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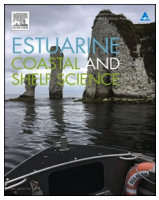

Constancy and change in macrobenthic abundance, biodiversity and assemblage structure along the axis of a flood-tidal sand delta

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A B S T R A C T

Flood-tidal deltas commonly occur along microtidal coasts in the mouths of those inlets kept open by tidal currents, but they have seldom been studied ecologically. Such a delta of fine sand occurs in the Knysna estuarine bay, South Africa, extending for some 2 km upstream. Although macrofaunal assemblage metrics (overall abundance, observed and estimated species density, geometric mean morphospecies abundance, evenness, and patchiness) varied little along the deltaic axis, faunal composition changed markedly though without species replacement except in the paraonid polychaetes. Unusually, the sand was dominated by these paraonids (especially *Paradoneis lyra capensis*) and, over its proximal half, also by the amphipod *Urothoe pulchella*, but worms steadily increased in importance upstream whilst crustaceans decreased. Noteworthily, a psammodrilid was present - the first record from Africa. The flood-tidal shore fauna contrasted in composition with that of the facing ebb-channel shore (dominated by *Dipolydora*) and areas upstream of the mouth.

1. Introduction

Along microtidal coasts, the mouths of those marine inlets kept open by tidal currents typically develop extensive flood-tidal deltas of sediment (Harris et al., 1992; Austin et al., 2018), and they are a common feature of estuaries in the Cape provinces of South Africa (Reddering and Rust, 1990). One such is in the Knysna estuarine bay in the Western Cape (Cooper, 2001), where the sediment concerned is largely fine-grained silica sand (mean particle size 0.18–0.25 mm) containing up to 25 % calcareous shell debris (Reddering and Esterhuysen, 1987; Cooper and Green, 2023). Its source is the major Tertiary-Pleistocene fossil coastal dune system immediately to the west of the mouth (Reddering and Esterhuysen, 1987; Illenberger, 1996). Sand eroded from the dune face is brought in by the flooding tide and deposited along the south-western shore of a bay island, itself a former flood-tidal sand bank created when local sea level was higher than at present (Flemming, 1977). This sediment forms a broad sandflat at LWS extending into the estuarine bay for 1.8 km as a single linear intertidal bank that gradually decreases in height. Tidal channels then occupy the western portion of the 15 m deep mouth region although the flood-tidal delta and channel are separated from the western ebb-tidal channel and shore by an elongate sand bank ('Pansy Bank') (Fig. 1).

Estuarine sands have been rather neglected relative to those of exposed oceanic beaches (McLachlan and Defeo, 2017), and likewise those of relatively mobile flood-tidal deltas have received less study than more stable sheltered sands in general. Very few have specifically considered the benthic macrofauna of flood-tidal delta sands as a habitat system in its own right, and although they are abundant in South Africa this situation applies to that country too. Studies that have been conducted include work in the deltas developed along the inlet between the Danish barrier island of Rømø and the German one of Sylt in the European.

Wadden Sea (Lackschewitz and Reise, 1998) and that in the mouth of the South African Nahoon Estuary (Bursey and Wooldridge, 2002, 2003). The Wadden Sea study was mainly directed towards the polychaete *Arenicola* and its burrow-commensal amphipod *Urothoe poseidonis*, whilst that in the Nahoon Estuary was particularly concerned with a faunal comparison of the delta with a sandy beach outside the estuary's mouth with which the delta was confluent, and with the estuarine regions further upstream, together with variation at different tidal heights. Here, species of *Urothoe* (*U. serrulidactylus* and *U. coxalis*) were also dominant members of the delta fauna. No study, however, seems to have investigated whether the faunal assemblages in the delta sands themselves change along their axial gradients, notwithstanding that they clearly often show linear habitat change from an exposed and unstable area near the mouth to their more sheltered zones upstream (e.g. Austin et al., 2018; Gong et al., 2023). Degree of exposure is after all considered to be one of the main environmental variables influencing macrofaunal assemblage composition (Jacquot et al., 2024).

Variation along the Rainbow Channel that cuts through the 140 km^2 flood-delta sands of the Eastern Banks region of Moreton Bay, Queensland, was indeed studied by Barnes (2023), but that investigation was

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restricted to such seagrass habitats as were present. In the seagrass, assemblage metrics of the associated macrofauna (faunal abundance, species richness, evenness and composition) remained effectively unchanged along the 12+ km length of the delta. It was considered likely, however, that seagrass systems constitute a special case because they create their own microclimate, including decoupling renewal times of the overlying water and local organic enrichment/decomposition state, permitting relative faunal constancy along environmental gradients. In contrast, bare sand does not achieve this, and its assemblages are known to vary more than those of adjacent seagrass beds along the general upstream gradient of an estuary (Barnes, 2022a). At least one area of the Rainbow Channel delta sand is also known to be dominated by a haustorioid amphipod, in this case by *Urohaustorius* (Barnes and Cottrell, 2024), the Australian equivalent of *Urothoe*. The Knysna estuarine bay is in several respects intermediate between the two huge leaky-lagoonal systems above (Wadden Sea and Moreton Bay) and the small narrow Nahoon Estuary, whilst the Queensland delta is structurally similar to the Knysna one in that the sand derives from immediately adjacent fossil coastal-barrier dune fields of equivalent age (Patton et al., 2019).

Although as a whole the Knysna estuarine bay is much studied, not least because of its biodiversity and conservation importance (Hayes et al., 2022; Whitfield et al., 2023), very little is known of its delta fauna and that only at its sheltered, north-western upstream end. Here, Allanson et al., 2000a repeated a transect carried out 50 years earlier (Day et al., 1951) from high to low water in the seagrass present at the time, and Barnes and Barnes (2014) took some samples in the same general area to compare adjacent seagrass and unvegetated sand faunas. This small area investigated to date suggested that faunistically the delta sands were markedly different from all other regions of the estuarine bay (Barnes, 2021). An equivalent conclusion has been reached in other systems, for example in respect of the small flood-tidal delta in the mouth of the Gamtoos Estuary, Eastern Cape (Schlacher and Wooldridge, 1996). The available Knysna samples, however, only represent a very small part of its flood-tidal delta system (especially those taken in a seagrass bed that no longer occurs over much of the shore), and no information is available on variation in faunal assemblage characteristics along its length. Such habitat variation in an ebb-tidal sand delta (offshore of the Ameland/Terschelling passage in the Dutch section of the European Wadden Sea) has recently been shown to be reflected by changes in the occupying zoobenthic assemblages (Holzhauer et al., 2022).

The present study therefore compared bare-sand sites along the whole longitudinal upstream axis of the Knysna flood-tide delta to examine the null hypothesis that macrofaunal invertebrate assemblages show no linear variation in their taxonomic composition or assemblage metrics. To place the delta sands in the context of the estuarine mouth zone as a whole, the investigation also compared the flood-tidal sand fauna with that on the immediately opposite western coast, alongside the deep and narrow, ebb-tidal channel, the null hypothesis here being no faunal difference between the two facing but contrasting shores. The

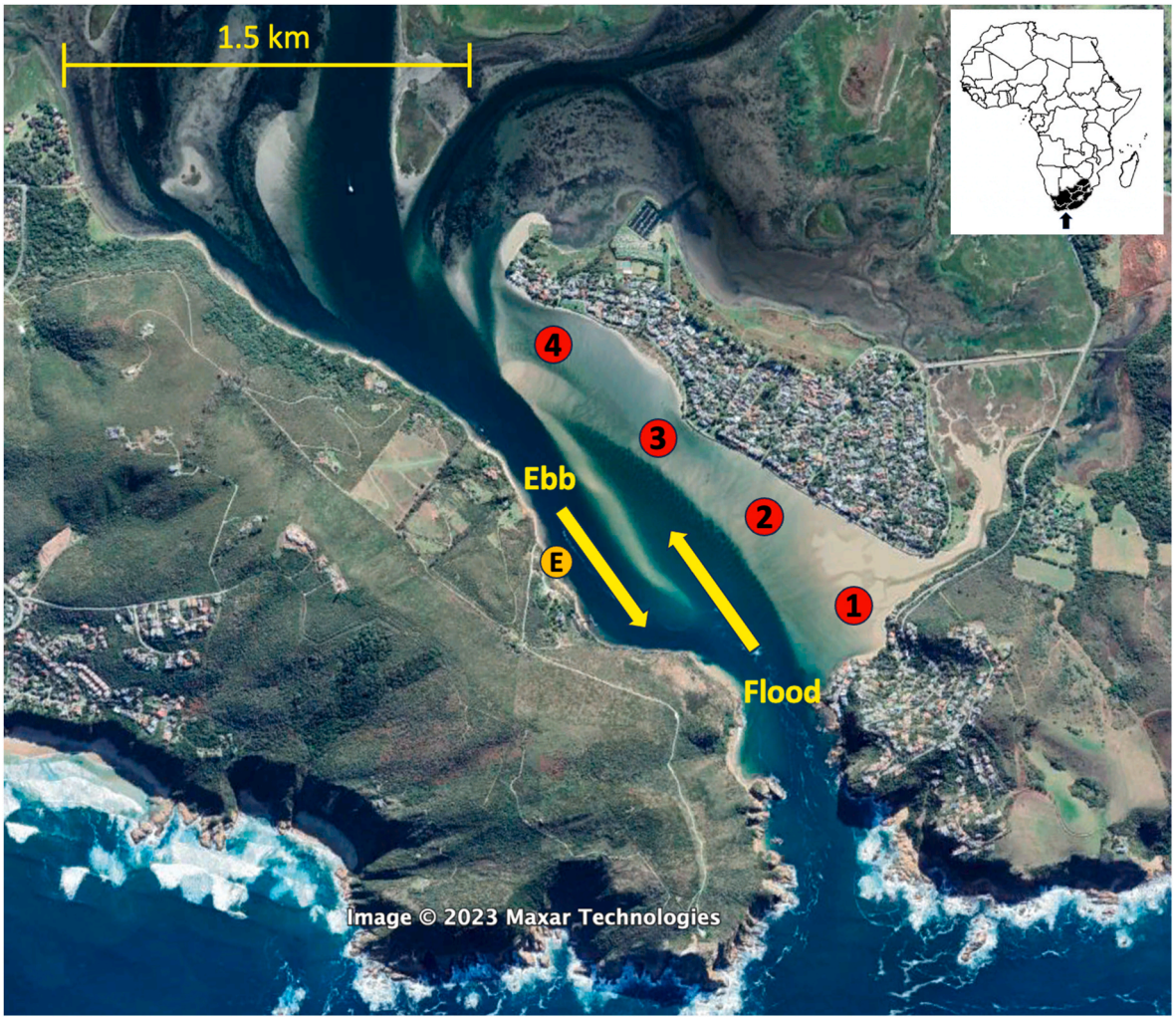

Fig. 1. Google Earth view of the mouth of Knysna estuarine bay, showing the tidal channels and sampling sites along the eastern flood-tidal delta sandflat and the western ebb-tidal shore: sites 1–4 upstream along the southwest shore of Leisure Isle; site E in the centre of the opposite ebb-tidal channel coast.

western coast possesses a shoreline formed by steep, narrow beaches that appear to have originated in situ from wave and current erosion of the sheltered landward face of the coastal dune system immediately behind them (see Marker, 2000); no information at all is available on their fauna or ecology. Faunal relationships between the delta and the other areas of the estuarine bay were assessed by comparison with equivalent historical datasets taken in 2021–2023 from comparable LWS areas of bare sediment across a representative range of Knysna sites, including one on the northern limit of the tidal-delta sand (Mendeley Data VI https://doi.org/10.17632/nmwsrpd738.1 and/d7fmxgx95t.1).

2. Methodology

Four flood-tidal sites spaced at equal distances along the length of the delta were selected between 34°04′25″S,23°03′41″E and 34°03′53″S,23°03′01″E, each such site being located in the centre of the intertidal flat that extends between the tidal channels and the seawall protecting Leisure Isle (Fig. 1). In so far as could be judged from observations of tidal movements along the delta, all sites were at more or less the same height in relation to the tide to avoid complications due to differential elevation (Dewenter et al., 2023). For comparison with the delta sands, a site along the shore of the western, ebb-tidal side of the estuarine mouth, directly opposite the mid point of the flood-tidal delta coastline, was also examined (at 34°04′16″S,23°03′00″E) (Fig. 1). This region supports sand at higher tidal levels than the eastern coast but below mean low water the shore comprises only a surface coating of sand above rock fragments. All these sites are exposed only during spring tidal cycles. Although the flood-tidal delta extends along part of the longitudinal estuarine axis, there is no diminution in salinity along its length, the whole delta being located in the fully-marine mouth region of the seawater-dominated estuarine bay, a region characterised by a very large spring-tidal prism of 19×10^6 m^3 with an average tidal flux of 1000 m^3 s^{-1} (Allanson et al., 2000b; Largier et al., 2000).

Studying tidal-sandflat and shallow-subtidal harbour sediments in Newfoundland, Clinton et al., 2024 found that 'typical sampling effort for coastal benthic studies, for example of <5 push cores of <0.0038 m^2 area' failed adequately to capture macroinfaunal assemblage composition and several biodiversity metrics, and could result in erroneous conclusions. They considered that for assessment of species density and evenness, ≥20 such cores per site were needed, although diversity (measured as the Shannon or Simpson indices) required fewer. This roughly equates to ≥14 cores of 0.0054 m^2 and therefore, here, two stations, at least 25 m apart, were worked at each site, each station comprising 16 randomly-located push core samples of 0.0054 m^2 cross-sectional area and 0.1 m depth. Stations yielded an average of 174 animals (minimum 120), well above the number required for robust multivariate comparisons, there being no high levels of evenness (Forcino et al., 2015). All cores were taken some 60 min before low tide when the stations were still covered by 15+ cm of water. Sampling was undertaken during in the austral spring, and all sampled areas were without any covering of macroalgae or seagrass. This sampling regime collects the smaller and most numerous members of the macrofauna that constitute the large majority of invertebrate biodiversity, at least insofar as molluscs are representative (Albano et al., 2011). All samples were gently sieved on site through 500 μm mesh, and all retained material from each core was then transported immediately to a local laboratory. There it was placed in a 30 × 25 cm dish over a LED pad in which the living fauna was located by visual inspection using 3.5x magnifying spectacles. The recent historical datasets from upstream of the delta were obtained in identical fashion (although sieved through 710 μm mesh).

Because of prevailing taxonomic uncertainty, even amongst numerically-dominant South African animal groups (see e.g. Simon et al., 2022), identification of collected fauna was generally attempted only to morphologically-based operational taxonomic units ('morphospecies'), an appropriate procedure to detect spatial patterns of numbers of taxa and their differential abundance (Dethier and Schoch, 2006; Gerwing et al., 2020). Although this incurs a risk of failing to distinguish closely similar animals, experience of taxonomic resolution/sufficiency in equivalent soft-sediment macrobenthic studies (e.g. Warwick, 1988; Tataranni et al., 2009) indicates that operating at various levels from species up to family all produce similar conclusions. Wherever possible, however, all animals of particular interest were identified to the lowest taxonomic level using names currently recognised. Nomenclature is as given by the World Register of Marine Species (WoRMS, www.marinespecies.org, accessed December 2024), except in respect of '*Assiminea*' *capensis* (see Barnes, 2018) which is listed in WoRMS as *Rissoa capensis* and as a *taxon inquirendum* [= the '*A.*' aff *capensis* of Miranda et al., 2014, but not their '*A*'. cf *capensis*].

Numbers per unit area (i.e. per core, station, and site) of each component zoobenthic morphospecies were subjected to similarity analysis, and assemblage metrics were derived and compared via *PAST* 4.15 multivariate software (Hammer et al., 2001) or Microsoft Excel for Mac 16.91 with the StatPlus:mac Pro 8.0.4 add-on, all metrics being based on animal numerical abundance. Univariate metrics assessed were those argued to have a major influence on local-scale biodiversity patterns (Santini et al., 2017; Blowes et al., 2022): (1) overall faunal abundance (presented below as numbers m^{-2}); (2) geometric mean morphospecies abundance m^{-2}; (3) relative evenness (=equitability) of individual taxon abundances (Pielou's *J*); and (4) observed and predicted likely real numbers of morphotaxa per unit area ('taxon density' *sensu* Gotelli and Colwell, 2001), estimated here as the absolute effective density (*ED*) (Gatti et al., 2020), incorporating Hill's H_0, H_1 and H_2 metrics (Gotelli et al., 2024) [i.e. by the expression $H_0 + [(H_1^2)/(2*H_2)]$, where H_0 is the observed taxon density, H_1 is the exponential of their Shannon entropy, and H_2 is the corresponding inverse Simpson concentration]. In addition, (5) local spatial variation in assemblage abundance was also assessed (by Lloyd's I_p index of patchiness, with significance of departures from random dispersal tested by Monte Carlo simulation with 9999 iterations). Interspecific relationships between assemblage-component abundances and occupancies were compared across sites by ANCOVA, with, as earlier at Knysna (Barnes, 2022b), occupancies being presented as logit transformed values [i.e. as occupancy/(1-occupancy)]. Relative importance of individual species within the macrofaunal assemblage at each site was assessed by the Index of Numerical Importance (INI) which combines data from both relative abundance and relative occupancy (Barnes, 2014).

Similarities between sites will be heavily influenced by numerically dominant species if no transformation is applied to the raw data, and the present data do show marked dominance by one or two species at all sites. Although therefore there are strong arguments in favour of transformation (Thorne et al., 1999), dominance by a few species is a feature of great ecological significance, especially where they alter the nature of the substratum. Hence here comparisons are presented both in untransformed and fourth-root transformed forms. Multivariate statistical comparison of quantitative assemblage composition was carried out by ANOSIM (using Euclidean distance), PerMANOVA (using Morisita's similarity index, see Wolda, 1981; Barwell et al., 2015), SIMPER (using Bray-Curtis similarity), all with 9999 permutations, and affinities between sites throughout the estuarine bay were expresed by nMDS. Qualitative faunal similarity was assessed as the β-2 index of Harrison et al. (1992), which uses incidence data, ranges from 0 (complete similarity) to 1 or 100 % (complete dissimilarity), and is a 'narrow sense' non-directional index in the terminology of Koleff et al. (2003). Contributions of species turnover and nestedness to β diversity were assessed as per Baselga (2010).

3. Results

The macrofauna of the Knysna flood-tidal sand delta was clearly dominated by paraonid polychaetes (*Paradoneis* and *Levinsenia*) which comprised >50 % of all sampled individuals and by haustorioid

amphipods (principally *Urothoe* but with a few *Indischnopus*). These two higher taxa plus the cumacean *Iphinoe* and the polychaetes *Orbinia* and *Cirratulus* comprised 80 % of all animals sampled. Nevertheless, although the delta is less than 2 km long, there were marked faunal changes along its length, most obviously in the relative importance of worms and crustaceans (Fig. 2). Indeed there were significant faunal differences between all four sites whether the data were fourth-root transformed or not (PerMANOVA overall $F > 36$, $P < 0.0001$; between individual sites $F > 7$, $P < 0.0001$). *Levinsenia*, for example, occurred at a density of almost 700 m^{-2} at the site nearest the mouth, but was absent from other sites where it was replaced by *Paradoneis* at a mean density of 1256 m^{-2}. *Urothoe* dominated the half of the linear delta nearest the mouth (at a mean 540 m^{-2}) but only a single individual was found in the entire distal half. Only *Iphinoe*, *Orbinia*, an elongate *Tetrastemma*-like four-eyed nemertine, the isopod *Cyathura*, bivalve *Hiatula* and polychaete *Simplisetia* (in decreasing order of abundance) were present at all four sites.

Which adjacent sites were most similar faunistically depended on whether the abundance data were transformed or not, but overall the two distal sites (3 and 4) were most similar, whilst most change occurred between sites 1 and 2 (see Tables 1 and 2). The taxa whose changing untransformed abundances were most responsible for differences between the sites were, in decreasing order, *Paradoneis*, *Urothoe*, *Levinsenia*, *Iphinoe*, *Cirratulus*, *Orbinia* and the gastropod '*Assiminea*' (cumulative SIMPER total 80 %), and after fourth-root transformation the same seven taxa were still those responsible, although *Cirratulus* and *Orbinia* changed places in the rank order (cumulative SIMPER total 62 %). The interspecific relationships at each site between the abundances of the various component species and their logit occupancy differed, both in respect of means (ANCOVA $F = 3.95$, $P = 0.01$) and slopes (ANCOVA $F = 23.0$, $P \ll 0.0001$). However, there was no consistent trend related to the sequence of sites along the delta (Fig. 3). Site 3 was the clear outlier but the slopes of sites 1, 2 and 4 also differed significantly (ANCOVA $F = 6.9$, $P < 0.002$) although not their means (ANCOVA $F = 1.15$, $P > 0.3$).

In total 45 morphospecies were recorded from the 128 flood-tidal delta samples, of which 22 % were singletons and 16 % were doubletons. Overall, abundance was 2010 ind m^{-2}. Values of assemblage metrics were relatively constant across sites (coefficients of variation within a range of 0.11–0.27, mean 0.16) (Patel et al., 2001), and there were no trends for variation in any metric with progress along the deltaic axis (Table 3), although site 4 supported both the fewest morphospecies and least abundance per core sample whilst site 3 showed the greatest abundance and site 2 the most species per core (ANOVA $F_{3,124} > 5.9$, $P < 0.001$). The fauna at sites 1 and 2 included a psammodrilid polychaete, constituting the first record of this group from African waters [Global Biodiversity Information Facility (www.gbif.org) and Ocean Biodiversity Information System (obis.org) databases (accessed Nov 2024)].

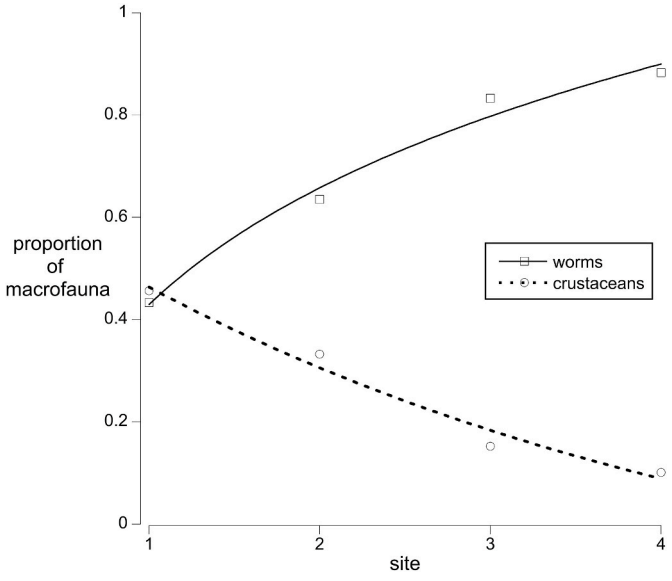

Fig. 2. Proportion of the total macrofaunal individuals comprised by worms (nemertines and annelids) and crustaceans along the upstream axis of the Knysna flood-tide sand delta.

Table 1
Compositional similarity of the macrobenthic assemblages in equal-area LWS samples at adjacent stations along the Knysna flood-tidal sand delta, as assessed by ANOSIM R, Morisita'a similarity index, and the β-2 diversity of Harrison et al. (1992). All three metrics are presented as similarity values so that 0 indicates complete dissimilarity and 1 complete similarity; the ANOSIM and Morisita's index values are quantitative, the Harrison β-2 diversity qualitative. Where appropriate, values are presented as untransformed/fourth-root transformed alternatives.

Sites	1 - (ANOSIM R)	Morisita	1 - (Harrison et al.'s β-2)
1 : 2	0.73/0.36	0.26/0.51	0.77
2 : 3	0.72/0.79	0.89/0.77	0.77
3 : 4	0.61/0.83	0.99/0.78	0.72
1 : 4	0.43/0.10	0.01/0.31	0.50

Table 2
Divergence in the three most important macrobenthic taxa at LWS in the mouth region of the Knysna estuarine bay from equal-area samples along the eastern flood-tidal sand delta and in the western beach on the ebb-tidal channel shore, together with their percentage importance (INI) rating.

Site	1st	2nd	3rd
Eastern flood-tidal sand delta			
1	*Urothoe pulchella* (32)	*Levinsenia gracilis* (31)	'*Assiminea*' *capensis* (12)
2	*Paradoneis lyra capensis* (31)	*Urothoe pulchella* (14)	*Iphinoe truncata* (9)
3	*Paradoneis lyra capensis* (45)	*Iphinoe truncata* (14)	*Orbinia angrapequensis* (9)
4	*Paradoneis lyra capensis* (50)	*Orbinia angrapequensis* (10)	*Schistomeringos ? neglecta* (6)
Western ebb-tidal beach			
E	*Dipolydora socialis* (5)	*Iphinoe truncata* (0.5)	*Urothoe pulchella* (0.5)

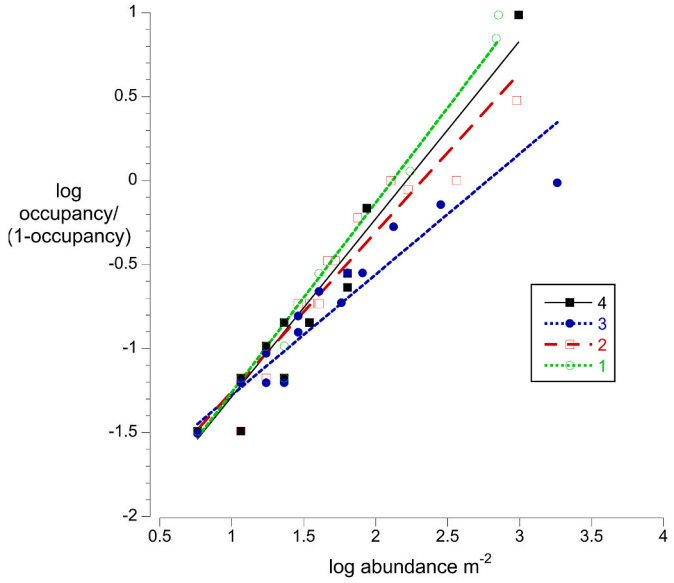

Fig. 3. Abundance-occupancy relationships of the macrobenthic assemblages at the four sampling sites along the upstream axis of the Knysna flood-tidal sand delta.

Table 3
Biodiversity metrics of the equal-area sites along the eastern flood-tidal sand delta and on the opposite western ebb-tidal coast at the mouth of the Knysna estuarine bay (see Fig. 1): observed (obs *N*) and estimated true (est *N*) numbers of morphospecies, overall numbers of macrobenthos m^{-2} (*A*), geometric mean abundance m^{-2} (*G*), evenness (Pielou's *J*), and Lloyd's index of patchiness (I_p). All values of I_p are significantly patchy at $P < 0.004$.

Site	obs *N*	est *N*	*A*	*G*	*J*	I_p
1	20	24	1820	19	0.53	1.08
2	31	38	2078	18	0.59	1.40
3	25	29	2708	21	0.44	1.29
4	22	27	1435	18	0.48	1.19
Mean flood-tide sandflat	24.5	29.5	2010	19	0.51	1.24
Ebb-tide beach	39	51	2031	17	0.62	2.01

Although species density was similar across all four sites, apart from the two paraonid species there was no evidence of species replacement along the delta. '*Assiminea*' occurred only towards the mouth but no microphytobenthically-feeding micro- (or indeed macro-) gastropod was present upstream, likewise no peracaridan took the place of *Urothoe* upstream, and no linear sequence of polychaetes was apparent. Nevertheless, species turnover contributed 0.35–0.55 to β diversity; nestedness only 0.02–0.13.

Upstream of the mouth, the lagoonal section of the estuarine bay is floored by aeolian sand from the same enclosing fossil dune system and the estuarine zone of the Knysna River by fluvial deposits, both systems with a surface veneer of mud especially in the estuary and in backwater saltmarsh-enclosed areas (Reddering and Esterhuysen, 1987). The abundance of macrofauna in the sand delta was marginally less than in those upstream muddy-sand sites (ANOVA $F_{1,9} = 5.23$, $P = 0.048$) but there was no significant difference in their species density (ANOVA $F_{1,9} = 0.60$, $P = 0.45$). Although the sand fauna on the opposite, ebb tidal-channel, side of the mouth region also included *Iphinoe* and *Urothoe* amongst its dominants (Table 2), it differed quite markedly from that of the delta (PerMANOVA $F > 14$, $P < 0.0001$), not least in the effective absence of paraonids (only four individuals being observed, each one in a different sample) and in the local dominance of maldanids and especially the polydorine spionid *Dipolydora*, all largely or completely absent from the delta. Morisita similarity of the ebb-tidal shore with the two opposite flood-tidal sites (numbers 2 and 3) was <0.11. Overall, the ebb-tidal site supported more species than any flood-tidal one, but abundance levels were comparable as were the other assemblage metrics except that of patchiness (Table 3).

Faunal affinity between the flood-tidal delta sites, the ebb-tidal shore one, and those upstream in the other notional compartments of the system (bay, lagoonal, estuarine and backwater) is displayed in Fig. 4. The flood-tidal sites away from the immediate vicinity of the mouth (sites 1.2–1.4 & 2) together with the two other sites within the marine bay region (3 & A) form one cluster, as do those upstream sites along the main channel within the lagoonal and estuarine compartments (sites 4–7), whilst the ebb-tidal mouth site (1E) and that nearest the mouth in the flood-tidal delta (1.1), dominated by *Dipolydora* and *Levinsenia* respectively, form very isolated outliers.

4. Discussion

Knysna appears most unusual in supporting a sandflat system dominated by paraonids or jointly by paraonids and *Urothoe*. *Urothoe* is a characteristic, small, worldwide though largely temperate burrower in marine soft sediments, and specifically *U. pulchella* is a typical dominant of relatively sheltered, but still clean and mobile, fine sands around the coasts of northwestern Europe and the western part of the Mediterranean (e.g. Marques and Bellan-Santini, 1993). The only other area from which it has been recorded is the south coast of South Africa, although the conspecificity of this disjunct population may be open to question. Griffiths (1974) recorded it from clean sand near the mouth of South African estuaries, exactly its habitat in Knysna and in other local systems such as Mngazana (Branch and Grindley, 1979). Whitfield (1989) recorded it from the nearby Swartvlei in a sand community that included *Iphinoe truncata*, with which it also occurs in Knysna. In Swartvlei, however, it occurred throughout the sandy estuary, although it does not appear to occur on exposed sandy shores, at least in South Africa (McLachlan et al., 1981). Thus in the Nahoon delta it is rare in the open-ocean facing sands, but within the flood-tidal sand bank it achieves densities of 600–2100 m^{-2} (c.f. 500-900 m^{-2} at the Knysna stations at which it is dominant).

Paraonid polychaetes have been recorded as being common subtidally (Aguirrezabalaga and Gil, 2008; Arriaga-Hernández et al., 2013), especially in the deep sea (Ranauro et al., 2020) and in some tropical mudflats (Barrio Froján et al., 2005). Very few accounts of sandflats,

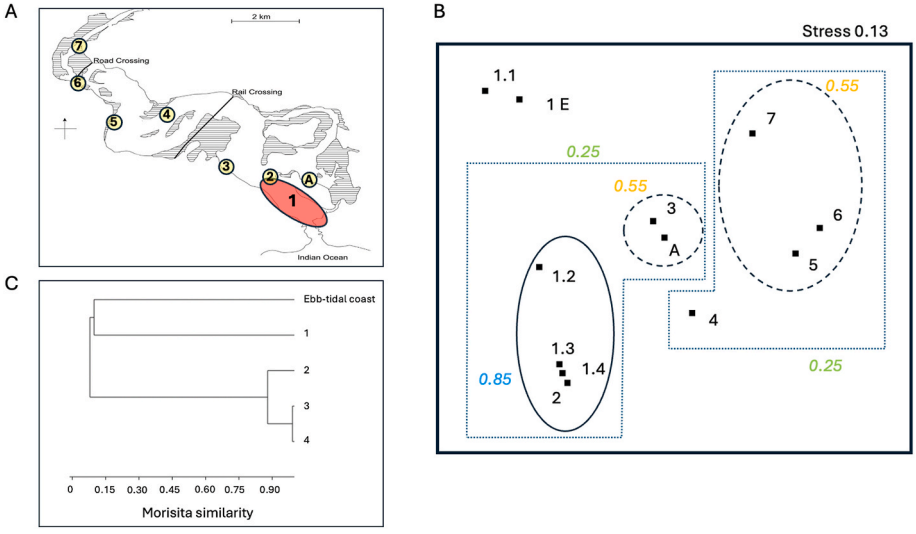

Fig. 4. (A) Map of the Knysna estuarine bay showing the location of bare soft-sediment sampling sites. (B) nMDS diagram (using Morisita's similarity index from series of 32 core samples) of the LWS macrofaunal assemblages at those sites: 1.1–1.4 & 2, the flood-tidal sand delta; 1.E, the ebb tidal-channel beach; 3–7, muddy-sand regions upstream of the mouth along the main channel; and A, a backwater creek (*sensu* Barnes, 2022a). Envelopes enclose sites at the stated levels of Morisita similarity. Sites 2–7 & A from recent historical datasets (see text). (C) Detail of Morisita similarity of the various group 1 sites: 1–4 along the flood-tide delta and one on the facing ebb coast.

however, mention them as dominant members of the fauna. Of those that do, Tillin et al. (2024:3) record *Paraonis fulgens* as a dominant inhabitant of *the biotope that occurs mainly on the mid and lower shore of moderately wave-exposed coasts, with medium and fine clean sand which remains damp throughout the tidal cycle and contains little organic matter. The sediment is often rippled*. This habitat description is of parts of the eastern cool-temperate coast of the UK (e.g. *c*.54°N) but it serves equally well for that of the sand delta at warm-temperate 34°S. The only other relevant mention appears to be Bulmer et al. (2017) who also describe *Paradoneis lyra lyra* (together with *Prionospio aucklandia*) as dominating an area of sandflat in Whangamata Harbour in New Zealand's North Island (*Prionospio* is abundant throughout much of the Knysna estuarine bay, but not in the delta). [Although Nehmer and Kröncke (2003) do record *P. fulgens*, together with the amphipod *Haustorius*, as subdominant macrofauna of the highly dynamic subtidal inter-sandbank channels within the flood-tidal delta landwards of the gap between Norderney and Baltrum barrier islands in the German Wadden Sea.] No such paraonid-dominance records hail from South Africa, however. Bursey and Wooldridge (2002) only mention paraonids as occurring at one of their 14 sites (and then at a density of only 0.3 m^{-2}) within the Nahoon estuary flood-tidal delta, whilst Schlacher and Wooldridge (1996) do not mention them at all in respect of the mouth of the Gamtoos estuary. *P. lyra lyra* has a worldwide but especially North Atlantic distribution, whereas *P. lyra capensis* was described from Knysna and still remains known only from one or two other Western Cape localities, including near the mouth of the nearby Keurbooms estuary which possesses a very similar fauna to Knysna (Barnes et al., 2024), but there only at a density of <13 m^{-2}.

The peculiarity of the Knysna delta system also includes what appears not to be present there. Cirolanid isopods are highly typical of South African intertidal sands (McLachlan et al., 1981), and the isopod *Excirolana latipes* characterises the Nahoon delta, in densities of up to 200 m^{-2}. No *Excirolana* were observed in the Knysna delta sand (in 1389 animals sampled), however, notwithstanding that Knysna is well within its geographical range and it occurs at equivalent shore heights in the nearby Swartvlei (Whitfield, 1989; Barnes, pers. obs.). Only a total of six individual cirolanids (all *Eurydice*) were found in the Knysna delta samples. Unfortunately, at present the Nahoon flood-tidal sand delta is really the only one with which it is possible to compare Knysna. There, Bursey and Wooldridge (2002) recorded *Scolelepis*, *Scoletoma* (as *Lumbrineris*) and *Solen* as being indicative of the delta sands. All three were also present at Knysna though only as totals of ten, eight and two individuals respectively. Besides *Urothoe*, only the bivalve *Hiatula* could be described as a characteristic member of both sandflats.

A further possible peculiarity is the marked faunal change over such a short distance in what is visually a uniform sandflat with similar environmental conditions of salinity, sediment type, etc. along its length. On the basis of the untransformed abundance data, the Morisita similarity between site 1 nearest the mouth and site 4 furthest away was a mere 0.01. To a considerable extent, this results from *Urothoe*, *Levinsenia* and '*Assiminea*' comprising 87 % of the total faunal individuals at site 1 but zero at site 4, and conversely *Paradoneis*, the polychaete *Schistomeringos* and large ostracod *Cylindroleberis* comprising zero at site 1 but 75 % at site 4. Since so few flood-tidal deltas have been investigated ecologically it is impossible to know the extent to which the Knysna system is typical in this respect. It does appear typical, however, in the coupling of such marked macrobenthic compositional change with relatively constant biodiversity metrics; a feature demonstrated over time in the Italian Tortoli Lagoon (Giampaoletti et al., 2025) and spatially in *Zostera* meadows along the Breton coast by Boyé et al. (2017), amongst others. In spite of this marked change in assemblage composition along the delta, apart from the two paraonids, somewhat unexpectedly there was no evidence of any species replacement within functional groups taking place, although turnover was a considerably more significant factor (Medeiros et al., 2016) than nestedness (Menegotto et al., 2019). Although there was no apparent difference between site 1 and sites 2–4 in the nature of the habitat available, the fauna responded as if the two areas were totally different.

Although not listed as one of the 'opportunistic' polychaete families by Dauvin et al. (2016), paraonids are so regarded by some authors (e.g. Quintana et al., 2015; Tillin et al., 2024). In that regard it is interesting that if the Knysna delta paraonids are included in this opportunistic category for the calculation of biotic indices such as the BO2A of Dauvin et al. (2016), the clean sands of the delta yield an overall value equivalent to the 'poor' end of the 'moderate' Ecological Quality Status band in the European Water Framework Directive (OJEC, 2000). Over the northern end of the delta where *Urothoe* is absent, the quality value would fall well into the 'poor' category. This could be taken to indicate moderately to heavily polluted local conditions (e.g. Dauvin and Ruellet, 2007) which is certainly not the case, and they strongly suggest that in this instance at least the dominant paraonids are not opportunistic indicators of pollution in the sense underlying such indices.

The presence of a psammodrilid in the sand delta is particularly noteworthy. Psammodrilids are distinctive 1–8 mm long interstitial annelids of uncertain relationships (Jumars et al., 2015) that occur in shallow sandy marine substrata but which are easily overlooked and hence very poorly known. Although the group is currently only represented by seven species, it is likely that many more await discovery through most areas of the world (Worsaae et al., 2021). The species present in Knysna closely resembles *P. balanoglossoides*, a morphotype that has been reported from the northeastern and northwestern Atlantic, White Sea, Florida and New Zealand. It joins the minute gastropod *Cornirostra* (Barnes, 2010) and benthic chaetognath *Spadella* (Barnes and Seath, 2025) as tiny macrofaunal species present in the Knysna estuarine bay but not otherwise known from Africa — this is very unlikely to be a true reflection of their distribution.

The Knysna estuarine bay is a complex system, divisible into a number of different biological/hydrographic compartments each with its own individual nested subset of the Knysna soft-sediment macrofauna (Barnes, 2021). It also possesses a distinctive unity, with some elements, including the systematically isolated and endemic South African microgastropod '*Assiminea*' *capensis*, occurring in all such compartments, both inter- and subtidally, including that exposed part of the flood-tidal sand delta nearest the mouth and the sheltered, muddy, low-salinity conditions at the estuarine head. Even the *Paradoneis lyra capensis* that is the most characteristic element of the delta sands occurs almost throughout the estuarine bay, i.e. in all compartments except the estuary of the Knysna River (all sites in Fig. 4 except numbers 6 and 7). Although it can achieve densities of up to 7000 m^{-2} (Barnes et al., 2024), like the psammodrilids it can easily be overlooked (being 0.1 mm wide and <10 mm long), and hence its real South African distribution may still be unappreciated.

Granted the nature of the delta substratum and the fact that the delta is the only place within the estuarine bay where such clean fine sand is present, it is not unexpected that the flood-tidal sands of the system's mouth possess a macrofauna distinct from those upstream (as is the case in other South African estuaries, see Millard and Harrison, 1954; Branch and Grindley, 1979; etc.) and distinct from the immediately facing ebb-tidal shore, although its unusual assemblage composition dominated by paraonids remains a mystery. The Knysna system possesses a diverse fauna, both within and across its various regions. This is boosted by the presence of the sand delta at its mouth, an effect that equivalent deltas may achieve in other areas. They are clearly worth more ecological attention than they currently receive.

Data availability

Data on the abundance of each morphospecies in each sample from each site are deposited in Mendeley Data and can be assessed at https://data.mendeley.com/datasets/pwj6rsd2b3.1.

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Data availability

Data deposited in Mendeley Data.

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