Affinities of some common estuarine macroinvertebrates to salinity and sediment type: empirical data from Eastern Cape estuaries, South Africa

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Fourteen species of subtidal macrobenthos present in thirteen Eastern Cape estuaries, South Africa, were compared with regard to correlations with two important environmental variables (salinity and sediment mud content). Species were divided into five different faunal components based on their affinity with one of the two variables, namely marine species, oligohaline species, estuarine sand species, estuarine mud species, and species whose distribution seemed independent of either environmental variable. Although most species exhibited wide tolerance ranges to both environmental variables, preference ranges could be identified in many cases. Among the fourteen species studied, three were found mostly at high salinities, two were confined to sandy substratum, and four showed a clear preference for muddy sediment. The crab Paratylodiplax algoense was identified as a euryhaline marine species and the larvae of chironomid midges, previously believed to be oligohaline species, were found to be tolerant to near-seawater salinities.

Key words: subtidal macrobenthos, true estuarine species, estuary, salinity, substratum.

INTRODUCTION

The fauna in estuaries consists of calm-water species (Day 1959, 1981), and distribution patterns of these within estuarine systems are most frequently studied by focusing on salinity (e.g. Chapman & Brinkhurst 1981; Wolff 1983; Holland et al. 1987; Peterson & Ross 1991; Dauer 1993; Cyrus & Blaber 1992; Peterson 1996; Maes et al. 1998; Cervetto et al. 1999). The obvious reason for this is the highly variable nature of salinity distribution both in time and space, a characteristic unique to estuaries. In order to survive fluctuations and extremes in salinity, species living in estuaries either osmoregulate, or employ strategies that help avoid or reduce exposure to the surrounding medium during periods of rapid salinity change.

The salinity variation encountered in estuaries has led many researchers to conclude that the distribution of organisms within an estuarine system depends mainly on their ability to tolerate a certain range of salinities (e.g. Kinne 1963; Remane & Schlieper 1971; Day 1951, 1967a; McLusky et al. 1982, McLusky 1986). However, other environmental variables also influence distribution patterns of species in estuaries (e.g. Day 1964; McLachlan & Grindley 1974; Wu & Richards 1981; Jones & Simons 1982; De Decker & Bally 1985; Roast et al. 1998; Vivier & Cyrus 1999), and the nature of the sediment seems to be of major importance to benthic species in particular. While salinity is important in limiting the distribution of stenohaline and euryhaline marine species and freshwater species, the distribution of ‘true estuarine species’ seems to be relatively independent of the salinity of the surrounding water (Boesch 1977; Teske & Wooldridge 2001, 2003). For most South African estuarine species, a salinity range of 5–55 is considered non-lethal (de Villiers et al. 1999).

Owing to the relative independence of true estuarine species from salinity, and because of their numerical dominance, dividing Eastern Cape estuaries into regions characterized by a certain type of sediment (e.g. a sand zone and a mud zone) can be considered more appropriate to account for observed distribution patterns than dividing them into polyhaline, mesohaline and oligohaline zones. In the present paper, this point

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is elaborated on by presenting empirical data from some of the numerically dominant representatives of the different groups of estuarine macro-invertebrates (retained by a 500 µm mesh) present in Eastern Cape estuaries. These data are analysed using a more sensitive method than the one employed in Teske & Wooldridge (2003).

METHODS

The thirteen estuaries sampled in this study are located in the western part of the Eastern Cape province (Fig. 1). The sampling area stretches from the Kromme Estuary in the west to the Keiskamma Estuary in the east. As most of the species dealt with in this paper are represented in both open and temporarily open/closed estuaries, no distinction was made between these two types of estuaries.

Samples were obtained on two successive sampling expeditions during June 1998 and December/January 1999. Subtidal benthic macrofauna was sampled at selected sampling sites that varied in number between two and nine, depending on the length of individual estuaries. Large estuaries, such as the Sundays or Kariega, had up to nine sampling sites, whereas smaller estuaries had proportionally fewer. Sites spanned the entire length of each estuary in order to incorporate possible salinity and sediment changes. Prior to sampling, near-bottom salinity was measured using a Valeport CTD meter, and a sediment sample was collected using a van Veen grab (200 cm² in area, sampling down to 10 cm). Nine grab samples were taken per site, and sampling and laboratory procedures followed the protocol described previously (Teske & Wooldridge 2001, 2003). Mud content was used as a variable representing the sediment, because it was previously found to explain distribution patterns well. Sediment grain size and organic content showed similar trends. The fact that only subtidal macro-benthos was sampled was crucial to this study. Unlike intertidal benthos, sampling of subtidal benthos is independent from the level of the tide, and the effect of dehydration, slope, and tidal range is eliminated.

The species focused on in greater detail in this study are listed in Table 1 and were selected as follows: several of them were previously identified as being important representatives of the estuarine faunas inhabiting either the sand zone...
Table 1. Presence of selected estuarine taxa in Eastern Cape estuaries. Estuarine systems and taxa are divided into categories based on criteria of Teske & Wooldridge (2001) and Teske & Wooldridge (2003).

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<tr>
<th>Taxon name</th>
<th>Acronym</th>
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1Faunal components: 1) high salinity species; 2) estuarine sand zone species; 3) estuarine mud zone species; 4) oligohaline species; 5) uncertain.

2Acronyms for Eastern Cape estuaries: SU = Sundays; GF = Great Fish; KE = Keiskamma; SW = Swartkops; KA = Kariega; EK = East Kleinemond; MP = Mpekweni; MT = Mtati; KJ = Kabeljous; VS = Van Stadens; OW = Old Woman's.
or the mud zone (Teske & Wooldridge 2001) during both seasons. Representatives of the estuarine sand zone fauna include the amphipod _Urothoe serrulidactylus_ and the cumacean _Iphinoe truncata_; the estuarine mud zone fauna is represented by the isopod _Cyathura estuaria_, the bivalve _Macoma litoralis_, the tanaid _Apsides digitalis_, and the polychaete _Dendronereis arborifera_. Other common estuarine species included two species of the polychaete genus _Prionospio_, namely _P. sexoculata_ and a new species of _Prionospio_; a representative of the polychaete species complex _Capitella capitata_; the amphipod _Corophium triaenonyx_; and larvae of a local species of chironomid midges. To compare salinity and sediment preferences of the above taxa to representatives of the less numerous stenohaline marine fauna and the oligohaline fauna, the following species were also included: first, the polychaete _Levinsenia oculata_ was chosen, because it was the numerically dominant species of the stenohaline marine fauna. It was present in the lower reaches of the marine-dominated Kromme, Swartvlei and Kariega Estuaries only. Second, a species of oligochaete was included, which was found exclusively at sites characterized by low salinity in the upper regions of the river-dominated Sundays, Great Fish and Keiskamma Estuaries (Table 1).

Clusters associated with a certain mud content or salinity value may be due to the greater frequency of sampling sites having that specific attribute. It was therefore considered important to derive some measure of preference for a particular environmental variable, so mean abundance of a taxon was determined using abundance records of all the estuaries in which that taxon occurred during a particular sampling period. If the taxon’s abundance at a site in a specific estuary fell below the mean, the status of that particular taxon was classified as ‘present’. If abundance was equal to, or greater than the mean, the taxon was considered ‘abundant’ at that site. At sites where the taxon was not only abundant, but also enjoyed a high ranking (i.e. the taxon was the most abundant or the second most abundant of all taxa at the site, and also had its highest or second highest level of abundance at that site in the same estuary), then the taxon was considered ‘prominent’ at that site. Finally, for each taxon, a geometric symbol representing the abundance rating was superimposed on salinity or percentage mud content encountered at the respective site.

**RESULTS**

The polychaete _Levinsenia oculata_ and the oligochaetes were confined to high and low salinity conditions, respectively (Fig. 2), although in the case of oligochaetes, this was apparent during summer only. During winter, this species was comparatively rare, as salinity values in the upper reaches of river-dominated estuaries approached near-freshwater conditions in the Great Fish and Sundays Estuaries only. _Levinsenia oculata_ was not found at salinities below 26.

As expected, the true estuarine species were found over a wide range of salinities (Fig. 2). This was particularly apparent during summer, when two mud zone species _Cyathura estuaria_ and _Apsides digitalis_ were prominent at near-freshwater salinities.

The two species of the genus _Prionospio_ differed considerably in their salinity preferences. While _P. sexoculata_ was restricted to salinity values not deviating much from seawater (it rated ‘prominent’ at salinities close to seawater and was not abundant below 32), _Prionospio_ sp. was abundant at a salinity of 13 during both seasons. The polychaete _Capitella capitata_ was mostly found at high salinities, but in one case it was ‘prominent’ at a salinity of 19. The sand zone species _Urothoe serrulidactylus_ and _Iphinoe truncata_ also exhibited wide salinity tolerance ranges, and _I. truncata_ was even present at salinities approaching that of freshwater during both seasons. The four mud zone species had similarly wide salinity tolerance ranges. _C. estuaria_ and _A. digitalis_ were both ‘prominent’ from almost freshwater to around seawater, and _Dendronereis arborifera_ was even ‘prominent’ at hypersaline conditions several times. The crab _Paratyldiplax algoense_ was found at high salinities during both seasons. Even though chironomid larvae were common at low salinities, they were also found at salinities close to that of sea water several times, and at one of the lower sites within the marine-dominated Kromme Estuary, this species even rated ‘prominent’ at a salinity of 35.

A separation between estuarine sand and mud faunas was evident from sediments with a mud content of about 20%, although both groups were also found at higher and lower mud concentrations, respectively (Fig. 3). _Urothoe serrulidactylus_ and _I. truncata_ were not ‘prominent’ above this level, whereas mud zone species were not ‘prominent’ in pure sand. The distribution of the other estuarine species seemed to be relatively independent of the nature of the sediment. The amphip-
Corophium triaenonyx, for example, was abundant both on pure sand and at mud concentrations up to 72%.

DISCUSSION

The results of this study show that even species known to be primarily associated with a certain salinity range or type of sediment may be found over a wide range of environmental conditions. The method of deriving a preference for a particular environmental condition by incorporating information on abundance, numerical dominance at a particular site, and intraspecific numerical maxima within an estuary considerably improved interpretability of the data, but nevertheless, results were not always clear-cut.

Numerical counts from biological surveys are challenging because they are often clumped, with zero values and potential outliers. In the present study, several factors are likely to have influenced the accuracy of the results. First, the effect of temporary deviations from long-term salinity values at individual sites during the sampling period may have caused salinity values at which
species were 'abundant' or 'prominent' to be above or below their actual optima. Estuarine species may avoid unfavourable conditions for a while by horizontal or vertical 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). Only if unfavourable conditions persist for a longer period will a species become excluded from a particular region of an estuary.

This would have been problematic, particularly in the three river-dominated, open estuaries, where salinities fluctuated extensively during summer because of increased freshwater inflow. In the case of mud content, the fact that sediment may not always have been completely homogenous could have influenced the results.

Because of these shortcomings, Figs 2 and 3 should be considered to depict general trends rather than absolute tolerance and optimum ranges. Nevertheless, the habitat preferences of

![Percentage mud](image-url)

**Fig. 3.** Abundance ratings of selected taxa at mud concentrations at which they were recorded; a) winter data; b) summer data. Encircled data points are discussed in the text. See Table 1 for names of taxa represented by acronyms.
some species can be recognized. *Levinsenia oculata* and *Prionospio sexoculata* were both found only at higher salinities. The fact that the former was exclusively present in marine-dominated, open estuaries, whereas the latter was found in four out of the six temporarily open/closed and all of the open estuaries studied, suggests that *L. oculata* is a stenohaline marine species, whereas *P. sexoculata* is euryhaline, and hence much better adapted to survive in estuaries. A similar preference for high salinities was identified in the crab *Paratryloidiplax algoense*. Although this species was previously grouped with estuarine mud zone species (Teske & Wooldridge 2003), the more sensitive categorization system employed in this study clearly indicates that *P. algoense* may not be an estuarine species at all, but rather a euryhaline marine species. The fact that it was present in all open estuaries, but in only one of the temporarily open/closed systems (Table 1) suggests that this species requires access to the sea because it has marine larval stages. The affinity of *P. algoense* with muddy sediment seems to be of secondary importance.

Oligochaetes and chironomid larvae were previously identified as members of an oligohaline fauna present particularly in the upper reaches of river-dominated estuaries (Teske & Wooldridge 2001, 2003). However, both taxa were found at salinities considerably higher than that of freshwater. In the case of oligochaetes, the single occurrence at a salinity of 19 in the upper reaches of the Keiskamma Estuary during the winter of 1998 may merely be an artifact of considerable fluctuations in salinity during that period. Chironomid larvae, on the other hand, were repeatedly found at higher salinity values, particularly in the freshwater-deprived Kromme Estuary. Hence, although this species seems to prefer low salinities and is sometimes considered a freshwater organism (Blaber *et al.* 1984; Davies 1984; De Decker & Bally 1985), it is likely that it is able to acclimatize to higher salinities in estuaries characterized by little variation in the salinity regime.

True estuarine species were commonly found at higher salinities (13–35). Although extremes in salinity may become stressful even to species that are good osmoregulators (e.g. Jones 1981; Campbell & Jones 1990), the main reason for this may be that salinity values were within this range at most of the sites sampled during both seasons. In individual cases, mud zone species were prominent at near freshwater salinity values, or at salinities higher than that of seawater. The preferences of some of the true estuarine species to a certain sediment type has long been known (e.g. Griffiths 1976; Kensley 1978; Kilburn & Rippey 1982), and in this study, affinities with certain concentrations of mud in the sediment were defined quite clearly: *U. serrulidactylus* and *I. truncata* were mostly present on pure sand, and the four mud zone species were mostly absent from such sites. Individual sites at which sand zone species were abundant in muddy sediment, and mud zone species were abundant in sediment containing very low mud concentrations, are focused on in more detail: *U. serrulidactylus* and *I. truncata* were both prominent at a site in the lower reaches of the Kromme Estuary where patches of muddy shell debris lying on pure sand occurred. It is likely that both species were present on the sandy portions of these sediment samples only, and hence, their presence at a mud concentration of 17% may be misleading. During winter, *Dendronereis arborifera* was the only mud zone species abundant at sites having sediment that contained less than 10% mud. Both of these sites were located in the small, temporarily open/closed Old Woman’s Estuary. In small estuaries, there tends to be an overlap of the distributions of faunal components that in larger estuaries are spatially separated, possibly because of the short distances between sites characterized by pure sand and sites characterized by higher sediment mud concentrations (Teske & Wooldridge 2003). The majority of sites at which mud zone species were found on sandy substrata (although they were not abundant in most cases) were sites within small estuaries. During summer, the mud zone species *Cyathura estuaria* and *Macoma litoralis* were abundant at a site located immediately downstream from muddy sites in the temporarily open/closed Mpekweni Estuary. In this case, the presence of small clumps of mud washed down onto an otherwise sandy substratum as a result of flushing during the rainy season may explain the presence of large numbers of mud zone species in this portion of the estuary. If one excludes these possible outliers from the analyses, then the estuarine sand zone and mud zone faunas separate at a sediment mud content of approximately 10%.

The remaining three species, the polychaetes *Capitella capitata* and *Prionospio* sp. and the amphipod *Corophium triaenonyx*, could previously not be grouped with any of the other estuarine faunal components, because their distributions seemed...
to be relatively independent of both salinity and sediment particle size. C. capitata polychaetes (present in all 13 estuaries studied, Table 1) remain in the sediment (Day 1967b), which increases their independence from salinity, as salinity fluctuations in the substratum are usually less pronounced than in the free water above (Kinne 1967). The presence of Prionospio sp. in all seven temporarily open/closed estuaries suggests that this could be a true estuarine species whose distribution is relatively independent of the nature of the sediment, a notion that is corroborated by the fact that the two members of the genus Prionospio studied are characterized by very different salinity tolerance ranges. The amphipod C. triaenonyx was frequently found on pure sand, but unlike the estuarine sand zone species, it was also very common on sediment characterized by high mud concentrations. C. triaenonyx constructs tubes of fine sand or silt particles on the surface of solid objects on the substratum, enabling it to exploit a greater variety of habitats (Cyrus & Martin 1988). The relative independence of Prionospio sp. and C. triaenonyx from sediment mud content indicates that although the nature of the substratum seems to be an important environmental variable responsible for limiting the distribution of true estuarine benthic macroinvertebrates, it cannot explain the distribution of all of them.

Redefining ‘true estuarine species’

It must be noted that some of the taxa referred to as ‘true estuarine species’ in this study do not qualify as such according to Day (1981), who defined this faunal component as ‘species that have not been recorded in the sea or in freshwater’, and for that reason have also been referred to as ‘estuarine endemics’ (Day 1967a). For example, the amphipod U. serrulidactylus, which is an important estuarine sand zone species, also occurs on sand-banks outside estuaries (Griffiths 1976). Day (1981) stated that true estuarine species are dominant at low salinities only (i.e. in the upper reaches of estuaries). By contrast, the species previously referred to as ‘estuarine endemics’ by Teske & Wooldridge (2001, 2003) and Teske et al. (2003) were dominant along the entire length of estuaries. Despite low species richness, this group represents the most abundant component (as measured by number of individuals per unit area) of the subtidal macroinvertebrate fauna in temporarily open/closed estuaries of the Eastern Cape, where it comprises up to 85% of the total number of individuals, and up to 50% of the individuals in open estuaries. This result was based on the alternative definition that ‘true estuarine species’ are characterized by distributions that seemed independent of salinity, suggesting that these species are specifically adapted for long-term survival in the periodically catastrophic estuarine systems, and that the estuarine habitat may represent a primary ecological niche. Just like marine species are able to establish themselves in the lower reaches of estuaries (at least temporarily), the relative independence of true estuarine species from salinity should enable them to survive in the marine habitat, provided that other environmental parameters are favourable. In fact, invertebrate species previously believed to be exclusively estuarine have subsequently been found in the marine habitat (e.g. Harris 1970), and macroinvertebrates characterized by broad salinity tolerance ranges are abundant in the freshwater-deprived Kromme and Kariega Estuaries (Teske & Wooldridge 2003), although these systems are considered mere extensions of the sea. The term ‘estuarine endemic’ may thus be inappropriate, and the reason why true estuarine species are rarely found in the marine habitat may be due to the relatively low number of indendations along the highly exposed South African open coast (Cooper 2001), competition with marine species (McLusky 1981), unfavourable environmental conditions not directly related to salinity (e.g. absence of dense plant growth or unsuitable sediment) and possibly also insufficient sampling. The fact that even species considered to be ‘estuarine endemics’ based on Day’s stricter definition are widely distributed along the South African coast (e.g. Corophium triaenonyx occurs from Hermanus Lagoon to Mozambique; Cyathura estuaria occurs from Hermanus Lagoon to St Lucia; and Exosphaeroma hylocoetes occurs from the Mkomazi to Milnerton Lagoon; Day 1974; note that none of these has planktonic larvae) suggests that the marine habitat may not represent a significant barrier to the dispersal of these species. Lastly, some benthic species included in the present study as representatives of the estuarine mud fauna, which have also been found in the marine habitat and were previously considered ‘euryhaline marine species’ (Day 1974, 1981), do not actually seem to require access to the sea. Examples include D. arborifera, M. litoralis and A. digitals, all of which were common in the temporarily open/closed Gqutywa...
Estuary during a period of mouth closure between February 1998 and December 1999 (Teske & Wooldridge 2001). The tanaid A. digitalis was even found in freshwater in the Nhlabanwe coastal lake system 20 years after the construction of a barrage, which cut this system off from the sea (Vivier & Cyrus 1999).

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