the effects of reduced river inflows and floods on estuarine fish communities. Several workers have studied the fish community structure in submerged macrophyte and salt marsh habitats within estuaries (e.g. Beckley, 1983; Hanekom & Baird, 1984; Whitfield *et al*., 1989; Ter Morshuizen & Whitfield, 1994; Paterson & Whitfield, 1996), particularly the potential nursery role that these habitats perform. The fish communities in degraded or polluted estuaries have been examined (e.g. Blaber *et al*., 1984; Ramm *et al*., 1987) and the sources of these anthropogenic disturbances identified. A number of comparative studies have also been undertaken in various parts of the country (e.g. Begg, 1984a; Bennett, 1989; Dundas, 1994; Whitfield *et al*., 1994; Harrison & Whitfield, 1995; Vorwerk *et al*., 2001), with particular emphasis on structural and functional differences between the different fish communities and estuary types.

While much research relating to estuarine fishes has been undertaken in South African estuaries, each investigation has had its own specific focus with regards the estuaries investigated and the aims and objectives of each study. No dedicated studies have considered the southern African region in its entirety. Regional analyses of estuarine fish communities in other parts of the world such as Australia (e.g. Pease, 1999), Europe (e.g. Elliott & Dewailly, 1995), South and Central America (e.g. Viera & Musick, 1993; 1994) and the United States (e.g. Monaco *et al*., 1992) have largely relied on limited field collections and / or existing data from other research.

Based on an extensive regional sampling program, spanning the entire South African coastline, this study aims to describe and compare the ichthyofauna of South African estuaries at a regional scale and to explain zoogeographic variations in fish communities.

## MATERIALS & METHODS

### Field methods

The ichthyofauna of some 250 coastal outlets between the Orange River and Kosi Bay were sampled over the period 1993 to 1999. Using information contained in Begg (1978), Heydorn & Tinley (1980) and Whitfield (1995), the coastline was divided into arbitrary sections, each containing approximately 40 estuaries (Figure 1). This grouping was based on the number of systems that could be adequately surveyed within each annual sampling period. The estuaries in each section of coast were sampled during the spring / summer period and a new section was covered each year until the entire coastline was completed.

The ichthyofauna of each estuary was sampled using a 30m x 1.7m x 15mm bar mesh seine net fitted with a 5mm bar mesh purse and, where possible, a fleet of gill nets. Each gill net had a range of mesh sizes and comprised three 45mm, 75mm and 100mm stretch mesh monofilament panels and was either 10m or 20m in length and 1.7m deep. Seine netting was carried out during daylight hours and was limited to shallow (<1.5m deep), unobstructed areas with gently sloping banks. Specimens collected by seine netting were, where possible, identified in the field, measured to the nearest mm 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. Gill netting was generally carried out in deep (>1m) open, mid-channel waters with the nets being deployed in the evening (18h00-19h00) and lifted the following morning (06h00-07h00). In most cases, only the larger, deeper systems were sampled with gill nets. 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.

The sampling effort undertaken in each estuary varied depending on the size of the system, and usually took one to three days to complete. Sampling was carried out until no new species were collected or until all habitats within each estuary had been sampled. An example of the relationship between sampling effort and the number of taxa captured in representative closed and open estuaries (see below) from each coastal sector are given in Figures 2 and 3.

**Laboratory methods**

Preserved specimens were identified in the laboratory by reference to Skelton (1993) and Smith & Heemstra (1995). At least 25 specimens of the abundant species were measured (mm SL) and weighed to the nearest 0.01g; the remaining specimens were counted and batch weighed. Voucher specimens were also sent to the South African Institute for Aquatic Biodiversity, Grahamstown for verification.

**Data analyses**

Estuary typology

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 account for the effect of the latter, representative estuaries were selected according to a broad agreement between two physical / morphological classification schemes.

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. These were:

- open non-barred estuaries
- predominantly open small estuaries (mean annual runoff <15 x $10^6 m^3$)
- predominantly open moderate to large estuaries (mean annual runoff >15 x $10^6 m^3$)
- predominantly closed small estuaries (surface

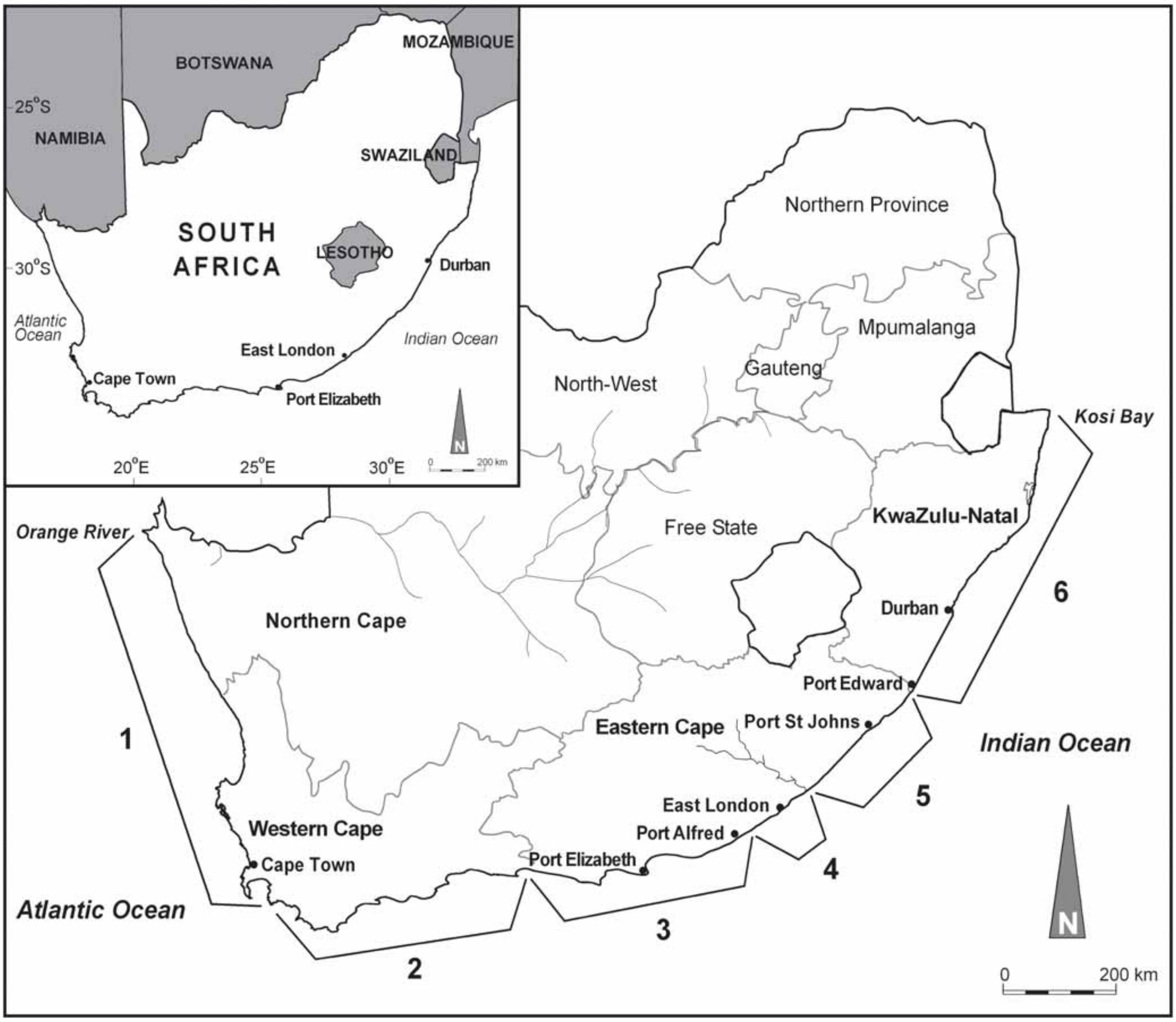


Figure 1. Map of South Africa showing the division of the coastline into six sampling sectors.

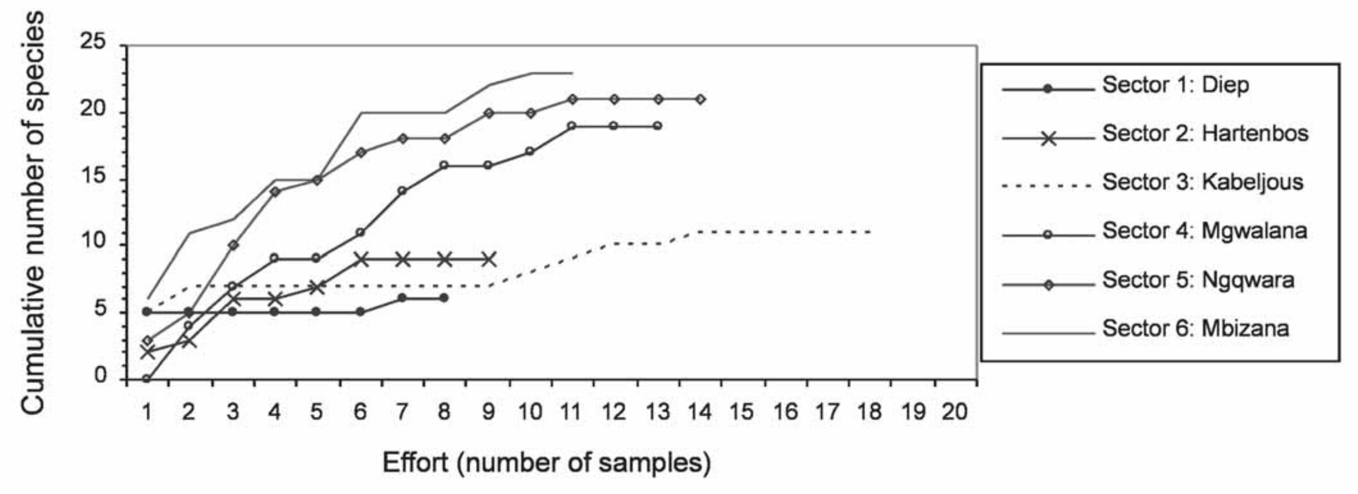


Figure 2. Relationship between sampling effort (seine and gill netting) and number of species captured in representative closed estuaries from each coastal sector.

area <2ha)

- predominantly closed moderately sized estuaries (surface area 2-150ha)
- predominantly closed large estuaries (surface area >150ha)

Whitfield (1992; 2000) identified and classified South Africas estuaries into five broad types based on a combination of physiography, hydrography and salinity:

- permanently open estuaries
- temporarily open / closed estuaries
- estuarine lakes
- estuarine bays
- river mouths

Representative estuaries were then selected according to a broad agreement between both classification schemes. This was to ensure that similar estuarine types were compared on a regional basis.

According to Harrison *et al.* (2000), 44 systems (18%) were not considered estuaries on the basis of their very small size, regular dry or hypersaline conditions, extensive human modification or almost permanent isolation from the sea (Table 1). Eleven systems (4%) were classified as open non-barred estuaries, 34 (14%) were small open estuaries and 62 (25%) were large open systems. Twenty-seven estuaries (11%) were classified as small closed systems, 71 (28%) were moderately sized closed estuaries, and only two (1%) were large closed systems. From Whitfield (2000), 51 (20%) of the systems were not considered estuaries either due to a loss of function or due to their extremely small size. Forty-five systems (18%) were classified as permanently open estuaries, 134 (53%) were temporarily open / closed estuaries, 12 (5%) were river mouths, eight (3%) were estuarine lakes and one was an estuarine bay (Table 1).

A total of 109 estuaries were selected for further analysis; these were divided into two basic types namely open estuaries and closed estuaries. Forty-two systems were open estuaries and comprised representatives of permanently open estuaries of Whitfield (2000) and large open estuaries of Harrison *et al.* (2000). Sixty-seven estuaries were closed systems representing temporarily open / closed estuaries of Whitfield (2000) and medium closed estuaries of Harrison *et al.* (2000) (Table 1). The remaining systems were excluded from further analysis.

Biogeography

Based on their fish communities, Harrison (2002) identified three biogeographic regions for South African estuaries. A cool-temperate region extends along the west and southwest coasts, a warm-temperate region stretches along the south, southeast and east coasts and a subtropical region extends along the northeast coast (Figure 4).

The selected open and closed estuaries were divided into three biogeographic regions described by Harrison (2002). These included cool-temperate estuaries between the Orange River and Cape Agulhas, warm-temperate estuaries from Cape Agulhas to, and including, the Mdumbi estuary, and subtropical estuaries from the Mdumbi estuary to Kosi Bay (Figures 5 & 6).

Species composition

Only taxa that were identified to species level were considered for further investigation. All alien species were also omitted from the analysis while translocated indigenous taxa (e.g. *Oreochromis mossambicus*) were adjusted by removing occurrences outside their natural range. An initial analysis of the inclusion / exclusion of this group revealed that they contributed very little to the overall abundance or biomass of the fish community in the estuaries (generally <0.1%).

The total species composition, both by number and by mass, of the fish community within each system was established. The relative biomass contribution of each species was calculated using actual recorded masses and masses derived from length-weight relationships presented in Harrison (2001).

Although the sampling strategy adopted during this study was designed to capture all available taxa that were susceptible to the gear used (Figures 2 & 3), the sampling effort within each estuary varied somewhat. To ensure that the fish communities of the various

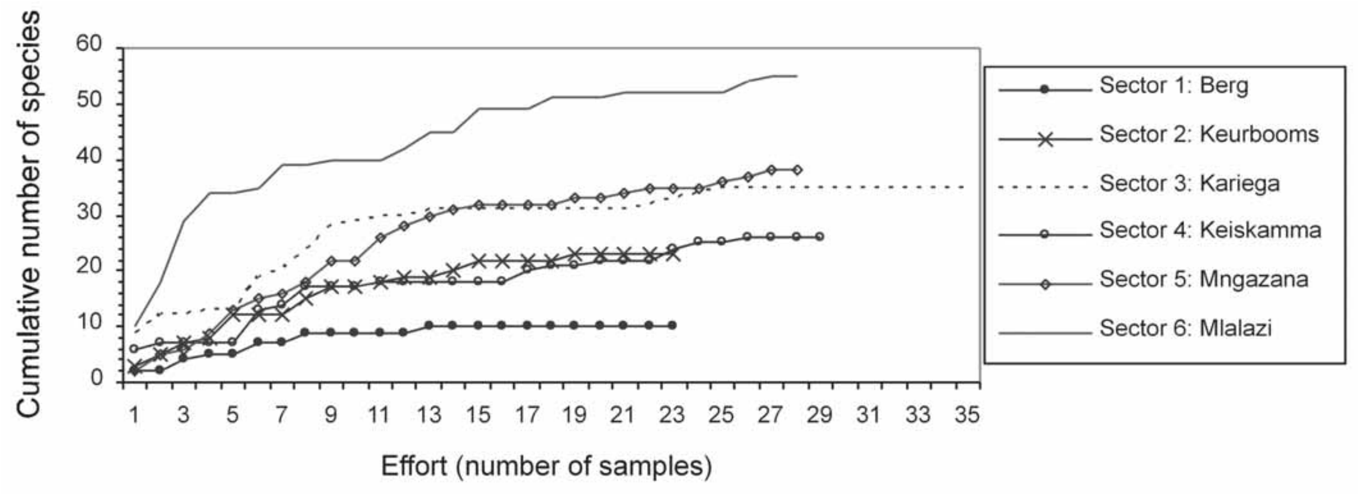


Figure 3. Relationship between sampling effort (seine and gill netting) and number of species captured in representative open estuaries from each coastal sector.

estuaries were comparable, all the data was standardised by computing the relative (%) abundance / biomass of each species within each estuary.

The average number of taxa (±SD) as well as the frequency of occurrence of each species was calculated for open and closed estuaries within each biogeographic region. In addition, the mean (±SD) contribution of each species, both in terms of abundance and biomass, to the overall fish assemblage of open and closed estuaries within each biogeographic region was determined.

A similarity breakdown (SIMPER) using the Plymouth Routines In Multivariate Ecological Research (PRIMER) was also performed on the data. In this analysis, the closed and open estuaries were grouped into the three biogeographic regions and the average Bray-Curtis similarity coefficient for each group calculated based on presence / absence, abundance and biomass. For abundance and biomass analyses, the data was first 4th root transformed; this has the effect of scaling down the importance of abundant species so that they do not swamp the other data (Field *et al.*, 1982; Clarke & Warwick, 1994). The contribution of each species to the average similarity within a group of estuaries (*S*) was calculated and the major species that account for this similarity identified (Clarke, 1993; Clarke & Warwick, 1994). The more abundant a species (*i*) is within a group, the more it will tend to contribute to the intra-group similarity. A species typifies that group if it is found at a consistent abundance throughout; so the standard deviation of its contribution (SD [*Si*]) is low and the ratio of its average similarity to the standard deviation (*Si* / SD [*Si*]) high (Clarke, 1993).

The SIMPER analysis was also used to identify those species that account for the differences (or dissimilarities) between the estuaries from the various biogeographic regions. In this analysis, the dissimilarity contribution of each species (ä*i*) to the average dissimilarity (ä) between two groups of estuaries is calculated. If the standard deviation of the contribution of a species (SD [ä*i*]) is small, and the ratio of its average dissimilarity (ä*i*) to the standard deviation (ä*i* / SD [ä*i*]) high, then that species not only contributes much to the dissimilarity between two groups of estuaries but it also does so consistently (Clarke, 1993; Clarke & Warwick, 1994). Cool-temperate and warm-temperate estuaries, and warm-temperate and subtropical systems were compared using the SIMPER routine.

## RESULTS

### Closed estuaries

Species composition

Eleven species representing eight families were recorded in closed cool-temperate estuaries with an average of 4.5 (SD±4.04) taxa being captured per estuary (Table 2). *Liza richardsonii* was the most frequently captured species (100%), followed by *Mugil cephalus* (75%), *Caffrogobius nudiceps* (50%) and *Heteromycteris capensis* (50%). In terms of abundance, *L. richardsonii* (56.7%), *Gilchristella aestuaria* (19.5%), *M. cephalus* (18.1%), *C. nudiceps* (3.0%) and *Atherina breviceps* (2.2%) were the dominant species. *Liza richardsonii* (49.9%), *M. cephalus* (43.8%) and *Lichia amia* (5.4%) dominated the overall species mass composition (Table 2).

Closed cool-temperate estuaries had average similarities ranging between 38.3% and 54.2% (Table 3). Four species accounted for over 90% of the similarity within this group, namely *C. nudiceps*, *H. capensis*, *L. richardsonii* and *M. cephalus*.

In the warm-temperate region, 43 species and 20 families were represented with an average of 15.5 (SD±4.85) species being captured per estuary (Table 4). The most frequently recorded taxa included *G. aestuaria* and *L. richardsonii* (100%), *Rhabdosargus holubi* (98%), *Monodactylus falciformis* (93%), *M. cephalus* and *Myxus capensis* (90%), *A. breviceps* and *Glossogobius callidus* (88%), *Liza dumerili* (83%), *Lithognathus lithognathus* and *Liza tricuspidens* (76%), *Psammogobius knysnaensis* (71%), and *O. mossambicus* and *Pomadasys commersonnii* (61%) (Table 5). In terms of abundance, *G. aestuaria* (35.8%), *A. breviceps* (18.3%), *R. holubi* (17.6%), *L. richardsonii* (6.7%), *M.*

*capensis* (5.6%), *G. callidus* (3.2%), *L. lithognathus* (2.9%), *L. dumerili* (2.6%), *M. cephalus* (1.8%), *L. tricuspidens* (1.1%) and *P. knysnaensis* (1.1%) were the dominant taxa. The biomass composition was dominated by *L. richardsonii* (28.4%), *M. cephalus* (11.5%), *R. holubi* (10.3%), *L. tricuspidens* (7.1%), *O. mossambicus* (6.6%), *Argyrosomus japonicus* (6.5%), *M. capensis* (5.8%), *P. commersonnii* (4.5%), *L. dumerili* (4.4%), *L. lithognathus* (3.7%), *L. amia* (3.3%), *Elops machnata* (1.7%) and *G. aestuaria* (1.6%) (Table 4).

Average similarities in closed warm-temperate estuaries varied between 60.6% and 69.1% (Table 5). Fourteen species accounted for over 90% of the similarity within this group and these included *A. breviceps*, *G. aestuaria*, *G. callidus*, *L. lithognathus*, *L. dumerili*, *L. richardsonii*, *L. tricuspidens*, *M. falciformis*, *M. capensis*, *O. mossambicus*, *P. commersonnii*, *P. knysnaensis* and *R. holubi* (Table 5).

Forty-nine species representing 22 families were reported in closed subtropical estuaries; an average of 15.9 (SD±5.19) species was captured per estuary (Table 6). Frequently recorded taxa included *M. capensis* and *O. mossambicus* (100%), *M. cephalus* (91%), *Valamugil cunnesius* (86%), *G. callidus* and *R. holubi* (82%), *L. dumerili* and *M. falciformis* (77%), *G. aestuaria* (73%), *Liza macrolepis* and *P. commersonnii* (68%), *Liza alata* (64%), *Terapon jarbua* and *Valamugil robustus* (55%), and *Ambassis ambassis* (50%) (Table 6). In terms of abundance, *G. aestuaria* (25.8%) was the dominant species overall followed by *O. mossambicus* (18.7%), *M. capensis* (14.1%), *M. cephalus* (7.8%), *R. holubi* (6.7%), *V. cunnesius* (5.2%), *L. dumerili* (3.7%), *G. callidus* (3.3%), *M. falciformis* (2.6%), *L. macrolepis* (2.2%), *V. robustus* (2.0%) and *A. ambassis* (1.9%). The overall species mass composition was dominated by *Clarias gariepinus* (18.1%), *O. mossambicus* (17.7%), *M. cephalus* (15.2%), *M. capensis* (14.0%), *L. alata* (6.6%), *L. macrolepis* (5.1%), *V. cunnesius* (3.9%), *P. commersonnii* (3.1%), *L. dumerili* (2.9%), *V. robustus* (2.8%), *R. holubi* (2.6%), *A. japonicus* (2.2%), *G. aestuaria* (1.4%) and *A. ambassis* (1.0%) (Table 6).

Closed subtropical estuaries had average similarities of between 52.3% and 58.7% (Table 7). Fifteen species accounted for over 90% of the similarity within this group. These taxa included *C. gariepinus*, *G. aestuaria*, *G. callidus*, *L. alata*, *L. dumerili*, *L. macrolepis*, *M. falciformis*, *M. cephalus*, *M. capensis*, *O. mossambicus*, *P. commersonnii*, *R. holubi*, *T. jarbua*, *V. cunnesius* and *V. robustus* (Table 7).

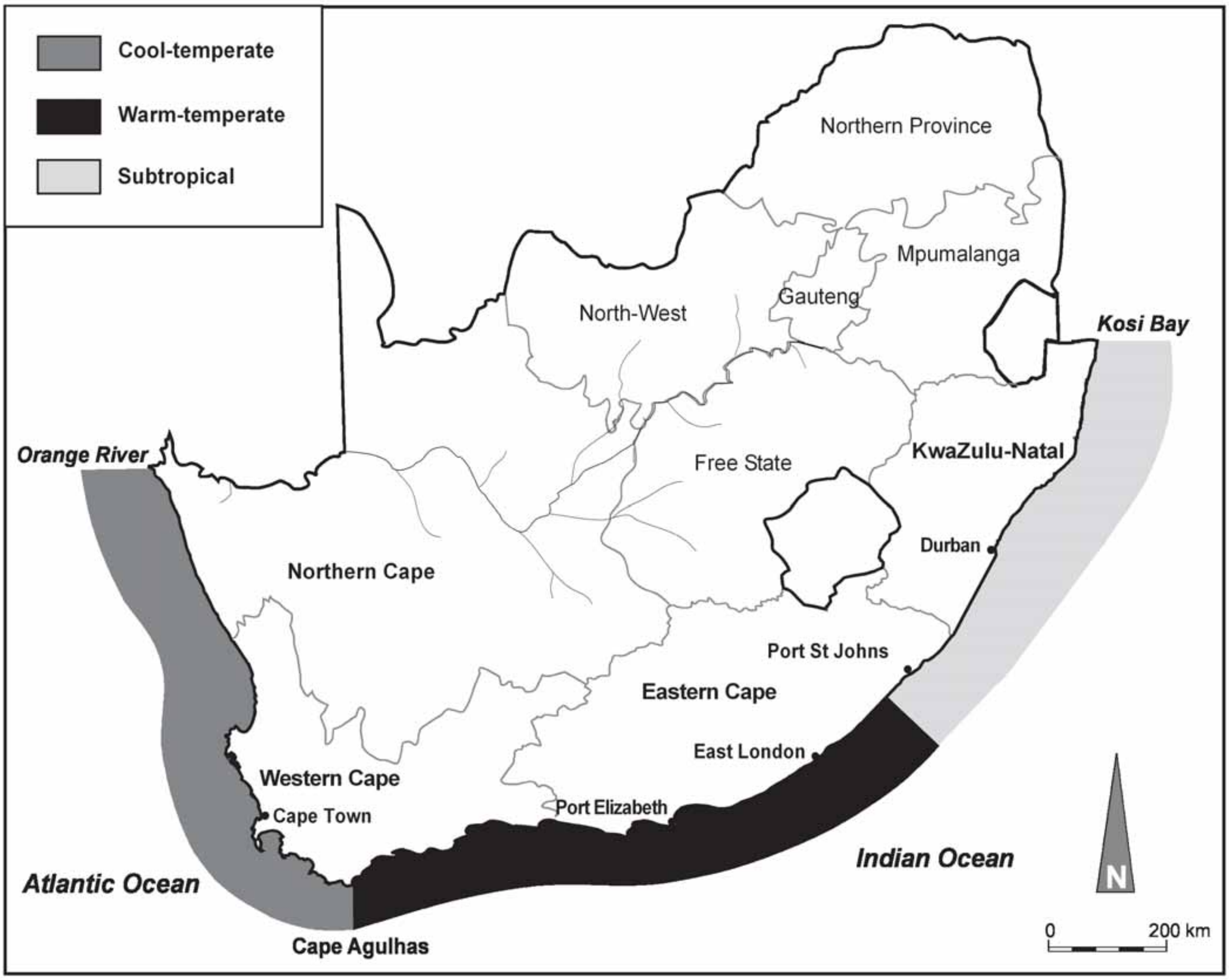


Figure 4. Map of South Africa indicating the three biogeographic provinces, based on estuarine fish communities.

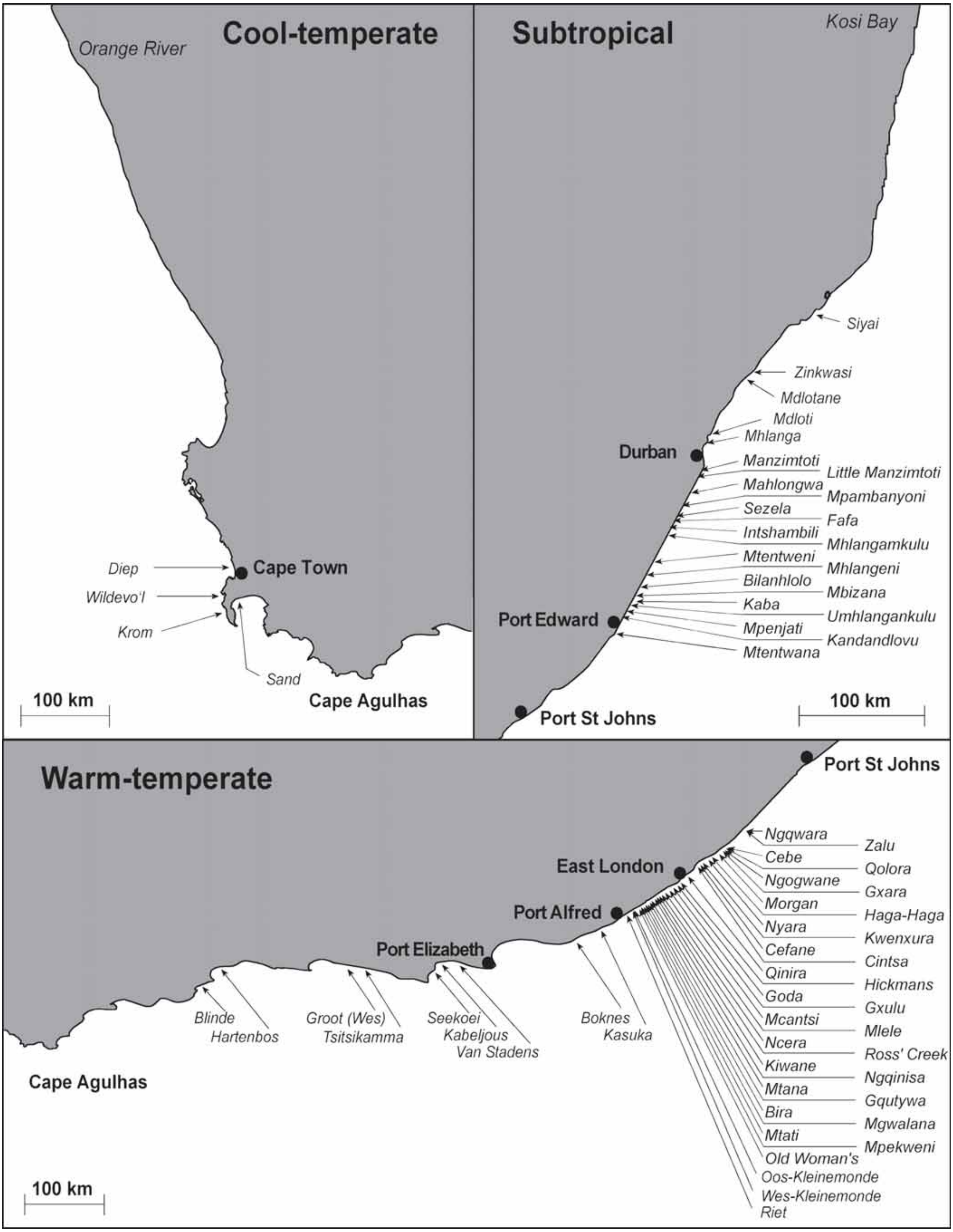


Figure 5. Map of closed estuaries in the cool-temperate, warm-temperate and subtropical biogeographic regions included in this study. The relative positions of the estuaries included in the study are indicated with arrows.

Inter-regional comparisons

In terms of their dissimilarities, the SIMPER analysis revealed that closed cool- and warm-temperate systems had average dissimilarities of between 68.3% and 75.3% (Table 8). Taxa that accounted for over 50% of this dissimilarity included *A. breviceps*, *G. aestuaria*, *G. callidus*, *L. lithognathus*, *L. dumerili*, *L. tricuspidens*, *M. falciformis*, *M. cephalus*, *M. capensis*, *O. mossambicus* and *R. holubi*.

Closed warm-temperate and subtropical estuaries had average dissimilarities of between 54.7% and 62.4% (Table 9). Taxa that accounted for over 50% of the dissimilarity included *A. ambassis*, *A. japonicus*, *A. breviceps*, *C. gariepinus*, *G. aestuaria*, *G. callidus*, *L. lithognathus*, *L. alata*, *L. dumerili*, *L. macrolepis*, *L. richardsonii*, *L. tricuspidens*, *M. cephalus*, *O. mossambicus*, *P. commersonnii*, *P. knysnaensis*, *R. holubi*, *T. jarbua*, *V. cunnesius* and *V. robustus*.

## Open estuaries

Species composition

Twelve species, representing 10 families were recorded in open cool-temperate estuaries with an average of 6.8 (SD±3.2) species captured per estuary (Table 10). *Liza richardsonii* and *P. knysnaensis* were the most frequently reported taxa (100%), followed by *A. breviceps*, *Galeichthys feliceps* and *M. cephalus* (75%) and, *G. aestuaria*, *Pomatomus saltatrix* and *Syngnathus temminckii* (50%). Numerically dominant species included *L. richardsonii* (85.7%), *A. breviceps* (11.5%) and *G. aestuaria* (1.2%) with *L. richardsonii* (76.1%), *A. breviceps* (10.1%), *Argyrosomus* sp. (3.9%), *P. saltatrix* (3.8%), *M. cephalus* (1.9%), *G. feliceps* (1.8%) and *Haploblepharus pictus* (1.3%) dominating the overall biomass (Table 10).

Open estuaries in the cool-temperate region had average similarity values of between 55.8% and 59.9% (Table 11). Species that accounted for over 90% of the overall similarity within these systems included *A. breviceps*, *G. feliceps*, *L. richardsonii*, *M. cephalus* and *P. knysnaensis*.

Seventy-three species representing 35 families were captured in open warm-temperate estuaries with an average of 25.3 (SD±6.18) species being captured per system (Table 12). *Argyrosomus japonicus*, *L. dumerili* and *L. tricuspidens* were the most frequently reported species (100%), followed by *Caffrogobius gilchristi*, *L. richardsonii*, *P. knysnaensis* and *R. holubi* (96%), *G. aestuaria* and *M. cephalus* (93%), *P. commersonnii* (89%), *A. breviceps*, *M. falciformis* and *S. bleekeri* (86%), *L. lithognathus* (79%), *E. machnata* (71%), *G. feliceps*, *G. callidus*, *H. capensis*, *L. amia* and *M. capensis* (64%), *Diplodus capensis* (57%), *C. nudiceps* (54%) and *L. macrolepis* (50%) (Table 12). In terms of abundance, *G. aestuaria* (30.4%), *R. holubi* (15.1%), *L. richardsonii* (12.0%), *L. dumerili* (7.8%), *M. cephalus* (6.4%), *A. breviceps* (4.7%), *C. gilchristi* (3.1%), *P. commersonnii* (3.0%), *G. callidus* (2.9%), *P. knysnaensis* (1.7%), *M. capensis* (1.5%), *S. bleekeri* (1.4%), *D. capensis* (1.3%), *A. japonicus* (1.2%) and *L. tricuspidens* (1.1%) were the dominant taxa. The overall biomass composition was dominated by *L. richardsonii* (15.5%), *E. machnata* (14.1%), *A. japonicus* (12.7%), *P. commersonnii* (8.9%), *M. cephalus* (8.9%), *G. feliceps* (8.7%), *L. tricuspidens* (7.2%), *L. dumerili* (4.9%), *L. amia* (4.6%), *R. holubi* (3.2%), *Valamugil buchanani* (2.9%), *L. lithognathus* (1.8%) and *G. aestuaria* (1.1%) (Table 12).

Open warm-temperate estuaries had overall similarities ranging between 57.9% and 63.0% (Table 13). Twenty-one species accounted for over 90% of the similarity within this group. These taxa included *A. japonicus*, *A. breviceps*, *C. gilchristi*, *D. capensis*, *E. machnata*, *G. feliceps*, *G. aestuaria*, *G. callidus*, *H. capensis*, *L. amia*, *L. lithognathus*, *L. dumerili*, *L. richardsonii*, *L. tricuspidens*, *M. falciformis*, *M. cephalus*, *M. capensis*, *P. commersonnii*, *P. knysnaensis*, *R. holubi* and *S. bleekeri* (Table 13).

In open subtropical estuaries, 76 species representing 31 families were captured with an average of 35.8 (SD±9.96) species being captured per estuary (Table 14). The most frequently recorded species included *A. japonicus*, *E. machnata*, *G. callidus*, *L. alata*, *L. dumerili*, *L. macrolepis*, *M. cephalus*, *P. commersonnii*, *R. holubi*, *T. jarbua* and *V. cunnesius* (100%), followed by *Acanthopagrus vagus*, *Caranx sexfasciatus*, *Hilsa kelee*, *Leiognathus equula* and *M. capensis* (90%), *Ambassis natalensis*, *Caranx ignobilis*, *G. aestuaria*, *Oligolepis acutipennis* and *Oligolepis keiensis* (80%), *L. tricuspidens*, *Scomberoides lysan*, *S. bleekeri*, *V. buchanani* and *V. robustus* (70%), *Amblyrhynchotes honckenii* (60%), and *Ambassis dussumieri*, *C. gilchristi*, *Lutjanus argentimaculatus*, *Thryssa vitrirostris* and *Valamugil seheli* (50%). The most abundant species overall were *G. aestuaria* (15.7%), *L. dumerili* (14.7%), *A. dussumieri* (6.9%), *R. holubi* (6.9%), *V. cunnesius* (6.8%), *L. macrolepis* (6.0%), *G. callidus* (4.2%), *M. cephalus* (3.4%), *P. commersonnii* (3.3%), *L. equula* (3.2%), *A. natalensis* (2.2%), *C. sexfasciatus* (1.8%), *C. ignobilis* (1.6%), *S. lysan* (1.6%), *C. gilchristi* (1.5%), *T. jarbua* (1.5%), *S. bleekeri* (1.3%), *M. capensis* (1.1%), *V. buchanani* (1.1%), *A. honckenii* (1.0%), *V. robustus* (1.0%) and *H. kelee* (1.0%). The biomass composition was dominated by *Liza alata* (14.9%), *E. machnata* (10.3%), *M. cephalus* (10.2%), *A. japonicus* (9.0%), *V. buchanani* (8.7%), *H. kelee* (4.7%), *L. dumerili* (4.6%), *P. commersonnii* (4.2%), *L. macrolepis* (3.9%), *M. capensis* (3.6%), *C. sexfasciatus* (3.6%), *V. cunnesius* (3.5%), *Megalops cyprinoides* (3.1%), *L. argentimaculatus* (2.3%), *C. gariepinus* (2.2%), *A. vagus* (1.2%), *T. vitrirostris* (1.1%), *L. amia* (1.0%), *L. tricuspidens* (1.0%) and *R. holubi* (1.0%) (Table 14).

The average similarities in open subtropical region estuaries ranged between 58.2% and 61.9% (Table 15). Thirty species accounted for over 90% of the similarity within this group and these were represented by *A. vagus*, *A. natalensis*, *A. honckenii*, *A. japonicus*, *C. ignobilis*, *C. sexfasciatus*, *E. machnata*, *G. aestuaria*, *G. callidus*, *H. kelee*, *L. equula*, *L. alata*, *L. dumerili*, *L. macrolepis*, *L. tricuspidens*, *L. argentimaculatus*, *M. cephalus*, *M. capensis*, *O. acutipennis*, *O. keiensis*, *P. commersonnii*, *R. holubi*, *S. lysan*, *S. bleekeri*, *T. jarbua*, *T. vitrirostris*, *V. buchanani*, *V. cunnesius*, *V. robustus* and *V. seheli* (Table 15).

Inter-regional comparisons

Open cool-temperate and warm-temperate estuaries had average dissimilarities of between 68.6% and 73.6%

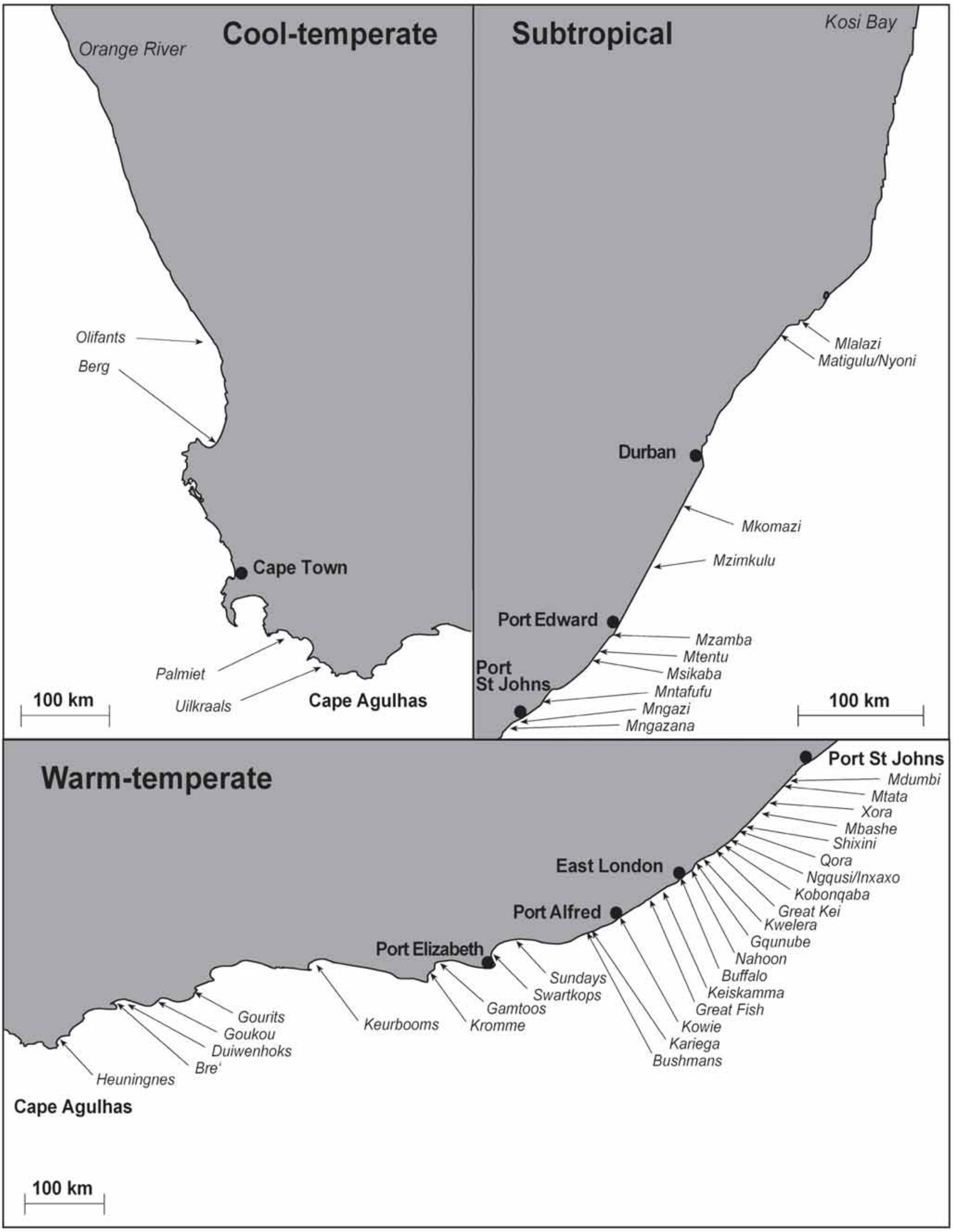


Figure 6. Map of open estuaries in the cool-temperate, warm-temperate and subtropical biogeographic regions included in this study. The relative positions of the estuaries included in the study are indicated with arrows.

(Table 16). *Argyrosomus japonicus, A. breviceps, C. gilchristi, E. machnata, G. feliceps, G. aestuaria, G. callidus, H. capensis, L. amia, L. lithognathus, L. dumerili, L. macrolepis, L. richardsonii, L. tricuspidens, M. falciformis, M. cephalus, M. capensis, P. commersonnii, R. holubi* and *S. bleekeri* were among the species that accounted for over 50% of the dissimilarity.

Average dissimilarities between warm-temperate subtropical systems ranged between 61.5% and 64.3% (Table 17). Species accounting for over 50% of this dissimilarity included *A. vagus, A. natalensis, A. breviceps, C. gilchristi, C. sexfasciatus, D. capensis, E. machnata, G. feliceps, G. aestuaria, G. callidus, H. capensis, H. kelee, L. equula, L. amia, L. lithognathus, L. alata, L. macrolepis, L. richardsonii, L. tricuspidens, M. falciformis, M. cephalus, M. capensis, O. acutipennis, O. keiensis, P. commersonnii, P. knysnaensis, R. holubi, S. lysan, T. jarbua, V. buchanani, V. cunnesius, V. robustus* and *V. seheli*.

## DISCUSSION

### Closed estuaries

Cool-temperate estuaries

Mugilids, *L. richardsonii* and *M. cephalus*, were the most frequently recorded species in closed cool-temperate estuaries and were also among the dominant taxa both in terms abundance and biomass. Other important taxa included *A. breviceps, C. nudiceps, G. aestuaria* and *L. amia*, with *H. capensis* also occasionally recorded (Table 2).

Similar fish communities have also been reported from closed cool-temperate estuaries. In the Diep estuary, for example, *L. richardsonii* was found to be the most common species with *M. cephalus* also present in lower numbers; other frequently reported species included *A. breviceps, C. nudiceps, G. aestuaria, H. capensis, L. lithognathus, P. knysnaensis* and *R. globiceps* (Millard & Scott, 1954; Grindley & Dudley, 1988). Limited sampling in the Wildevoël estuary revealed the presence of both *L. richardsonii* and *M. cephalus* (Heinecken, 1985). Notable species reported in the Sand estuary included *A. breviceps, C. nudiceps, G. aestuaria, L. amia, L. lithognathus, L. richardsonii, M. cephalus, P. saltatrix, P. knysnaensis* and *R. globiceps* (Morant & Grindley, 1982; Clark *et al.*, 1994; Quick & Harding, 1994).

Warm-temperate estuaries

Important taxa in terms of frequency of occurrence, numerical contribution and biomass in closed warm-temperate estuaries included *G. aestuaria, L. lithognathus, L. dumerili, L. richardsonii, L. tricuspidens, M. cephalus, M. capensis* and *R. holubi*. Frequently captured species that were also numerically important were *A. breviceps, G. callidus* and *P. knysnaensis* while *O. mossambicus* and *P. commersonnii* were important in terms of biomass. *Argyrosomus japonicus, E. machnata* and *L. amia*, were among the important taxa in terms of biomass, but were not regularly recorded. Although it did not contribute significantly toward the overall abundance or biomass in closed warm-temperate estuaries, *M. falciformis* was frequently captured in these systems (Table 4).

Studies in closed warm-temperate estuaries have also reported comparable fish assemblages. Bickerton (1982), for example, found that *L. dumerili, L. richardsonii* and *M. falciformis* were among the most abundant species in the Hartenbos system. Important species in the Seekoei estuary, in terms of abundance and / or biomass, included *A. breviceps, G. feliceps, G. aestuaria, L. amia, L. lithognathus, L. dumerili, L. richardsonii, M. falciformis, M. cephalus* and *R. holub*, while in the Kabeljous estuary *A. japonicus, A. breviceps, G. aestuaria, L. amia, L. lithognathus, L. richardsonii, L. tricuspidens, M. falciformis, M. cephalus, O. mossambicus, P. commersonnii, Pomadasys olivaceum* and *R. holubi* dominated the catch composition either numerically and / or in terms of biomass (Bickerton & Pierce, 1988; Dundas, 1994). The dominant species captured in the Van Stadens estuary included *A. breviceps, L. amia, L. lithognathus, L. dumerili, L. richardsonii, M. falciformis, M. cephalus, Myliobatis aquila, P. commersonnii* and *R. holubi* (Dundas, 1994). From Cowley & Whitfield (2001) the numerically dominant fishes in the Oos-Kleinemond estuary included *A. breviceps, G. aestuaria, G. callidus, L. lithognathus, L. dumerili, L. richardsonii, M. falciformis, M. cephalus, M. capensis* and *R. holubi*. Similarly, Vorwerk *et al.* (2001) found that *A. breviceps, G. aestuaria, G. callidus, L. dumerili, L. richardsonii, M. falciformis, M. capensis, O. mossambicus* and *R. holubi* were generally the most abundant fishes in the Oos-Kleinemond, Mpekweni, Mtati, Mgwalana, Bira and Gqutywa estuaries. Taxa such as *E. machnata, L. lithognathus, M. cephalus, P. commersonnii* and *P. saltatrix* were also among the dominant species in some of these systems.

Subtropical estuaries

Taxa that were frequently captured and were also important in terms of abundance and biomass in closed subtropical estuaries included *A. ambassis, G. aestuaria, L. dumerili, L. macrolepis, M. cephalus, M. capensis, O. mossambicus, R. holubi, V. cunnesius* and *V. robustus*. Species such as *G. callidus* and *M. falciformis* were regularly recorded and were also numerically important while *L. alata* and *P. commersonnii* were among the dominant species in terms of biomass. *Argyrosomus japonicus* and *C. gariepinus* were seldom captured but were important in terms of biomass. Although it did not comprise an important component, either numerically or by mass, *T. jarbua* was frequently reported in these systems (Table 6).

A number of studies have provided information on the fish communities of closed subtropical estuaries. Ramm *et al.* (1987) found that the most abundant fishes recorded in the Sezela estuary included *A. ambassis, O. mossambicus, V. cunnesius, M. capensis, M. falciformis* and *G. aestuaria*. Important species, either numerically and / or in terms of biomass in the Mhlanga estuary included *A. ambassis, A. japonicus, G. aestuaria, G. callidus, L. amia, L. alata, L. dumerili, L. macrolepis, M. cephalus, M. capensis, O. mossambicus, P. commersonnii, R. holubi, T. jarbua* and *V. cunnesius* (Whitfield, 1980a; 1980b; 1980c; Harrison &

Whitfield, 1995). *Ambassis ambassis*, *L. alata*, *L. macrolepis*, *M. cephalus*, *M. capensis*, *O. mossambicus* and *V. cunnesius* were also among the most frequently reported species in the Mdloti estuary (Blaber *et al.*, 1984). Begg (1984a; 1984b) used a beam trawl to sample fishes in normally closed KwaZulu-Natal systems and found that the dominant species were *G. aestuaria*, *Glossogobius* spp. and *O. mossambicus*.

**Open estuaries**

Cool-temperate estuaries

In open cool-temperate estuaries, *A. breviceps* and *L. richardsonii* were important species in terms of frequency of occurrence, numerical contribution and biomass. *Gilchristella aestuaria* was also frequently recorded and was a key species in terms of abundance while *G. feliceps*, *M. cephalus* and *P. saltatrix* were important in terms of biomass. *Argyrosomus* sp. and *H. pictus* were also important in terms of biomass, but were uncommon. *Argyrosomus* sp. was only recorded in the Olifants estuary and *H. pictus* in the Berg estuary. Although not well represented either numerically or in terms of biomass, *P. knysnaensis* and *S. temminckii* were recorded in a number of estuaries (Table 10).

Day (1981) found that the most common species in the Olifants estuary were *A. breviceps*, *G. aestuaria* and *L. richardsonii* with a few *L. lithognathus* also reported. In the Berg estuary, *A. breviceps*, *C. nudiceps*, *G. aestuaria*, *L. richardsonii* and *P. knysnaensis* were found to be among the most important species (Day, 1981; Bennett, 1994). Surveys of the Palmiet estuary also revealed that *A. breviceps*, *L. lithognathus*, *L. richardsonii* and *P. knysnaensis* were the dominant taxa, both in terms of abundance and / or biomass (Branch & Day, 1984; Bennett, 1989). Limited sampling in the Uilkraals estuary recorded taxa such as *C. nudiceps*, *L. lithognathus*, Mugilidae and *P. knysnaensis* in the system (Heydorn & Bickerton, 1982).

Warm-temperate estuaries

In open warm-temperate estuaries, *A. japonicus*, *G. aestuaria*, *L. dumerili*, *L. richardsonii*, *L. tricuspidens*, *M. cephalus*, *P. commersonnii* and *R. holubi* were all frequently reported taxa and also important in terms of abundance and biomass. Frequently captured species that were also abundant, included *A. breviceps*, *C. gilchristi*, *D. capensis*, *G. callidus*, *M. capensis*, *P. knysnaensis* and *S. bleekeri*, while *E. machnata*, *G. feliceps*, *L. amia* and *L. lithognathus* made major contributions to the overall biomass. *Valamugil buchanani* was not frequently recorded, but it was important in terms of biomass. Although they did not contribute to the overall abundance or biomass, *C. nudiceps*, *H. capensis*, *L. macrolepis* and *M. falciformis* were frequently captured (Table 12).

On an individual estuary basis, the dominant fish communities reported in open warm-temperate estuaries were somewhat similar to those recorded during this study. Numerically important species reported in the Breë estuary included *A. japonicus*, *G. feliceps*, *L. amia*, *L. lithognathus*, *L. richardsonii*, *M. falciformis*, *M. cephalus* and *P. commersonnii* (Ratte, 1982; Coetzee & Pool, 1991).

In the Kromme estuary dominant taxa, either numerically and / or in terms of biomass, included *A. japonicus*, *A. breviceps*, *C. gilchristi*, *G. feliceps*, *G. aestuaria*, *G. callidus*, *L. amia*, *L. dumerili*, *L. richardsonii*, *L. tricuspidens*, *M. falciformis*, *P. commersonnii*, *P. knysnaensis* and *R. holubi* (Marais, 1983a; Hanekom & Baird, 1984; Bickerton & Pierce, 1988).

The dominant taxa recorded in the Gamtoos estuary, both numerically and in terms of biomass, were *A. japonicus*, *G. feliceps*, *L. amia* and Mugilidae (*L. dumerili*, *L. richardsonii*, *L. tricuspidens*, *M. cephalus* and *M. capensis*) (Marais, 1983b).

The most abundant fishes reported in the Swartkops estuary included *A. japonicus*, *A. breviceps*, *C. gilchristi*, *D. capensis*, *E. machnata*, *Engraulis japonicus*, *G. feliceps*, *G. aestuaria*, *L. amia*, *L. lithognathus*, *L. dumerili*, *L. richardsonii*, *L. tricuspidens*, *M. cephalus*, *P. commersonnii*, *P. saltatrix*, *P. knysnaensis* and *R. holubi* (Marais & Baird, 1980; Beckley, 1983; Baird *et al.*, 1988).

Important species, either numerically and / or in terms of biomass, in the Sundays estuary included *A. japonicus*, *C. gilchristi*, *G. feliceps*, *G. aestuaria*, *H. capensis*, *L. dumerili*, *L. richardsonii*, *M. falciformis*, *M. cephalus* and *P. commersonnii P. knysnaensis*, *R. holubi* and *S. bleekeri* (Marais, 1981; Beckley, 1984).

Numerically dominant taxa in the Kariega estuary included *A. breviceps*, *C. superciliosus*, *G. aestuaria*, *G. callidus*, *D. capensis*, *L. dumerili*, *M. falciformis*, *M. cephalus* and *R. holubi* (Ter Morshuizen & Whitfield, 1994; Paterson & Whitfield, 1996).

In the Kowie estuary the most abundant species reported were *A. breviceps*, *A. japonicus*, *D. capensis*, *G. feliceps*, *G. aestuaria*, *L. amia*, *L. dumerili*, *L. richardsonii*, *L. tricuspidens*, *M. cephalus*, *M. capensis*, *P. commersonnii*, *P. olivaceum* and *R. holubi* (Whitfield *et al.*, 1994).

From various studies in the Great Fish estuary *A. dussumieri*, *A. japonicus*, *C. nudiceps*, *G. feliceps*, *G. aestuaria*, *H. capensis*, *L. lithognathus*, *L. dumerili*, *L. richardsonii*, *L. tricuspidens*, *M. cephalus*, *M. capensis*, *P. commersonnii*, *P. olivaceum*, *P. knysnaensis*, *R. holubi*, and *S. bleekeri* were found to be among the most abundant species reported (Whitfield *et al.*, 1994; Ter Morshuizen *et al.*, 1996a; 1996b; Vorwerk *et al.*, 2001).

Numerically important species in the Keiskamma estuary were *A. breviceps*, *A. japonicus*, *C. gilchristi*, *C. nudiceps*, *G. feliceps*, *G. aestuaria*, *L. dumerili*, *L. richardsonii*, *L. tricuspidens*, *M. cephalus*, *M. capensis*, *P. commersonnii*, and *R. holubi* (Vorwerk *et al.*, 2001).

Dominant species, both in terms of number and biomass, from gill nets in the Great Kei estuary included *A. japonicus*, *L. richardsonii*, *L. tricuspidens*, *M. cephalus*, *M. capensis* and *P. commersonnii* (Plumstead *et al.*, 1985).

Fishes captured by gill nets in the Mbashe estuary were dominated by *A. japonicus*, *E. machnata*, *L. amia*, *L. tricuspidens*, *M. cephalus*, *M. capensis*, *P. commersonnii* and *V. buchanani* (Plumstead *et al.*, 1989a). Species such as *L. dumerili*, *L. richardsonii*, *R. holubi* and *V. robustus* were also fairly common.

The dominant gill netted taxa, both numerically and in terms of biomass, reported in the Mtata estuary were *A. japonicus*, *C. leucas*, *E. machnata*, *J. dorsalis*, *L. equula*, *L. amia*, *L. alata*, *M. cephalus*, *P. commersonnii*, *P. kaakan*, *T. vitrirostris* and *V. buchanani* (Plumstead *et al*., 1989b).

Subtropical estuaries

Important taxa in open subtropical estuaries in terms of frequency of occurrence, abundance and biomass, included *C. sexfasciatus*, *H. kelee*, *L. dumerili*, *L. macrolepis*, *M. cephalus*, *M. capensis*, *P. commersonnii*, *R. holubi*, *V. buchanani* and *V. cunnesius*. Frequently reported species that were also abundant included *A. dussumieri*, *A. natalensis*, *A. honckenii*, *C. gilchristi*, *C. ignobilis*, *G. aestuaria*, *G. callidus*, *L. equula*, *S. lysan*, *S. bleekeri*, *T. jarbua* and *V. robustus*. Species such as *A. vagus*, *A. japonicus*, *E. machnata*, *L. alata*, *L. tricuspidens*, *L. argentimaculatus* and *T. vitrirostris* were also regularly reported and were important in terms of biomass. Although they did not contribute greatly to the overall abundance or biomass, *O. acutipennis*, *O. keiensis* and *V. seheli* were frequently reported in these estuaries. *Clarias gariepinus*, *L. amia* and *M. cyprinoides* were infrequently recorded but did make important contributions to the overall biomass in these systems (Table 14).

Species that were common to abundant in the Mngazana estuary included *A. natalensis*, *A. breviceps*, *C. gilchristi*, *C. nudiceps*, *Eleotris fusca*, *G. aestuaria*, *G. callidus*, *L. dumerili*, *L. macrolepis*, *M. argenteus*, *M. cephalus*, *O. acutipennis*, *P. knysnaensis*, *R. holubi*, *S. salpa* and *T. jarbua* (Branch & Grindley, 1979).

In the Mntafufu estuary, *A. japonicus*, *Caranx* spp., *Chanos chanos*, *E. machnata*, *H. kelee*, *L. equula*, *L. amia*, *L. alata*, *L. macrolepis*, *L. tricuspidens*, *M. falciformis*, *M. cephalus*, *M. capensis*, *P. commersonnii*, *P. saltatrix*, *R. sarba*, *Sphyraena acutipinnis*, *T. vitrirostris*, *V. buchanani* and *V. cunnesius* were the dominant gill netted taxa both numerically and / or in terms of biomass (Plumstead *et al*., 1991).

The main species captured by gill net in the Mzamba estuary included *A. japonicus*, *Caranx* spp., *C. chanos*, *H. kelee*, *L. equula*, *L. amia*, *L. alata*, *L. macrolepis*, *M. cephalus*, *M. capensis*, *P. saltatrix*, *Scomberoides tol*, *T. vitrirostris* and *V. buchanani* (Plumstead *et al*., 1991).

Important taxa in the Matigulu system included Ambassidae, *A. japonicus*, *E. machnata*, *L. equula*, *L. macrolepis* and *Pomadasys* spp. (Hemens *et al*., 1986).

Common to abundant fishes reported in the Mlalazi estuary by Hill (1966) comprised Ambassidae, *Arothron immaculatus*, *L. dumerili*, *M. cephalus*, *Periopthalmus* sp., *R. holubi*, *T. jarbua* and *V. seheli*.

According to Begg (1984a; 1984b), open estuaries on the subtropical KwaZulu-Natal coast are dominated by a wide variety of marine teleosts including *A. vagus*, *A. japonicus*, *Pomadasys* spp., *Rhabdosargus* spp. and Mugilidae.

**Inter-regional comparisons**

This study revealed that subtropical systems are characterised by fish assemblages of predominantly tropical origin. Tropical species that were largely restricted to subtropical estuaries (e.g. *A. vagus*, *Ambassis* spp., *C. sexfasciatus*, *C. gariepinus*, *H. kelee*, *L. equula*, *L. alata*, *L. macrolepis*, *Oligolepis* spp., *S. lysan*, *T. jarbua*, *V. cunnesius*, *V. robustus*, *V. seheli*) also accounted for some of the dissimilarity between warm-temperate and subtropical estuaries (Tables 9 & 17).

The dispersal of tropical Indo-Pacific fishes into southern African waters is facilitated by the warm Agulhas Current off the east coast of South Africa (Wallace & van der Elst, 1975; Day *et al*., 1981). As the Agulhas Current flows south, however, it moves offshore and consequently inshore sea temperatures decline; this limits the dispersal of tropical species into warm-temperate estuaries (Wallace & van der Elst, 1975; Day *et al*., 1981; Whitfield, 1998). Maree *et al*. (2000) have suggested that summer upwelling events on the southeast coast also acts as a barrier to the southward distribution of tropical species, particularly in the Algoa Bay region. An upwelling cell that extends from Port Alfred northward to the Mbashe estuary and even as far as Port St Johns (Lutjeharms *et al*., 2000) is probably the first thermal barrier encountered by tropical species. This also corresponds with the subtropical / warm-temperate biogeographic boundary region described by Harrison (2002).

Some tropical species (e.g. *A. japonicus*, *E. machnata*, *M. falciformis*, *O. mossambicus*, *P. commersonnii*), however, do extend into warm-temperate estuaries and are often an important part of the ichthyofauna (Marais & Baird, 1980; Marais, 1981; Marais, 1983b; Whitfield *et al*., 1994; Vorwerk *et al*., 2001). Briggs (1974) noted that a conspicuous faunal element that inhabits warm-temperate shelf regions is the eurythermic tropical group, which consists of species that range in both tropical and warm-temperate waters. Although some tropical species occur in both warm-temperate and subtropical estuaries, they did contribute toward the dissimilarity between these estuaries (Tables 9 & 18). This was mainly due to differences in the relative proportions of these species recorded in each region.

Warm temperate estuaries are mainly dominated by endemic taxa; this is probably enhanced through the restriction of tropical species to estuaries further north, thus reducing competition. Endemic taxa (e.g. *A. breviceps*, *G. feliceps*, *H. capensis*, *L. lithognathus*, *L. richardsonii*, *P. knysnaensis*) also accounted for some of the dissimilarity between warm-temperate and subtropical estuaries (Tables 9 & 18). Some endemic species (e.g. *G. aestuaria*, *G. callidus*, *L. dumerili*, *L. tricuspidens*, *M. capensis*, *R. holubi*) also extended into subtropical estuaries, however, their contribution toward the dissimilarity between warm-temperate and subtropical estuaries was mainly due to differences in the relative proportions of these species within each region (Table 9 & 17).

Cool-temperate estuaries did not appear to contain any unique taxa, but rather comprised a mix of widespread (e.g. *M. cephalus*) and endemic species that appear to prefer cooler waters (e.g. *A. breviceps*, *L. richardsonii*). Tropical species that occur in warm-temperate estuaries (e.g. *A. japonicus*, *E. machnata*, *M. falciformis*, *O. mossambicus*, *P. commersonnii*) as well as endemic taxa that extend into subtropical estuaries (e.g. *G. callidus*, *L. dumerili*, *L. tricuspidens*, *M. capensis*, *R. holubi*, *S. bleekeri*) accounted for some of the dissimilarity between the warm- and cool-temperate estuaries (Tables 8 & 16). Although the cold, upwelled water associated with the Benguela Current system has been identified as a barrier to the distribution of tropical species into southwest and west coast estuaries (Whitfield, 1983; 1996), it may also serve as a barrier to many endemic species. *R. holubi* in west coast estuaries, for example, is only represented by a few stragglers (Whitfield, 1999). Species that were important in both warm- and cool-temperate systems (e.g. *A. breviceps*, *G. feliceps*, *G. aestuaria*, *L. lithognathus*, *L. richardsonii*, *M. cephalus*) also accounted for some of the dissimilarity between these estuaries. This was mainly due to differences in the relative proportions of the species collected in the estuaries within each region (Tables 8 & 16).

Because no two estuaries are identical in terms of either biotic or abiotic characteristics, it could be argued that the ichthyofaunas of each estuary will also differ. Whitfield (1999), however, postulated that if the fishes in estuaries respond to the environment in a consistent manner, then the communities occupying similar types of estuaries in a particular region would be expected to reflect this similarity. Monaco *et al*. (1992) also noted that estuaries with similar habitats and environmental regimes often support similar species assemblages. This study has demonstrated that the fish communities of estuaries within each biogeographic region contain somewhat distinctive fish communities. The dominant fish species within each biogeographic region were also found to be similar to those reported from other studies; this is in spite of the fact that each study differed in its specific aims, timescale and sampling methodologies. These findings suggest that estuarine fish communities are relatively consistant and are dominated by a characteristic group of taxa.

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Table 1. Comparison of classification of South African estuaries after Harrison *et al*. (2000) and Whitfield (2000).

| | Whitfield (2000) | | | | | | |
|---|---|---|---|---|---|---|---|
| **Harrison *et al.* (2000)** | Non-estuary | Permanently open | Temporarily open/closed | River mouth | Estuarine lake | Estuarine bay | **Total** |
| Non-estuary | 42 | - | 2 | - | - | - | **44** |
| Open, non-barred | - | 3 | 2 | 6 | - | - | **11** |
| Open, small | 2 | - | 31 | - | 1 | - | **34** |
| Open, large | - | 42 | 11 | 5 | 3 | 1 | **62** |
| Closed, small | 5 | - | 21 | 1 | - | - | **27** |
| Closed, medium | 2 | - | 67 | - | 2 | - | **71** |
| Closed, large | - | - | - | - | 2 | - | **2** |
| **Total** | **51** | **45** | **134** | **12** | **8** | **1** | **251** |

Table 2. Percent frequency of occurrence, mean percent abundance and mean percent biomass composition of fishes in closed cool-temperate estuaries (n = number of estuaries, SD = standard deviation).

| **Family** | **Species** | **Frequency** | | **Abundance** | | **Biomass** | |
|---|---|---|---|---|---|---|---|
| | | **%** | **n** | **%** | **SD** | **%** | **SD** |
| Atherinidae | *Atherina breviceps* | 25 | 1 | 2.21 | 4.41 | 0.11 | 0.23 |
| Carangidae | *Lichia amia* | 25 | 1 | 0.08 | 0.16 | 5.43 | 10.86 |
| Clupeidae | *Gilchristella aestuaria* | 25 | 1 | 19.50 | 39.00 | 0.54 | 1.07 |
| Gobiidae | *Caffrogobius nudiceps* | 50 | 2 | 3.01 | 5.94 | 0.14 | 0.28 |
| | *Psammogobius knysnaensis* | 25 | 1 | 0.02 | 0.03 | 0.00 | 0.01 |
| Mugilidae | *Liza dumerili* | 25 | 1 | 0.06 | 0.13 | 0.05 | 0.11 |
| | *Liza richardsonii* | 100 | 4 | 56.69 | 43.60 | 49.85 | 39.84 |
| | *Mugil cephalus* | 75 | 3 | 18.09 | 33.60 | 43.83 | 33.03 |
| Soleidae | *Heteromycteris capensis* | 50 | 2 | 0.24 | 0.37 | 0.01 | 0.01 |
| Sparidae | *Rhabdosargus globiceps* | 25 | 1 | 0.05 | 0.10 | 0.00 | 0.00 |
| Syngnathidae | *Syngnathus temminckii* | 25 | 1 | 0.05 | 0.10 | 0.03 | 0.06 |

Table 3. Major species accounting for the similarity within closed cool-temperate estuaries; *Si* is the average similarity contribution of each species; % *Si* is the percent contribution to the overall similarity (*S*); SD (*Si*) is the standard deviation of each species to the total similarity. Similarities are based on presence/absence, abundance and biomass.

| | **Presence/absence** | | | **Abundance** | | | **Biomass** | | |
|---|---|---|---|---|---|---|---|---|---|
| **Species** | ***Si*** | **% *Si*** | ***Si* / SD(*Si*)** | ***Si*** | **% *Si*** | ***Si* / SD(*Si*)** | ***Si*** | **% *Si*** | ***Si* / SD(*Si*)** |
| *C. nudiceps* | | | | 1.4 | 3.69 | 0.41 | | | |
| *H. capensis* | 2.2 | 5.09 | 0.41 | | | | | | |
| *L. richardsonii* | 29.5 | 67.47 | 1.49 | 26.4 | 69.06 | 1.84 | 35.8 | 66.15 | 2.26 |
| *M. cephalus* | 9.8 | 22.36 | 0.82 | 9.2 | 24.15 | 0.85 | 17.3 | 31.92 | 0.89 |
| **Total *S*** | **43.67** | | | **38.26** | | | **54.19** | | |

Table 4. Percent frequency of occurrence, mean percent abundance and mean percent biomass composition of fishes in closed warm-temperate estuaries (n = number of estuaries; SD = standard deviation).

| **Family** | **Species** | **Frequency** | | **Abundance** | | **Biomass** | |
|---|---|---|---|---|---|---|---|
| | | **%** | **n** | **%** | **SD** | **%** | **SD** |
| Ambassidae | *Ambassis dussumieri* | 2 | 1 | 0.00 | 0.01 | 0.00 | 0.00 |
| Ariidae | *Galeichthys feliceps* | 20 | 8 | 0.02 | 0.05 | 0.36 | 1.31 |
| Atherinidae | *Atherina breviceps* | 88 | 36 | 18.33 | 18.61 | 0.84 | 1.17 |
| Blenniidae | *Parablennius lodosus* | 2 | 1 | 0.00 | 0.01 | 0.00 | 0.00 |
| Carangidae | *Caranx sexfasciatus* | 5 | 2 | 0.02 | 0.15 | 0.34 | 1.96 |
| | *Lichia amia* | 41 | 17 | 0.05 | 0.10 | 3.26 | 4.60 |
| Cichlidae | *Oreochromis mossambicus* | 61 | 25 | 0.79 | 1.83 | 6.56 | 10.47 |
| Clupeidae | *Gilchristella aestuaria* | 100 | 41 | 35.78 | 22.29 | 1.62 | 1.63 |
| Elopidae | *Elops machnata* | 17 | 7 | 0.04 | 0.14 | 1.73 | 6.71 |
| Gerreidae | *Gerres methueni* | 2 | 1 | 0.00 | 0.01 | 0.01 | 0.05 |
| Gobiidae | *Caffrogobius gilchristi* | 27 | 11 | 0.13 | 0.26 | 0.02 | 0.05 |
| | *Caffrogobius natalensis* | 5 | 2 | 0.00 | 0.02 | 0.00 | 0.00 |
| | *Caffrogobius nudiceps* | 5 | 2 | 0.06 | 0.37 | 0.01 | 0.04 |
| | *Glossogobius callidus* | 88 | 36 | 3.24 | 3.91 | 0.41 | 0.67 |
| | *Oligolepis keiensis* | 5 | 2 | 0.01 | 0.03 | 0.00 | 0.00 |
| | *Psammogobius knysnaensis* | 71 | 29 | 1.12 | 3.91 | 0.05 | 0.07 |
| Haemulidae | *Pomadasys commersonnii* | 61 | 25 | 0.24 | 0.48 | 4.52 | 5.73 |
| | *Pomadasys olivaceus* | 7 | 3 | 0.01 | 0.03 | 0.00 | 0.01 |
| Lutjanidae | *Lutjanus argentimaculatus* | 2 | 1 | 0.00 | 0.01 | 0.14 | 0.89 |
| Monodactylidae | *Monodactylus falciformis* | 93 | 38 | 0.71 | 0.82 | 0.94 | 1.11 |
| Mugilidae | *Liza alata* | 2 | 1 | 0.01 | 0.04 | 0.08 | 0.50 |
| | *Liza dumerili* | 83 | 34 | 2.58 | 3.55 | 4.41 | 5.48 |
| | *Liza macrolepis* | 27 | 11 | 0.12 | 0.33 | 0.35 | 0.96 |
| | *Liza richardsonii* | 100 | 41 | 6.65 | 8.68 | 28.36 | 22.99 |
| | *Liza tricuspidens* | 76 | 31 | 1.13 | 1.76 | 7.11 | 10.31 |
| | *Mugil cephalus* | 90 | 37 | 1.80 | 3.67 | 11.46 | 13.36 |
| | *Myxus capensis* | 90 | 37 | 5.58 | 12.27 | 5.80 | 6.28 |
| | *Valamugil buchanani* | 5 | 2 | 0.01 | 0.02 | 0.16 | 0.75 |
| | *Valamugil cunnesius* | 5 | 2 | 0.03 | 0.17 | 0.02 | 0.11 |
| | *Valamugil robustus* | 7 | 3 | 0.04 | 0.19 | 0.04 | 0.19 |
| Pomatomidae | *Pomatomus saltatrix* | 15 | 6 | 0.09 | 0.48 | 0.72 | 2.92 |
| Sciaenidae | *Argyrosomus japonicus* | 44 | 18 | 0.14 | 0.29 | 6.45 | 9.92 |
| Soleidae | *Heteromycteris capensis* | 29 | 12 | 0.23 | 0.77 | 0.01 | 0.03 |
| | *Solea bleekeri* | 37 | 15 | 0.09 | 0.18 | 0.03 | 0.13 |
| Sparidae | *Acanthopagrus vagus* | 2 | 1 | 0.00 | 0.01 | 0.02 | 0.11 |
| | *Diplodus capensis* | 29 | 12 | 0.34 | 1.74 | 0.02 | 0.05 |
| | *Lithognathus lithognathus* | 76 | 31 | 2.91 | 7.56 | 3.70 | 5.13 |
| | *Rhabdosargus globiceps* | 5 | 2 | 0.00 | 0.01 | 0.00 | 0.01 |
| | *Rhabdosargus holubi* | 98 | 40 | 17.64 | 15.72 | 10.28 | 8.55 |
| | *Rhabdosargus sarba* | 5 | 2 | 0.00 | 0.02 | 0.18 | 0.94 |
| | *Sarpa salpa* | 17 | 7 | 0.04 | 0.11 | 0.00 | 0.01 |
| Teraponidae | *Terapon jarbua* | 7 | 3 | 0.03 | 0.13 | 0.01 | 0.05 |
| Tetraodontidae | *Amblyrhynchotes honckenii* | 2 | 1 | 0.00 | 0.01 | 0.00 | 0.02 |
| | | | | | | | |

Table 5. Major species accounting for the similarity within closed warm-temperate estuaries; *Si* is the average similarity contribution of each species; % *Si* is the percent contribution to the overall similarity (*S*); SD (*Si*) is the standard deviation of each species to the total similarity. Similarities are based on presence/absence, abundance and biomass.

| | **Presence/absence** | | | **Abundance** | | | **Biomass** | | |
|---|---|---|---|---|---|---|---|---|---|
| **Species** | ***Si*** | ***% Si*** | ***Si* / SD*(Si)*** | ***Si*** | ***% Si*** | ***Si* / SD*(Si)*** | ***Si*** | ***% Si*** | ***Si* / SD*(Si)*** |
| *A. breviceps* | 5.2 | 7.48 | 1.71 | 6.9 | 11.13 | 1.41 | 3.0 | 4.99 | 1.55 |
| *G. aestuaria* | 6.8 | 9.78 | 4.05 | 9.8 | 15.90 | 2.84 | 4.4 | 7.32 | 2.72 |
| *G. callidus* | 4.6 | 6.65 | 1.52 | 4.1 | 6.67 | 1.41 | 2.2 | 3.68 | 1.48 |
| *L. lithognathus* | 3.5 | 5.10 | 1.01 | 2.2 | 3.54 | 0.99 | 3.3 | 5.45 | 0.92 |
| *L. dumerili* | 4.5 | 6.56 | 1.39 | 3.7 | 5.98 | 1.30 | 3.9 | 6.43 | 1.29 |
| *L. richardsonii* | 6.9 | 10.00 | 4.23 | 6.4 | 10.37 | 3.25 | 10.7 | 17.68 | 2.88 |
| *L. tricuspidens* | 3.7 | 5.36 | 1.11 | 2.5 | 4.06 | 1.06 | 3.3 | 5.53 | 0.94 |
| *M. falciformis* | 5.4 | 7.86 | 1.97 | 3.5 | 5.61 | 1.84 | 3.2 | 5.32 | 1.75 |
| *M. cephalus* | 5.7 | 8.22 | 1.87 | 3.9 | 6.37 | 1.63 | 5.6 | 9.25 | 1.40 |
| *M. capensis* | 5.5 | 7.90 | 1.86 | 4.4 | 7.18 | 1.65 | 4.8 | 7.95 | 1.55 |
| *O. mossambicus* | 2.0 | 2.89 | 0.70 | | | | 2.2 | 3.58 | 0.66 |
| *P. commersonnii* | | | | | | | 2.3 | 3.72 | 0.72 |
| *P. knysnaensis* | 2.7 | 3.90 | 0.80 | 1.8 | 2.95 | 0.81 | | | |
| *R. holubi* | 6.7 | 9.77 | 3.10 | 7.6 | 12.29 | 2.79 | 6.8 | 11.15 | 2.37 |
| **Total *S*** | **69.05** | | | **61.84** | | | **60.61** | | |

Table 6. Percent frequency of occurrence, mean percent abundance and mean percent biomass composition of fishes in closed subtropical estuaries (n = number of estuaries, SD = standard deviation).

| Family | Species | Frequency | | Abundance | | Biomass | |
|---|---|---|---|---|---|---|---|
| | | % | n | % | SD | % | SD |
| Ambassidae | *Ambassis dussumieri* | 9 | 2 | 0.18 | 0.60 | 0.00 | 0.01 |
| | *Ambassis natalensis* | 23 | 5 | 0.37 | 1.14 | 0.01 | 0.02 |
| | *Ambassis ambassis* | 50 | 11 | 1.86 | 5.29 | 1.04 | 1.49 |
| Carangidae | *Caranx ignobilis* | 5 | 1 | 0.05 | 0.22 | 0.19 | 0.88 |
| | *Caranx papuensis* | 5 | 1 | 0.02 | 0.11 | 0.01 | 0.03 |
| | *Caranx sexfasciatus* | 36 | 8 | 0.17 | 0.39 | 0.51 | 0.99 |
| Chanidae | *Chanos chanos* | 5 | 1 | 0.03 | 0.14 | 0.17 | 0.80 |
| Cichlidae | *Oreochromis mossambicus* | 100 | 22 | 18.72 | 22.79 | 17.67 | 13.75 |
| | *Tilapia rendalli* | 9 | 2 | 0.18 | 0.73 | 0.15 | 0.63 |
| Clariidae | *Clarias gariepinus* | 41 | 9 | 0.88 | 1.85 | 18.13 | 28.02 |
| Clupeidae | *Gilchristella aestuaria* | 73 | 16 | 25.82 | 32.52 | 1.37 | 3.89 |
| Cyprinidae | *Barbus natalensis* | 5 | 1 | 0.01 | 0.03 | 0.00 | 0.00 |
| Eleotridae | *Eleotris fusca* | 9 | 2 | 0.01 | 0.03 | 0.00 | 0.00 |
| Elopidae | *Elops machnata* | 5 | 1 | 0.01 | 0.03 | 0.03 | 0.15 |
| Gerreidae | *Gerres methueni* | 18 | 4 | 0.35 | 1.14 | 0.09 | 0.34 |
| Gobiidae | *Awaous aeneofuscus* | 14 | 3 | 0.01 | 0.04 | 0.01 | 0.03 |
| | *Caffrogobius natalensis* | 18 | 4 | 0.07 | 0.21 | 0.00 | 0.00 |
| | *Glossogobius callidus* | 82 | 18 | 3.27 | 4.72 | 0.14 | 0.16 |
| | *Glossogobius giuris* | 27 | 6 | 0.18 | 0.57 | 0.01 | 0.02 |
| | *Mugillogobius merteni* | 5 | 1 | 0.00 | 0.02 | 0.00 | 0.00 |
| | *Oligolepis acutipennis* | 14 | 3 | 0.09 | 0.25 | 0.01 | 0.03 |
| | *Oligolepis keiensis* | 9 | 2 | 0.05 | 0.19 | 0.00 | 0.00 |
| | *Oxyurichthys opthalmonema* | 5 | 1 | 0.01 | 0.03 | 0.00 | 0.00 |
| | *Psammogobius knysnaensis* | 14 | 3 | 0.24 | 0.70 | 0.01 | 0.02 |
| | *Redigobius dewaali* | 5 | 1 | 0.01 | 0.03 | 0.00 | 0.00 |
| Haemulidae | *Pomadasys commersonnii* | 68 | 15 | 0.64 | 1.35 | 3.10 | 4.17 |
| | *Pomadasys kaakan* | 5 | 1 | 0.02 | 0.09 | 0.02 | 0.07 |
| Leiognathidae | *Leiognathus equula* | 9 | 2 | 0.06 | 0.28 | 0.02 | 0.09 |
| Lutjanidae | *Lutjanus argentimaculatus* | 14 | 3 | 0.02 | 0.05 | 0.05 | 0.14 |
| | *Lutjanus fulviflamma* | 5 | 1 | 0.00 | 0.02 | 0.00 | 0.00 |
| Megalopidae | *Megalops cyprinoides* | 9 | 2 | 0.12 | 0.42 | 0.39 | 1.26 |
| Monodactylidae | *Monodactylus argenteus* | 5 | 1 | 0.02 | 0.09 | 0.01 | 0.03 |
| | *Monodactylus falciformis* | 77 | 17 | 2.64 | 8.06 | 0.94 | 1.72 |
| Mugilidae | *Liza alata* | 64 | 14 | 0.48 | 0.68 | 6.57 | 11.53 |
| | *Liza dumerili* | 77 | 17 | 3.70 | 5.54 | 2.92 | 3.84 |
| | *Liza macrolepis* | 68 | 15 | 2.21 | 4.26 | 5.09 | 10.20 |
| | *Liza tricuspidens* | 14 | 3 | 0.04 | 0.13 | 0.01 | 0.03 |
| | *Mugil cephalus* | 91 | 20 | 7.80 | 8.49 | 15.17 | 11.09 |
| | *Myxus capensis* | 100 | 22 | 14.08 | 12.71 | 13.97 | 13.34 |
| | *Valamugil buchanani* | 18 | 4 | 0.08 | 0.25 | 0.37 | 1.27 |
| | *Valamugil cunnesius* | 86 | 19 | 5.19 | 8.74 | 3.91 | 8.05 |
| | *Valamugil robustus* | 55 | 12 | 1.97 | 3.24 | 2.78 | 5.64 |
| | *Valamugil seheli* | 14 | 3 | 0.18 | 0.56 | 0.04 | 0.14 |
| Sciaenidae | *Argyrosomus japonicus* | 36 | 8 | 0.14 | 0.23 | 2.23 | 4.28 |
| Sillaginidae | *Sillago sihama* | 5 | 1 | 0.01 | 0.03 | 0.00 | 0.01 |
| Soleidae | *Solea bleekeri* | 27 | 6 | 0.29 | 0.83 | 0.02 | 0.06 |
| Sparidae | *Acanthopagrus* spp. | 14 | 3 | 0.07 | 0.23 | 0.13 | 0.55 |
| | *Rhabdosargus holubi* | 82 | 18 | 6.67 | 10.98 | 2.55 | 5.82 |
| | *Rhabdosargus sarba* | 9 | 2 | 0.11 | 0.45 | 0.01 | 0.02 |
| Teraponidae | *Terapon jarbua* | 55 | 12 | 0.86 | 1.65 | 0.16 | 0.38 |
| | | | | | | | |

Table 7. Major species accounting for the similarity within closed subtropical estuaries; *Si* is the average similarity contribution of each species; % *Si* is the percent contribution to the overall similarity (*S*); SD (*Si*) is the standard deviation of each species to the total similarity. Similarities are based on presence/absence, abundance and biomass.

| | Presence/absence | | | Abundance | | | Biomass | | |
|---|---|---|---|---|---|---|---|---|---|
| **Species** | ***Si*** | **% *Si*** | *Si* / SD(*Si*) | ***Si*** | **% *Si*** | *Si* / SD(*Si*) | ***Si*** | **% *Si*** | *Si* / SD(*Si*) |
| *C. gariepinus* | | | | | | | 2.0 | 3.56 | 0.40 |
| *G. aestuaria* | 3.7 | 6.35 | 0.97 | 5.0 | 9.56 | 0.81 | 1.6 | 2.93 | 0.80 |
| *G. callidus* | 4.5 | 7.60 | 1.32 | 3.6 | 6.82 | 1.19 | 1.8 | 3.29 | 1.19 |
| *L. alata* | | | | 1.2 | 2.37 | 0.74 | 2.7 | 4.93 | 0.78 |
| *L. dumerili* | 4.0 | 6.77 | 1.14 | 3.2 | 6.18 | 1.10 | 3.1 | 5.60 | 1.10 |
| *L. macrolepis* | 2.1 | 3.51 | 0.75 | 1.8 | 3.48 | 0.79 | 2.1 | 3.78 | 0.76 |
| *M. falciformis* | 3.0 | 5.10 | 0.98 | 2.3 | 4.37 | 1.11 | 2.2 | 4.02 | 1.02 |
| *M. cephalus* | 6.1 | 10.42 | 1.87 | 5.1 | 9.79 | 1.67 | 8.0 | 14.56 | 1.84 |
| *M. capensis* | 7.3 | 12.44 | 4.37 | 7.8 | 14.89 | 2.92 | 7.7 | 14.00 | 2.30 |
| *O. mossambicus* | 6.8 | 11.59 | 2.70 | 7.1 | 13.65 | 2.27 | 9.4 | 17.02 | 2.86 |
| *P. commersonnii* | 3.0 | 5.20 | 0.88 | 1.8 | 3.47 | 0.88 | 2.3 | 4.17 | 0.77 |
| *R. holubi* | 4.1 | 6.92 | 1.18 | 3.5 | 6.64 | 1.10 | 2.8 | 5.15 | 1.17 |
| *T. jarbua* | 1.6 | 2.80 | 0.61 | | | | | | |
| *V. cunnesius* | 5.1 | 8.72 | 1.56 | 4.0 | 7.71 | 1.48 | 3.9 | 7.13 | 1.50 |
| *V. robustus* | 1.6 | 2.73 | 0.60 | 1.2 | 2.29 | 0.60 | | | |
| **Total *S*** | **58.67** | | | **52.34** | | | **54.93** | | |

Table 8. Major species accounting for the dissimilarity between closed cool-temperate and closed warm-temperate estuaries; ä*i* is the average dissimilarity contribution of each species; % ä*i* is the percent contribution to the overall dissimilarity (ä); SD (ä*i*) is the standard deviation of each species to the total dissimilarity. Dissimilarities are based on presence/absence, abundance and biomass.

| | Presence/absence | | | Abundance | | | Biomass | | |
|---|---|---|---|---|---|---|---|---|---|
| **Species** | **δ*i*** | **% δ*i*** | δ*i* / SD(δ*i*) | **δ*i*** | **% δ*i*** | δ*i* / SD(δ*i*) | **δ*i*** | **% δ*i*** | δ*i* / SD(δ*i*) |
| *A. breviceps* | 4.03 | 5.52 | 1.36 | 7.45 | 9.89 | 1.43 | | | |
| *G. aestuaria* | 4.58 | 6.28 | 1.51 | 9.11 | 12.10 | 1.81 | 3.51 | 5.14 | 1.72 |
| *G. callidus* | 4.44 | 6.09 | 1.96 | 5.02 | 6.67 | 1.69 | | | |
| *L. lithognathus* | 4.06 | 5.57 | 1.38 | | | | 4.24 | 6.21 | 1.21 |
| *L. dumerili* | | | | 4.13 | 5.48 | 1.49 | 4.03 | 5.91 | 1.56 |
| *L. tricuspidens* | 3.99 | 5.47 | 1.55 | | | | 4.41 | 6.45 | 1.31 |
| *M. falciformis* | 4.89 | 6.71 | 2.28 | | | | | | |
| *M. cephalus* | | | | | | | 5.62 | 8.22 | 1.40 |
| *M. capensis* | 4.95 | 6.79 | 2.10 | 4.87 | 6.47 | 1.99 | 5.07 | 7.42 | 1.90 |
| *O. mossambicus* | | | | | | | 3.64 | 5.32 | 1.00 |
| *R. holubi* | 5.57 | 7.64 | 2.61 | 7.78 | 10.33 | 2.75 | 6.37 | 9.32 | 2.63 |
| **Total δ** | **72.90** | | | **75.30** | | | **68.31** | | |

Table 9. Major species accounting for the dissimilarity between closed warm-temperate and closed subtropical estuaries; ä*i* is the average dissimilarity contribution of each species; % ä*i* is the percent contribution to the overall dissimilarity (ä); SD (ä*i*) is the standard deviation of each species to the total dissimilarity. Dissimilarities are based on presence/absence, abundance and biomass.

| | Presence/absence | | | Abundance | | | Biomass | | |
|---|---|---|---|---|---|---|---|---|---|
| **Species** | **δ*i*** | **% δ*i*** | **δ*i* / SD(δ*i*)** | **δ*i*** | **% δ*i*** | **δ*i* / SD(δ*i*)** | **δ*i*** | **% δ*i*** | **δ*i* / SD(δ*i*)** |
| *A. ambassis* | 1.49 | 2.72 | 0.89 | | | | | | |
| *A. japonicus* | | | | | | | 2.38 | 3.82 | 1.06 |
| *A. breviceps* | 3.08 | 5.62 | 2.31 | 5.63 | 9.30 | 1.77 | | | |
| *C. gariepinus* | | | | | | | 2.87 | 4.59 | 0.77 |
| *G. aestuaria* | | | | 4.61 | 7.61 | 1.47 | | | |
| *G. callidus* | | | | 2.33 | 3.84 | 1.25 | | | |
| *L. lithognathus* | 2.55 | 4.66 | 1.50 | 1.90 | 3.13 | 1.34 | 2.78 | 4.46 | 1.30 |
| *L. alata* | 1.61 | 2.95 | 1.08 | | | | 2.69 | 4.31 | 1.20 |
| *L. dumerili* | | | | 2.16 | 3.56 | 1.28 | | | |
| *L. macrolepis* | 1.87 | 3.42 | 1.13 | | | | | | |
| *L. richardsonii* | 3.56 | 6.50 | 4.19 | 4.03 | 6.65 | 3.45 | 6.17 | 9.89 | 2.84 |
| *L. tricuspidens* | 2.41 | 4.40 | 1.39 | 2.22 | 3.66 | 1.42 | 2.96 | 4.74 | 1.34 |
| *M. cephalus* | | | | | | | 2.30 | 3.68 | 1.13 |
| *O. mossambicus* | 1.71 | 3.13 | 0.88 | 3.22 | 5.32 | 1.28 | 3.38 | 5.42 | 1.30 |
| *P. commersonnii* | 1.85 | 3.38 | 1.01 | | | | 2.36 | 3.79 | 1.23 |
| *P. knysnaensis* | 2.13 | 3.89 | 1.16 | | | | | | |
| *R. holubi* | | | | 3.07 | 5.07 | 1.40 | 2.57 | 4.12 | 1.47 |
| *T. jarbua* | 1.75 | 3.20 | 1.03 | | | | | | |
| *V. cunnesius* | 2.95 | 5.38 | 1.93 | 2.91 | 4.80 | 1.62 | 2.80 | 4.48 | 1.84 |
| *V. robustus* | 1.74 | 3.18 | 1.02 | | | | | | |
| **Total δ** | **54.72** | | | **60.58** | | | **62.42** | | |

Table 10. Percent frequency of occurrence, mean percent abundance and mean percent biomass composition of fishes in open cool-temperate estuaries (n = number of estuaries, SD = standard deviation).

| **Family** | **Species** | **Frequency** | | **Abundance** | | **Biomass** | |
|---|---|---|---|---|---|---|---|
| | | **%** | **n** | **%** | **SD** | **%** | **SD** |
| Ariidae | *Galeichthys feliceps* | 75 | 3 | 0.05 | 0.05 | 1.80 | 1.55 |
| Atherinidae | *Atherina breviceps* | 75 | 3 | 11.52 | 16.22 | 10.10 | 17.15 |
| Clupeidae | *Gilchristella aestuaria* | 50 | 2 | 1.20 | 1.76 | 0.90 | 1.55 |
| Gobiidae | *Caffrogobius nudiceps* | 25 | 1 | 0.30 | 0.59 | 0.21 | 0.43 |
| | *Psammogobius knysnaensis* | 100 | 4 | 0.88 | 0.97 | 0.07 | 0.05 |
| Mugilidae | *Liza richardsonii* | 100 | 4 | 85.72 | 18.01 | 76.08 | 23.80 |
| | *Mugil cephalus* | 75 | 3 | 0.19 | 0.25 | 1.86 | 2.25 |
| Pomatomidae | *Pomatomus saltatrix* | 50 | 2 | 0.07 | 0.10 | 3.79 | 5.08 |
| Scianidae | *Argyrosomus* sp. | 25 | 1 | 0.01 | 0.02 | 3.89 | 7.79 |
| Scyliorhinidae | *Haploblepharus pictus* | 25 | 1 | 0.01 | 0.02 | 1.29 | 2.57 |
| Syngnathidae | *Syngnathus temminckii* | 50 | 2 | 0.03 | 0.04 | 0.01 | 0.02 |
| Triglidae | *Chelidonichthys capensis* | 25 | 1 | 0.01 | 0.03 | 0.00 | 0.00 |
| | | | | | | | |

Table 11. Major species accounting for the similarity within open cool-temperate estuaries; *Si* is the average similarity contribution of each species; % *Si* is the percent contribution to the overall similarity (*S*); SD (*Si*) is the standard deviation of each species to the total similarity. Similarities are based on presence/absence, abundance and biomass.

| | Presence/absence | | | Abundance | | | Biomass | | |
|---|---|---|---|---|---|---|---|---|---|
| **Species** | ***Si*** | **% *Si*** | *Si* / SD(*Si*) | ***Si*** | **% *Si*** | *Si* / SD(*Si*) | ***Si*** | **% *Si*** | *Si* / SD(*Si*) |
| *A. breviceps* | 6.9 | 11.51 | 0.89 | 4.4 | 7.65 | 0.75 | 3.8 | 6.86 | 0.62 |
| *G. feliceps* | 6.9 | 11.51 | 0.89 | 2.8 | 4.89 | 0.86 | 5.5 | 9.93 | 0.91 |
| *L. richardsonii* | 16.1 | 26.95 | 3.40 | 34.4 | 59.84 | 3.73 | 33.2 | 59.44 | 2.95 |
| *M. cephalus* | 9.6 | 15.97 | 0.87 | 4.2 | 7.25 | 0.90 | 4.6 | 8.17 | 0.76 |
| *P. knysnaensis* | 16.1 | 26.95 | 3.40 | 8.5 | 14.79 | 2.55 | 5.1 | 9.09 | 2.61 |
| **Total *S*** | **59.92** | | | **57.50** | | | **55.78** | | |

Table 12. Percent frequency of occurrence, mean percent abundance and mean percent biomass composition of fishes in open warm-temperate estuaries (n = number of estuaries, SD = standard deviation).

| Family | Species | Frequency | | Abundance | | Biomass | |
|---|---|---|---|---|---|---|---|
| | | % | n | % | SD | % | SD |
| Ambassidae | *Ambassis dussumieri* | 14 | 4 | 0.21 | 0.83 | 0.01 | 0.02 |
| | *Ambassis natalensis* | 4 | 1 | 0.00 | 0.02 | 0.00 | 0.00 |
| | *Ambassis ambassis* | 7 | 2 | 0.00 | 0.02 | 0.00 | 0.01 |
| Anguillidae | *Anguilla mossambica* | 7 | 2 | 0.01 | 0.05 | 0.01 | 0.05 |
| Antennariidae | *Antennarius striatus* | 4 | 1 | 0.00 | 0.00 | 0.00 | 0.00 |
| Ariidae | *Galeichthys feliceps* | 64 | 18 | 0.58 | 1.03 | 8.74 | 13.08 |
| Atherinidae | *Atherina breviceps* | 86 | 24 | 4.68 | 9.53 | 0.17 | 0.37 |
| Blenniidae | *Omobranchus woodi* | 4 | 1 | 0.00 | 0.00 | 0.00 | 0.00 |
| Carangidae | *Caranx ignobilis* | 4 | 1 | 0.00 | 0.01 | 0.00 | 0.00 |
| | *Caranx sexfasciatus* | 11 | 3 | 0.01 | 0.04 | 0.28 | 1.35 |
| | *Lichia amia* | 64 | 18 | 0.11 | 0.14 | 4.60 | 5.96 |
| | *Trachinotus spp.* | 4 | 1 | 0.00 | 0.02 | 0.00 | 0.00 |
| | *Trachurus trachurus* | 4 | 1 | 0.00 | 0.00 | 0.00 | 0.00 |
| Cichlidae | *Oreochromis mossambicus* | 7 | 2 | 0.02 | 0.09 | 0.02 | 0.12 |
| Clinidae | *Clinus superciliosus* | 36 | 10 | 0.36 | 1.25 | 0.03 | 0.11 |
| Clupeidae | *Etrumeus whiteheadi* | 4 | 1 | 0.00 | 0.01 | 0.00 | 0.00 |
| | *Gilchristella aestuaria* | 93 | 26 | 30.42 | 21.82 | 1.07 | 1.55 |
| | *Sardinops sagax* | 18 | 5 | 0.03 | 0.07 | 0.00 | 0.02 |
| Dasyatidae | *Dasyatis kuhlii* | 4 | 1 | 0.00 | 0.00 | 0.14 | 0.75 |
| Elopidae | *Elops machnata* | 71 | 20 | 0.27 | 0.34 | 14.14 | 14.56 |
| Engraulidae | *Stolephorus holodon* | 18 | 5 | 0.03 | 0.07 | 0.00 | 0.01 |
| Gobiidae | *Caffrogobius gilchristi* | 96 | 27 | 3.10 | 4.45 | 0.13 | 0.16 |
| | *Caffrogobius natalensis* | 36 | 10 | 0.17 | 0.41 | 0.01 | 0.01 |
| | *Caffrogobius nudiceps* | 54 | 15 | 0.60 | 1.18 | 0.03 | 0.06 |
| | *Glossogobius callidus* | 64 | 18 | 2.86 | 4.64 | 0.17 | 0.31 |
| | *Oligolepis acutipennis* | 11 | 3 | 0.02 | 0.11 | 0.00 | 0.00 |
| | *Oligolepis keiensis* | 21 | 6 | 0.08 | 0.18 | 0.00 | 0.00 |
| | *Psammogobius knysnaensis* | 96 | 27 | 1.73 | 1.65 | 0.04 | 0.04 |
| Haemulidae | *Pomadasys commersonnii* | 89 | 25 | 3.02 | 4.85 | 8.92 | 11.62 |
| | *Pomadasys kaakan* | 7 | 2 | 0.01 | 0.02 | 0.00 | 0.01 |
| | *Pomadasys olivaceus* | 29 | 8 | 0.31 | 0.91 | 0.04 | 0.13 |
| Hemiramphidae | *Hemiramphus far* | 11 | 3 | 0.03 | 0.15 | 0.00 | 0.01 |
| Leiognathidae | *Leiognathus equula* | 7 | 2 | 0.01 | 0.05 | 0.03 | 0.16 |
| | *Secutor ruconius* | 4 | 1 | 0.00 | 0.02 | 0.00 | 0.00 |
| Lutjanidae | *Lutjanus argentimaculatus* | 4 | 1 | 0.00 | 0.02 | 0.05 | 0.25 |
| Monodactylidae | *Monodactylus falciformis* | 86 | 24 | 0.44 | 0.45 | 0.72 | 1.07 |
| Mugilidae | *Liza dumerili* | 100 | 28 | 7.76 | 8.46 | 4.86 | 3.38 |
| | *Liza macrolepis* | 50 | 14 | 0.23 | 0.80 | 0.42 | 0.68 |
| | *Liza richardsonii* | 96 | 27 | 12.03 | 17.94 | 15.46 | 15.38 |
| | *Liza tricuspidens* | 100 | 28 | 1.09 | 1.61 | 7.21 | 6.49 |
| | *Mugil cephalus* | 93 | 26 | 6.38 | 9.73 | 8.89 | 16.88 |
| | *Myxus capensis* | 64 | 18 | 1.54 | 4.52 | 0.88 | 1.37 |
| | *Valamugil buchanani* | 39 | 11 | 0.08 | 0.21 | 2.89 | 6.43 |
| | *Valamugil cunnesius* | 18 | 5 | 0.04 | 0.11 | 0.01 | 0.03 |
| | *Valamugil robustus* | 32 | 9 | 0.10 | 0.30 | 0.15 | 0.56 |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| Myliobatidae | *Myliobatis aquila* | 4 | 1 | 0.01 | 0.05 | 0.05 | 0.26 |
| Odontaspididae | *Carcharias taurus* | 7 | 2 | 0.00 | 0.01 | 0.72 | 2.88 |
| Platycephalidae | *Platycephalus indicus* | 21 | 6 | 0.09 | 0.41 | 0.11 | 0.27 |
| Pomatomidae | *Pomatomus saltatrix* | 46 | 13 | 0.10 | 0.29 | 0.47 | 1.68 |
| Rajidae | *Raja miraletes* | 4 | 1 | 0.00 | 0.00 | 0.00 | 0.00 |
| Sciaenidae | *Argyrosomus japonicus* | 100 | 28 | 1.15 | 1.88 | 12.69 | 9.01 |
| | *Johnius dorsalis* | 4 | 1 | 0.00 | 0.02 | 0.01 | 0.05 |
| Siganidae | *Siganus sutor* | 4 | 1 | 0.00 | 0.01 | 0.00 | 0.00 |
| Sillaginidae | *Sillago sihama* | 4 | 1 | 0.00 | 0.00 | 0.00 | 0.00 |
| Soleidae | *Heteromycteris capensis* | 64 | 18 | 0.46 | 0.77 | 0.01 | 0.01 |
| | *Solea bleekeri* | 86 | 24 | 1.39 | 3.28 | 0.04 | 0.05 |
| Sparidae | *Acanthopagrus vagus* | 21 | 6 | 0.39 | 1.92 | 0.20 | 0.64 |
| | *Diplodus hottentotus* | 21 | 6 | 0.02 | 0.06 | 0.00 | 0.02 |
| | *Diplodus capensis* | 57 | 16 | 1.29 | 3.75 | 0.03 | 0.08 |
| | *Gymnocrotaphus curvidens* | 4 | 1 | 0.00 | 0.01 | 0.00 | 0.00 |
| | *Lithognathus lithognathus* | 79 | 22 | 0.73 | 1.17 | 1.81 | 3.74 |
| | *Rhabdosargus globiceps* | 39 | 11 | 0.30 | 0.72 | 0.03 | 0.10 |
| | *Rhabdosargus holubi* | 96 | 27 | 15.06 | 13.39 | 3.24 | 2.49 |
| | *Rhabdosargus sarba* | 4 | 1 | 0.00 | 0.01 | 0.06 | 0.29 |
| | *Sarpa salpa* | 32 | 9 | 0.52 | 1.97 | 0.08 | 0.26 |
| Sphyraenidae | *Sphyraena jello* | 4 | 1 | 0.01 | 0.03 | 0.09 | 0.47 |
| Syngnathidae | *Hippichthys spicifer* | 4 | 1 | 0.00 | 0.01 | 0.00 | 0.00 |
| | *Syngnathus temminckii* | 32 | 9 | 0.04 | 0.09 | 0.00 | 0.01 |
| | *Syngnathus watermeyeri* | 4 | 1 | 0.00 | 0.01 | 0.00 | 0.00 |
| Teraponidae | *Terapon jarbua* | 11 | 3 | 0.02 | 0.06 | 0.01 | 0.06 |
| Tetraodontidae | *Amblyrhynchotes honckenii* | 21 | 6 | 0.02 | 0.04 | 0.01 | 0.03 |
| Torpedinidae | *Torpedo fuscumaculata* | 14 | 4 | 0.01 | 0.02 | 0.11 | 0.31 |
| | *Torpedo sinusperci* | 14 | 4 | 0.01 | 0.01 | 0.08 | 0.23 |

Table 13. Major species accounting for the similarity within open warm-temperate estuaries; *Si* is the average similarity contribution of each species; % *Si* is the percent contribution to the overall similarity (*S*); SD (*Si*) is the standard deviation of each species to the total similarity. Similarities are based on presence/absence, abundance and biomass.

| | **Presence/absence** | | | **Abundance** | | | **Biomass** | | |
|---|---|---|---|---|---|---|---|---|---|
| **Species** | ***Si*** | **% *Si*** | ***Si* / SD(*Si*)** | ***Si*** | **% *Si*** | ***Si* / SD(*Si*)** | ***Si*** | **% *Si*** | ***Si* / SD(*Si*)** |
| *A. japonicus* | 1.4 | 2.15 | 0.97 | 1.5 | 2.52 | 2.47 | 7.0 | 11.46 | 4.39 |
| *A. breviceps* | 2.7 | 4.35 | 1.38 | 2.9 | 4.97 | 1.24 | 1.0 | 1.71 | 1.13 |
| *C. gilchristi* | 2.8 | 4.39 | 1.47 | 2.4 | 4.15 | 1.63 | 1.7 | 2.72 | 2.20 |
| *D. capensis* | 1.3 | 2.02 | 0.67 | 0.9 | 1.60 | 0.64 | | | |
| *E. machnata* | 1.9 | 3.04 | 0.98 | 1.3 | 2.27 | 0.92 | 3.4 | 5.58 | 0.96 |
| *G. feliceps* | 1.8 | 2.82 | 0.80 | 1.2 | 2.11 | 0.77 | 2.5 | 4.03 | 0.76 |
| *G. aestuaria* | 3.8 | 5.99 | 2.19 | 4.7 | 8.13 | 2.04 | 2.7 | 4.39 | 2.07 |
| *G. callidus* | 1.6 | 2.49 | 0.82 | 1.7 | 2.94 | 0.75 | | | |
| *H. capensis* | 1.6 | 2.52 | 0.80 | 1.1 | 1.98 | 0.77 | | | |
| *L. amia* | 1.6 | 2.62 | 0.81 | 0.9 | 1.60 | 0.81 | 2.1 | 3.37 | 0.79 |
| *L. lithognathus* | 2.7 | 4.22 | 1.20 | 1.7 | 2.93 | 1.13 | 1.7 | 2.72 | 0.90 |
| *L. dumerili* | 4.5 | 7.07 | 5.13 | 5.3 | 9.19 | 3.53 | 5.2 | 8.49 | 4.29 |
| *L. richardsonii* | 4.1 | 6.58 | 2.89 | 5.1 | 8.79 | 1.85 | 6.3 | 10.29 | 2.19 |
| *L. tricuspidens* | 3.2 | 5.00 | 1.83 | 2.1 | 3.71 | 2.62 | 5.4 | 8.91 | 3.57 |
| *M. falciformis* | 3.1 | 4.87 | 1.58 | 2.1 | 3.56 | 1.48 | 1.7 | 2.78 | 1.21 |
| *M. cephalus* | 3.6 | 5.79 | 2.15 | 3.4 | 5.83 | 1.81 | 4.1 | 6.79 | 1.71 |
| *M. capensis* | 1.6 | 2.54 | 0.79 | 1.1 | 1.91 | 0.74 | | | |
| *P. commersonnii* | 2.3 | 3.68 | 1.19 | 1.8 | 3.10 | 1.36 | 4.2 | 6.93 | 1.42 |
| *P. knysnaensis* | 4.1 | 6.56 | 2.89 | 3.9 | 6.68 | 2.73 | 1.4 | 2.21 | 2.37 |
| *R. holubi* | 4.1 | 6.46 | 2.94 | 6.3 | 10.82 | 2.48 | 4.0 | 6.55 | 2.47 |
| *S. bleekeri* | 3.0 | 4.82 | 1.58 | 2.3 | 4.03 | 1.42 | 1.0 | 1.64 | 1.42 |
| **Total *S*** | **62.97** | | | **57.86** | | | **61.07** | | |

Table 14. Percent frequency of occurrence, mean percent abundance and mean percent biomass composition of fishes in open subtropical estuaries (n = number of estuaries, SD = standard deviation).

| Family | Species | Frequency | | Abundance | | Biomass | |
|---|---|---|---|---|---|---|---|
| | | % | n | % | SD | % | SD |
| Ambassidae | *Ambassis dussumieri* | 50 | 5 | 6.94 | 11.72 | 0.35 | 0.56 |
| | *Ambassis natalensis* | 80 | 8 | 2.17 | 2.70 | 0.05 | 0.06 |
| | *Ambassis ambassis* | 40 | 4 | 0.20 | 0.27 | 0.21 | 0.43 |
| Atherinidae | *Atherina breviceps* | 20 | 2 | 0.61 | 1.30 | 0.02 | 0.04 |
| Bothidae | *Pseudorhombus arsius* | 10 | 1 | 0.05 | 0.16 | 0.01 | 0.04 |
| Carangidae | *Caranx heberi* | 10 | 1 | 0.00 | 0.01 | 0.00 | 0.00 |
| | *Caranx ignobilis* | 80 | 8 | 1.62 | 1.56 | 0.94 | 1.84 |
| | *Caranx papuensis* | 30 | 3 | 0.03 | 0.06 | 0.19 | 0.39 |
| | *Caranx sexfasciatus* | 90 | 9 | 1.77 | 1.92 | 3.59 | 5.21 |
| | *Lichia amia* | 20 | 2 | 0.02 | 0.04 | 1.03 | 2.40 |
| | *Scomberoides lysan* | 70 | 7 | 1.55 | 3.81 | 0.03 | 0.06 |
| Cichlidae | *Oreochromis mossambicus* | 30 | 3 | 0.16 | 0.35 | 0.26 | 0.64 |
| | *Tilapia rendalli* | 10 | 1 | 0.01 | 0.04 | 0.00 | 0.00 |
| Clariidae | *Clarias gariepinus* | 30 | 3 | 0.07 | 0.11 | 2.17 | 3.81 |
| Clupeidae | *Gilchristella aestuaria* | 80 | 8 | 15.70 | 22.85 | 0.52 | 1.00 |
| | *Hilsa kelee* | 90 | 9 | 0.95 | 0.95 | 4.67 | 4.52 |
| Eleotridae | *Eleotris fusca* | 10 | 1 | 0.01 | 0.02 | 0.00 | 0.00 |
| Elopidae | *Elops machnata* | 100 | 10 | 0.41 | 0.31 | 10.34 | 8.17 |
| Engraulidae | *Engraulis japonicus* | 20 | 2 | 0.16 | 0.44 | 0.00 | 0.00 |
| | *Stolephorus holodon* | 40 | 4 | 0.77 | 1.91 | 0.01 | 0.02 |
| | *Thryssa setirostris* | 20 | 2 | 0.02 | 0.04 | 0.00 | 0.00 |
| | *Thryssa vitrirostris* | 50 | 5 | 0.93 | 1.33 | 1.14 | 1.91 |
| Gerreidae | *Gerres longirostris* | 10 | 1 | 0.07 | 0.23 | 0.00 | 0.01 |
| | *Gerres macracanthus* | 10 | 1 | 0.01 | 0.04 | 0.00 | 0.00 |
| | *Gerres methueni* | 30 | 3 | 0.88 | 1.67 | 0.07 | 0.18 |
| Gobiidae | *Caffrogobius gilchristi* | 50 | 5 | 1.54 | 3.27 | 0.03 | 0.07 |
| | *Caffrogobius natalensis* | 20 | 2 | 0.05 | 0.10 | 0.00 | 0.00 |
| | *Favonigobius reichei* | 20 | 2 | 0.07 | 0.17 | 0.00 | 0.00 |
| | *Glossogobius callidus* | 100 | 10 | 4.19 | 5.57 | 0.07 | 0.11 |
| | *Glossogobius giuris* | 40 | 4 | 0.24 | 0.54 | 0.01 | 0.02 |
| | *Oligolepis acutipennis* | 80 | 8 | 0.69 | 0.92 | 0.01 | 0.01 |
| | *Oligolepis keiensis* | 80 | 8 | 0.61 | 0.73 | 0.01 | 0.01 |
| | *Periopthalmus koelreuteri* | 20 | 2 | 0.01 | 0.03 | 0.00 | 0.00 |
| | *Psammogobius biocellatus* | 10 | 1 | 0.02 | 0.06 | 0.00 | 0.00 |
| | *Psammogobius knysnaensis* | 30 | 3 | 0.10 | 0.27 | 0.00 | 0.00 |
| | *Silhouettea sibayi* | 10 | 1 | 0.04 | 0.14 | 0.00 | 0.00 |
| Haemulidae | *Pomadasys commersonnii* | 100 | 10 | 3.33 | 3.01 | 4.15 | 5.03 |
| | *Pomadasys kaakan* | 30 | 3 | 0.23 | 0.50 | 0.23 | 0.48 |
| | *Pomadasys olivaceus* | 10 | 1 | 0.90 | 2.86 | 0.02 | 0.06 |
| Leiognathidae | *Leiognathus equula* | 90 | 9 | 3.21 | 4.64 | 0.64 | 0.79 |
| Lutjanidae | *Lutjanus argentimaculatus* | 50 | 5 | 0.06 | 0.08 | 2.33 | 5.24 |
| | *Lutjanus fulviflamma* | 10 | 1 | 0.01 | 0.02 | 0.00 | 0.00 |
| Megalopidae | *Megalops cyprinoides* | 40 | 4 | 0.12 | 0.20 | 3.14 | 6.71 |
| Monodactylidae | *Monodactylus argenteus* | 20 | 2 | 0.03 | 0.06 | 0.02 | 0.03 |
| | *Monodactylus falciformis* | 40 | 4 | 0.05 | 0.12 | 0.05 | 0.11 |
| Mugilidae | *Liza alata* | 100 | 10 | 0.92 | 0.94 | 14.86 | 14.31 |
| | *Liza dumerili* | 100 | 10 | 14.73 | 11.57 | 4.57 | 3.08 |
| | *Liza macrolepis* | 100 | 10 | 6.04 | 6.95 | 3.88 | 2.74 |
| | *Liza melinoptera* | 20 | 2 | 0.01 | 0.03 | 0.06 | 0.13 |
| | *Liza tricuspidens* | 70 | 7 | 0.34 | 0.63 | 1.03 | 2.82 |
| | *Mugil cephalus* | 100 | 10 | 3.36 | 3.06 | 10.16 | 6.19 |
| | *Myxus capensis* | 90 | 9 | 1.13 | 1.29 | 3.63 | 4.51 |
| | *Valamugil buchanani* | 70 | 7 | 1.06 | 1.52 | 8.69 | 11.57 |
| | *Valamugil cunnesius* | 100 | 10 | 6.77 | 9.73 | 3.50 | 4.70 |
| | *Valamugil robustus* | 70 | 7 | 0.96 | 1.83 | 0.78 | 0.87 |
| | *Valamugil seheli* | 50 | 5 | 0.85 | 2.43 | 0.04 | 0.07 |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| Mullidae | *Upeneus vittatus* | 20 | 2 | 0.09 | 0.20 | 0.01 | 0.01 |
| Platycephalidae | *Platycephalus indicus* | 30 | 3 | 0.13 | 0.24 | 0.24 | 0.49 |
| Polynemidae | *Polydactylus plebeius* | 10 | 1 | 0.00 | 0.01 | 0.03 | 0.08 |
| Pomatomidae | *Pomatomus saltatrix* | 30 | 3 | 0.06 | 0.09 | 0.10 | 0.31 |
| Scianidae | *Argyrosomus japonicus* | 100 | 10 | 0.72 | 0.71 | 8.97 | 11.40 |
| Serranidae | *Epinephelus malabaricus* | 30 | 3 | 0.04 | 0.07 | 0.01 | 0.03 |
| Silliaginidae | *Sillago sihama* | 20 | 2 | 0.07 | 0.19 | 0.01 | 0.03 |
| Soleidae | *Solea bleekeri* | 70 | 7 | 1.26 | 1.76 | 0.03 | 0.04 |
| Sparidae | *Acanthopagrus* spp. | 90 | 9 | 0.88 | 0.74 | 1.21 | 1.54 |
| | *Diplodus capensis* | 10 | 1 | 0.02 | 0.06 | 0.05 | 0.15 |
| | *Lithognathus lithognathus* | 10 | 1 | 0.00 | 0.01 | 0.06 | 0.19 |
| | *Rhabdosargus holubi* | 100 | 10 | 6.91 | 6.12 | 0.99 | 1.02 |
| | *Rhabdosargus sarba* | 40 | 4 | 0.35 | 0.82 | 0.24 | 0.48 |
| Sphyraenidae | *Sphyraena jello* | 30 | 3 | 0.05 | 0.08 | 0.30 | 0.66 |
| Syngnathidae | *Hippichthys heptagonus* | 10 | 1 | 0.01 | 0.02 | 0.00 | 0.00 |
| | *Hippichthys spicifer* | 10 | 1 | 0.01 | 0.02 | 0.00 | 0.00 |
| Teraponidae | *Terapon jarbua* | 100 | 10 | 1.46 | 1.31 | 0.13 | 0.08 |
| Tetraodontidae | *Amblyrhynchotes honckenii* | 60 | 6 | 0.99 | 1.70 | 0.07 | 0.10 |
| | *Arothron immaculatus* | 20 | 2 | 0.03 | 0.05 | 0.01 | 0.03 |
| | *Chelonodon laticeps* | 40 | 4 | 0.12 | 0.27 | 0.04 | 0.13 |
| | | | | | | | |

Table 15. Major species accounting for the similarity within open subtropical estuaries; *Si* is the average similarity contribution of each species; % *Si* is the percent contribution to the overall similarity (*S*); SD (*Si*) is the standard deviation of each species to the total similarity. Similarities are based on presence/absence, abundance and biomass.

| **Species** | ***Si*** | **% *Si*** | ***Si* / SD(*Si*)** | ***Si*** | **% *Si*** | ***Si* / SD(*Si*)** | ***Si*** | **% *Si*** | ***Si* / SD(*Si*)** |
|---|---|---|---|---|---|---|---|---|---|
| *Acanthopagrus* spp. | 2.5 | 3.97 | 1.87 | 1.9 | 3.23 | 1.75 | 1.8 | 2.90 | 1.74 |
| *A. natalensis* | 1.8 | 2.93 | 1.17 | 1.6 | 2.71 | 1.16 | 0.7 | 1.10 | 1.05 |
| *A. honckenii* | 0.6 | 0.92 | 0.44 | 0.7 | 1.14 | 0.54 | | | |
| *A. japonicus* | 1.3 | 2.07 | 1.11 | 1.4 | 2.40 | 2.71 | 3.9 | 6.48 | 3.70 |
| *C. ignobilis* | | | | 0.7 | 1.21 | 1.03 | 1.1 | 1.85 | 1.10 |
| *C. sexfasciatus* | 1.3 | 2.17 | 1.29 | 1.2 | 2.13 | 1.74 | 2.1 | 3.39 | 1.25 |
| *E. machnata* | 3.2 | 5.22 | 5.65 | 2.2 | 3.76 | 4.95 | 4.2 | 7.01 | 2.58 |
| *G. aestuaria* | 1.9 | 3.01 | 1.23 | 2.0 | 3.48 | 1.00 | 0.9 | 1.55 | 1.00 |
| *G. callidus* | 3.2 | 5.22 | 5.65 | 3.2 | 5.42 | 2.79 | 1.1 | 1.90 | 3.24 |
| *H. kelee* | 2.5 | 3.97 | 1.87 | 1.9 | 3.32 | 1.83 | 3.0 | 5.02 | 1.90 |
| *L. equula* | 2.5 | 3.97 | 1.87 | 2.1 | 3.68 | 1.64 | 1.6 | 2.72 | 1.69 |
| *L. alata* | 3.2 | 5.22 | 5.65 | 2.4 | 4.20 | 4.02 | 4.9 | 8.09 | 2.67 |
| *L. dumerili* | 3.2 | 5.22 | 5.65 | 5.5 | 9.43 | 3.84 | 4.0 | 6.55 | 4.09 |
| *L. macrolepis* | 3.2 | 5.22 | 5.65 | 3.6 | 6.26 | 4.44 | 3.6 | 5.97 | 3.82 |
| *L. tricuspidens* | 0.9 | 1.41 | 0.67 | 0.7 | 1.26 | 0.84 | 0.6 | 1.05 | 0.80 |
| *L. argentimaculatus* | 0.6 | 0.96 | 0.52 | | | | 0.6 | 0.97 | 0.49 |
| *M. cephalus* | 2.2 | 3.60 | 2.07 | 1.8 | 3.14 | 3.11 | 5.0 | 8.20 | 3.30 |
| *M. capensis* | 0.8 | 1.30 | 0.86 | 1.0 | 1.73 | 1.54 | 2.1 | 3.46 | 1.23 |
| *O. acutipennis* | 1.9 | 3.10 | 1.23 | 1.4 | 2.43 | 1.18 | 0.6 | 0.97 | 1.16 |
| *O. keiensis* | 1.9 | 3.01 | 1.23 | 1.3 | 2.30 | 1.18 | | | |
| *P. commersonnii* | 3.2 | 5.22 | 5.65 | 3.0 | 5.12 | 4.83 | 3.0 | 5.03 | 3.39 |
| *R. holubi* | 3.2 | 5.22 | 5.65 | 3.8 | 6.51 | 2.51 | 2.3 | 3.77 | 2.65 |
| *S. lysan* | 1.0 | 1.55 | 0.71 | 0.8 | 1.34 | 0.84 | | | |
| *S. bleekeri* | 1.4 | 2.26 | 0.90 | 1.3 | 2.15 | 0.84 | | | |
| *T. jarbua* | 2.5 | 4.05 | 2.40 | 2.2 | 3.86 | 2.46 | 1.7 | 2.83 | 7.27 |
| *T. vitrirostris* | 0.6 | 1.00 | 0.52 | | | | | | |
| *V. buchanani* | 0.9 | 1.40 | 0.77 | 0.9 | 1.47 | 0.82 | 1.9 | 3.20 | 0.79 |
| *V. cunnesius* | 3.2 | 5.22 | 5.65 | 3.2 | 5.45 | 3.94 | 2.7 | 4.49 | 2.87 |
| *V. robustus* | 1.5 | 2.36 | 0.91 | 1.2 | 1.99 | 0.88 | 1.1 | 1.84 | 0.80 |
| *V. seheli* | 0.8 | 1.37 | 0.53 | | | | | | |
| **Total *S*** | **61.85** | | | **58.21** | | | **60.51** | | |

Table 16. Major species accounting for the dissimilarity between open cool-temperate and open warm-temperate estuaries; **ä***i* is the average dissimilarity contribution of each species; % **ä***i* is the percent contribution to the overall dissimilarity (**ä**); SD (**ä***i*) is the standard deviation of each species to the total dissimilarity.

| | **Presence/absence** | | | **Abundance** | | | **Biomass** | | |
|---|---|---|---|---|---|---|---|---|---|
| **Species** | **δ*i*** | **% δ*i*** | **δ*i* / SD(δ*i*)** | **δ*i*** | **% δ*i*** | **δ*i* / SD(δ*i*)** | **δ*i*** | **% δ*i*** | **δ*i* / SD(δ*i*)** |
| *A. japonicus* | | | | | | | 5.75 | 7.82 | 3.66 |
| *A. breviceps* | | | | 3.71 | 5.18 | 1.37 | 2.91 | 3.95 | 1.26 |
| *C. gilchristi* | 2.80 | 4.08 | 1.85 | 2.69 | 3.75 | 1.58 | | | |
| *E. machnata* | 2.23 | 3.25 | 1.51 | | | | 4.16 | 5.66 | 1.45 |
| *G. feliceps* | | | | | | | 2.89 | 3.93 | 1.23 |
| *G. aestuaria* | 1.91 | 2.78 | 0.94 | 3.31 | 4.62 | 1.31 | | | |
| *G. callidus* | 2.01 | 2.92 | 1.30 | 2.72 | 3.80 | 1.15 | | | |
| *H. capensis* | 2.10 | 3.06 | 1.26 | | | | | | |
| *L. amia* | 2.11 | 3.08 | 1.25 | | | | 2.86 | 3.89 | 1.24 |
| *L. lithognathus* | 2.73 | 3.98 | 1.66 | 2.14 | 2.99 | 1.45 | | | |
| *L. dumerili* | 3.54 | 5.16 | 3.88 | 5.01 | 6.99 | 3.30 | 4.37 | 5.94 | 4.08 |
| *L. macrolepis* | | | | | | | | | |
| *L. richardsonii* | | | | 4.98 | 6.96 | 1.92 | 3.69 | 5.01 | 1.83 |
| *L. tricuspidens* | 2.98 | 4.34 | 2.17 | | | | 4.74 | 6.44 | 3.26 |
| *M. falciformis* | 2.88 | 4.19 | 2.15 | 2.19 | 3.06 | 1.94 | | | |
| *M. cephalus* | | | | 2.31 | 3.22 | 1.62 | | | |
| *M. capensis* | 2.09 | 3.05 | 1.24 | | | | | | |
| *P. commersonnii* | 2.49 | 3.63 | 1.74 | | | | 4.42 | 6.00 | 1.68 |
| *R. holubi* | 3.37 | 4.91 | 3.09 | 5.94 | 8.29 | 2.95 | 3.65 | 4.96 | 3.05 |
| *S. bleekeri* | 2.85 | 4.16 | 2.16 | 2.51 | 3.51 | 1.65 | | | |
| **Total δ** | **68.59** | | | **71.61** | | | **73.56** | | |

Table 17. Major species accounting for the dissimilarity between open warm-temperate and open subtropical estuaries; **ä***i* is the average dissimilarity contribution of each species; % **ä***i* is the percent contribution to the overall dissimilarity (**ä**); SD (**ä***i*) is the standard deviation of each species to the total dissimilarity.

| **Species** | **δ*i*** | **% δ*i*** | **δ*i* / SD(δ*i*)** | **δ*i*** | **% δ*i*** | **δ*i* / SD(δ*i*)** | **δ*i*** | **% δ*i*** | **δ*i* / SD(δ*i*)** |
|---|---|---|---|---|---|---|---|---|---|
| *Acanthopagrus* ***vagus*** | 1.36 | 2.18 | 1.56 | 1.26 | 1.96 | 1.88 | 1.35 | 2.20 | 1.92 |
| *A. natalensis* | 1.40 | 2.25 | 1.67 | 1.33 | 2.07 | 1.62 | | | |
| *A. breviceps* | 1.26 | 2.04 | 1.42 | 2.00 | 3.12 | 1.44 | | | |
| *C. gilchristi* | 1.33 | 2.14 | 1.83 | 1.36 | 2.11 | 1.44 | | | |
| *C. sexfasciatus* | 1.14 | 1.84 | 1.73 | | | | 1.82 | 2.97 | 1.41 |
| *D. capensis* | 1.01 | 1.62 | 1.08 | 1.10 | 1.71 | 0.99 | | | |
| *E. machnata* | | | | | | | 1.71 | 2.77 | 1.22 |
| *G. feliceps* | 1.20 | 1.93 | 1.28 | 1.10 | 1.71 | 1.16 | 2.06 | 3.35 | 1.14 |
| *G. aestuaria* | | | | 1.43 | 2.22 | 1.06 | | | |
| *G. callidus* | | | | 1.64 | 2.55 | 1.50 | | | |
| *H. capensis* | 1.14 | 1.83 | 1.27 | | | | | | |
| *H. kelee* | 1.64 | 2.64 | 2.64 | 1.45 | 2.26 | 2.44 | 2.28 | 3.71 | 2.66 |
| *L. equula* | 1.54 | 2.49 | 2.12 | 1.74 | 2.71 | 1.91 | 1.27 | 2.07 | 2.05 |
| *L. amia* | 1.07 | 1.73 | 1.14 | | | | 1.67 | 2.71 | 1.21 |
| *L. lithognathus* | 1.36 | 2.19 | 1.53 | 1.28 | 1.98 | 1.40 | 1.31 | 2.13 | 1.16 |
| *L. alata* | 1.88 | 3.02 | 5.27 | 1.59 | 2.47 | 3.11 | 3.39 | 5.52 | 2.65 |
| *L. macrolepis* | 1.43 | 2.31 | 1.82 | 1.72 | 2.68 | 2.22 | 1.73 | 2.82 | 1.81 |
| *L. richardsonii* | 1.81 | 2.92 | 3.65 | 3.07 | 4.78 | 2.09 | 3.31 | 5.38 | 2.43 |
| *L. tricuspidens* | | | | | | | 1.98 | 3.21 | 1.82 |
| *M. falciformis* | 1.09 | 1.76 | 1.12 | 1.10 | 1.71 | 1.51 | | | |
| *M. cephalus* | | | | 1.22 | 1.90 | 1.48 | 1.25 | 2.03 | 1.20 |
| *M. capensis* | | | | | | | 1.49 | 2.43 | 1.38 |
| *O. acutipennis* | 1.35 | 2.18 | 1.57 | 1.09 | 1.70 | 1.52 | | | |
| *O. keiensis* | 1.22 | 1.97 | 1.36 | | | | | | |
| *P. commersonnii* | | | | | | | 1.30 | 2.12 | 1.20 |
| *P. knysnaensis* | 1.28 | 2.07 | 1.38 | 1.74 | 2.70 | 2.06 | | | |
| *R. holubi* | | | | 1.71 | 2.66 | 1.61 | | | |
| *S. lysan* | 1.06 | 1.71 | 1.16 | | | | | | |
| *T. jarbua* | 1.59 | 2.56 | 2.62 | 1.46 | 2.02 | 2.27 | | | |
| *V. buchanani* | | | | | | | 1.98 | 3.23 | 1.18 |
| *V. cunnesius* | 1.63 | 2.62 | 2.36 | 2.10 | 3.27 | 2.26 | 1.93 | 3.13 | 2.58 |
| *V. robustus* | 1.07 | 1.73 | 1.11 | | | | | | |
| *V. seheli* | 1.03 | 1.65 | 0.98 | | | | | | |
| **Total δ** | **62.09** | | | **64.31** | | | **61.48** | | |

## SMITHIANA

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### STYLE OF THE HOUSE

Hyphens: Certain substantive compounds are hyphenated: gill-raker, soft-ray, type-species, type-locality, type-series, type-specimen. Other words often used together are not hyphenated unless they are used in adjectival expressions before a noun: anal fin / anal-fin rays; lateral line / lateral-line scales; gill arch / gill-arch filaments, etc.

Word usage: Although the following word pairs are often used interchangeably, we believe that consistent use of the first word as a noun and the second as an adjective will improve the precision of our writing: mucus / mucous; maxilla / maxillary; opercle / opercular, operculum / opercular. The operculum (= gill cover) comprises (usually) four separate bones: opercle, subopercle, preopercle and interopercle. The words preoperculum, suboperculum and interoperculum are unnecessary substitutes and not to be used for preopercle, subopercle and interopercle. The plural of operculum is opercula.

Decimal comma versus decimal point: Contrary to most journals published in South Africa and some European countries, we will not use a comma in place of a decimal point. Most computers do not read a comma as a decimal point. In addition, it is common in ichthyological papers to give sequences of measurements that include decimal numbers, with each measurement separated by a comma. If the comma is used to separate items in a series, as well as being used to indicate a decimal number, it will cause considerable confusion.

Fin formulae: Fin formulae will be designated as follows: D XII,10-12 indicates on continuous fin with 12 spines and 10-12 soft (segmented) rays; DX / I,10-12 indicates a fin divided to the base in front of the last spine; and D X+I,12 indicates two separate dorsal fins, the first with 10 spines and the second with 1 spine and 12 soft rays. If it is necessary to differentiate branched and unbranched soft-rays, lower-case Roman numerals will be used for unbranched rays and Arabic numerals for branched rays, e.g. D iii,S. Principal caudal-fin rays are defined as those that touch the hypural bones. The number of principal caudal rays is usually the number of branched rays plus two. If the principal caudal rays are in two separate groups, the number of rays in the dorsal group is given first: thus, "principal caudal rays 8+7" means that there are 15 principal caudal rays, with 8 rays in the dorsal group and 7 in the ventral group.

Abbreviations: Abbreviations normally end with a full stop: et al., e.g., etc., n.b., (note: these commonly used abbreviations of Latin words are not italicized). Dr (Doctor) and Mr (Mister) and compass directions (north, west, northwest, etc.) are abbreviated using capital letters without full stops: N, W, NW. We recommend the following abbreviations for ichthyological terms: SL - standard length, TL - total length, FL - fork length, GR - gill-rakers, LL - lateral line.

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