



# Biodiversity differentials between seagrass and adjacent bare sediment change along an estuarine gradient

R.S.K. Barnes<sup>a,b</sup>

<sup>a</sup> Department of Zoology and Entomology, Rhodes University, Makhanda, Eastern Cape, 6140, South Africa

<sup>b</sup> Department of Zoology & Conservation Research Institute, University of Cambridge, Cambridge, UK

## ARTICLE INFO

### Keywords:

Biodiversity  
Estuary  
Knysna  
Macrobenthos  
Mudflat  
Seagrass

## ABSTRACT

Differentials between the invertebrate biodiversity of seagrass (S) and of adjacent bare sediment (B) were investigated at 8 localities spaced along the axial gradient of an estuarine system, that at Knysna in South Africa; various assemblage metrics being compared at paired S/B stations. Little or no S:B differentials were found near the mouth, but significant increase in those between both levels of overall assemblage abundance and of taxon richness did occur upstream (in abundance from <1 near the mouth to >2 towards the head, and in taxon richness from 1 to 2). The habitat supporting greater abundance therefore switched along the gradient. The differential between numbers of co-dominant species in the assemblages also increased upstream, whereas that between levels of taxonomic distinctness decreased. Functional diversity, evenness and patchiness differentials, however, showed no significant upstream change; neither did values of Bray-Curtis similarity between the two habitat types. Most affected were the epibenthic- and subsurface-feeding assemblage components. As predicted, macrobenthic assemblages of seagrass and bare sediment reacted differently to the gradient, and seagrass enhanced macrobenthic biodiversity much more upstream. However, location along the estuarine gradient appeared an equally important influence on assemblage composition to presence or absence of seagrass. The evident context-dependent nature of such differentials urges considerable caution in the extrapolation of ecological indicators derived from local areas to wider regions.

## 1. Introduction

The distribution of estuarine macrobenthos has been generalised in two classic paradigms. Their assemblages comprise a suite of predominantly sheltered-coastal, soft-sediment species (Day, 1959) that can also penetrate waters of lower salinity to various degrees, each dependent on its own tolerance limits (Barnes, 1989; Montague and Ley, 1993; Attrill, 2002; Attrill and Rundle, 2002). Consequently, a pattern of gradual decline in species richness/density is usually observed upstream as more and more species drop out of the fauna and are not replaced (Whitfield et al., 2012; Wildsmith et al., 2017; although see Morais et al., 2016). The sharper the gradient, the steeper is the decline (Reizopoulou et al., 2014). Although this 'Remane paradigm' (Remane, 1934, 1971) is the standard model for macrofaunal diversity patterns along estuarine gradients (Attrill, 2002), it was originally described for the non-tidal Baltic Sea and is clearly subject to a number of qualifications when applied not to stable inland brackish seas but to rapidly fluctuating estuaries (Day, 1981; Attrill, 2002; Teske and Wooldridge, 2004; Whitfield et al., 2012).

One such qualifying factor may be the occurrence of a covering of seagrass. In the warm-temperate Knysna estuarine bay, South Africa, the seagrass *Zostera* (*Zosterella*) *capensis* [*Nanozostera capensis* in the revision

of the Zosteraceae by Coyer et al., 2013] occurs virtually throughout the whole system, including over a salinity gradient of <5–35 (Maree, 2000). Along this gradient, Barnes and Ellwood (2012) found zones of considerable stability in the macrobenthic faunal biodiversity associated with the *Zostera*, separated by relatively sharp discontinuities. They suggested that, equivalently to the effect of macroalgae on microclimates on rocky-coasts (Scrosati, 2017; Monteiro et al., 2017), the presence of seagrass might have a further dampening effect on the already reduced environmental variation near, at or below the sediment surface compared to that in the overlying water (see, e.g., Misturini and Colling, 2021), thereby permitting increased penetration of the estuary by relatively stenotopic species.

Within or adjacent to expanses of seagrass are often located areas lacking angiosperm cover (e.g. Nakaoka, 2005; Hirst and Attrill, 2008) (Fig. 1), and qualitative and quantitative differences between the macrofaunal assemblages of such bare areas and those of the adjacent seagrass are the subject of the second paradigm (Hemminga and Duarte, 2000). Classically, seagrass supports assemblages of macrobenthic invertebrates with different composition and with considerably greater abundance and species density than adjacent areas without this cover (Stoner, 1980; Barnes and Barnes, 2012; van der Zee et al., 2016;

<https://doi.org/10.1016/j.ecss.2022.107951>

Received 4 April 2022; Received in revised form 5 June 2022; Accepted 14 June 2022

Available online 16 June 2022

0272-7714/© 2022 The Author. Published by Elsevier Ltd. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

Alsaffar et al., 2020; Surugiu et al., 2021; etc.). These contrasts have been attributed to the supposed refuge from nektonic predation, greater food availability, increased larval entrainment, and greater habitat structure provided by the vegetation (Reise, 1978; Edgar, 1999; Boström et al., 2006; Siebert and Branch, 2007; etc), especially for epifaunal species (Murphy et al., 2021) but also for the infauna (Brun et al., 2021). This situation has obvious impact on the relative conservation importance of seagrass and on the potential consequences of its loss on local biodiversity (Pillay et al., 2010; Alsaffar et al., 2020).

Processes associated with both these paradigms may potentially interact in the upstream zones of an estuary. If a seagrass cover does render the habitat less labile in terms of environmental fluctuation than the bare sediment alone, differentials between macrofaunal composition, abundance and biodiversity in seagrass and in adjacent bare sediment should be most evident in relatively hostile areas, and should therefore be greatest in the upstream zones of lower salinity that are known to induce stress in basically marine species (Namba and Nakaoka, 2021). The macrobenthic assemblages of seagrass and bare sediment should thus react differently to estuarine gradients. Hence the study described here examines differentials in ecological metrics between the macrobenthic assemblages associated with seagrass and with adjacent areas of bare sediment on progression up the main axial channel of an estuarine system. Tested null hypotheses were that the macrofaunal assemblages of vegetated and bare sediments do not react differently to the gradient and that biodiversity-differential indices between the two habitat types therefore remain more or less constant and biased in favour of seagrass.

## 2. Materials and methods

### 2.1. Protocol and study area

The study took place in the Knysna estuarine bay from its Indian-Ocean-influenced sandy mouth to the more typically estuarine muddy reaches near its head. This system is located within the Garden Route National Park and the research was approved by South African National Parks (SANParks) and was conducted in accordance with their scientific research regulations and requirements. It should be noted that, following the publication of Largier et al. (2000), studies at Knysna

including this one regard only the most upstream region of the system as a river estuary in hydrographic and biotic terms, although the whole estuarine bay would be considered a drowned river-valley estuary in the classification recommended by Whitfield and Elliott (2011). As in most semi-enclosed coastal circumstances, and regardless of how much of the system might be a 'true' estuary, the upstream gradient from mouth to head is a complex one reflecting not only changes in mean salinity and magnitude of salinity variation, but also changes in silt and organic content of the substratum, in water residence time, in shelter from wave action, and in width and slope of the shore and width of the channel, all of which might be expected to impinge on the distribution and abundance of the fauna (Terrados et al., 1998; Tagliapietra et al., 2012; Gross et al., 2019; Magni et al., 2022).

Macrofaunal sampling took place during the 2021/2022 austral spring and summer at six localities set at intervals along that section of the estuarine system supporting seagrass, each a c.150-m linear stretch of shoreline between tidal heights of mean low water and low water spring. Sampling localities were selected (1) to represent the three varieties of muddy-sand macrobenthic assemblage previously shown to characterise contrasting environmental conditions ('bay', 'lagoon' and 'estuary') arranged like beads on a string along the system's long-axial channel (see Barnes, 2021a), and (2) to support both beds of *Zostera capensis* and adjacent areas of bare sediment. As elsewhere in comparable circumstances (e.g. van Houte-Howes et al., 2004; Barry et al., 2021), differences between macrofaunal assemblages in these various zones are mainly consequent on variation in the relative importance of members of a common suite of numerically-dominant estuarine species (Barnes, 2021a), rather than serial replacement or turnover of faunas (e.g. Namba et al., 2020). In upstream order, the six (Fig. 2) were: 'Kingfisher' (34°03.7'S,23°03.1'E) and 'Brenton' (34°03.5'S,23°02.0'E) representing the marine bay; 'Point' (34°02.4'S,23°01.1'E) and 'Belvidere' (34°01.9'S,22°59.5'E) and 'Westford' (34°01.1'S,23°00.0'E) within the estuary of the Knysna River. Earlier data from two other localities were also available: i.e. from 'Bollard' (34°03.9'S,23°03.2'E) in the sandy tidal-delta mouth region (Barnes and Barnes, 2014), and 'Red Bridge' (34°01.0'S,23°00.1'E) in the upper estuary. In respect of the latter, seagrass disappeared from there in late 2020/early 2021 and a comparison was possible only between the seagrass macrobenthic



Fig. 1. Part of the Brenton foreshore in the Knysna estuarine bay illustrating the patchwork of *Zostera capensis* and bare sediment.

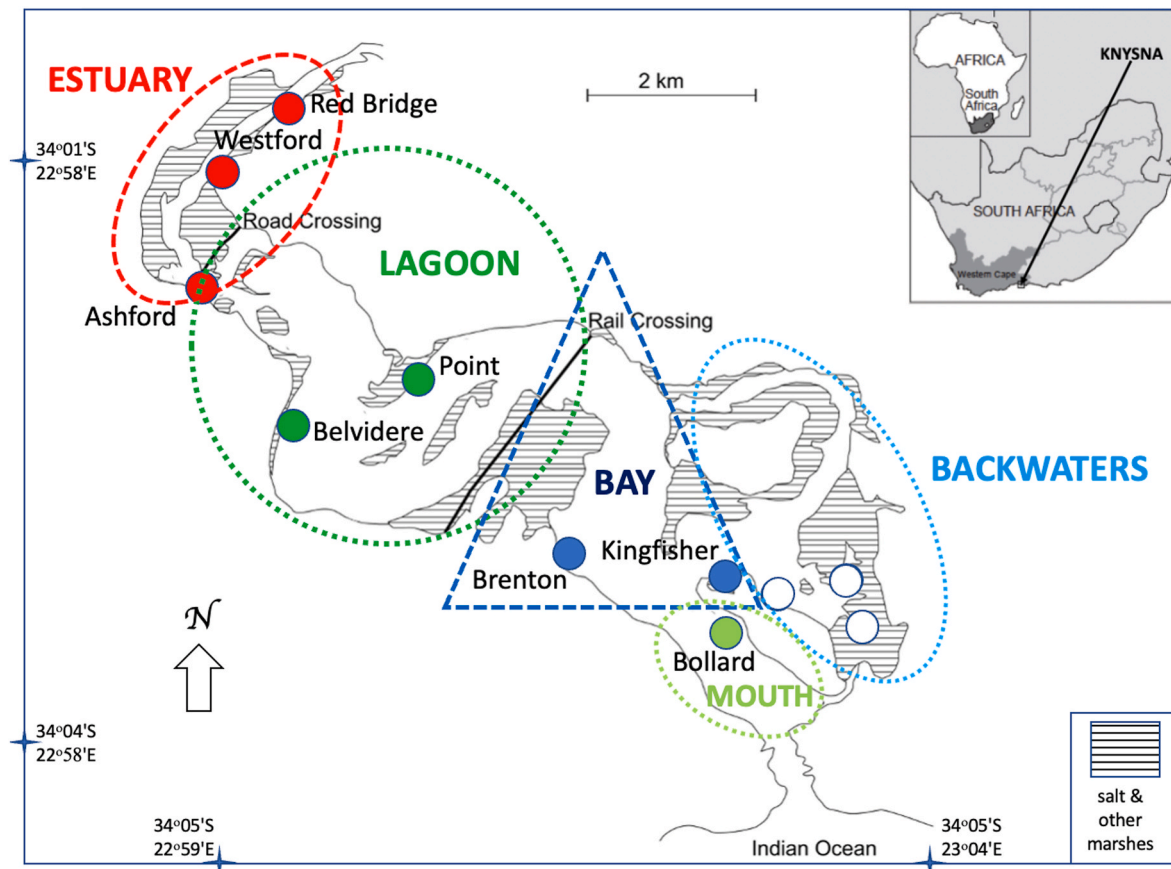


Fig. 2. Position of the eight sampling localities along Knysna's longitudinal axis, with indication of approximate extent of its four different axial macrofaunal seagrass assemblages as recognised by Barnes (2021a). White circles mark localities investigated earlier in respect of seagrass/bare-sediment differentials within the faunistically-distinct saltmarsh-enclosed backwater-channel region (Barnes and Barnes, 2014); data from their equivalent locality in the sandy mouth region ('Bollard') are re-used in present analyses.

assemblage present at one site there in summer 2019 (Barnes, 2019a) and its replacement bare-sediment assemblage in summer 2022. Earlier work at Knysna (Barnes, 2019b) has shown that such temporal comparisons at a locality produced similar patterns to spatial comparisons. In all cases, strong bioturbators (such as the sandprawn *Kraussillichirus kraussi*, which dominates many other South African estuaries) were absent from both seagrass and bare-sediment sites (see Barnes and Barnes, 2014).

At each locality except Red Bridge, adjacent seagrass and bare-sediment stations at the same tidal height were sampled at two replicate sites, >100 m apart, each station by 20 replicate cores at ~1 m intervals parallel to the water line; at Red Bridge only a single sampling site was possible. Samples were taken at least 2 m away from habitat interfaces to avoid any possible edge effects (Nakaoka, 2005; Barnes and Hamylton, 2016). For comparability with previous studies at Knysna, individual cores were of 0.0054 m<sup>2</sup> area and 10 cm 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), though not any scarcer megafaunal or deeply-burrowing species such as adult mudprawn *Upogebia africana*. This relatively large crustacean, although present and ecologically co-dominant with the *Zostera* throughout the sampled area, occurs at a maximum density unlikely anywhere to exceed <1 per core sample (Hodgson et al., 2000). All samples were collected during daylight hours, just before tidal ebb from the area of shore concerned whilst it was still covered by > 15 cm of water, and were gently sieved on site through 710 µm mesh. Retained material from each seagrass 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 immediately to a local laboratory, and (3) was there placed in a 30 × 25 cm dish over a A4 LED pad in which the living fauna was located by visual inspection using a pair of 3.5x magnifying spectacles. Bare-sediment cores were treated similarly except that stage (1) was omitted. As macrofaunal assemblages 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 65% standard for estuarine *Zostera*. The earlier cores from Bollard and Red Bridge were previously collected and sorted in identical fashion, and subsets for reuse here were taken randomly from the historical databases concerned.

Because of taxonomic uncertainty, identification of collected fauna was generally attempted only to morphologically-based operational taxonomic units ('taxa'), 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 et al., 2006; Tataranni et al., 2009; Brind'Amour et al., 2014) indicates that operating at various levels from species up to family all produce similar conclusions. Taxa were distinguished under a x25 binocular microscope, were counted, and individuals were then returned to their habitat. All nomenclature below is as given by the World Register of Marine Species (WoRMS, [www.marinespecies.org](http://www.marinespecies.org), accessed March 2022), except in respect of the unlisted 'Assimineae' (see Barnes, 2018). 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 (e.g. *Siphonaria compressa*)

that had become detached from the seagrass leaves during sampling.

## 2.2. Data analysis

Numbers of each component zoobenthic taxon at each station were subjected to similarity analysis, and per-station assemblage metrics were derived and compared via PAST 4.0.9 (Hammer et al., 2001) or Microsoft Excel for Mac 16.59 with the StatPlus:mac Pro 8.0.1 add-on, all metrics being based on animal abundance (Beck et al., 2013). Curves were fitted using KaleidaGraph 5.0, and their slopes were compared with each other and with predicted values using ANCOVA.

Univariate metrics assessed per station were those known to have a major influence on local biodiversity (Blowes et al., 2022); i.e. (1) overall faunal numbers, (2) observed numbers of taxa, i.e. Hill's  $N_0$  ['species density' sensu (Gotelli and Colwell, 2001)], and (3) relative evenness (= equitability) of taxon abundances (Pielou's  $J$ ); together with (4) taxonomic distinctness ( $\Delta^*$ ) (Clarke and Warwick, 1998), (5) functional-group  $\alpha$  diversity, and (6) assemblage patchiness (as estimated by Lloyd's  $I_p$ ). Assemblage structure is determined largely by its more numerous component taxa (Pos et al., 2014; Wang et al., 2018; Sgarbi et al., 2020); so, using the logic of Gaston (1994), in addition (7) number of co-dominant common to abundant taxa was assessed as those above the median density value for each station. Following Barnes (2021b), taxon  $\alpha$  diversity was not measured. Functional-group diversity was assessed as per Barnes and Hendy (2015) using the groupings listed in their Table 1 except that *Nassarius kraussianus* was here, following Pillay et al. (2007), regarded as largely a surface-biofilm consumer rather than a scavenger. Correlations with position along the estuarine gradient were assessed as Spearman's rank coefficient,  $\rho$ .

Multivariate comparison of assemblage composition used hierarchical clustering analysis of  $S_{17}$  Bray-Curtis similarity (Legendre and Legendre, 1998), one-way ANOSIM, SIMPER, and ordination by non-metric multidimensional scaling (nMDS) carried out on untransformed and on square-root transformed taxon abundances, all with 9999 permutations. All transformed datasets yielded the same outcomes as untransformed ones, and only the latter are presented here. Likewise, for data yielding very low values of ANOSIM R, relative magnitudes and statistical significance of macrofaunal (dis)similarities were confirmed using PerMANOVA, but no differences in patterns of significance were forthcoming. The relative influences of location along the gradient and presence/absence of seagrass on macrobenthic assemblage composition were determined using two-way ANOSIM.

## 3. Results

Analyses were based on a total sample of >13,000 macrobenthic animals representing 125 taxa, of which 7788 individuals and 47 taxa were annelids, 3039 individuals and 33 taxa were molluscs and 2086

**Table 1**  
Similarity of macrofaunal assemblage composition in within- and across-habitat comparisons along the axis of the Knysna estuarine system: Values of Bray-Curtis compositional similarity and of ANOSIM dissimilarity R, values for across-habitat comparisons being the average of the two replicate sites at each locality. Asterisk values of R indicate no significant difference ( $P > 0.05$ ).

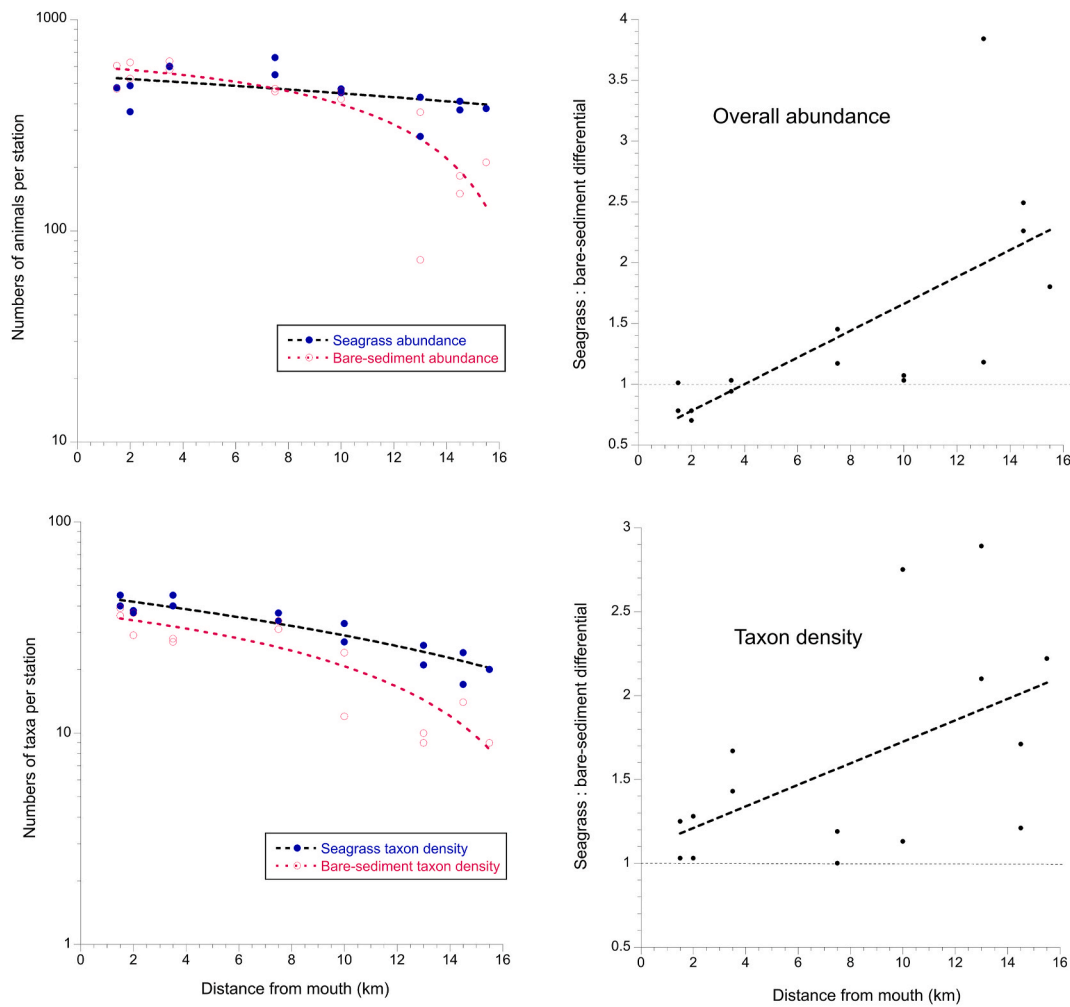
Locality	Between seagrass sites		Between bare sites		Between seagrass and bare sites	
	B-C s	ANOSIM R	B-C s	ANOSIM R	B-C s	ANOSIM R
Bollard	0.62	0.14	0.47	0.61	0.45	0.68
Kingfisher	0.62	0.36	0.84	0.13	0.37	0.72
Brenton	0.80	0.07	0.73	0.17	0.35	0.85
Point	0.65	0.30	0.79	0.16	0.46	0.58
Belvidere	0.68	0.21	0.72	0.25	0.54	0.48
Ashford	0.60	0.19	0.28	0.65	0.55	0.45
Westford	0.82	0.01*	0.79	0.02*	0.50	0.43
Red Bridge	–	–	–	–	0.38	0.87

individuals and 32 taxa were crustaceans.

In total, the Knysna seagrass stations supported 9% more macrobenthic individuals and 12% more taxa than those in the bare sediment, only 56% of all sampled taxa being common to both habitats: these 70 shared taxa, however, contributed 97% of all individuals. Chao1 estimates of likely total number of taxa were 113 (seagrass) and 111 (bare). As would be expected, numbers of individuals and of taxa per station declined upstream, both in the seagrass and in the bare sediment, but the rate of decline of each metric was lower in the seagrass (Fig. 3), so that abundance in the seagrass was effectively unchanged over much of the gradient. Number of individuals was larger in the bare sediment than in the seagrass near the marine mouth and bay regions, but this reversed upstream so that by the lagoonal zone those in the seagrass were the more abundant. Number of taxa was never greater in the bare sediment, although near the mouth they were subequal with those in seagrass, but upstream a marked differential developed in favour of the seagrass (Fig. 3).

For neither abundance nor taxon richness were indicator differentials between the assemblage metrics in the two adjacent habitats constant. Instead their magnitude was positively correlated with distance upstream (Spearman  $\rho_{\text{abundance}} = 0.86$ ,  $P < 0.0001$ ;  $\rho_{\text{taxa}} = 0.53$ ,  $P < 0.05$ ), so that the slopes of the relationships significantly departed from the 1:1 no-change differential (ANCOVA  $F > 5.5$ ;  $P < 0.03$ ). The same was true for numbers of common species in each assemblage (those more abundant than the median value), the seagrass increasingly supporting more co-dominant assemblage components than the bare sediment (Spearman  $\rho = 0.6$ ;  $P < 0.02$ . ANCOVA  $F = 5.9$ ;  $P < 0.03$ ). The differential in taxonomic distinctness, however, showed a significant decrease upstream (Spearman  $\rho = -0.54$ ,  $P < 0.04$ ; ANCOVA  $F = 4.89$ ,  $P < 0.04$ ). There were no changes in the differentials between the other assessed assemblage metrics (Fig. 4) along the axial gradient, although an upstream decrease in that of functional diversity came close to significance (Spearman  $\rho = -0.46$ ,  $P = 0.08$ ). The differentials in functional diversity and evenness significantly departed in favour of the seagrass assemblage (ANOVA  $F_{1,28} > 6.8$ ,  $P < 0.01$ ), however; although those for patchiness did not significantly depart from 1 (ANOVA  $F_{1,28} = 0.01$ ,  $P > 0.9$ ) indeed displayed a mean value of 1.

Bray-Curtis similarity between adjacent seagrass and bare-sediment stations did not change upstream (Table 1; Spearman  $\rho = 0.31$ ,  $P > 0.25$ ; ANCOVA  $F = 1.7$ ,  $P > 0.2$ ); a mean value of 0.45 with a variance of only 0.02. Within-versus across-habitat patterns of assemblage compositional similarity at a given locality depended on geographical context, i.e. whether compared at the local or regional level. Compositional similarity of the replicate within-habitat sites at each locality, whether assessed by Bray-Curtis similarity or via ANOSIM R, was greater than that of the local cross-habitat (seagrass versus bare-sediment station) comparisons (ANOVA  $F_{2,26} > 7.9$ ;  $P < 0.008$ ) (summarised in Table 1). However, at the larger, between-locality, spatial scale, a somewhat different picture emerged. Bray-Curtis grouped the seagrass and bare-sediment assemblages at a given locality together at the same level of similarity that the seagrass there showed to the equivalent seagrass systems in the two adjacent upstream and downstream localities (means of 0.52 and 0.53 respectively; Mann-Whitney  $P = 1$ ), and they were more similar (though not significantly so) to each other than were the local bare-sediment habitats (mean of 0.41; Mann-Whitney  $P = 0.13$ ). Two-way ANOSIM (using the mouth/bay/lagoon/estuary locational regions of Fig. 2) showed both habitat type and location within the estuary as having a highly significant influence on assemblage composition ( $P < 0.002$ ) but with location being responsible for greater differences (ANOSIM habitat R 0.47 vs region R 0.68) (and see Fig. 5). Table 2 illustrates the high level of faunal similarity within localities and the regional differences between them. It also shows that SIMPER identified the same taxon that was the dominant element in both habitat types at a locality as often being one of those most responsible for the differences between them by virtue of its differential proportional abundances. Further, the same taxon could be a particularly important



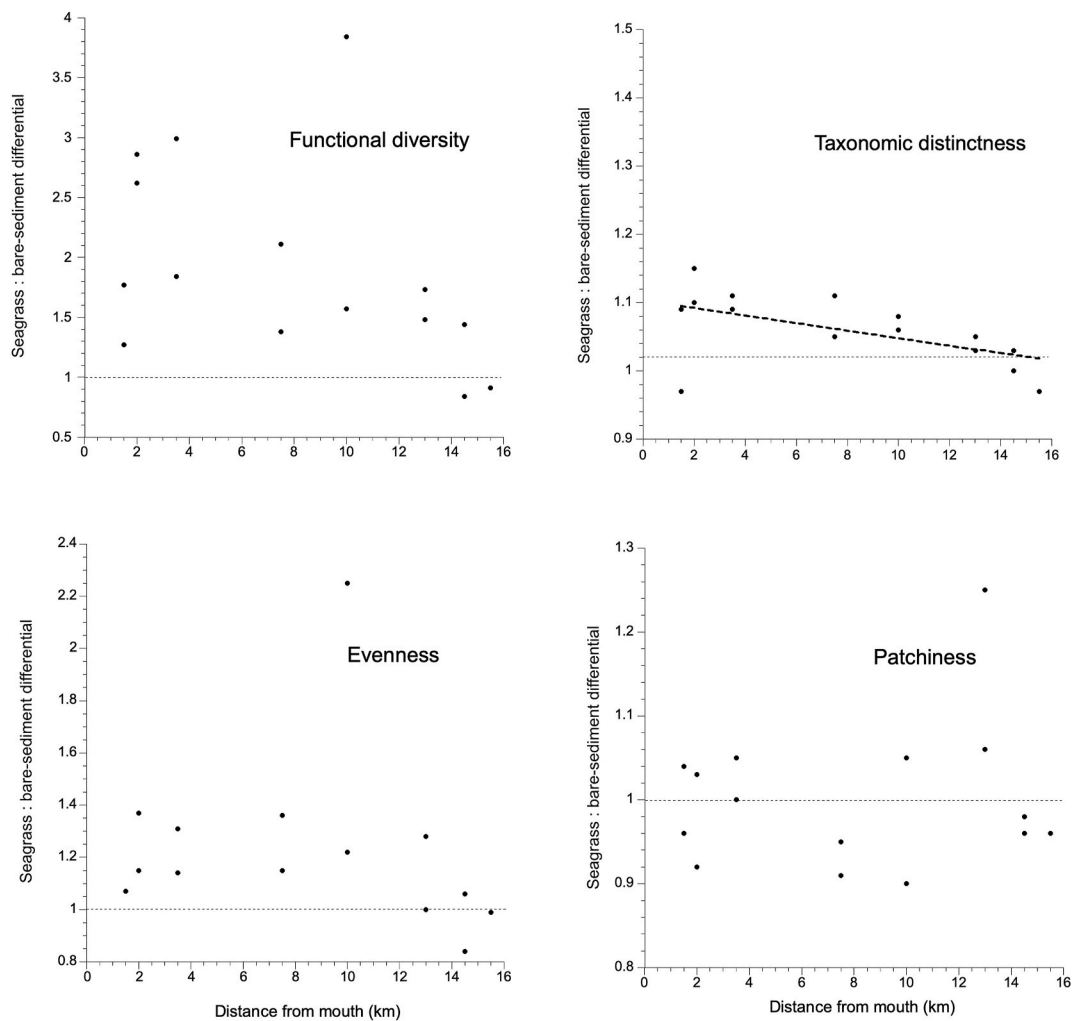
**Fig. 3.** Variation upstream in values of, and differentials between, the macrobenthic assemblages of seagrass and of adjacent bare sediment in respect of overall abundance and taxon-richness metrics. For differentials, bare-sediment values are set at 1.

component of one of the two habitat types at one locality but of the other habitat at a different locality. Thus the relative abundance of *Prionospio* in the local bare sediment was one of the three to five components responsible for >50% of the difference between the two habitats at four localities (Kingfisher, Brenton, Belvidere and Red Bridge); however it was the high proportion of *Prionospio* in the seagrass at three others (Point, Ashford and Westford) that made it one of the two to four taxa responsible for >50% of the differences between the two habitats there (SIMPER). Likewise, 'excess' *Simplisetia* were present in the seagrass at Westford, but in the bare sediment at Brenton.

Annelids tended to dominate the bare-sediment (in which they averaged 76% of individuals; c.f. 44% in the seagrass) whilst crustaceans and molluscs were more numerous in the seagrass (23% and 30% in seagrass vs 8% and 15% in bare, respectively). The differential between numbers of annelid individuals in the seagrass and in bare sediment changed upstream in an equivalent manner to that of the invertebrate assemblages as a whole (Fig. 6). The upstream declines in number of annelid taxa in the two habitat types were very similar (ANCOVA  $F = 1.1$ ;  $P > 0.30$ ) (Fig. 6). Both crustacean abundance and number of taxa in each habitat decreased upstream (Fig. 6). Although there was much scatter in the data, number of molluscan individuals did not show any upstream decrease; indeed the proportion of bivalve molluscs in the assemblages increased upstream in both seagrass and bare sediment (Spearman  $\rho > 0.78$ ;  $P < 0.0007$ ). Echinoderms were virtually absent from the bare-sediment stations, and they were absent from the estuarine zone. Over the whole gradient [and excluding all relatively rare

species (those each comprising <0.5% of total numbers)], relative abundance of the two polychaetes *Prionospio* and *Simplisetia* was responsible for 28% of the compositional difference between seagrass and bare-sediment assemblages (SIMPER); together the two also comprised 30% of all animals in the samples.

Allocating the individual taxa to the various feeding-location guilds of Macdonald et al. (2010), there was no difference between the number (ANOVA  $F_{1,28} = 0.66$ ;  $P > 0.4$ ) or proportion of total individuals (72.9% and 73.5%, respectively) feeding at the sediment surface in the seagrass and in the bare areas; epibenthic animals were essentially non-existent over the bare sediment (but formed 11% of those in the seagrass); whilst subsurface feeders were >1.4 times more numerous there. The numbers of subsurface feeders declined upstream in both the seagrass and the bare sediment (Spearman  $\rho > -0.90$ ;  $P < 0.0001$ ), and epibenthic ones did so in the seagrass (Spearman  $\rho > -0.89$ ;  $P < 0.0001$ ). Those of surface feeders were unaffected by the gradient (Spearman  $\rho < 0.51$ ;  $P > 0.05$ ) (Fig. 7); nevertheless, the lagoon marked a change in their seagrass: bare sediment differential from a mean 0.7 to seawards to a mean 2.6 in the estuary. The same pattern was displayed in respect of number of component taxa, except that the number of surface-feeding taxa was greater in the seagrass than in the bare sediment (ANOVA  $F_{1,28} = 7.4$ ;  $P < 0.01$ ) and the number in each habitat type did decrease upstream (Spearman  $\rho > -0.80$ ;  $P < 0.0001$ ), those in the bare sediment showing the faster decline (ANCOVA  $F = 4.0$ ;  $P < 0.05$ ). As with abundance, the lagoon also marked a change in the taxon-density differential in the surface feeders from a mean 1.2 to seawards to one of 2.1



**Fig. 4.** Variation upstream in differentials between the macrobenthic assemblages of seagrass and of adjacent bare sediment (set at 1) in respect of metrics of functional diversity, taxonomic distinctness, evenness, and patchiness.

in the estuary.

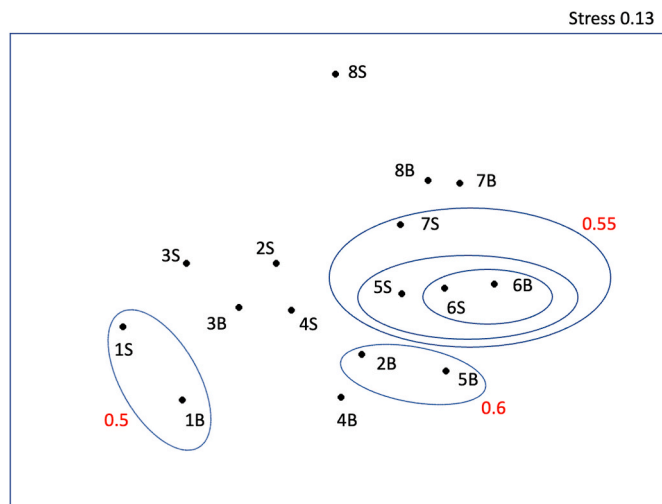
#### 4. Discussion

If adjacent faunal assemblages react differently to any common environmental, geographical or other gradient, biodiversity differentials between them would be expected to change along its length. The present results do indeed demonstrate that differentials in the more usually assessed metrics of seagrass versus bare-sediment biodiversity (abundance and observed number of taxa) are far from constant, changing along the axial gradient at Knysna in direction and/or magnitude even over relatively short distances. They also present a consistent picture. Number of taxa per station was never smaller in the seagrass than in adjacent bare sediment, and increasingly changed from being subequal in areas influenced directly by the Indian Ocean to being larger away from that influence. Near the mouth the number of individuals was greater in bare sediment, but this changed markedly upstream so that away from the marine embayment number of individuals was greater in the seagrass. Although these overall trends were statistically significant, there was much ‘noise’ both between and within localities especially upstream, such possibly being associated with the evident variation in local nature of the bare sediment there dependent on current patterns (i. e. bare sediments exposed to more water flow being sandier). Some individual upstream stations even maintained the subequal status of overall abundance and/or taxon density in the two habitat types that

characterised the mouth region.

The only comparable study along such a gradient is that of [Magni et al. \(2017\)](#) who investigated the macrobenthic fauna of both seagrass (*Zostera marina*) and bare sediment in the boreal Furen Lagoon in Hokkaido. Furen is a system supporting a species-poor but otherwise similar fauna at the generic level to that at Knysna, although only one of the seven most numerically dominant species there was an annelid. They also found that number of species was always larger in *Zostera* than in bare areas but that there, in marked contrast to Knysna, number of individuals was only larger in the seagrass in the area nearest the mouth and was much more equitably distributed in upstream regions (paralleling the intertidal versus subtidal upstream comparisons of [Barnes and Claassens, 2020](#), in Knysna seagrass). Macrofaunal abundance was there also more patchily dispersed in the seagrass than in the bare sediment, which was not the case at Knysna. As they only investigated three points along the system (relatively small distances apart), however, it was not possible to test for systematic change in differentials between the two habitat types. In any event, Magni et al.’s sites probably more closely resembled the three most upstream (estuarine) Knysna stations, rather than reflecting a mouth-upstream gradient, not least in that the Furen locations were all characterised by organically-enriched muddy conditions. They are therefore only partially comparable.

In spite of reviews cautioning against over-generalisation (e.g. [Nakaoka, 2005](#)), it continues to be stated without qualification in the literature that “one of the most important functions of seagrasses is ...



**Fig. 5.** Pattern of compositional similarity between the macrobenthic assemblage components of seagrass and of adjacent bare sediment at the various localities along the estuarine-bay gradient, as indicated by ordination by nMDS of superimposed locality-average  $S_{17}$  Bray-Curtis similarities of untransformed abundances. Envelopes enclose those points clustered at  $\geq 0.5$ . Key: 1 Bollard, 2 Kingfisher, 3 Brenton, 4 Point, 5 Belvidere, 6 Ashford, 7 Westford, 8 Red Bridge; S seagrass, B bare sediment. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

**Table 2**

The identity of the two most numerically-dominant taxa in seagrass and in adjacent bare sediment along the axis of the Knysna estuarine system, demonstrating both regionalisation and that the same taxa frequently dominated both habitat types at a given locality. Asterisked taxa are ones identified by SIMPER as being particularly responsible for the difference between the two habitat types in the localities concerned by virtue of their greater proportional abundance in the habitat indicated.

	Seagrass	Bare sediment
Bollard	<i>Turritella</i> & <i>Alaba</i> *	<i>Turritella</i> * & <i>Paradoneis</i> *
Kingfisher	<i>Orbinia</i> & ? <i>Cylindroleberis</i> *	<i>Prionospio</i> * & <i>Orbinia</i> *
Brenton	? <i>Cylindroleberis</i> * & <i>Caulleriella</i> *	<i>Simplisetia</i> * & <i>Paradoneis</i> *
Point	<i>Caulleriella</i> * & <i>Prionospio</i> *	<i>Cirratulus</i> * & <i>Prionospio</i>
Belvidere	<i>Prionospio</i> & <i>Nassarius</i> *	<i>Prionospio</i> * & <i>Orbinia</i>
Ashford	<i>Prionospio</i> * & <i>Nassarius</i> *	<i>Prionospio</i> & <i>Dosinia</i>
Westford	<i>Prionospio</i> * & <i>Salmacoma</i> *	<i>Salmacoma</i> & <i>Prionospio</i>
Red Bridge	<i>Hydrobia</i> * & <i>Simplisetia</i>	<i>Simplisetia</i> & <i>Prionospio</i> *

supporting higher biodiversity levels than bare areas” (Brun et al., 2021) or “the macrobenthic communities of seagrass meadows are more abundant and species-rich than those of bare sediment since seagrass beds provide more food, larval entrainment, habitat structure, and refuge from predation” (Hu et al., 2022), to give just two recent examples. Indeed for many years the paradigm of a marked differential between overall abundance and species richness supported by each of these two broad habitat types has been used to stress the importance and relative conservation value of a seagrass cover (e.g. Virnstein et al., 1983; Arrivillaga and Baltz, 1999; Fredriksen et al., 2010; Brun et al., 2021; etc.). Thus McHenry et al. (2021) felt able to generalise that the 7800 km<sup>2</sup> of current seagrass beds along the gulf coast of Florida supported 43–64% more species than unvegetated habitats and that appropriate seagrass restoration would increase biodiversity there by 43–45% above unvegetated levels, the local ‘biodiversity enhancement value’ of seagrass. These Knysna results, however, confirm that in fact seagrass: bare-sediment differentials are not always so clear-cut; indeed in some circumstances they may be not biased in favour of seagrass at all (see also van Houte-Howes et al., 2004; Schultz and Krushel, 2010; Barnes and Barnes, 2014). In the Adriatic Novigrad lagoon, Schultz and

Kruschel (2010), for example, found that abundance and diversity of mobile macrobenthos were both greater on bare sediment than in neighbouring seagrass, and attributed this to the dominant presence of larger and more efficient ambush-hunting predatory fish in the seagrass beds. The magnitude and direction of such differentials are clearly context dependent, changing sometimes radically as at Knysna along an environmental gradient. The present results from the sandy mouth-region of the main estuarine channel confirming earlier data from the saltmarsh-enclosed marine backwater channels of the Knysna bay region (Barnes and Barnes, 2014) that demonstrated that there the bare sediment supported almost as many species as the local seagrass and even larger numbers of individuals (mainly of truncatelloid microgastropods), 1.5x as many on average.

Overall differentials may be further complicated by the varied responses of the different higher taxonomic groups that occur across both habitat types. Like most temperate mudflats (Dissanayake et al., 2018), the soft sediments at Knysna are dominated by polychaetes, possibly because of their ability to seek refuges during periods of environmental adversity via burrowing or swimming (Lowe et al., 2022). Polychaetes as a whole have been described as not showing greater biodiversity in seagrass (Barrio Froján et al., 2006; 2009) whilst molluscs have been described as doing so (Rueda et al., 2009; Hyman et al., 2019). At Knysna, differentials within these important taxa were not so specific however: they also changed along the estuarine gradient. In the annelids, for example, the differentials in both abundance and species richness increased from mouth towards the head, where the annelids *did* display the greater biodiversity in the seagrass. Like the crustaceans there were nearly always more mollusc taxa in the seagrass, but not always more individuals.

The single term ‘seagrass’ obscures a wide range of differing plant species and shoot densities (Nakaoka, 2005), and the associated macrofauna may react directly or indirectly to such variation resulting in an equally wide range of seagrass-associated animal abundance and biodiversity (Leopardus et al., 2014; McCloskey and Unsworth, 2015; Ambo-Rappe, 2016; Barnes, 2020; Rodil et al., 2021). For this amongst other reasons, past attention has focussed on seagrass as the controlling variable in differentials between the two habitats by virtue of its potential to enhance biodiversity above bare-sediment levels. As the present results make clear, however, it is not always the seagrass that is the more important variable. Along the Knysna long-axial channel, change in the seagrass: bare-sediment abundance differential was mainly consequent on upstream changes in the bare-sediment compartment. Number of individuals (and to a lesser extent taxa) supported by the seagrass along much of the gradient was relatively uniform, in conformity with the general notion that seagrass beds support macrofaunal assemblages that display spatial and temporal stability of abundance and composition, and high levels of resilience (Blake et al., 2014; Gartner et al., 2015). Both number of taxa and individuals in the bare sediment, however, declined more rapidly and to a greater proportional extent, thereby creating the differentials observed.

It was also notable that, granted changes in their metrics and relative importance of different taxa, the difference in magnitude of assemblage compositional changes between seagrass and bare sediment, as measured by Bray-Curtis, that might have been expected along the gradient was not observed. Assemblages near the relatively benign mouth were just as (dis)similar to each other as at the more environmentally-hostile upstream localities, in spite of marked differences in taxonomic composition and overall abundance, at least in the bare sediment. Over most of the gradient, seagrass samples contained fewer annelid and more crustacean and mollusc individuals than bare-sediment ones, but the animal individually responsible for more of the difference between paired habitat types across the various localities than any other taxon, the polychaete *Prionospio*, was more abundant in the seagrass in some localities and in the bare-sediment in others, and to a lesser extent the same was also true of *Simplisetia*, again emphasising local context dependence.

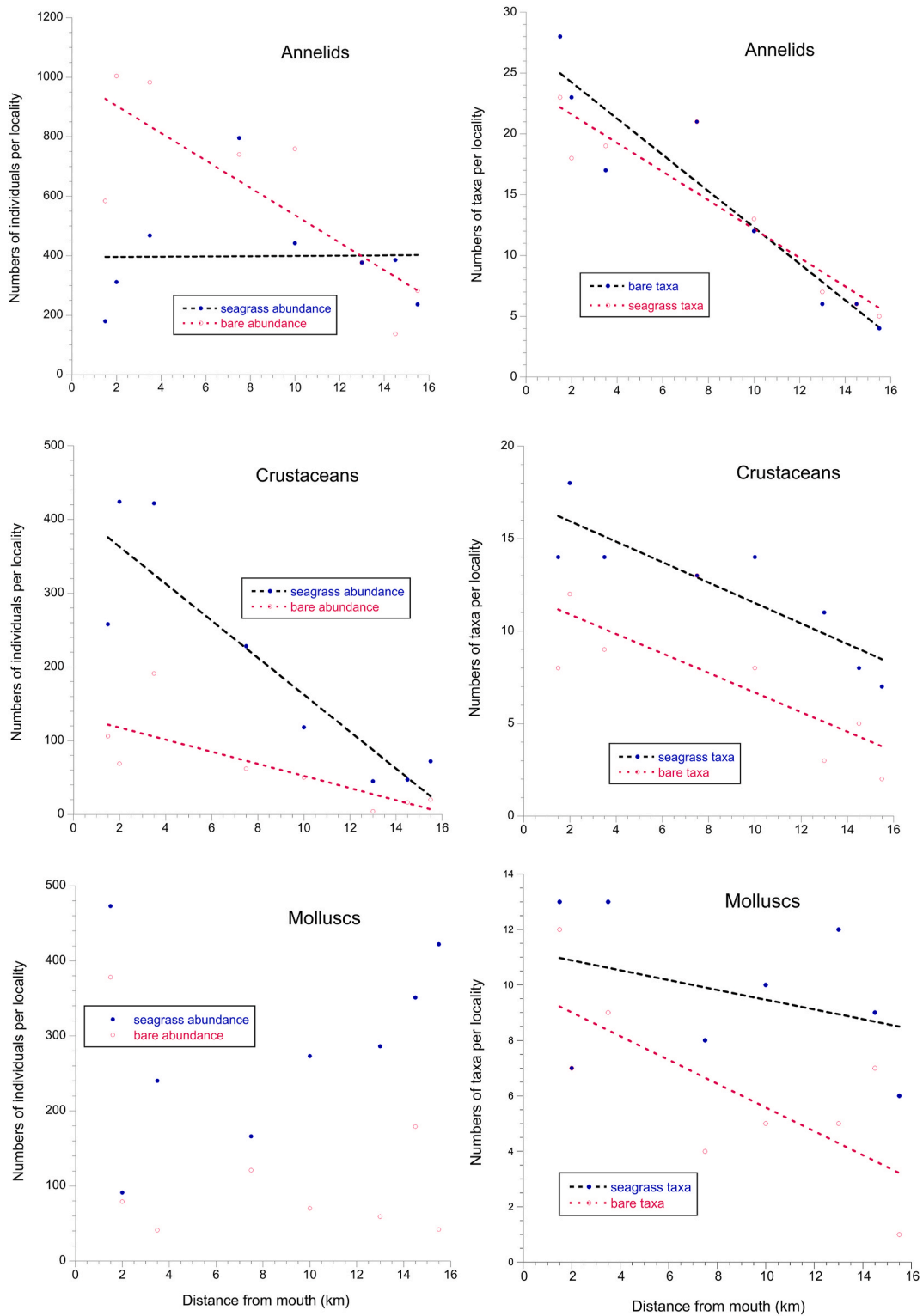


Fig. 6. Variation upstream in the annelid, crustacean and molluscan components of the macrobenthic assemblages of seagrass and of adjacent bare sediment in respect of overall abundance and taxon-richness metrics.

Similarity between adjacent seagrass and bare-sediment faunas has been suggested particularly to depend on the relative importance of infaunal and epifaunal components. Törnroos et al. (2013), for example, have shown infaunal assemblages in the two habitat types in the northern Baltic to be more similar to each other taxonomically than either were to the seagrass epifauna. It is difficult, however, to categorise most of the Knysna macrofauna as either ‘epifauna’ or ‘infauna’ as

most straddle the sediment-water interface; the more mobile species roaming over the surface to feed and retreating beneath it for safety or at some states of the tide, and the more sedentary ones displaying a life-style with part of the body above and part below the surface (true of both *Prionospio* and *Simplisetia* above). Relatively few taxa occupy only one of the two notional compartments, and for many purposes the feeding-location guilds of ‘epibenthic’, ‘surface’ and ‘subsurface’ of

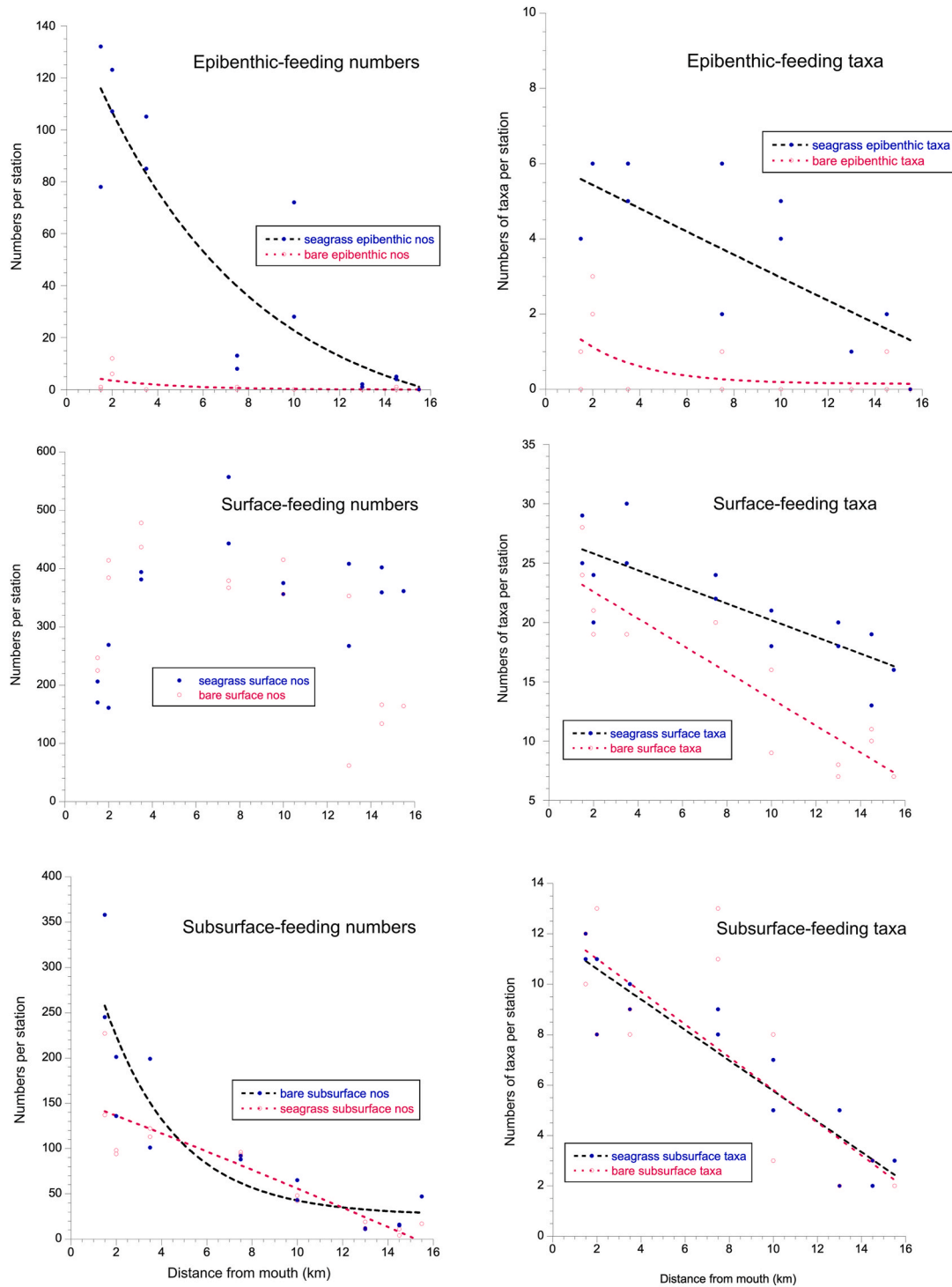


Fig. 7. Variation upstream in values of overall abundance and taxon-richness metrics for the epibenthic-feeding, surface-feeding, and subsurface-feeding components of macrobenthic seagrass assemblages and those of adjacent bare-sediment.

Macdonald et al. (2010) comprise a much more realistic classification of mudflat/seagrass fauna, and hence this approach was adopted here. In terms of those feeding guilds, as would be expected there were effectively no epibenthic feeders over the bare sediment, and those that were present in the seagrass, together with the subsurface feeders in both habitat types, decreased in abundance along the gradient. That seagrass supported fewer subsurface feeders than the bare sediment is presumably a reflection of the limitation of space and difficulty of movement imposed by seagrass root-rhizome systems (Berkenbusch and Rowden,

2007). Somewhat surprisingly, however, the surface-feeding taxa showed no significant decrease upstream in abundance, neither in the bare sediment nor in the seagrass, although they did so in taxon richness.

Overall, the two tested null hypotheses — that the macrobenthic assemblages of vegetated and bare sediments do not react differently to an estuarine gradient and that biodiversity-metric differentials between the two habitat types remain unchanged upstream — were disproved. The evidence strongly indicates that the presence of seagrass near the mouth of the Knysna estuary had little or no effect on relative

biodiversity of the invertebrate fauna, but that it did so increasingly upstream, relative abundance and taxon richness within the bare sediment departing more and more from the seagrass state. Does this then indicate amelioration of the micro-environment of the sediment-water interface by the seagrass cover? At Knysna its effect on the abundance of the macrobenthic assemblages was considerably more marked than on their taxon richness, which suggests that its main effect is to provide more habitat and/or greater potential food availability at least for epibenthic and subsurface feeding taxa. Granted, however, that the upstream rate of decline of sediment-surface feeding taxa was greater in the bare areas than in the seagrass, it does also suggest a degree of amelioration of the physical environment permitting some species to penetrate further upstream within its shelter than would otherwise be the case.

Are these Knysna results likely to be a special case? Like most South African systems (Schlacher and Wooldridge, 1996), Knysna is certainly a low-freshwater-input estuary and the distribution of *Z. capensis* there does contrast markedly with those of the related *Zostera* species *Z. marina* and *Z. noltei* which, at least in non-tidal lagoonal situations, have been described as critically affected by salinity (positively) and nearness to sources of freshwater (negatively) (Boscutti et al., 2015). It may well be, therefore, that the range of seagrass at Knysna down to salinities of <5 (Maree, 2000) is unusual (Adams and Bate, 1994, cite 10 as the lower limit of *Z. capensis*), but other aspects of the Knysna gradient, i.e. the increasing proportion of fine particles, increasing slope of the shore, and decreasing width of the channel upstream, all otherwise appear typically estuarine. Is it then estuaries in general that are atypical in their pattern of differentials? Here it is relevant that the supposedly 'unusual' lack of major differentials between seagrass and bare-sediment abundance and taxon richness is a feature only of the fully marine, outer embayment region, and cannot be ascribed to any estuarine influence (other than increased shelter). Whether or not the lack of significant differentials there is due to the absence of bio-turbation (Barnes and Barnes, 2014) or to some other cause can only be answered by more studies in other relevant localities. It is certainly not the case in all other estuarine bays, e.g. in Moreton Bay, Australia (Barnes and Barnes, 2012). But even if the lack of differentials near the mouth proves atypical, it would still appear likely that the predicted and observed increasing differentials up the gradient of environmental hostility, from whatever starting point, will be characteristic of other estuarine environments as well, all other things being equal.

Although the *Zostera* does enhance benthic biodiversity in the more environmentally hostile estuarine regions, however, general location along the gradient appears to have had at least as important a role in influencing assemblage structure as did the presence or absence of seagrass. Faunal assemblages in adjacent seagrass and bare sediment were as similar to each other as were the local seagrass assemblages to those in the same habitat type in the localities immediately upstream and downstream. It must also be stressed that whilst the presence of seagrass enhances estuarine biodiversity towards the head, it is the more marine end of the system that supports the greater overall macrobenthic biodiversity, whether in the seagrass or in the bare sediment, and here there was very little if any enhancement due the vegetation cover. The seagrass simply delays the inevitable upstream changes.

This still leaves many questions unanswered: Why does the compositional similarity of adjacent assemblages not change in magnitude along the gradient? Why does the bare sediment support the larger abundances and subequal taxon richness near the mouth, when it does not do at several other studied marine locations? Why is there such a marked contrast between the Furen Lagoon studied by Magni et al. (2017) and Knysna in respect of their patterns of differential abundances in seagrass and bare sediment? etc. What it does make clear, however, is that the context-dependent nature of the differentials emphasises the need for considerable caution in the extrapolation of relative biodiversity indicators derived from local areas across wider geographical regions and in situations where environmental gradients of any sort are

likely to be present.

## Data statement

Historical datasets of Knysna seagrass macrobenthos are deposited in the Rondevlei Office of SANParks Scientific Services and are available in electronic format on request (<http://dataknpsanparks.org/sanparks/mecat/Nerinak.23.11/sanparks>); the 2021/2022 data, and subsets of earlier data re-used here, can be found online at Mendeley Data, VI, <https://doi.org/10.17632/nmwsrpd738.1>.

## Funding

This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

## Ethical approval

All applicable international, national and/or institutional guidelines for sampling, care and experimental use of organisms for the study were followed and all necessary permissions and approvals were obtained in respect of the original collections of the data.

## CRediT authorship contribution statement

**R.S.K. Barnes:** Writing – review & editing, Writing – original draft, Project administration, Investigation, Formal analysis, Data curation, Conceptualization.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Data availability

The data are deposited in a Mendeley data file (specified in the text).

## Acknowledgements

I am most grateful to: Rhodes University Research Committee for support; Ruth Farre of the South African Navy Hydrographic Office for advance information on Knysna tidal data; Brian McCabe for statistical advice; SANParks Garden Route Scientific Services (Rondevlei) and Knysna Lakes Area Manager, Megan Taplin, for permission to undertake fieldwork in the Knysna Section of the Garden Route National Park under permit BARN-RSK/2019-034; and the Knysna Senior Section Ranger, Owen Govender, for logistical assistance.

## References

- Adams, J.B., Bate, G.C., 1994. The ecological implications of tolerance to salinity by *Ruppia cirrhosa* (Petagna) Grande and *Zostera capensis* Setchell. Bot. Mar. 37, 449–456. <https://doi.org/10.1515/botm.1994.37.5.449>.
- Albano, P.G., Sabelli, B., Bouchet, P., 2011. The challenge of small and rare species in marine biodiversity surveys: microgastropod diversity in a complex tropical coastal environment. Biodivers. Conserv. 20, 3233–3237. <https://doi.org/10.1007/s10531-011-0117-x>.
- Alsaffar, Z., Pearman, J.K., Cúrdia, J., Ellis, J., Calleja, M.L., Ruiz-Compean, R., Roth, F., Villalobos, R., Jones, B.H., Morán, X.A.G., Carvalho, S., 2020. The role of seagrass vegetation and local environmental conditions in shaping benthic bacterial and macroinvertebrate communities in a tropical coastal lagoon. Sci. Rep. 10, 13550 <https://doi.org/10.1038/s41598-020-70318-1>.
- Ambo-Rappe, R., 2016. Differences in richness and abundance of species assemblages in tropical seagrass beds of different structural complexity. J. Environ. Sci. Tech. 9, 246–256. <https://doi.org/10.3923/jest.2016.246.256>.
- Arrivillaga, A., Baltz, D.M., 1999. Comparison of fishes and macroinvertebrates on seagrass and bare-sand sites on Guatemala's Atlantic coast. Bull. Mar. Sci. 65, 301–319.

- Attrill, M.J., 2002. A testable linear model for diversity trends in estuaries. *J. Anim. Ecol.* 71, 262–269. <https://doi.org/10.1046/j.1365-2656.2002.00593.x>.
- Attrill, M.J., Rundle, S.D., 2002. Ecotone or ecocline: ecological boundaries in estuaries. *Estuar. Coast Shelf Sci.* 55, 929–936. <https://doi.org/10.1006/ecss.2002.1036>.
- Barnes, R.S.K., 1989. What, if anything, is a brackish-water fauna? *Trans. R. Soc. Edinb. Earth Sci.* 80, 235–240. <https://doi.org/10.1017/S0263593300028674>.
- Barnes, R.S.K., 2018. Little-known and phylogenetically obscure South African estuarine microgastropods (Mollusca: truncatelloidea) as living animals. *J. Nat. Hist.* 52, 87–113. <https://doi.org/10.1080/00222933.2017.1408867>.
- Barnes, R.S.K., 2019a. Local patchiness of macrobenthic faunal abundance displays homogeneity across the disparate seagrass systems of an estuarine bay. *Mar. Environ. Res.* 148, 99–107. <https://doi.org/10.1016/j.marenvres.2019.05.001>.
- Barnes, R.S.K., 2019b. Context dependency in the effect of *Ulva*-induced loss of seagrass cover on estuarine macrobenthic abundance and biodiversity. *Aquat. Conserv.* 29, 163–174. <https://doi.org/10.1002/aqc2977>.
- Barnes, R.S.K., 2020. Do different sympatric seagrasses support macrobenthic faunas of differing composition, abundance, biodiversity or patchiness? *Mar. Environ. Res.* 160, 104983 <https://doi.org/10.1016/j.marenvres.2020.104983>.
- Barnes, R.S.K., 2021a. Patterns of seagrass macrobenthic biodiversity in the warm-temperate Knysna estuarine bay, Western Cape: a review. *Aquat. Ecol.* 55, 327–345. <https://doi.org/10.1007/s10452-021-09848-3>.
- Barnes, R.S.K., 2021b. What does measuring species diversity in estuarine seagrass systems actually assess? *Mar. Environ. Res.* 172, 105500 <https://doi.org/10.1016/j.marenvres.2021.105500>.
- Barnes, R.S.K., Barnes, M.K.S., 2012. Shore height and differentials between macrobenthic assemblages in vegetated and unvegetated areas of an intertidal sandflat. *Estuar. Coast Shelf Sci.* 106, 112–120. <https://doi.org/10.1016/j.ecss.2012.05.011>.
- Barnes, R.S.K., Barnes, M.K.S., 2014. Biodiversity differentials between the numerically-dominant macrobenthos of seagrass and adjacent unvegetated sediment in the absence of sandflat bioturbation. *Mar. Environ. Res.* 99, 34–43. <https://doi.org/10.1016/j.marenvres.2014.05.013>.
- Barnes, R.S.K., Claassens, L., 2020. Do beds of subtidal estuarine seagrass constitute a refuge for macrobenthic biodiversity threatened intertidally? *Biodivers. Conserv.* 29, 3227–3244. <https://doi.org/10.1007/s10531-020-02019-0>.
- Barnes, R.S.K., Ellwood, M.D.F., 2012. Spatial variation in the macrobenthic assemblages of intertidal seagrass along the long axis of an estuary. *Estuar. Coast Shelf Sci.* 112, 173–182. <https://doi.org/10.1016/j.ecss.2012.07.013>.
- Barnes, R.S.K., Hamylton, S., 2016. On the very edge: faunal and functional responses to the interface between benthic seagrass and unvegetated-sand assemblages. *Mar. Ecol. Prog. Ser.* 553, 33–48. <https://doi.org/10.3354/meps11800>.
- Barnes, R.S.K., Hendy, I.W., 2015. Seagrass-associated macrobenthic functional diversity and functional structure along an estuarine gradient. *Estuar. Coast Shelf Sci.* 164, 233–243. <https://doi.org/10.1016/j.ecss.2015.07.050>.
- Barrio Froján, C.R.S., Kendall, M.A., Paterson, G.L.J., Hawkins, L.E., Nimsantjaroen, S., Aryuthaca, C., 2006. Patterns of polychaete diversity in selected tropical intertidal habitats. *Sci. Mar.* 70 (S3), 239–248.
- Barrio Froján, C.R.S., Kendall, M.A., Paterson, G.L.J., Hawkins, L.E., Nimsantjaroen, S., Aryuthaca, C., 2009. The importance of bare marine sedimentary habitats for maintaining high polychaete diversity and the implications for the design of marine protected areas. *Aquat. Conserv.* 19, 748–757. <https://doi.org/10.1002/aqc.1031>.
- Barry, S.C., Hyman, A.C., Jacoby, C.A., Reynolds, L.K., Kowalewski, M., Frazer, T.K., 2021. Variation in seagrass-associated macroinvertebrate communities along the Gulf Coast of peninsular Florida: an exploration of patterns and ecological consequences. *Front. Mar. Sci.* 8, 596966 <https://doi.org/10.3389/fmars.2021.596966>.
- Beck, J., Holloway, J.D., Schwanghart, W., 2013. Undersampling and the measurement of beta diversity. *Methods Ecol. Evol.* 4, 370–382. <https://doi.org/10.1111/2041-210x.12023>.
- Berkenbusch, K., Rowden, A.A., 2007. An examination of the spatial and temporal generality of the influence of ecosystem engineers on the composition of associated assemblages. *Aquat. Ecol.* 41, 129–147. <https://doi.org/10.1007/s10452-006-9053-3>.
- Blake, R.E., Duffy, J.E., Richardson, J.P., 2014. Patterns of seagrass community response to local shoreline development. *Estuar. Coast* 37, 1549–1561. <https://doi.org/10.1007/s12237-014-9784-7>.
- Blowes, S.A., Daskalova, G.N., Dornelas, M., et al., 2022. Local biodiversity change reflects interactions among changing abundance, evenness and richness. *bioRxiv*. <https://doi.org/10.1101/2021.08.29.458087>.
- Boscutti, F., Marcorin, I., Sigura, M., Bressan, E., Tamberlich, F., Vianello, A., Casolo, V., 2015. Distribution modeling of seagrasses in brackish waters of Grado-Marano lagoon (Northern Adriatic Sea). *Estuar. Coast Shelf Sci.* 164, 183–193. <https://doi.org/10.1016/j.ecss.2015.07.035>.
- Boström, C., O'Brian, K., Roos, C., Ekeboom, J., 2006. Environmental variables explaining structural and functional diversity of seagrass macrofauna in an archipelago landscape. *J. Exp. Mar. Biol. Ecol.* 335, 52–73. <https://doi.org/10.1016/j.jembe.2006.02.015>.
- Brind'Amour, A., Laffargue, P., Morin, J., Vaz, S., Foveau, A., Le Bris, H., 2014. Morphospecies and taxonomic sufficiency of benthic megafauna in scientific bottom trawl surveys. *Continent. Shelf Res.* 72, 1–9. <https://doi.org/10.1016/j.csr.2013.10.015>.
- Brun, F.G., Cobo-Diaz, J.F., González-Ortiz, V., Varela, J.L., Pérez-Lloréns, J.L., Vergara, J.J., 2021. Seagrass patch complexity affects macroinfaunal community structure in intertidal areas: an in situ experiment using seagrass mimics. *Diversity* 13, 572. <https://doi.org/10.3390/d13110572>.
- Clarke, K.R., Warwick, R.M., 1998. A taxonomic distinctiveness index and its statistical properties. *J. Appl. Ecol.* 35, 523–531. <https://doi.org/10.1046/j.1365-2664.1998.3540523.x>.
- Coyer, J.A., Hoarau, G., Kuo, J., Tronholm, A., Veldsink, J., Olsen, J.L., 2013. Phylogeny and temporal divergence of the seagrass family Zosteraceae using one nuclear and three chloroplast loci. *Syst. Biodivers.* 11, 271–284. <https://doi.org/10.1080/14772000.2013.821187>.
- Davidson, I.C., Crook, A.C., Barnes, D.K.A., 2004. Quantifying spatial patterns of intertidal biodiversity: is movement important? *Mar. Ecol.* 25, 15–34. <https://doi.org/10.1111/j.1439-0485.2004.00015.x>.
- Day, J.H., 1959. The biology of Langebaan Lagoon: a study of the effect of shelter from wave action. *Trans. Roy. Soc. S. Afr.* 35, 475–547. <https://doi.org/10.1080/00359195909519025>.
- Day, J.H. (Ed.), 1981. *Estuarine Ecology with Particular Reference to Southern Africa*. Balkema, Rotterdam, ISBN 9789061912057.
- Dethier, M.N., Schoch, G.C., 2006. Taxonomic sufficiency in distinguishing natural spatial patterns on an estuarine shoreline. *Mar. Ecol. Prog. Ser.* 306, 41–49. <https://doi.org/10.3354/meps306041>.
- Dissanayake, N., Frid, C.J.L., Drylie, T.P., Caswell, B.A., 2018. Ecological functioning of mudflats: global analysis reveals both regional differences and widespread conservation of functioning. *Mar. Ecol. Prog. Ser.* 604, 1–20. <https://doi.org/10.3354/meps12728>.
- Edgar, G.J., 1999. Experimental analysis of structural versus trophic importance of seagrass beds. 1. Effects on macrofaunal and meiofaunal invertebrates. *Vie Milieu* 49, 239–248. ISSN:0240-8759.
- Fredriksen, S., De Backer, A., Boström, C., Christie, H., 2010. Infauna from *Zostera marina* L. meadows in Norway. Differences in vegetated and unvegetated areas. *Mar. Biol.* Res. 6, 189–200. <https://doi.org/10.1080/17451000903042461>.
- Gartner, A., Lavery, P.S., Lonzano-Montes, H., 2015. Trophic implications and faunal resilience following one-off and successive disturbances to an *Amphibolis grillifithii* seagrass system. *Mar. Pollut. Bull.* 94, 131–143. <https://doi.org/10.1016/j.marpolbul.2015.03.001>.
- Gaston, K.J., 1994. *Rarity*. Chapman & Hall, London.
- Gerwing, T.G., Cox, K., Allen Gerwing, A.M., Campbell, L., Macdonald, T., Dudas, S.E., Juanes, F., 2020. Varying intertidal invertebrate taxonomic resolution does not influence ecological findings. *Estuar. Coast Shelf Sci.* 232, 106516 <https://doi.org/10.1016/j.ecss.2019.106516>.
- Gotelli, N.J., Colwell, R.K., 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecol. Lett.* 4, 379–391. <https://doi.org/10.1046/j.1461-0248.2001.00230.x>.
- Gross, C., Donoghue, C., Pruitt, C., Trimble, A.C., Ruesink, J.L., 2019. Nekton community responses to seagrass differ with shoreline slope. *Estuar. Coast* 42, 1156–1168. <https://doi.org/10.1007/s12237-019-00556-8>.
- Hammer, Ø., Harper, D.A.T., Ryan, P.D., 2001. PAST: paleontological statistics software package for education and data analysis. *Palaeontol. Electron.* 4 (1), 9.
- Hemminga, M.A., Duarte, C.M., 2000. *Seagrass Ecology*. Cambridge University Press, Cambridge, ISBN 9780521052498.
- Hirst, J.A., Attrill, M., 2008. Small is beautiful: an inverted view of habitat fragmentation in seagrass beds. *Estuar. Coast Shelf Sci.* 78, 811–818. <https://doi.org/10.1016/j.ecss.2008.02.020>.
- Hodgson, A.N., Allanson, B.R., Cretchley, R., 2000. An estimation of the standing stock and population structure of *Upogebia africana* (Crustacea: thalassinidae) in the Knysna Estuary. *Trans. Roy. Soc. S. Afr.* 55, 187–196. <https://doi.org/10.1080/00359190009520443>.
- Hu, C., Liu, Y., Yang, X., Shui, B., Zhang, X., Wang, J., 2022. Functional trait responses of macrobenthic communities in seagrass microhabitats of a temperate lagoon. *Mar. Pollut. Bull.* 177, 113491 <https://doi.org/10.1016/j.marpolbul.2022.113491>.
- Hyman, A.C., Frazer, T.K., Jacoby, C.A., Frost, J.R., Kowalewski, M., 2019. Long-term persistence of structured habitats: seagrass meadows as enduring hotspots of biodiversity and faunal stability. *Proc R Soc B* 286, 20191861. <https://doi.org/10.1098/rspb.2019.1861>.
- Largier, J.L., Attwood, C., Harcourt-Baldwin, J.L., 2000. The hydrographic character of the Knysna Estuary. *Trans. Roy. Soc. S. Afr.* 55, 107–122. <https://doi.org/10.1080/00359190009520437>.
- Legendre, P., Legendre, L., 1998. In: *Numerical Ecology*, 2<sup>nd</sup> English Edn. Elsevier, Amsterdam, ISBN 9780080523170.
- Leopardus, V., Uy, W., Nakaoka, M., 2014. Benthic macrofaunal assemblages in multispecific seagrass meadows of the southern Philippines: variation among vegetation dominated by different seagrass species. *J. Exp. Mar. Biol. Ecol.* 457, 71–80. <https://doi.org/10.1016/j.jembe.2014.04.006>.
- Lowe, V., Frid, C.J.L., Venarsky, M., Burford, M.A., 2022. Responses of a macrobenthic community to seasonal freshwater flow in a wet-dry tropical estuary. *Estuar. Coast Shelf Sci.* 265, 107736 <https://doi.org/10.1016/j.ecss.2021.107736>.
- Macdonald, T.A., Burd, B.J., Macdonald, V.I., van Roodselaar, A., 2010. *Taxonomic and Feeding Guild Classification for the Marine Benthic Macroinvertebrates of the Strait of Georgia, British Columbia*, vol. 2874. *Can Techn Rep Fish Aquat Sci*, p. 63.
- Magni, P., Como, S., Kamijo, A., Montani, S., 2017. Effects of *Zostera marina* on the patterns of spatial distribution of sediments and macrozoobenthos in the boreal lagoon of Furen (Hokkaido, Japan). *Mar. Environ. Res.* 131, 90–102. <https://doi.org/10.1016/j.marenvres.2017.09.013>.
- Magni, P., Semprucci, F., Gravina, M.F., 2022. Joint analysis of macrofaunal and meiofaunal assemblages improves the assessment of lagoonal environmental heterogeneity. *Estuar. Coast Shelf Sci.* 266, 107740 <https://doi.org/10.1016/j.ecss.2021.107740>.
- Maree, B., 2000. Structure and status of the wetlands of the Knysna estuary. *Trans. Roy. Soc. S. Afr.* 55, 163–176. <https://doi.org/10.1080/00359100009520441>.

- McCloskey, R.M., Unsworth, R.F., 2015. Decreasing seagrass density negatively influences associated fauna. *PeerJ* 3 (6), e1053. <https://doi.org/10.7717/peerj.1053>.
- McHenry, J., Rassweiler, A., Hernan, G., Uejio, C.K., Pau, S., Dubel, A.K., Lester, S.E., 2021. Modelling the biodiversity enhancement value of seagrass beds. *Divers. Distrib.* 27, 2036–2049. <https://doi.org/10.1111/ddi.13379>.
- McKenzie, L.J., 2003. *Guidelines for the Rapid Assessment and Mapping of Tropical Seagrass Habitats*. Queensland Department of Primary Industries, Cairns.
- Misturini, D., Colling, L.A., 2021. Can short-term meteorological events alter subtropical estuarine macrobenthic assemblages in seagrass meadows (Patos Lagoon Estuary - southern Brazil)? *Estuar. Coast Shelf Sci.* 261, 107532. <https://doi.org/10.1016/j.ecss.2021.107532>.
- Montague, C.L., Ley, J.A., 1993. A possible effect of salinity fluctuation on abundance of benthic vegetation and associated fauna in northeastern Florida Bay. *Estuaries* 16, 703–717. <https://doi.org/10.2307/1352429>.
- Monteiro, C., Zardi, G.I., McQuaid, C.D., Serrão, E.A., Pearson, G.A., Nicastro, K.R., 2017. Canopy microclimate modification in central and marginal populations of a marine macroalga. *Mar. Biodivers.* 49, 415–424. <https://doi.org/10.1007/s12526-017-0824-y>.
- Morais, G.C., Camargo, M.G., Lana, P., 2016. Intertidal assemblage variation across a subtropical estuarine gradient: how good conceptual and empirical models are? *Estuar. Coast Shelf Sci.* 170, 91–101. <https://doi.org/10.1016/j.ecss.2015.12.020>.
- Murphy, C.E., Orth, R.J., Lefcheck, J.S., 2021. Habitat primarily structures seagrass epifaunal communities: a regional-scale assessment in the Chesapeake Bay. *Estuar. Coast* 44, 442–452. <https://doi.org/10.1007/s12237-020-00864-4>.
- Nakaoka, M., 2005. Plant-animal interactions in seagrass beds: ongoing and future challenges for understanding population and community dynamics. *Popul. Ecol.* 47, 167–177. <https://doi.org/10.1007/s10144-005-0226-z>.
- Namba, M., Hashimoto, M., Ito, M., Momota, K., Smith, C., Yorise, T., Nakaoka, M., 2020. The effect of environmental gradient on biodiversity and similarity of invertebrate communities in eelgrass (*Zostera marina*) beds. *Ecol. Res.* 35, 61–75. <https://doi.org/10.1111/1440-1703.12086>.
- Namba, M., Nakaoka, M., 2021. Increased salinity stress changes plant productivity and biomass by altering the top-down controls in eelgrass beds. *Ecosphere* 12, e03852. <https://doi.org/10.1002/ecs2.3852>.
- Pillay, D., Branch, G.M., Forbes, A.T., 2007. The influence of bioturbation by the sandprawn *Callinassa kraussi* on feeding and survival of the bivalve *Eumarcia paupercula* and the gastropod *Nassarius kraussianus*. *J. Exp. Mar. Biol. Ecol.* 344, 1–9. <https://doi.org/10.1016/j.jembe.2006.10.044>.
- Pillay, D., Branch, G.M., Griffiths, C.L., Williams, C., Prinsloo, A., 2010. Ecosystem change in a South African marine reserve (1960–2009): role of seagrass loss and anthropogenic disturbance. *Mar. Ecol. Prog. Ser.* 415, 35–48. <https://doi.org/10.3354/meps08733>.
- Pos, E., Andino, J.E.G., Sabatier, D., et al., 2014. Are all species necessary to reveal ecologically important patterns? *Ecol. Evol.* 4, 4626–4636. <https://doi.org/10.1002/ece3.1246>.
- Reise, K., 1978. Experiments on epibenthic predation in the wadden sea. *Helgol. Wiss. Meeresunters.* 31, 51–101. <https://doi.org/10.1007/BF02296991>.
- Reizopoulou, S., Simboura, N., Barbone, E., Aleffi, F., Basset, A., Nicolaidou, A., 2014. Biodiversity in transitional waters: steeper ecotone, lower diversity. *Mar. Ecol.* 35 (Suppl. 1), 78–84. <https://doi.org/10.1111/maec.12121>.
- Remane, A., 1934. Die brackwasserfauna. *Verh. Dtsch. Zool. Ges.* 36, 34–74. ISSN:0070-4342.
- Remane, A., 1971. Ecology of brackish water. In: Remane, A., Schlieper, C. (Eds.), *Biology of Brackish Water*, 2nd. Schweizerbart'sche, Stuttgart, ISBN 978-3-510-40034-8, pp. 1–210 (English) Edn.
- Rodil, I.F., Lohrer, A.M., Attard, K.M., Hewitt, J.E., Thrush, S.F., Norkko, A., 2021. Macrofauna communities across a seascape of seagrass meadows: environmental drivers, biodiversity patterns and conservation implications. *Biodivers. Conserv.* 30, 3023–3043. <https://doi.org/10.1007/s10531-021-02234-3>.
- Rueda, J.L., Marina, P., Urra, J., Salas, C., 2009. Changes in the composition and structure of a molluscan assemblage due to eelgrass loss in southern Spain (Alboran Sea). *J. Mar. Biol. Ass. UK* 89, 1319–1330. <https://doi.org/10.1017/S0025315409000289>.
- Schlacher, T.A., Wooldridge, T.H., 1996. Ecological responses to reductions in freshwater supply and quality in South Africa's estuaries: lessons for management and conservation. *J. Coast Conserv.* 2, 115–130. <https://doi.org/10.1007/BF02743045>.
- Schultz, S.T., Kruschel, C., 2010. Frequency and success of ambush and chase predation in fish assemblages associated with seagrass and bare sediment in an Adriatic lagoon. *Hydrobiologia* 649, 25–37. <https://doi.org/10.1007/s10750-010-0256-1>.
- Scrosati, R.A., 2017. Community-level facilitation by macroalgal foundation species peaks at an intermediate level of environmental stress. *ALGAE* 32, 41–46. <https://doi.org/10.4490/algae.2017.32.2.20>.
- Sgarbi, L.F., Bini, L.M., Heino, J., et al., 2020. Sampling effort and information quality provided by rare and common species in estimating assemblage structure. *Ecol. Indic.* 110, 105937. <https://doi.org/10.1016/j.ecolind.2019.105937>.
- Siebert, T., Branch, G.M., 2007. Influences of biological interactions on community structure within seagrass beds and sandprawn-dominated sandflats. *J. Exp. Mar. Biol. Ecol.* 340, 11–24. <https://doi.org/10.1016/j.jembe.2006.08.007>.
- Stoner, A.W., 1980. The role of seagrass biomass in the organization of benthic macrofaunal assemblages. *Bull. Mar. Sci.* 30, 537–551.
- Surugiu, V., Teaca, A., Svedu, I., Quijón, P.A., 2021. A hotspot in the Romanian Black Sea: eelgrass beds drive local biodiversity in surrounding bare sediments. *Front. Mar. Sci.* 8, 745137. <https://doi.org/10.3389/fmars.2021.745137>.
- Tagliapietra, D., Sigovini, M., Magni, P., 2012. Saprobity: a unified view of benthic succession models for coastal lagoons. *Hydrobiologia* 686, 15–28. <https://doi.org/10.1007/s10750-012-1001-8>.
- Tataranni, M., Maltagliati, F., Floris, A., Castelli, A., Lardicci, C., 2009. Variance estimates and taxonomic resolution: an analysis of macrobenthic spatial patterns at different scales in a western Mediterranean coastal lagoon. *Mar. Environ. Res.* 67, 219–229. <https://doi.org/10.1016/j.marenvres.2009.02.003>.
- Terrados, J., Duarte, C.M., Fortes, M.D., et al., 1998. Changes in community structure and biomass of seagrass communities along gradients of siltation in SE Asia. *Estuar. Coast Shelf Sci.* 46, 757–768. <https://doi.org/10.1006/ecss.1997.0304>.
- Teske, P.R., Wooldridge, T.H., 2004. Affinities of some common estuarine macroinvertebrates to salinity and sediment type: empirical data from Eastern Cape estuaries, South Africa. *Afr. Zool.* 39, 183–192. <https://doi.org/10.1080/15627020.2004.11657215>.
- Törnroos, A., Nordström, M.C., Bonsdorff, E., 2013. Coastal habitats as surrogates for taxonomic, functional and trophic structures of benthic faunal communities. *PLoS One* 8 (10), e78910. <https://doi.org/10.1371/journal.pone.0078910>.
- van der Zee, E.M., Angelini, C., Govers, L.L., et al., 2016. How habitat-modifying organisms structure the food web of two coastal ecosystems. *Proc R Soc B* 283, 20152326. <https://doi.org/10.1098/rspb.2015.2326>.
- van Houte-Howes, K.S.S., Turner, S.J., Pildich, C.A., 2004. Spatial differences in macroinvertebrate communities in intertidal seagrass habitats and unvegetated sediment in three New Zealand estuaries. *Estuaries* 27, 945–957. <https://doi.org/10.1007/BF02803421>.
- Virnstein, R., Mikkelsen, P.S., Cairns, K.D., Capone, M.A., 1983. Seagrass beds versus sand bottoms: the trophic importance of their associated benthic invertebrates. *Fla. Sci.* 46, 363–381, 131.111/98.148.
- Wang, X., Ellwood, M.D.F., Ai, D., Zhang, R., Wang, G., 2018. Species abundance distributions as a proxy for the niche-neutrality continuum. *J. Plant Ecol.* 11, 445–452. <https://doi.org/10.1093/jpe/rtx013>.
- Warwick, R.M., Dashfield, S.L., Somerfield, P.J., 2006. The integral structure of a benthic infaunal assemblage. *J. Exp. Mar. Biol. Ecol.* 330, 12–18. <https://doi.org/10.1016/j.jembe.2005.12.013>.
- Whitfield, A., Elliott, M., 2011. Ecosystem and biotic classifications of estuaries and coasts. In: Wolanski, E., McLusky, D.S. (Eds.), *Treatise on Estuarine and Coastal Science*, vol. 1. Academic Press, Waltham, pp. 99–124.
- Whitfield, A.K., Elliott, M., Basset, A., Blaber, S.J.M., West, R.J., 2012. Paradigms in estuarine ecology – a review of the Remane diagram with a suggested revised model for estuaries. *Estuar. Coast Shelf Sci.* 97, 78–90. <https://doi.org/10.1016/j.ecss.2011.11.026>.
- Wildsmith, M.D., Valesini, F.J., Robinson, S.F., 2017. The value of enduring environmental surrogates as predictors of estuarine macroinvertebrate assemblages. *Estuar. Coast Shelf Sci.* 197, 159–172. <https://doi.org/10.1016/j.ecss.2017.08.006>.