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Cinderella effects in conservation assessment: Re-evaluating biodiversity merit in a South African estuarine system

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ABSTRACT

Two adjacent estuaries in South Africa differ markedly in their assessed biodiversity, conservation status and management style: one, a flagship site, is considered to support the richest estuarine biodiversity in the country, receives the management and protection of a National Park, and attracts much research attention; the other is regarded as having an impoverished macrobenthic fauna, bears no formal conservation status, and is much less studied. To test whether these supposed contrasts in biodiversity are simply a reflection of differential levels of scientific attention, the biodiversity, abundance and nature of the macrobenthos in a representative habitat, beds of the endangered seagrass *Nanozostera capensis* that dominate both estuaries, were compared in apparently equivalent upstream (estuarine and lagoonal) locations of the two systems using identical field research effort and methodology. There the neglected and supposed impoverished estuary (the Keurbooms/Bitou) was found to support as great, if not greater, macrobenthic biodiversity, in greater abundance, and with more numerous rare endemics than the flagship conservation site (the Knysna estuarine bay). Its previously considered species poverty appears entirely due to inadequate earlier investigation, particularly in respect of its invertebrate fauna. Of the two, Keurbooms/Bitou also has the merit of being less accessible and less anthropogenically impacted. This study highlights the consequences of basing conservation assessments on incomplete biodiversity data, and stresses that a uniform programme of investigative fieldwork is critical for the meaningful ranking of sites. It also emphasises the extent to which non-bait species of invertebrate are often ignored in estuarine management protocols to the detriment of local and overall conservation management aims.

1. Introduction

Money and manpower for effective habitat protection and management are everywhere in short supply, even during times of economic prosperity, and are never enough to achieve all conservation goals (Pienkowski et al., 2021). This means (or should mean) rigorous prioritisation of sites to receive the most intensive management, the choice of which in turn requires *inter alia* accurate information on supported biodiversity and on species of particular concern. Inevitably, however, some sites will be better known than others, and seldom will the data available have been collected in a consistent manner. Here we investigate the extent to which assessment of the relative conservation merit of two different estuaries, and consequently the degree or type of management afforded them, might be dependent not on real differences in their supported biodiversity but on differential quantity and quality of the data available on the two systems.

The Knysna and Keurbooms/Bitou estuarine systems are two adjacent waterbodies that discharge into the Indian Ocean along the warm-temperate Southern Cape coast of South Africa (Fig. 1). They share a number of features; for example, being two of the only three known localities of the rare and endangered fully-estuarine seahorse, *Hippocampus capensis* (Teske et al., 2003), and the presence of important beds of Cape dwarf-eelgrass, *Nanozostera capensis*, a globally vulnerable seagrass that in South Africa is also in the endangered category (Skowno et al., 2019) but covers ≥30 % of the beds of those two estuaries. Regions of both systems also appear to possess benthic communities dominated by a suite of unusual and nationally rare animals that are not typical members of the South African estuarine fauna [as per the listings of Day (1981) and Knox et al. (2004)]. These local specialities include the three endemic South African microgastropods *Alaba pinnae*, '*Assiminea*'

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capensis (*sensu* Criscione and Ponder, 2013), and '*Hydrobia*' *knysnaensis* (*sensu* Wilke et al., 2013), and the polychaete *Paradoneis lyra capensis*. [*n.b.* '*Assiminea*' and '*Hydrobia*' are here names of convenience, both await the description of the new genera required, and for '*Assiminea*' possibly a new subfamily or family (Fukuda and Ponder, 2010)].

Although, unusually in the South African context, both estuaries are permanently open to the ocean and have large tidal prisms, their present nature, size, shape and hydrography otherwise differ quite considerably. Knysna is a large drowned river valley forming an estuarine bay *sensu* Van Niekerk et al. (2020) with a water surface area of some 19 km^2 (Russell et al., 2010; Whitfield et al., 2023). Like most South African estuaries (Whitfield, 2005), freshwater inflow is limited, and the whole system is dominated by sea water. The smaller (3 km^2) Keurbooms/Bitou system comprises a typical longshore back-barrier lagoon (the Keurbooms Lagoon), that receives at its head the estuaries of both the Bitou and Keurbooms rivers. Its relatively large freshwater input, with episodic flood incidents (Schumann, 2015), maintains a mouth that migrates in position along the 4 km long enclosing sand bar (Reddering, 1983; Schumann, 2021).

The two estuaries also differ markedly in perceived conservation and biodiversity importance and consequently in the nature and intensity of their management. Since work in the late 1940s (Day et al., 1951), Knysna has been regarded as supporting the richest estuarine fauna in the country, both in terms of numbers of individual animals and number of species. Accordingly, over the last eight decades it has received very much more scientific attention than neighbouring estuaries including the Keurbooms/Bitou (see summaries in Hayes et al., 2022; Whitfield et al., 2023), and it remains top of the overall national estuarine biodiversity rankings (Turpie, 2004; Turpie and Clark, 2007). Indeed it was recently described as the 'Jewel of the Garden Route' (Whitfield et al., 2023). Because of its biological richness, it forms a special section of the Garden Route National Park and is managed as a 'Protected Area'. In contrast, although rated as 'highly important' in the South African context (Turpie et al., 2012a,b) not least because of the *Hippocampus* and 112 ha of *Nanozostera* it too supports, the current management plan for the Keurbooms/Bitou system (CapeNature, 2023a, p. 12) states that the density of its benthic invertebrates is "well below expected levels" and that their species richness is "low". The few available pre-2020 accounts of its benthos do all suggest a very limited benthic fauna, totalling only a paltry 40 soft-sediment species for the whole Keurbooms/Bitou system (Duvenage and Morant, 1984; Turpie et al., 2004; Adams et al., 2015). Not surprisingly because of this apparent species poverty, it has received very much less ecological attention than its larger neighbour, and enjoys no formal protection, other than, like all South African estuaries, management under the prescriptions of the National Estuarine Management Protocol (Creecy, 2021), in this case by CapeNature (the Western Cape Nature Conservation Board).

Recently, however, Barnes et al. (2024), investigating the mouth regions of the two estuarine systems, questioned whether this marked difference in biodiversity between their benthic faunas might be an artefact of differential research attention. They employed identical sampling methodology and intensity to quantify the abundance and biodiversity of the benthic assemblages present in and alongside those *N. capensis* beds that were present in seemingly similar circumstances near their mouths. When investigated with the same intensity, the seagrass and adjacent sandflat macrobenthos near low-water spring tide

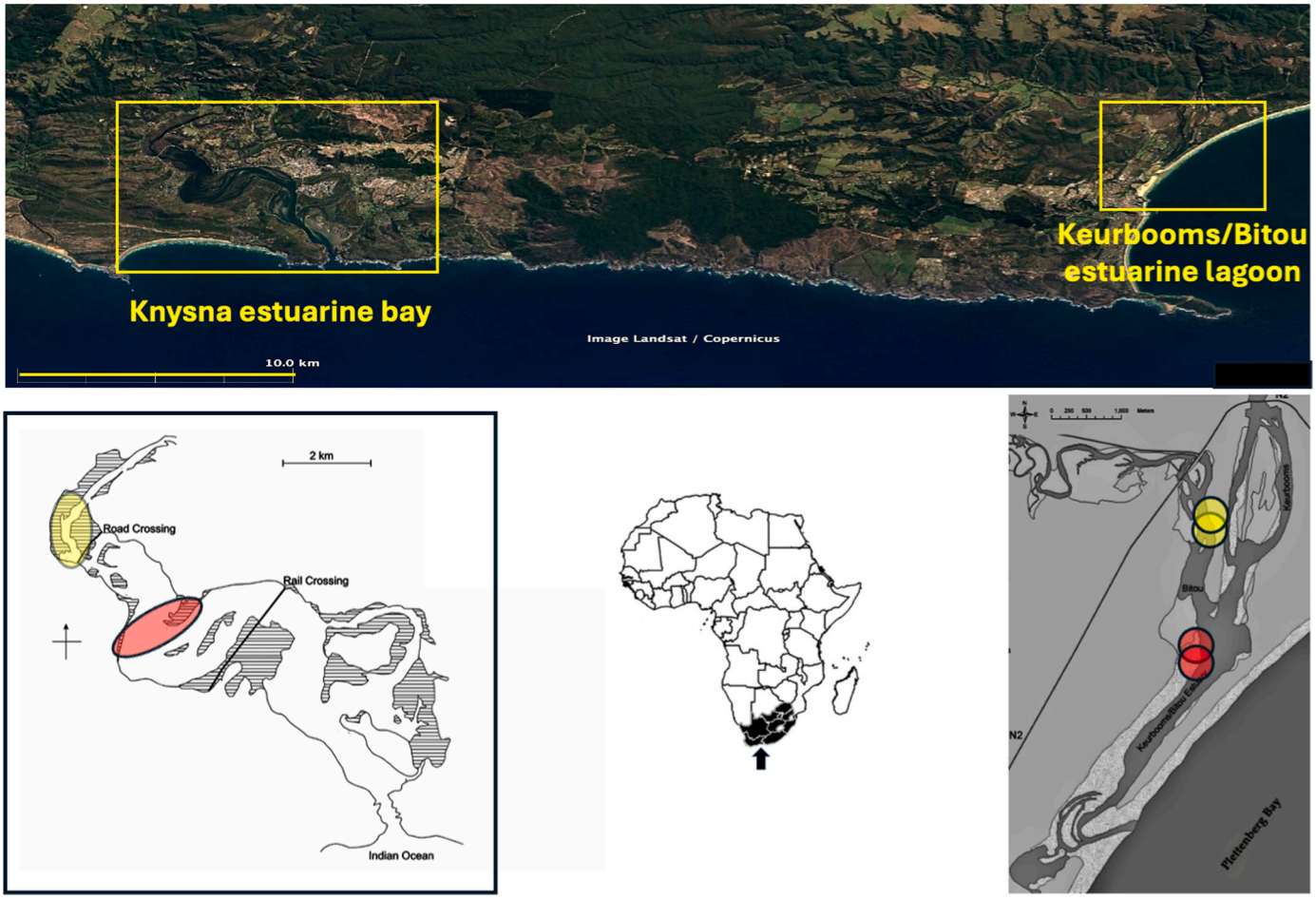

Fig. 1. Part of the Southern Cape coast of South Africa showing the location of the two waterbodies under study, and, within each system, the sites investigated (estuarine localities in yellow and lagoonal ones in red).

(LWS) there proved just as biodiverse in 'impoverished' Keurbooms/-Bitou as in the 'especially rich' Knysna. For example, the equal-area sites in the Keurbooms/Bitou supported 53 observed (63 estimated total) species at a density of 7800 m^{-2} in the seagrass, whilst in Knysna the corresponding values were 52 observed (67 estimated) species at a density of 6700 m^{-2}. The equivalent data for adjacent areas of bare sediment were 33 vs 35 observed species, 38 vs 40 estimated ones, and 4500 vs 4200 individual animals. During this survey, more macrobenthic species were observed in a 0.15 m^2 area of seagrass in Keurbooms than had previously been recorded from the entire estuarine system.

The Knysna estuarine environment can be considered basically a linear chain of hydrologically (Largier et al., 2000) and faunistically (Barnes, 2021a) differing compartments, essentially: marine embayment, lagoon and estuary. Although much smaller, to a degree the Keurbooms/Bitou system can also be similarly subdivided, having a particularly marine-influenced area near its mouth, the long linear Keurbooms Lagoon, and at its head the two separate Bitou and Keurbooms estuaries, that of the Keurbooms River being larger and of lower salinity than the Bitou. Like Knysna, these different compartments might be expected to support faunal assemblages with contrasting ecological features. The Barnes et al. (2024) investigation encompassed only the areas adjacent to the mouth in the marine-embayment compartment of each system. It could be argued that the mouth regions of the two systems would be expected to share many characteristics simply because they are similar habitats both in immediate contact with the same stretch of coastal Indian Ocean, and that the supposed marked disparity in the faunal richness of Knysna and Keurbooms/Bitou is really a feature of their more isolated upstream portions.

Therefore the present study sought to investigate whether these supposed differences in relative biodiversity of the upstream zones of the Knysna and Keurboom/Bitou estuaries could also be more apparent than real, and to set them in the context of the two estuarine systems as a whole. Thus, in the present study the same near-LWS horizon examined earlier was investigated in the lagoonal and estuarine reaches of Keurbooms/Bitou, to test the null hypothesis that there is no difference between macrobenthic nature, abundance and biodiversity within the representative habitat of *N. capensis* beds in that allegedly impoverished system compared to those previously documented in equivalent sites in the flagship Knysna estuarine bay. This research has much wider relevance than the two South African estuaries concerned, highlighting the general consequences of assessing conservation and management needs on the basis of previously published databases of varying quality, coverage, and/or of unknown levels of completeness, and exemplifying the imperative of uniformity of investigative fieldwork when constructing rank orders of site importance.

2. Materials and methods

2.1. Protocol and study areas

Previous work on benthic macrofaunas within individual *Nanozostera* meadows has demonstrated a high degree of constancy in assemblage metrics across quite wide ranges of environmental conditions, despite variation in assemblage composition (Barnes, 2022, 2023; Barnes et al., 2022) [and see Boyé et al. (2017) in respect of *Zostera*]. Hence precise site location within the estuarine systems concerned was not considered to be too critical a potential variable. Two of the Knysna regions recently surveyed by Barnes and Claassens (2020) and Barnes (2021b, 2022) — Belvidere/Point (34°03′S,23°00′E) and Crabs Creek/-Westford (34°02′S,22°59′E) — appear typical of the lagoonal and estuarine zones of that system, with salinities in the normal ranges of 25–32 and 15–20, respectively (Allanson et al., 2000; Largier et al., 2000). The relevant historical data taken from those regions in areas supporting the subtidal, long-leafed phenotype of *Nanozostera capensis* (Lawrence, 2025) represented Knysna. Localities in the Keurbooms/Bitou system selected for comparison were located in equivalent positions (Fig. 1), and insofar as habitat data are available were similar to those at Knysna in terms of sediment, salinity, etc. (see Adams et al., 2015), as well as in shore height and seagrass form and cover; these were at 34°01′S,23°23′E (Keurbooms Lagoon, where salinity may fall to 23) and 34°01′S,23°24′E (Bitou estuary, where it may fall to <20).

At each locality, the *Nanozostera* beds were sampled during the austral summer at two replicate sites, >50 m. All samples were taken at least 2 m away from habitat interfaces to avoid any possible edge effects (Nakaoka, 2005; Barnes and Hamylton, 2016), and each site was represented by 16 randomly-located replicate cores. These replicate sample numbers and timings were fixed to conform to those in the specific historical Knysna datasets being compared, so that all site comparisons were based on the same number and size of samples, size range of animals, total sampled area, and the same type of habitat. On the basis of past experience of the habitats under consideration at Knysna and at the mouth of the Keurbooms/Bitou system, 16 such cores could be expected to yield a total of at least 230 animals (in fact they totalled >1100), well above the number required for robust multivariate comparisons (Forcino et al., 2015). Also to conform to the datasets previously collected from Knysna, individual core samples were of 0.0054 m^2 area and 0.1 m depth, thus collecting 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). Recent experience in both the lagoonal and estuarine regions at Knysna suggests that a total sample of 32 cores per locality would collect at least 60 % of estimated total macrofaunal morphospecies present in each region but that the remaining 40 % would all be rare, some 40 % of all the taxa recorded from the lagoonal and estuarine reaches each occurring in <0.33 % of samples (Fig. 2). It would therefore require a disproportionately large number of samples to increase the sampled proportion beyond 60 % which was deemed unacceptable in a sensitive and endangered environment.

As previously at Knysna, all samples were collected during daylight hours through >15 cm of water, and were gently sieved on site through 710 μm mesh. Retained material from each core: (1) was placed in a large polythene bag of local estuary water within which all seagrass was shaken vigorously to dislodge all but sessile animals and then discarded; (2) was then re-sieved and transported to a local laboratory, and (3) was there placed in a translucent dish over a LED light pad in which the living fauna was located by visual inspection, identified and counted, and finally returned to their habitat. As macrofaunal assemblage characteristics may vary with the degree of seagrass cover (McCloskey and Unsworth, 2015), all seagrass samples were taken from areas with coverages greater than the McKenzie (2003) maximum 75 % standard for estuarine dwarf-eelgrass. The earlier samples from Knysna were previously sorted in identical fashion and taken during the same months of the year. Where multiple such sets of samples have recently (2019–2021) been obtained from the Knysna localities, they were represented here by the mean value of individual sets of 2 x 16 cores: these historical Knynsa estuarine and lagoonal zone datasets are available online at https://data.mendeley.com/datasets/w3cpzdtrh3/1. Those of Knysna's marine, near-mouth region at available at https://data.mendeley.com/datasets/nj2mvv8fn5/1; and the historical data on the Keurbooms Lagoon mouth region can likewise be found at https://data.mendeley.com/datasets/d7fmxgx95t/1.

Because of taxonomic uncertainty, including amongst numerically-dominant local 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 any closely similar species, experience of taxonomic resolution/sufficiency in equivalent soft-sediment macrobenthic studies (e.g. Warwick, 1988; Tataranni et al., 2009; Kokesh et al., 2022) indicates that operating at

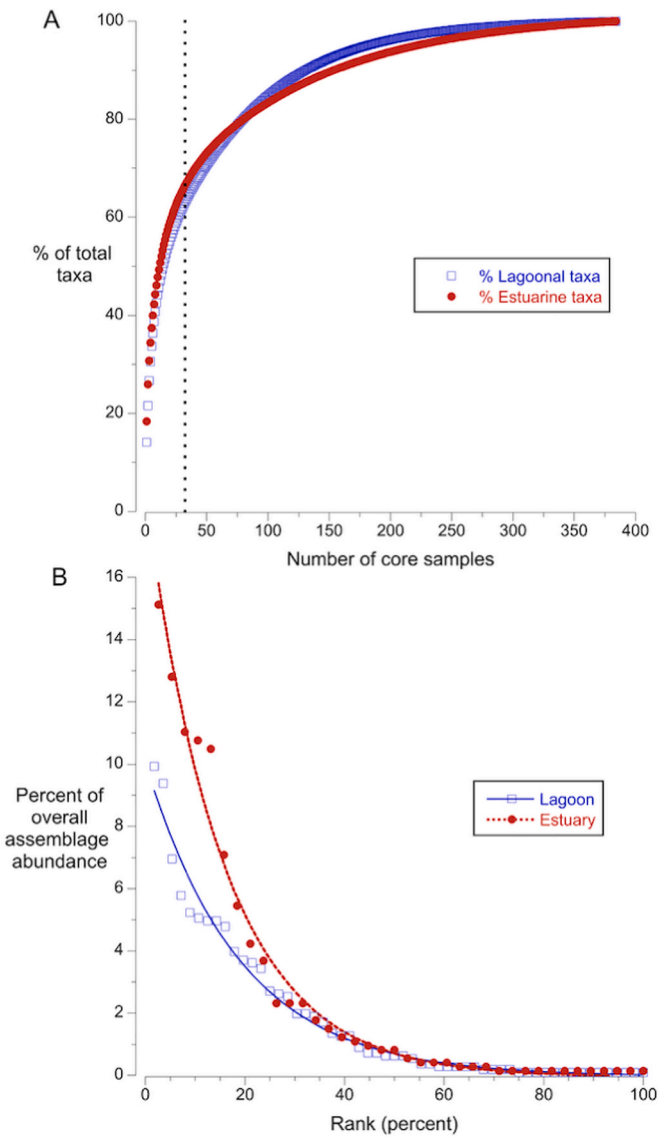

Fig. 2. Assemblage structure of the seagrass-associated macrofauna from three localities in each of the Knysna lagoonal and estuarine regions (from 2019 to 2021 data). A: Mao-tau distribution of the percentage of total morphospecies observed as a function of number of samples taken, extrapolated to its asymptote from a sample of 96 cores each of 0.0054 m^2 area. The 32 cores adopted here as the sampling unit would yield some 60 % of the likely total in both notional lagoonal and estuarine compartments. B: Species abundance diagram (as per Passey, 2016), showing the preponderance of relatively rare taxa at each site (R^2s > 0.98).

various levels from species up to family all produce similar conclusions. The same morphospecies recognised by Barnes et al. (2024) were used again in the present study, although, again as before, wherever possible, all animals of particular interest were identified to the lowest taxonomic category currently recognised locally. Nomenclature below is as given by the World Register of Marine Species (WoRMS, www.marinespecies.org, accessed August 2025), except in respect of '*Assiminea*' *capensis* (see Barnes, 2018) which is listed in WoRMS as *Rissoa capensis* and as a *taxon inquirendum*, and of the genera of the Zosteracea which follow the recent revision by Sullivan and Short (2023). All data collected are available at https://data.mendeley.com/datasets/n3x2w7y366.1. Sessile and mobile species can differentially influence spatial patterns of biodiversity (Davidson et al., 2004), and this study excluded any sessile or semi-sessile animals that had become detached from the seagrass leaves during sampling.

2.2. Data analysis

Numbers per unit area (per core, site, and locality) of component zoobenthic morphotaxa were subjected to similarity analysis, and assemblage metrics were derived and compared via *PAST* 4.15 software (Hammer et al., 2001) or Microsoft Excel for Mac 16.93 with the Stat-Plus:mac Pro 8.0.4 add-on, all metrics being based on animal abundance. Ranking of dominant species was determined by the Barnes (2014a) index of numerical importance (INI). Univariate metrics assessed were those argued to have a major influence on local-scale biodiversity (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 morphospecies abundances (Pielou's *J*); and (4) observed and (5) estimated likely real numbers of morphospecies per unit area ('species density' *sensu* Gotelli and Colwell, 2001), represented 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) in 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. Likely real number of morphospecies at different sampling intensities was also estimated by sample rarefaction using Mao's tau (Colwell et al., 2004). In addition, (6) taxonomic diversity (*sensu* Clarke and Warwick, 1998) was also assessed.

Multivariate statistical comparison of quantitative assemblage composition used ANOSIM of Euclidian distance data, PerMANOVA of Morisita similarity [see Wolda (1981) and Barwell et al. (2015)] carried out on untransformed abundances, and SIMPER of Bray-Curtis data, all with probabilities determined by Monte Carlo bootstrap analysis using 9999 permutations. 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).

3. Results

3.1. Lagoonal zone

At all spatial scales investigated, the number of observed morphospecies per unit area was greater at the Keurbooms lagoonal locality than in the Knysna one, markedly so per core sample (ANOVA $F_{1,126} = 137$; $p \ll 0.0001$) and per site (Table 1): Keurbooms lagoonal-locality core sample mean 12.5 (95 % confidence limits 11.7–13.2; range 8–17); equivalent Knysna mean 7.4 (95 % confidence limits 7.0–7.8; range 3–13); per site values were 29 *vs* 20. Per locality values were more similar (32 *vs* 28). The Keurbooms Mao tau accumulation curve was approximately parallel to that of the mean Knysna one and the two showed little sign of eventually converging (Fig. 3A). Likewise, numbers of individuals per unit area was always greater in Keurbooms/Bitou than in Knysna and by a large margin at all spatial scales: Keurbooms/Bitou supported a mean 101 individuals per core sample (95 % confidence limits 78–124; range 24–300), Knysna only 19 (95 % confidence limits 17.7–20.4; range 5–35) (ANOVA $F_{1,126} = 154$; $p \ll 0.0001$) (see Table 1).

There was no overlap in the dominant species in the two systems (Table 2), and they supported very different faunal assemblages (PerMANOVA $F = 71$; $p < 0.0001$) (Table 3). Keurbooms/Bitou was dominated by the suite of unusual South African endemics (including '*Assiminea*', *Halmyrapseudes* and '*Hydrobia*') usually considered to typify the Knysna estuarine bay, where, however, they are more associated with backwater, saltmarsh-enclosed creeks than the main estuarine channel (i.e. the region demarcated in Barnes and Seath, 2025: Fig. 2). In contrast, with the exception of the unusual seagrass-associated cushion-star *Parvulastra*, the lagoonal region at Knysna was characterised by species regarded by Day (1981) as being common and relatively

Table 1
Per site biodiversity metrics of the benthic macrofaunal assemblages in comparable equal-area samples of *Nanozostera capensis* beds in equivalent estuarine and lagoonal stretches of the Knysna and Keurbooms/Bitou systems: Observed number of morphospecies (obs *N*), the Gatti et al. (2020) estimator of number of morphospecies really present (est *N*), overall macrobenthic abundance m^{-2} (*A*), geometric mean morphospecies abundance m^{-2} (*G*), Pielou evenness (*J*), and index of taxonomic diversity (*D*), with ranges given in parentheses. Knysna data are mean values from historical 2019–2021 samples.

	obs N	est N	A	G	J	D
LAGOONAL SITES						
Knysna	20	29	4054	62	0.75	3.88
	(14–24)	(19–38)	(2650–5984)	(46–83)	(0.68–0.80)	(3.62–4.07)
Keurbooms/Bitou	29	35	18756	127	0.60	3.40
	(28 & 30)	(34 & 37)	(12940 & 24572)	(97 & 157)	(0.58 & 0.63)	(3.23 & 3.58)
ESTUARINE SITES						
Knysna	16	21	2908	73	0.75	3.72
	(12–19)	(16–26)	(2234–3426)	(53–96)	(0.69–0.80)	(3.48–3.91)
Bitou	25	29	28356	148	0.52	3.05
	(23 & 27)	(27 & 32)	(28287 & 28426)	(142 & 154)	(0.50 & 0.54)	(3.02 & 3.08)

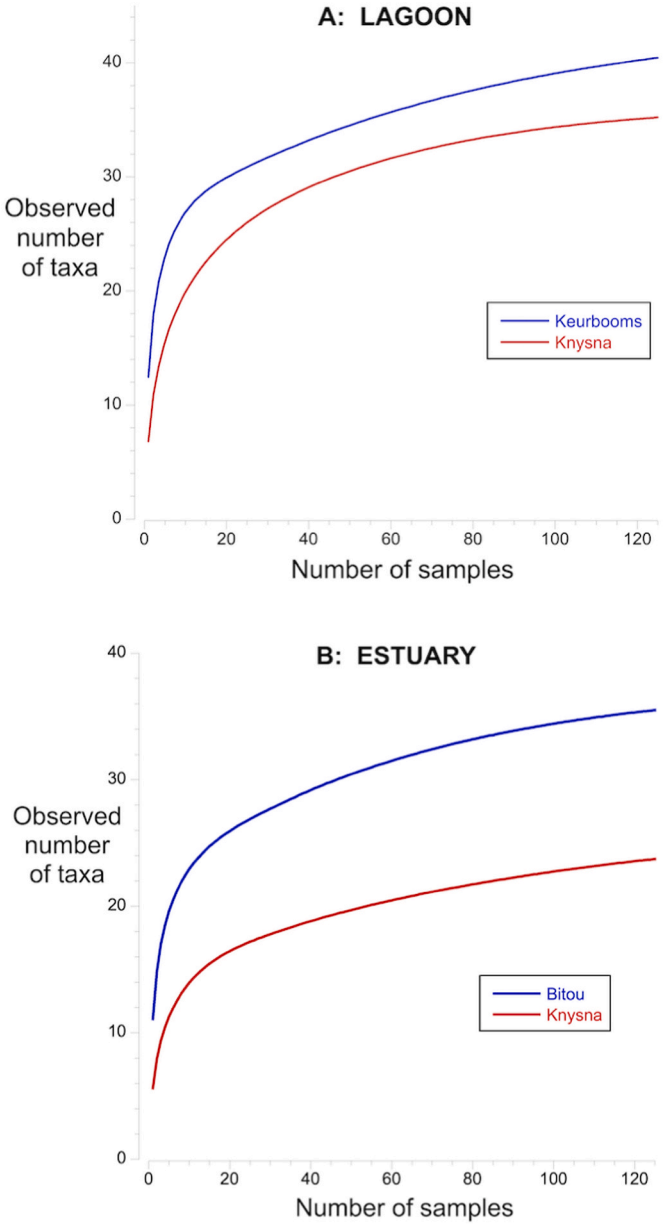

Fig. 3. Comparison of the number of seagrass-associated macrofaunal morphospecies by Mao-tau accumulation extrapolated to 125 samples in (A) lagoonal and (B) estuarine localities of the Knysna and Keurbooms/Bitou systems.

Table 2
The five most numerous macrobenthic taxa in comparable equal-area samples of *Nanozostera capensis* beds in equivalent estuarine and lagoonal stretches of the Knysna and Keurbooms/Bitou systems, together with their percentage importance (INI) rating. The taxon most responsible for the difference between the localities (according to SIMPER) bears an asterisk. Knysna data are mean values from historical sets of 2019–2021 samples.

LAGOONAL SEAGRASS			
KNYSNA		KEURBOOMS/BITOU	
*Prionospio sexoculata**	19 %	*'Assiminea' capensis**	22 %
Nassarius kraussianus	14 %	*Halmyrapseudes ?cooperi*	11 %
Salmacoma litoralis	9 %	*Melita zeylanica*	10 %
Arcuatula capensis	7 %	*Capitella* sp	9 %
Parvulastra exigua	7 %	*'Hydrobia' knysnaensis*	7 %
ESTUARINE SEAGRASS			
KNYSNA		BITOU	
*Prionospio sexoculata**	20 %	*'Assiminea' capensis**	29 %
Simplisetia erythraeensis	19 %	*Halmyrapseudes ?cooperi*	13 %
Salmacoma litoralis	16 %	*'Hydrobia' knysnaensis*	10 %
Arcuatula capensis	10 %	*Capitella* sp	7 %
Nassarius kraussianus	9 %	*Grandidierella lignorum*	6 %

Table 3
Compositional similarity of the benthic macrofaunal assemblages in comparable equal-area samples of *Nanozostera capensis* beds in equivalent estuarine and lagoonal stretches of the Knysna and Keurbooms/Bitou systems, assessed by ANOSIM R, Morisita similarity, and Harrison et al. *β*-2 diversity. 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 et al. *β*-2 diversity qualitative. Knysna data are mean values from historical sets of 2019–2021 samples.

	1 - ANOSIM R	Morisita	1 - Harrison et al. β-2
LAGOONAL SEAGRASS			
Knysna *vs* Keurbooms/Bitou	0.57	0.07	0.43
ESTUARINE SEAGRASS			
Knysna *vs* Bitou	0.38	0.19	0.55

widely-distributed in southern African estuaries (Table 2). The five most numerically important species in Keurbooms/Bitou only comprised <1 % of the Knysna fauna; conversely *Arcuatula* and *Parvulastra* did not occur in the Keurbooms lagoonal samples, *Salmacoma* was rare, whilst only *Prionospio* and *Nassarius* achieved ≥2 % of the fauna there. The differential importance of annelids, peracaridans and gastropods in the two systems is illustrated in Fig. 4A. At Keurbooms/Bitou, the various annelids usually labelled 'opportunistic' and often considered to indicate anthropologically degraded habitat comprised 16 % of the faunal individuals whereas disturbance-sensitive amphipods formed 13 %; Knysna, in contrast, displayed an opportunistic annelid total of 30 % and

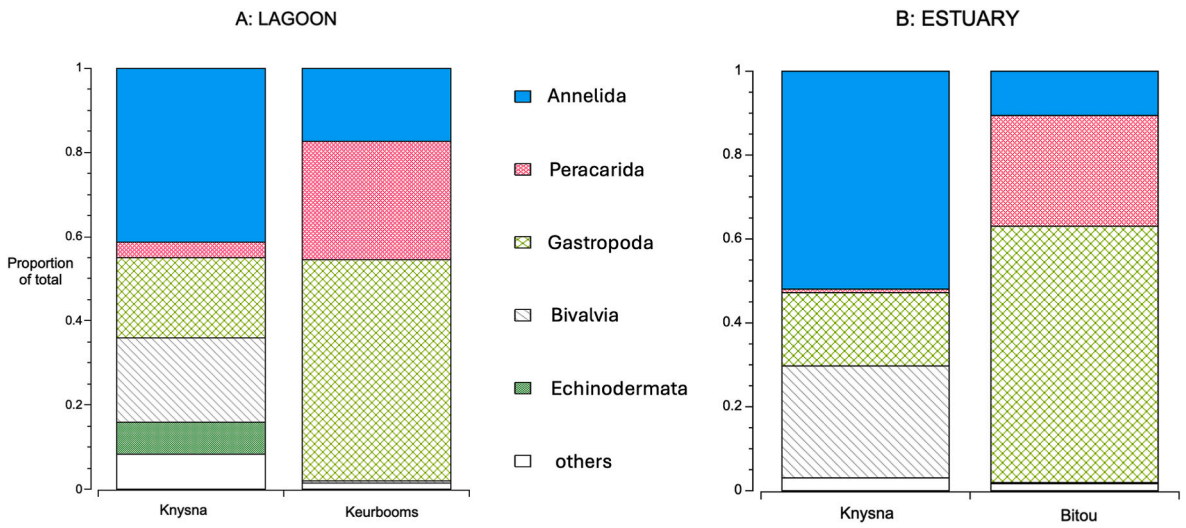

Fig. 4. Stacked-column diagrams illustrating the contrasting proportional abundance of different major taxa in macrobenthic assemblages of comparable *Nanozostera capensis* beds in equivalent lagoonal (A) and estuarine (B) stretches of the Knysna and Keurbooms/Bitou estuarine systems.

a sensitive amphipod total of <2 %.

3.2. Estuarine zone

Precisely the same patterns were replicated at the estuarine localities. At all spatial scales investigated, the number of observed morphospecies per unit area was greater in the Bitou Estuary than in that at Knysna, displaying twice the species density per core sample (95 % confidence limits of 5.2–6.0 for Knysna, and 10.4–12.2 in Bitou), as well as being greater with no overlap in numbers per site (Table 1), and with a mean of 18 at Knysna and 27 for the Bitou locality. Likewise, numbers of individuals per unit area was always greater in Bitou than in Knysna at all scales, and by the large factor of 10: Bitou supported 128–178 individuals per core sample (mean 153), Knysna only 5.2–6.0 (95 % confidence limits) (see Table 1). The Bitou Mao tau accumulation curve was again approximately parallel to that of the mean Knysna one with the two showing little sign of eventually converging (Fig. 3B).

As in the lagoonal sites, there was no overlap in the dominant estuarine species in the two systems (Table 2), and they supported very different faunal assemblages (PerMANOVA $F > 119$; $p < 0.0001$) (Table 3). The Bitou one was dominated by the same suite of morphospecies that characterised the Keurbooms/Bitou lagoonal site (with one amphipod, the common and relatively widespread *Grandidierella*, replacing another such, *Melita*, in the top five), and likewise the Knysna estuarine zone being dominated by the same species as its lagoonal region, except for the replacement of *Parvulastra* by *Simplisetia* (Table 2). The differential importance of annelids, peracaridans and gastropods in the two estuaries is illustrated in Fig. 4B. In the Bitou, the various opportunistic annelids comprised 2.5 % of the faunal individuals whereas disturbance-sensitive amphipods formed 8.5 %; Knysna, in contrast, displayed an opportunistic annelid total of 27 % and a sensitive amphipod total <0.1 %.

3.3. Overall

The same expected pattern of distribution of biodiversity along the length of their axial channels (Whitfield et al., 2012) was seen in the two systems (Table 4); i.e. a reduction in species richness upstream. As also expected there were significant faunal differences between the three notional Keurbooms/Bitou system compartments (PerMANOVA $F = 103$, $p < 0.0001$), even between the relatively similar lagoonal and estuarine ones, with or without fourth-root transformation of the data ($F = 9.3$, $p < 0.0001$). The relative abundance of '*Assiminea*', *Halmyrapseudes*, *Capitella*, *Melita*, '*Hydrobia*' and *Nassarius* in the lagoonal region, and the scarcity of *Simplisetia*, were responsible for >75 % of the difference between that compartment and the adjacent zone near the Keurbooms mouth (SIMPER), the two differing markedly in assemblage composition (PerMANOVA $F = 103$; $p < 0.0001$), in macrofaunal abundance (the lagoon supporting 2.4 x the mouth-region numbers) and in species density, the mouth with twice the total overall number of morphospecies, and but fewer per core sample (mouth mean 9.4, 95 % confidence limits 8.5–10.2; lagoon mean 12.5, 95 % confidence limits 11.7–13.2; ANOVA $F_{1,62} = 30$, $p < 0.0001$). The greater abundance of '*Assiminea*', *Halmyrapseudes* and '*Hydrobia*' in the estuary, and of *Capitella* and *Melita* in the lagoon was responsible for >75 % of the compositional difference between the two (SIMPER). Keurbooms/Bitou also supported a surprisingly large share of the overall local biodiversity held within the two systems combined, a proportion greater than that of Knysna (Table 4) in the compared samples.

Table 4
The total species density located in each of the different notional system compartments of the Knysna and Keurbooms/Bitou estuaries within and across the two systems. All data from samples of 32 cores in each representative system compartment; i.e. each estuary by 96 core samples.

compartment	Knysna	Keurbooms/ Bitou	taxa only in Knysna	taxa only in K/ Bitou	shared taxa
estuarine	53	84	15	47	38
lagoonal	59	68	37	35	27
mouth	62	70	30	38	32

Adding the earlier data for the marine Keurbooms/Bitou mouth compartment (Barnes et al., 2024) to that of the present lagoonal and estuarine localities, the number of observed macrofaunal morphospecies in the shallow *Nanozostera* beds fringing that system (from a total of 96 core samples) was 68, with estimates of between 77 (effective density) and 89 (Mao tau extrapolation) for the likely total number in the immediate sampled areas. A further 20 species were also earlier recorded from the subtidal seagrass at the system's mouth (Barnes et al., 2024), Mao tau extrapolation then indicating that the investigated areas of Keurbooms/Bitou *Nanozostera* are likely to support some 115 species. Granted that the 128 cores taken to date only sampled a total area of 0.7 m^2, the likely species total for the whole Keurbooms/Bitou cannot be other than much larger still.

Knysna, however, possesses some three to four times the area of

Nanozostera present in Keurbooms/Bitou, and hence an area effect would be expected (Gleason, 1922), with Knysna supporting the larger overall number of macrobenthic species in that more extensive habitat. Whether this is indeed so is difficult to gauge on present data. Excluding those only found in artificial marina basins, the known Knysna grand total of 191 seagrass-associated macrobenthic morphospecies derives from a total of 39350 individual animals from 2500 core samples taken from >30 localities spanning all the areas of *Nanozostera* present in the estuarine bay (subtidal and intertidal, main channel and backwaters, estuarine and marine), vastly more samples than available from Keurbooms/Bitou where most of the subtidal zone and all the low-salinity Keurbooms Estuary remain to be investigated. All *Nanozostera* macrofaunas investigated to date show the same species-abundance pattern, i.e. in rank order, an exponential decline equivalent to that of Fig. 2B. Assuming this similarity in relationship holds in the present instance, as a rough quide Mao-tau rarefaction suggests that the number of morphospecies in the Knysna assemblage expected from a random 128 core samples is in the order of 100 ± 10 (=53 % of the known overall total); the 88 ± 5 currently known from Keurbooms from the same number of samples overlaps with the estimated equivalent Knysna total and would translate to a grand total of some 166 ± 9.

4. Discussion

4.1. Biodiversity management in the Knysna and Keurbooms/Bitou systems

It is very clear from these results that when compared in an equivalent manner, using the same sampling intensity and target organisms, the macrofauna supported by the Keurbooms/Bitou seagrass per unit area is as biodiverse, if not more so, than that of the flagship Knysna estuarine bay, supposedly the richest and most biodiverse in South Africa, and it is even more abundant. Even the number of species in total that it supports appears likely to be comparable notwithstanding the difference in their areas. Further Keurbooms/Bitou holds greater abundance of several nationally rare endemic and unusual invertebrates than Knysna. It fulfills all the elements of biodiversity importance that score highly in the South African conservation-priority status assessment of estuarine environments. This all stands in extreme contrast to its supposed state of supporting well-below-expected species richness and abundance (CapeNature, 2023a). The only other invertebrate survey of the system to have been published since preparation of the current management plan (de Villiers et al., 2021), which was carried out in the seagrass of the low-salinity area of the Keurbooms Estuary, also found a rich fauna in the summer months totalling some 7500 m^{-2} and dominated by '*Hydrobia*' (>5000 m^{-2}) (N. de Villiers pers. com.).

Knysna is a large and diverse estuarine bay and seagrass is not the only habitat it supports, but seagrass is arguably the most important one and that of greatest conservation concern, both for its own sake as a threatened keystone plant (Adams, 2016) and for the fish and invertebrates that it shelters and supports (Chen et al., 2024). In Keurbooms/Bitou, what is true of the seagrass, however, does also seem to apply to the bare sediment as well, at least to that near the mouth which is the only area where it has received any attention (Barnes et al., 2024), and bare sand is the other main Knysna habitat below low-water neap tide level (Van Niekerk et al., 2019).

A town with 75000 inhabitants and some 500000 annual tourist visits extends along one shore of the Knysna estuarine bay and most of this eastern shore is now artificial (Claassens et al., 2020). Although the system lies within a National Park it is open-access and a 'common-pool resource'; hence its management cannot be other than a compromise between the socio-economic requirements of the local and tourist human population and the desirability of conservation of its natural resources (Roux et al., 2023). Virtually all of its intertidal seagrass beds are easily accessible, and all bear the obvious scars of having been (legally or illegally) pushed or pumped for bait-prawns or dug for bait-worms (see, e.g. Whitfield et al., 2023, Fig. 7.11), recreational and artisanal fishing being widespread (Table 5). Backwater channels immediately adjacent to the town and/or receiving small rivers draining township or industrial areas are degraded (Benjamin et al., 2025), and episodes of eutrophication-fuelled 'green-tide' algal blooms have impacted its seagrass beds (Claassens et al., 2020) (Table 5). It is still very rich in wildlife, however, thanks to the twice-daily flushing the main channel receives by virtue of its large tidal prism, but the effects of humanity are all too evident, and are unlikely to decrease in the future.

The Keurbooms/Bitou system (Table 5), on the other hand, does not have a conurbation along its shores (although homes do line much of the eastern shore of the Keurboom Estuary and the shoreline there has been reinforced by gabions), and most of its coast is difficult to access. Hence apart from near its northern and southern extremities, the intertidal zone shows less signs of bait harvesting; it is currently rated as still being in an unmodified, approximately natural state with few modifications (CapeNature, 2023a); and it has a higher level of estuary health than Knysna (Turpie et al., 2012a,b). Waterbirds are almost as diverse as at Knysna, 64 *vs* 72 species; and the fish it supports include the endangered white steenbras, *Lithognathus lithognathus* (CapeNature, 2023a) and a number of elasmobranchs for which it may be specially important as a nursery (Elston and Murray, 2024). It is currently rated as 'vulnerable' but as receiving only a low to moderate (and no formal) level of protective management (Turpie et al., 2012a,b; CapeNature, 2023a), although much of the surrounding area is so protected. The Keurbooms River immediately upstream of the estuary is managed as a Provincial Nature Reserve, for example; the Garden Route National Park extends both to its east and west but excludes it; and the adjacent open sea is within the Robberg Marine Protected Area (MPA). Somewhat paradoxically, then, in the 2018 South African National Biodiversity Assessment (Van Niekerk et al., 2019), the Keurbooms/Bitou was rated as 'a priority' by virtue of its extensive seagrass, seahorse and nursery function. The value of the Keurbooms/Bitou estuarine system has also been popularly recognised by inclusion in the 'Plettenberg Bay International Hope Spot' by the Sustainable Seas Trust/Mission Blue organisations (Knysna estuarine bay forms another such), although this does not carry with it any protected status. Granted the overturn in its apparent invertebrate biodiversity described herein, it would appear even more obvious that conservation of the warm-temperate estuarine biodiversity of South Africa is more likely to be achieved in a system like the Keurbooms/-Bitou than in most others, even though its enclosing sandy barrier is mobile and freshwater floods occur episodically. The clock is ticking, however; there are proposals to build further estates along its shores (see, e.g., Cape EAPrac, 2024): in South Africa, as elsewhere, urbanisation of estuaries is proceeding apace (Claassens et al., 2022).

Table 5
Summary of general characteristics and key anthropogenic pressures associated with the two studied estuarine systems (compiled by J.B. Adams from data in Van Niekerk et al., 2019).

	Knysna	Keurbooms/ Bitou
Catchment size (km^2)	417	1123
Mean annual runoff (x 10^6 m^3)	68	215
Protected area compared with size of estuarine functional zone (ha)	2984/ 3011	234/1641
Key pressures:		
flow modification	low	low
pollution	high	low
habitat loss	low	medium
fishing effort	high	low
Fish nursery importance	high	high
Estuarine Health score	78/100	88/100
Biodiversity importance	high	high

4.2. Neglect of benthic invertebrates in estuarine management assessments

That Keurbooms/Bitou currently bears no formal conservation designation or protective management as a nature reserve could appear solely a result of inadequate knowledge of its true biodiversity importance. However, there is another issue. More than one notion of what constitutes 'estuarine biodiversity' seems to occur, just as there is more than one view of what organisms are of potential relevance to biodiversity assessment (Ornellas et al., 2011). It has been well understood for almost a century that the dominant macrobenthic animals of the soft sediments characteristic of estuaries are mostly small (e.g. Thamdrup, 1935; Linke, 1939). However, unlike locally at Knysna (Day et al., 1951) and Swartvlei (Whitfield, 1989a), what little earlier benthic survey work taking place at Keurbooms/Bitou was concerned only with relatively large animals (see, e.g., Duvenage and Morant, 1984), and the legacy of this restricted interpretation of benthic biodiversity is evident today, not least in the designation of inappropriate management targets. The current Management Plan specifies that the densities "of each of the four numerically dominant benthic species" should be maintained at baseline levels. But lack of appropriate macrobenthic data has resulted in attention being directed to the wrong species: the animals specified to be the numerical dominants and hence to be the subject of this specific monitoring, i.e. *Upogebia, Kraussillichirus, Arenicola* and *Solen*, are all large and in fact are really very far from being the most numerically dominant.

All four, however, do share one particular feature: they are popularly collected for use as bait. Indeed, throughout South Africa there seems to be an assumption that the only estuarine invertebrates of any potential interest and relevance to management are those that can be used as bait. Just as in Knysna where the organisation responsible for managing the system could be accused of paying more attention to safeguarding the widespread and abundant bait mudprawn *Upogebia* than to the threatened *Nanozostera capensis* of conservation concern in which it lives (Barnes et al., 2024), so in Keurbooms/Bitou the organisms singled out for special management attention are all those in which humans have a direct interest. Because they are all exploited, it may be that they are considered likely to be potentially most at risk, but actually they are all common South African species whose populations seem stable in the face of exploitation (Hodgson et al., 2000; Simon et al., 2019), except possibly some of those of *Arenicola* (Simon et al., 2020). A cynic might comment that their harvesting also brings in revenue from bait-collection permits, as does the fishing that uses them. A far greater threat than to any bait species populations, however, is habitat loss or degradation (including that caused by trampling during bait collection).

In any event, it is evident from this study that in the Keurbooms/Bitou system the four macrobenthic species that are the real numerical dominants in the seagrass and those likely to be of greatest ecological importance are the gastropod '*Assiminea*' and tanaid crustacean *Halmyrapseudes* with mean densities $>1000\ m^{-2}$, and the polychaete *Capitella* and gastropod '*Hydrobia*' with mean densities of $>800\ m^{-2}$. From the information currently available on the bare sediment, it appears likely that its numerical dominant will also be the '*Assiminea*'. None of these receive any mention in Management Plans. Since all four are associated with the surface or near-surface of the sediment, monitoring their populations would certainly be very much less intrusive than that for deeply burrowing animals such as *Upogebia* and *Arenicola*.

Invertebrates "are vastly under-represented in studies of African diversity" (CapeNature, 2023b) and are largely ignored in conservation management protocols, as is exemplified by Keurbooms/Bitou. This is also evident in the national assessment of South African estuarine biodiversity conducted by Van Niekerk et al. (2019). They award regional red-list status to a total of 67 estuarine taxa: 35 birds, 20 fish, 7 plants, but only 5 invertebrates. Several rare polychaetes, ostracods, amphipods, isopods, gastropods and members of other invertebrate groups are endemic to South African estuaries and are each currently known only from a few individual sites, for some only a single locality. Yet the invertebrate red list does not include any of these rare South African endemics that almost by definition must fall into at least the vulnerable category. The five invertebrates to which the assessment did draw conservation attention are two decapod crustaceans widely distributed throughout the Indo-West-Pacific Ocean and (perhaps not-surprisingly considering the discussion above) three common bait species. Unfortunately, the overturn in apparent macrobenthic biodiversity status described here, and the presence of a number of rare endemic species, would have little or no effect on the position of Keurbooms/Bitou in the South African rank order of estuarine conservation importance because invertebrate biodiversity accounts for only a very small fraction (<7 %) of any system's overall importance score (Turpie, 2004), regardless of the rarity or conservation status of any of the individual animals concerned.

4.3. Conservation management of estuaries

Indeed, almost everywhere, management of estuarine, lagoonal and equivalent transitional environments to conserve their biological richness and productivity lags far behind that of terrestrial habitats, notwithstanding that estuaries are amongst the most productive yet most highly degraded of Earth's biomes (Edgar et al., 2000). Besides promoting biodiversity, their seagrass systems are known to structure soft-sediment dynamics, modulate critical coastal ecosystem processes including carbon storage and cycling, sequester pollutants, combat erosion and eutrophication, and support commercially-important crustacean and fish stocks (Rodil et al., 2022; Millot et al., 2024). Seagrass beds are a prime source of nature-based solutions to coastal problems (Lima et al., 2023; Marino et al., 2025), and monitoring their benthic macrofauna can provide a good indication of their ecological health and ability to continue to carry out these and other valuable functions (Magni et al., 2005; Blanchet et al., 2008; Lu et al., 2021). To achieve this end, and come to that any matter relating to estuarine or lagoonal habitat management, and to reach appropriate decisions on the relative importance of individual sites, biodiversity assessments should include an accurate quantitative and qualitative picture of the macrobenthos concerned. As well as data on the vertebrates, they should yield realistic estimates of invertebrate species composition, abundance, richness, spatial distribution and variability at any point in time, as an essential component of national estuarine management protocols.

Disparity of conservation status or ranking created by differential levels of investigation and knowledge will not be confined to estuarine environments nor indeed to South Africa: the example here of the Keurbooms/Bitou will certainly not be alone in that respect. Nor is the low conservation status accorded to invertebrates only of local South African concern. Conservation of estuarine birds and fish is high profile and attracts public support for management protocols to achieve it, and their presence may carry major ranking points for sites. The fact that the only part of the Keurbooms/Bitou estuarine system managed as a nature reserve is the breeding colony of a seagull species rated of 'least conservation concern' on the lagoon-enclosing sand bar somehow epitomises current estuarine conservation priorities. Such vertebrates are, however, the tip of the iceberg. The same public may not have any interest in small, charisma-deficient, mud-dwelling, non-bait worms, crustaceans and molluscs, and would certainly be unwilling to pay entry fees to observe them in a nature reserve, but the underlying trophic levels cannot be taken for granted, especially in light of the variation in their nature over short distances set out here. One feeds the other, as detailed in Swartvlei by Whitfield (1989b), and management of one without explicit and realistic consideration of the other will be pointless in the long run.

4.4. Knysna and Keurbooms/Bitou in their local setting: further research

As pointed out above, the smaller macrobenthos has been catalogued in many South African estuaries, but because of taxonomic uncertainty

identifications have often been tentative, especially in respect of worms (polyclad, nemertine or annelid), and the dominant microgastropods (Barnes, 2018). Hence, whether some, including the Knysna-area specialities, are really more widespread or are indeed very local and hence in need of active conservation management remains an open question (Barnes, 2025), part of an unfortunately general pattern (Kindsvater et al., 2018). Parity of treatment of the invertebrate macrobenthos with that accorded to vertebrates may be wishful-thinking, but focussed research into their status and potential conservation requirements is urgently needed in southern Africa and in many other parts of the world.

The marked contrast between the dominant faunal elements in the lagoonal and estuarine stretches of the Knysna and Keurbooms/Bitou seagrass systems (Table 2 and Fig. 4) is worthy of further investigation. Both are permanently open systems, and they are located close together geographically, yet spatial autocorrelation does not seem to apply to the most abundant faunal components in their shared *Nanozostera* beds. Dominance by the endemic microgastropods '*Assiminea*' *capensis* and '*Hydrobia*' *knysnaensis*, however, is also a feature of the upstream zones of the Swartvlei estuary to the west of Knysna, '*Assiminea*' comprising 52 % of the macrofauna in its *Nanozostera* and 26 % in the *Ruppia* there, and '*Hydrobia*' 24 % and 36 % respectively, in a combined overall density of >40000 m^{-2} (Ndhlovu et al., in prep.). Swartvlei differs markedly from Knysna and Keurbooms/Bitou in being a temporarily closed estuary; indeed it spends longer isolated by a sand barrier than being open to the Indian Ocean (SANParks, 2020), and permanently and only temporarily open estuarine systems usually display marked faunal and ecological dissimilarity in South Africa and elsewhere (Teske and Wooldridge, 2001). Thus the equivalent dominance of the two contrasting seagrass systems by the same two unusual microgastropods is unexpected: is it, as might appear possible (Barnes, 2025), a triumph of biogeography over ecology? Nevertheless because of its temporarily-closed state Swartvlei is relatively depauperate (the 96 seagrass samples of Ndhlovu et al., in prep., yielding only half the species density of the same number of samples from Keurbooms/Bitou). Although there are areas along Knysna's main channel that do support '*Assiminea*', for example in the clean sands near its mouth, '*Hydrobia*' is very scarce there. Both species are much more characteristic of the *Nanozostera* and associated bare sediment in Knysna's backwater, saltmarsh-enclosed creeks and channels.

The co-dominance of *Halmyrapseudes* in Keurbooms/Bitou is also of biodiversity and conservation interest in that tanaids have not been reported as dominant in any other South African seagrass system, although a closely related parapseudid, *Longiflagrum,* is one of the most abundant components of the macrobenthos of the *Nanozostera mulleri* fauna in the Moreton Bay Marine Park, Queensland (Barnes, 2014b), and *Halmyrapseudes* is also dominant in soft sediment in the temporarily closed uMdlotane Estuary and in Richards Bay harbour, KwaZulu/Natal (Izegaegbe et al., 2020; Carrasco et al., 2025). This tanaid has not been recorded from Swartvlei, and in Knysna seems to be restricted to backwater high-level pans and a borrow ditch enclosed within saltmarsh.

4.5. Overall conclusions

In no sense does the comparison conducted here diminish the standing of the flagship Knysna estuarine bay or suggest change in its management regime. The many person-hours of study devoted to it have disclosed a very rich biodiversity indeed, notwithstanding the human impact (Whitfield et al., 2023); a biodiversity that includes representatives of at least three families found nowhere else in Africa south of the Sahara. What it does show, however, is that other still relatively natural estuaries also occur in South Africa and that, albeit maybe relatively small, they may support biodiversity of highly significant national importance, including flourishing populations of some rare endemic species — levels of biodiversity that have been previously unrecognised because lack of investigation. These sites may currently receive little or no active management to conserve this biodiversity, but they could be of vital importance in stemming the decline in *Nanozostera*, its associated fauna, and estuarine organisms in general, and should therefore receive appropriate protective management. Keurbooms/Bitou is one such.

It is also evident that much greater emphasis needs to be placed on conservation of South Africa's rare or only locally-abundant endemic invertebrates, those that create the distinctive character of the country's or region's estuarine environments (*sensu* Van Niekerk et al., 2020). What is now needed is a uniformly-conducted national field census of estuarine invertebrate biodiversity, and where appropriate the implementation of Estuarine Protected Areas (as urged recently in respect of fish conservation by Whitfield and Smith, 2024). Previously, assessment of biodiversity held in individual South African estuaries was all too often only based on the scant available literature (Turpie et al., 2002, 2012). Such a census would not be just of academic interest: 99 % of South African estuarine environment already falls into the critically-endangered, endangered or vulnerable categories (Van Niekerk et al., 2019) despite the known importance, value and potential for nature-based remediation of this habitat type (Dowdall et al., 2022).

4.6. Postscript

Whilst this paper was in the final stage of consideration by *Ocean and Coastal Management*, we became aware of the existence of another [de Souza C, Griffiths CL, Lamberth SJ, Ndlovu T, Elston C and Botha TPA, 'Revealing the true macrofaunal biodiversity of the Keurbooms Estuary'] that is under consideration by another journal. The two papers arrive at identical conclusions concerning the true macrofaunal biodiversity and conservation merits of the Keurbooms system.

CRediT authorship contribution statement

R.S.K. Barnes: Writing – review & editing, Writing – original draft, Visualization, Supervision, Methodology, Investigation, Formal analysis, Conceptualization. **Minyonne Verster:** Writing – review & editing, Resources, Project administration, Investigation. **Janneke Whittle:** Writing – review & editing, Investigation. **G.M. Rishworth:** Writing – review & editing, Supervision, Resources, Project administration, Investigation.

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Data availability

Data deposited in Mendeley Data as specified in the article

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