What limits the distribution of subtidal macrobenthos in permanently open and temporarily open/closed South African estuaries? Salinity vs. sediment particle size

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Abstract

Thirteen estuaries in the Eastern Cape Province, South Africa, were assigned to one of four types of estuaries (river-dominated permanently open, marine-dominated permanently open, medium-sized temporarily open/closed and small temporarily open/closed), and macrobenthic zonation patterns were compared using multivariate statistics. Three major habitat zones were identified: two relating to substrate (a sand zone and a mud zone), and a third zone characterised by water of low salinity (<20). These zones are inhabited by four major groups of macrobenthos. The distribution of two of these (estuarine endemic sand fauna and estuarine endemic mud fauna) is limited by the nature of the substratum, whereas the distribution of the other two (fauna originating from the marine habitat and oligohaline fauna) is limited by salinity. Estuarine endemics were present in all four types of estuaries. Marine fauna was numerically important only in permanently open systems, while oligohaline fauna was abundant only in the upper reaches of river dominated open systems. Medium-sized temporarily open/closed estuaries lacked both marine and oligohaline forms, but these were present to a limited extent in small temporarily open/closed estuaries. Hence, salinity is not the primary environmental variable determining zonation patterns in Eastern Cape estuaries, and particularly in temporarily open/closed estuaries, it is of minor importance.

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1. Introduction

The importance of salinity and sediment composition in determining distribution patterns of estuarine benthic fauna has long been recognised, and numerous studies have investigated the relationship between macrobenthic community structure and either or both variables. The majority of such studies have attached greater importance to salinity (Carriker, 1967; Holland, Shaughnessy, & Hiegel, 1987; Pearse & Gunter, 1957; Wolff, 1983). Pearse and Gunter (1957), for example, found that within an estuarine system, salinity is generally the more obvious environmental factor. The reason for the structuring effect of salinity on macrobenthic communities is that the salinity gradient acts as a physiological barrier for stenohaline marine and freshwater species, and places environmental stress on euryhaline marine species. Wider fluctuations of salinity within the middle estuary heighten physiological stress and can result in a reduction in the number of species (Sanders, Mangelsdorf, & Hampson, 1965). Holland et al. (1987) concluded that salinity regulated macrofauna abundance in Chesapeake Bay on spatial and temporal scales. However, Holland (1985) found that the importance of salinity in Chesapeake Bay was not always obvious. Relationships between salinity and abundance were weaker in seasons when populations were dominated by adults. He concluded that the osmoregulatory capabilities of many adult species are greater than those of their larvae, making them more independent of salinity. In the same study, Holland identified three distinctive macrobenthic communities in a mesohaline region of...
Chesapeake Bay, that corresponded to the major sediment types sampled rather than to the salinity gradient: a nearshore sand community, a transitional muddy-sand community and a deep-water mud community. Although species composition of these communities was similar, relative abundances of component species differed among them. Boesch (1973) found that sediment composition rather than salinity was responsible for species distribution and diversity in the Hampton Roads area of Chesapeake Bay. In a subsequent study, Boesch (1977) differentiated between ‘homoiohaline systems’, represented by Chesapeake Bay, and ‘poikilohaline systems’, represented by the Brisbane River estuary in eastern Australia. He found that the Venice System of approximate ranges of salinity values in coastal waters (Anonymous, 1959) may extrapolate well to large eastern North American estuaries, but that the zonation patterns (i.e. distribution of groups of species having similar tolerance ranges to environmental conditions measured) along the estuarine gradient of the Brisbane River estuary do not relate in any meaningful way to existing estuarine classification schemes such as the Venice System. Designation of portions of the estuary as polyhaline, mesohaline, oligohaline, etc., seems futile, because the benthic habitats throughout most of the estuary are inhabited by estuarine endemic forms. Day (1967a) acknowledged that salinity was not the only environmental factor responsible for the presence of a species in a certain region of an estuary. He found that many so-called estuarine species are really calm-water species, and that the ability to survive in sheltered waters is just as important as tolerance to reduced salinity in determining the estuarine population. In Day (1964), he stated that the most important physical conditions, apart from the salinity regime, are the depth and permanence of the mouth, the clarity of the water, and the nature of the bottom sediments.

The importance of salinity variation in estuaries has led to biotic classification systems based on the relationship of species with the salinity of the surrounding water. A number of classification systems based on the organisms’ ability to osmoregulate and to tolerate certain salinity ranges were developed, for example, by Kinne (1963) and Day (1951, 1967a). The classification system suggested by Day (1967a) was based on the Venice system of approximate ranges of salinity values in coastal waters (Anonymous, 1959) and assigns estuarine animals to five groups: a stenohaline marine component (marine species that can tolerate a slight decrease in salinity only), a euryhaline marine component (marine species having a wide tolerance range for salinity), an estuarine component (species absent from both the riverine and the marine habitats), a freshwater component (riverine species which may penetrate estuaries), and a migratory component (species that may penetrate estuaries during a part of their life-cycle). Day’s work concentrated on prominent South African estuaries and bays such as the Knysna estuary, Langebaan lagoon and Durban bay, which are all marine dominated. However, estuaries of this type are rare in Southern Africa, and it is uncertain whether Day’s classification system is equally applicable to other types of South African estuaries. Of the 250 estuaries along the South African coastline, 182 (73% of the total) are classified as temporarily open/closed (Whitfield, 2000). These estuaries are not in contact with the sea for part of the year, because a sand bar forms in the mouth area as a result of low river flow and longshore winds. During periods of high rainfall, the water level inside such an estuary may rise sufficiently high to breach the sand bar, and the system then behaves temporarily like a true estuary (Whitfield, 1992; Wooldridge & McGwynne, 1996). The limited accessibility of these systems to marine species, and the inability of many marine species to complete their life cycles within estuaries probably manifests itself in numerical dominance of the estuarine endemic component within temporarily open/closed systems. Thus, the distribution of macrobenthos within these estuaries may be independent of salinity, as is the case with the Brisbane Estuary (Boesch, 1977). The relative importance of the steno- and euryhaline marine components within many permanently open estuaries in South Africa may also be less than in the estuarine bays and lagoons primarily studied by Day, Millard, and Harrison (1952), Day and Morgans (1956) and Day (1959, 1967a, 1981). First, the influence of the river on physical and chemical processes is often greater, which results in the exclusion of many marine species. Secondly, the mouth areas particularly of the estuaries of mud-rich rivers tend to be channel-like (Cooper, Wright, & Mason, 1999), which decreases the surface area available for colonisation by species associated with high salinities and sandy sediments.

The main aim of the present study was to evaluate the relative importance of salinity and sediment characteristics as factors influencing subtidal macrobenthic community structure in 13 South African estuaries having widely different attributes. The estuaries investigated are located in the Eastern Cape Province and range from permanently open estuaries with high freshwater input (strong horizontal salinity gradients), to freshwater deprived systems that are essentially extensions of the sea, and from temporarily open/closed systems with relatively high freshwater inputs to a hypersaline, lagoonal type estuary. Lower estuarine reaches usually have high salinity values and sandy bottoms, whereas higher estuarine reaches are characterised by lower salinity values and finer substrates (Day, 1951; McLusky, 1981). Thus, there is usually a high degree of correlation between these two variables. The inclusion of a wide range of estuarine types into the present study would make these
two variables (salinity and sediment type) more independent of each other.

1.1. Estuaries sampled

The 13 estuaries are located in the western part of the Eastern Cape Province, South Africa (Fig. 1). The sampling area stretches from the Kromme (KR) in the West, to the Keiskamma (KE) in the East. Each estuary has been assigned to one of four groups.

1.1.1. Medium-sized temporarily open/closed (MC) and small temporarily open/closed (SC)

Temporarily open/closed estuaries were subdivided into two groups, which differ from each other with regard to size and ecological indices (macrobenthic density, species richness and diversity) at individual sites (Teske & Wooldridge, 2001): Medium-sized temporarily open/closed estuaries (more than 1 km but below 10 km in length), and small temporarily open/closed estuaries (less than 1 km in length). Medium-sized estuaries include the East Kleinemond (EK), Mpekweni (MP), Mtati (MT) and the Gqutwywa Estuary (GQ). Small temporarily open/closed estuaries are represented by the Kabeljous (KJ), Old Woman’s (OW) and Van Stadens (VS) Estuaries. Note that the Gqutwywa Estuary was hypersaline during the study period (salinity range 35.5–39.6), but this had no significant effect on species composition and ecological indices (Teske & Wooldridge, 2001).

1.1.2. Marine-dominated open estuaries (OM)

Relatively large, freshwater deprived estuaries are represented by the Kromme (KR) and Kariega (KA) Estuaries. Even though base flow is kept to a minimum as a result of impoundments, both remain permanently open. Salinity values remain close to that of the sea along the estuaries’ entire length, and at times these estuaries become hypersaline, particularly in the upper reaches. Even though the Swartkops Estuary (SW) exhibits a salinity gradient (Baird, 1999), it has been included in this group. Because of a naturally low freshwater input, salinities approximate that of the sea (McLachlan & Grindley, 1974). Consequently, its species composition and magnitude of ecological indices are similar to the two freshwater deprived estuaries (Teske & Wooldridge, 2001). Although the effect of tides on the physical and chemical environment of marine dominated permanently open estuaries may be considerably greater than in estuaries assigned to the three other groups, the comparatively low tidal height along the South African coast (0–2 m; Schumann, Largier, & Slinger, 1999) suggests that environmental conditions do not change drastically both on a daily basis and during a lunar cycle. Cooper et al. (1999) stated that tidal

Fig. 1. Map of the sampling area. Estuaries sampled are labelled with acronyms, which are explained in the text. Any other estuaries and bodies of water in the sampling area that were not included in the analysis are numbered. Many of the larger rivers are not shown in their entire length.
range in South Africa is too small for tidally dominated systems on a global scale to be recognised.

1.1.3. River-dominated open estuaries (OR)

The remaining permanently open estuaries investigated have strong freshwater inputs and full salinity gradients along their horizontal axes. River-dominated permanently open estuaries are represented by the Great Fish (GF), Keiskamma (KE) and Sundays (SU) Estuaries. In comparison with many other parts of the world, the flow of freshwater into South African estuaries is limited (Schumann et al., 1999). The Sundays Estuary, for example, has an average flow rate of 1 m$^3$s$^{-1}$ during winter and 2.7 m$^3$s$^{-1}$ during summer (Scharler, Baird, & Winter, 1998) as compared to about 18 400 m$^3$s$^{-1}$ measured in the Mississippi (Milliman & Meade, 1983). Consequently, these estuaries do not flush dramatically during the rainy season, but merely experience a shift in the salinity regime downstream. Even though drastic changes in salinity regime and the nature of the sediment may occur during freshwater floods, it is possible that much of the estuarine macrobenthos survives floods. Reddering and Esterhuysen (1987) found that floods produced significant scour in the sandy lower reaches of three medium-sized (<10 km but >1 km) estuaries. The muddy middle section of the estuaries, on the other hand, was largely unaffected. No freshwater floods were recorded during the study period, suggesting that no dramatic changes in the composition and abundance of estuarine macrofauna occurred between the two sampling expeditions. Although a limited number of low-salinity taxa became more abundant in the upper reaches of river-dominated open estuaries (OR) during the rainy season, no significant differences in density, species richness and diversity of macrobenthos were found within each of the four estuarine groups between the seasons (Teske & Wooldridge, 2001).

Taking into account the above considerations regarding the effect of abiotic variables on zonation patterns and the presence of four types of estuaries, the following hypotheses were tested in this study:

1. The relative importance of salinity in determining macrobenthic zonation patterns decreases from marine-dominated open estuaries (dominated by marine species) to river-dominated open estuaries (large estuarine component) to temporarily open/closed estuaries (dominated by the estuarine component).
2. The four types of estuaries can be distinguished based on the relative abundance of Day’s (1967a) estuarine components within each type.
3. Seasonal differences in the relative abundance and species composition of Day’s (1967a) estuarine components exist among the four types of estuaries. These are particularly pronounced in marine-dominated open estuaries because of increased freshwater inflow during the rainy season.

2. Materials and methods

Two sampling surveys were undertaken and the data analysed. Whenever results from the two surveys were similar, only information collected during December 1998 and January 1999 (austral summer, rainy season in the Eastern Cape) is presented in figures. Results from the other sampling trip (undertaken in June 1998 during the austral winter) are contrasted if seasonal differences were evident.

2.1. Sampling procedure

Subtidal benthic macrofauna was sampled at sampling sites that varied in number, depending on estuarine size. Large estuaries, such as the Sundays or Kariega, had up to nine sampling sites, whereas smaller estuaries had fewer, but at least two. Sites spanned the entire length of each estuary in order to incorporate possible salinity variations, sediment changes and depth changes. Before sampling commenced at each particular site, temperature and salinity were measured at the bottom using a Valeport CTD meter, and depth was recorded. After that, a total of 10 grab samples per site were taken using a van Veen grab (200 cm$^2$ in area, depth sampled down to 10 cm). The grab sampler was operated from a small boat. The first grab sample was used as a sediment sample, while the other nine were used as macrobenthos samples. Sets of three grab samples were immediately transferred to large plastic bags and preserved in 10% formaldehyde. Each of the three replicates thus represented a sampling area of 3 $\times$ 200 cm$^2$. The mean calculated from the three replicates was subsequently corrected to number of individuals m$^{-2}$. Each of the three sets of samples was collected in a different spot and covered an area of about 10 m$^2$. Samples were taken in, or close to the main channel, to ensure that all sites were truly subtidal. In the intertidal area, some zonation along the tidal elevation gradient exists (Warwick, 1971), which might have obscured trends in zonation patterns along the long axes of the estuaries. Average depth was similar in all systems, ranging between 1 and 2 m in permanently open estuaries, and between 1 and 1.5 m in temporarily open/closed estuaries.

2.2. Laboratory procedure

Macrobenthos was extracted following the method outlined in Schlacher and Wooldridge (1996), with a modification in the protocol aimed at improving extractions from sandy samples.
samples were accomplished by repeated decantation. This was done at least three times, or until no more specimens could be detected. Remaining sand was examined for the presence of macrobenthic organisms too heavy to be effectively extracted by decantation (large bivalves and gastropods) before sediment was discarded. Muddy samples were spread on a sieve with 1 m² surface area and 0.25 mm aperture size and gently washed with a garden hose, until no more mud remained. Many of the samples from the upper reaches of estuaries contained large amounts of plant material, which was largely removed after washing it off thoroughly and carefully picking off any animals that clung to it. What remained was subjected to the decantation procedure. Much of the remaining plant matter, as well as pebbles and sand, could be effectively removed this way. All samples were then gently sieved through a mesh of 0.5 mm aperture size. This mesh-size was considered a good compromise between 1 mm, the level often used as the lower limit of macrobenthos size (Day, 1981), and 0.25 mm, which Schlacher and Wooldridge (1996) considered more useful for the determination of zonation patterns. All organisms were again preserved in 10% formaldehyde, containing the dye rose bengal. The two-step fixation procedure may not be ideal for dye uptake, but since the extraction procedure took several weeks, the purpose of the first formaldehyde fixation was to prevent rotting of the samples. All individuals from samples were identified as far as possible by means of taxon descriptions in Griffiths (1976), Kensley (1978), Kilburn & Rippey (1982), Branch, Branch, Griffiths & Beckley (1994), Ruppert & Barnes (1994) and Steyn & Lussi (1998) and counted under a binocular microscope.

Sediment samples were oven-dried at 100°C for 24 h. Approximately half of each sample was weighed, gently ground, and the mud (i.e. clay and silt) portions removed by washing them through a 63 μm mesh sieve. The remaining sediment was again dried at 100°C for 24 h, and re-weighed. The percentage of the initial mass lost represented the mud content (by dry mass) of a particular sample.

2.3. Data analysis

Species diversity has been shown to increase from an estuary’s head to its mouth (Remane & Schlieper, 1971). Assuming approximately equal densities in upper and lower reaches of Eastern Cape estuaries (see Teske & Wooldridge, 2001), individual species found in the upper reaches consequently tend to have higher densities than those in the lower reaches. Because individual taxa from the upper reaches were numerically dominant, and the lower reaches were in most cases inhabited by a mixture of estuarine and marine species, biotic zonation patterns were determined by using taxon groups rather than individual species. There is a paucity of information on environmental conditions required by most of the species identified, and requirements of their larval stages are largely unknown. Consequently, it was not feasible to group taxa on the basis of whether they are estuarine (i.e. complete all their life cycles within an estuary), anadromous or catadromous. Instead, taxa were grouped empirically by virtue of their affinities with either salinity or sediment particle size as identified by canonical correspondence analysis (CCA). Zonation patterns were then identified by means of non-metric multidimensional scaling (NMDS) using taxon groups. Details of this procedure, as well as additional investigations, are discussed subsequently.

2.3.1. Canonical correspondence analysis

Only taxa whose proportion of total abundance at any one site was greater than 5% were included in this and subsequent multivariate analyses. CCA is an eigenvalue ordination technique designed for direct analysis of the relationships between multivariate ecological data tables (ter Braak, 1986). A regression model is inserted in the ordination model with the result that the ordination axes appear in order of variance explained by linear combination of independent (environmental) variables. The multiple regression thus constrains the ordination scores. In this study, CCA was used as a method to investigate the affinity of the taxa sampled with environmental variables (inverse or r-type analysis). CCA was implemented using the program PC-ORD (McCune & Mefford, 1997). Data were standardised by centering and normalizing, and ordination scores were scaled by optimizing for taxa rather than sites. Taxa that exhibited similar affinities with specific environmental variables were grouped, and these groups were used to determine zonation patterns (see next paragraph).

2.3.2. Non-metric multidimensional scaling

NMDS is an ordination method that is well suited to data that are non-normal or are on arbitrary, discontinuous or otherwise questionable scales (McCune & Mefford, 1997). Being based on ranked distances, it linearises the relation between environmental distance and sociological (site or species) distance (Beals, 1984). MDS (as implemented in the PC-ORD package) was chosen as ordination method to identify zonation patterns based on site scores (normal or q-type analysis). The Sørensen coefficient was used to calculate distances between two site scores. Sørensen distance is measured as percent dissimilarity and is defined as $1 - 2w/(a + b)$, where $w$ is the sum of shared abundances and $a$ and $b$ are the sums of abundances in individual sample units.

Unlike in CCA, environmental variables do not influence the arrangement of site scores on NMDS ordination plots. To interpret which environmental variables are responsible for biotic patterns, a geometric shape representing the magnitude of the variable is
superimposed on to each site score, and the significance of
the variable is determined by visually assessing how
clustering of sites or species corresponded to geometrical
shapes of a certain size range. The number of dimen-
sions to be used was determined by plotting final stress
vs. the number of dimensions (‘scree test’, Cattell, 1966).

Given the volume of data from the 83 sites on 13 estu-
aries (summer data), differences between faunistic zones
were not sufficiently distinct for site clusters to form. In-
stead, biotic zones were identified by visually assessing
patterns shown by environmental variables and numeri-
cally dominant taxon groups associated with these. The
method is discussed in detail in Teske and Wooldridge
(2001). As zonation patterns were similar in both seasons,
only ordination plots for summer data are shown.

Information from the CCA analysis was used to plot
proportional abundances of taxon groups for each of
the four types of estuaries. The NMDS plots were then
used to determine proportional abundances of taxon
groups in different zones within estuarine types.

3. Results

3.1. Determination of zonation patterns

3.1.1. Canonical correspondence analysis

Ordination plots of the first two axes of both winter
and summer data are shown in Fig. 2. In both seasons,
% mud content was most highly correlated with the first
axis, while salinity was correlated with the second axis.
Temperature and depth are not represented by environ-
mental arrows in Fig. 2a because the difference between
correlations with axes 1 and 2 were considerably below
those determined for the other variables. Environmental
arrows of salinity and particularly mud content are
nearly orthogonal, indicating lack of correlation be-
tween these variables. In Fig. 2b, arrows representing
mud content and depth are nearly parallel (same direc-
tion, i.e. positively correlated), whereas those of salinity
and temperature are in opposite directions (i.e. nega-
tively correlated). The variation explained by the first
three axes was low both in winter (axis 1, 6.6%; axis
2, 5.3%; axis 3, 3.3%) and summer (axis 1, 7.5%; axis
2, 4.7%; axis 3, 3.4%). Nevertheless, the CCA plots were
suitable to assign most taxa to one of four taxon
groups (high-salinity taxa, oligohaline taxa, sand zone
taxa and mud zone taxa). Taxa that seemed independent
of either salinity or sediment characteristics (particularly
if affinities to environmental variables differed between
the seasons) were grouped together and treated as a fifth
group. This group also included taxa too rare to be con-
fidently placed into any of the other groups. Scientific
names and acronyms of taxa constituting the five taxon
groups are listed in Table 1.

3.1.2. Non-metric multidimensional scaling

Reducions in stress values were minimal beyond
three dimensions (k = 2, 4.0; k = 3, 12.6; k = 4, 9.5). Site
arrangement and salinity do not show any relationship
(Fig. 3a), suggesting that salinity plays only a minor role
in determining community patterns. Fig. 3b indicates
that the nature of the sediment, rather than salinity, is
the major determinant of observed faunistic zonation
patterns. Plots including water depth showed patterns
similar to those in Fig. 3b, but mud content showed the
trend more clearly. Note that this pattern does not change appreciably when using individual species rather
than taxon groups (Teske & Wooldridge, 2001).

Consequently, sites were grouped into two major
zones both based on the mud content and on the pres-
ence of typical estuarine species: a sand zone, whose sites
had a mud content not greater than 5%, and a mud
zone, where the sediment contained more than 5% mud.

In addition to the two major zones, an oligohaline
zone was identified in the upper reaches of the three
river-dominated estuaries during summer (rainy season).
The most characteristic taxa found were larvae of Chiro-
nomid sp. (Chi) and oligochaetes (O1), which were ab-
sent from most other sites. The amphipod Corophium
triaenonyx was also common in this zone, but as this spe-
cies was also abundant at salinities close to seawater at
individual sites, it was not grouped with the oligohaline
taxa.

3.1.3. Proportional abundance of taxon groups

Taxa associated high salinity dominated the mouth
areas of river-dominated open estuaries during winter
(Fig. 4a). During the rainy season, their proportional
abundance in this part of the estuary decreased, and cor-
respondingly, the proportion of oligohaline taxa found
in the upper reaches increased (Fig. 4b). Seasonal differ-
ces in the proportional abundance of taxa associated
with salinity ranges were also found in freshwater-
deprieved open estuaries and small, closed estuaries.
Paradoxically, Chironomid larvae (associated with low
salinities) were common in the lower reaches of both es-
tuarine types during the dry season. During the rainy
season, on the other hand, they were virtually absent
from both types of estuaries. The fauna of medium-sized,
closed estuaries was clearly divided into species associ-
ated with sand (mouth area), and species associated with
mud (remainder of estuaries). Taxa whose distribution is
limited by the salinity regime were absent, and seasonal
differences in faunal composition were minimal. Small,
closed estuaries differed considerably from their larger
counterparts. First, it was difficult to divide these estua-
ries into a sand zone and a mud zone, because despite
differences in sediment particle size, taxon compositions
did not change much with horizontal distance. Secondly,
the relative proportion of taxa that could not clearly be
associated with a particular salinity or sediment particle
size, was higher. Two estuarine species, the amphipod *Corophium triaenonyx*, and the polychaete *Ceratonereis keiskamma*, dominated this taxon group in small, closed systems.

### 4. Discussion

Two major trends emerged in this study. First, the nature of the sediment is more important than salinity in limiting the distribution of macrobenthos in all four types of estuaries studied. This may have been overlooked in previous studies because of the strong correlation between salinity and sediment particle size. Secondly, both variables have an effect on macrobenthic distribution patterns on a large scale (in terms of kilometres). The importance of salinity decreases away from the mouth, as the number of marine species decreases, and increases again towards the estuarine head (river dominated estuaries during the rainy season only).
Table 1
Taxon codes and scientific names of species identified in this study. Each species has been assigned to one of four taxon groups, depending on affinities with environmental variable identified in Fig. 2.

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<th>Sand zone taxa</th>
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P.R. Teske, T.H. Wooldridge / Estuarine, Coastal and Shelf Science 57 (2003) 225–238
The type of sediment-associated fauna also changes away from the mouth area (transition from sandy to muddy sediment), which is evident particularly in medium-sized temporarily open/closed estuaries, where both marine and low-salinity faunas are largely absent. This may set South African estuaries apart from estuarine systems in the Northern Hemisphere, where “salinity is the major factor influencing regional distributions, while sediment characteristics strongly influence local distributions” (Carriker, 1967). Both observations are the result of South African estuaries being dominated by species whose distribution is relatively independent of salinity, and to which the nature of the sediment and associated variables are consequently more important factors limiting their distribution.

Salinity tolerance for a given species is not constant but varies with season, salinity experience, and temperature (Castagna & Chanley, 1973). Apart from that, there are numerous ways in which estuarine organisms may evade temporarily unfavourable salinity conditions, which make it difficult to determine their salinity tolerance limits from distribution patterns. These include vertical or
horizontal migration, production of protective substances covering sensitive body surfaces, retreat into holes and burrows, withdrawal of sensitive body parts, closure of shells or comparable structures or transitions into resting stages (Kinne, 1967). Many estuarine organisms can thus survive periods of adverse salinity conditions, but if these conditions persist longer, they will have an effect on the distribution even of such species.

However, if the change in salinity is large enough and occurs rapidly, for most invertebrates the salinity effect will override substratum preferences (Culter, Mote Marine Laboratory, personal communication). Bassindale (1943) noted “if the salt content of the water in which they are living is changed sufficiently slowly, many animals can acclimatise themselves to large changes. Thus although the magnitude of the change is important, the rate of change is also significant”.

Experimental tests of the salinity tolerance of estuarine animals usually give the animals very little time to adapt. Examples include Castagna and Chanley (1973), Qiu and Qian (1999), Pechenik, Berard, and Kerr (2000) and Brito, Chimal, and Rosas (2000). Richmond and Woodin (1996) changed experimental salinities in a stepwise fashion (a salinity change each hour over a 6-h period) in order to mimic the salinity changes in an estuary after a storm event. In most South African estuaries, such drastic changes may be observed during freshwater floods. In general, however, the benthic fauna has considerably more time to adapt to gradual changes in the salinity regime. It is known that many benthic taxa in South African estuaries are able to tolerate a wide range of salinities. For most South African estuarine species a salinity range of 5–55 is usually considered non-lethal (de Villiers & Hodgson, 1999). Scylla serrata, a large swimming crab commonly found in estuaries along the South African coast, even has a salinity tolerance range from 2 to 89 (Hill, 1979). The distribution of many macroinvertebrates in South African estuaries is consequently relatively independent of salinity.

In all four types of estuaries studied, the proportional abundance of the estuarine component was greater than that of the marine and freshwater components combined. Medium-sized temporarily open/closed estuaries are even inhabited almost exclusively by estuarine species. Estuarine endemics are also an important component of the South African estuarine ichthyofauna. The contribution of estuarine species declined from 99% in the Bot River Estuary (closed for 3 years) to 81% in the seasonally open Kleinmond Estuary and to 46% in the permanently open Palmiet Estuary (Bennett, 1989), suggesting that the magnitude of the nekton’s proportional abundance depends on the temporal extent of mouth closure (Bennett, 1989). The importance of estuarine endemics in South African estuaries suggests that a classification system based entirely on salinity tolerance is not suitable to explain the zonation patterns observed. Even though a method of determining estuarine zones based on salinity tolerance of biological organisms has recently been developed (Bulger, Hayden, Monaco, Nelson, & McCormick-Ray, 1993), and even though Day’s (1967a, 1981) classification system is still considered useful by researchers studying Australian and South African estuaries (De Villiers & Hodgson, 1999; Jackson & Jones, 1999), such systems could be improved by adding sediment characteristics as an additional factor influencing the distribution of benthic organisms. A classification system for Eastern Cape estuaries following Day’s (1981) method of assigning estuarine species to different components is shown below. The migrant component is not included, as its presence did not clearly emerge in this study.

4.1. Components I and II

Steno- and euryhaline marine species. These two faunal groups are important in the lower reaches of permanently open estuaries only. Stenohaline marine forms are restricted to salinities close to seawater, whereas some euryhaline marine species are able to penetrate further up estuaries. In this study, the numerical abundance of individual marine species was too low to be able to assign any of them to either the steno- or euryhaline component with certainty.
4.2. Component III

A eurytolerant estuarine endemic sand fauna. In Eastern Cape permanently open systems, the zone inhabited by the sand fauna is also inhabited by marine fauna. Hence, it is difficult to separate the three components on the basis of distribution, as the presence of group III species is dependent on sandy sediment that mainly occurs near the estuary mouth. Because of this habitat sharing, the proportional abundance of estuarine endemic sand species is lower in open estuaries than in closed estuaries. In medium-sized temporarily open/closed systems, the estuarine endemic sand fauna is present in its pure form.

4.3. Component IV

An estuarine endemic mud fauna, also tolerant of a wide range in salinity. Diversity of this group is higher than that of the estuarine endemic sand fauna, but particularly in medium-sized temporarily open/closed estuaries, their densities are below those of component III species (Teske & Wooldridge, 2001). This explains why their proportional abundance is not much greater in this estuarine type, even though most sites contained muddy sediment.

4.4. Component V

An oligohaline fauna, to which sediment characteristics are less important than is the case in the previous two groups.

It is important to note that even though salinity and sediment type explain much of the zonation patterns observed in Eastern Cape estuaries, a large proportion of taxa seems to be relatively independent of either environmental variable. Among the more abundant species identified, the polychaetes Capitella capitata complex, Ceratonereis keiskamma and Prionospio sp., the amphipods Grandidierrella lignorum, G. lutosa and Corophium triaenonyx, as well as the isopod Xenathura sp. could not clearly be assigned to any of the above groups. Excluding some or all of these taxa from the databases used to construct CCA and NMDS plots considerably increased percentage of variation explained by each of the axes and site separation, respectively (not shown). The fact that most of the species in the group of taxa with 'uncertain' preferences were found in all four types of estuaries (Teske & Wooldridge, 2001) suggests that most of these are estuarine endemic species which are not closely associated with the sediment, but whose distribution is limited by physical, chemical or biological factors not investigated in this study. The polychaete of the C. capitata complex, however, may equally well be a euryhaline marine species. These worms live in the sediment (Day, 1967b), which increases their independence from salinity, as salinity fluctuations in the substrate are less pronounced than in the free water above (Kinne, 1967).

Sediment particle size may be equally important in determining the horizontal distribution of many intertidal macrobenthic species as it is for subtidal macrobenthos. McLachlan and Gridley (1974) found that in the Swartkops estuary, substrate is by far the most important limiting factor influencing the distribution of two anomurans, the mudprawn (Upogebia africana) and the sandprawn (Callianassa kraussi). Both species were found to be completely restricted to their preferred type of substrate, and no overlap between the two populations was found.

Day (1967a) stated that “there is every indication that the findings derived from the benthic fauna are applicable both to fishes and other nekton and to the plankton". Even though most of the recent studies on nekton in estuaries of the Southern Hemisphere did not include any sediment characteristics as environmental variables (Cyrus & Blaber, 1992; Loneragan, Potter, & Lenanton, 1989; Potter, Hyndes, & Baronie, 1993; Young, Potter, Hyndes, & de Lestang, 1997), zonation patterns of most estuarine fishes are probably independent of the type of substratum. For example, Loneragan, Potter, Lenanton, and Caputi (1986) found that changes in faunal composition in the Australian Peel-Harvey Estuary were most highly correlated with salinity. In the Swan Estuary, on the other hand, shifts in faunal composition were related first to distance from the estuary mouth and then to salinity (Loneragan & Potter, 1990). Exceptions include benthic fishes such as the Australian goby Pseudogobius olorum, which prefers sediment with a high silt content (Gill & Potter, 1993).

Strydom et al. (submitted for publication) found that salinity zones played a significant role in both species density and the presence or absence of species of ichthyoplankton in both permanently open and temporarily open/closed Eastern Cape estuaries. The mesohaline zone (salinity 5–17.9), which is associated with the river estuary interface (REI) present particularly in river-dominated open estuaries, was found to support the highest densities of larval fish. The high concentration of suspended particulate matter in this region is considered to form the basis for biological functioning in estuaries. Macrobenthic densities in river-dominated open estuaries are significantly lower than in the three other types of estuaries (Teske & Wooldridge, 2001). Furthermore, sites located in the mesohaline zone had among the lowest densities of any of the sites sampled in these estuaries, with some sites in the Great Fish and Sundays Estuaries being nearly devoid of macrobenthos.

The four types of estuaries could be distinguished on the basis of relative abundance of different components of estuarine fauna, and the importance of taxa
associated with a certain salinity environment decreased from river-dominated open estuaries to marine-domin- 
ated open estuaries to temporarily open/closed estu- 
aries. Interestingly, the larvae of Chironomus sp. (the 
sole representative of the oligohaline component in es-
tuaries other than river-dominated open systems) were 
more abundant in small estuaries than in medium-sized 
estuaries. They were also abundant in marine-domi-
inated open estuaries. This has been attributed to the 
fact that both types of estuaries experience less vari-
ation in salinity values because of low freshwater input, 
suggesting that Chironomus larvae are able to acclima-
tise to salinities approaching that of seawater if given 
sufficient time.

Even though two of the marine-dominated open es-
tuaries (Kariega and Kromme) are considered mere ex-
tensions of the sea, the importance of estuarine endemics 
in these systems is nevertheless considerable. The pro-
portion of endemic sand zone species is roughly equal 
to that of the marine component, whereas the number 
of endemic mud zone species is much greater. While 
the lack of salinity variation has enabled many steno-
haline marine species to survive in these estuaries, they 
have not replaced the estuarine endemics. As in river-
dominated permanently open estuaries, the marine com-
ponent is restricted to the lower reaches, where it shares 
habitat with the estuarine endemic sand fauna. This 
suggests that even though salinity is the primary variable 
limiting the distribution of the marine component, sandy 
sediment is also important to these species. The marine 
component is nearly absent from muddy sites within 
marine-dominated open estuaries, even though salinities 
were around seawater during the study period. As in 
medium-sized temporarily open/closed estuaries, this 
part of the estuaries is dominated by an estuarine en-
demic mud zone community.

As compared to river-dominated open estuaries, 
there is little support for the hypothesis that marine do-
nominated open systems have a greater proportion of taxa 
whose distribution is limited by salinity. During winter, 
the proportion of high-salinity taxa was even slightly 
greater in the river dominated systems. However, 
marine-dominated open estuaries contain a greater pro-
portion of taxa whose affinity to environmental vari-
ables is uncertain. The distribution of some of these 
may be limited by salinity, but this did not clearly 
emerge because of very low numerical abundances of 
most of the species in this group. Both types of tem-
porarily open/closed estuaries, on the other hand, are 
dominated by true estuarine species, supporting the 
hypothesis that these systems contain fewer species 
limited by salinity than either type of open estuary. 
The reason for the comparatively large number of spe-
cies in small estuaries that could not be assigned to any 
particular macrobenthos component may be related to 
the observation that sand zone and mud zone species 
were found to be less clearly separated than in medium-
sized estuaries. When such estuaries close, macrobenthic 
composition may change faster than sediment, and after 
some time, many ‘quiet-water species’ will be found in-
habitating ‘running-water sediments’, and vice versa.

A previous study using the same database found that 
macrobenthic density, species richness and abundance 
did not change significantly among sites within any of 
the estuaries studied between the seasons (Teske & 
Wooldridge, 2001). However, seasonal differences in 
proportional abundance of estuarine components were 
evident in river-dominated open estuaries, where the 
lower reaches were dominated by the marine component 
in winter, and the upper reaches were dominated by 
the oligohaline component during summer. No seasonal 
differences were evident in Medium-sized temporarily 
open/closed estuaries. This suggests that seasonal differ-
ences in faunal composition of estuaries are brought 
about by changes in the amount of freshwater inflow 
rather than changes in temperature.

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