



Patterns of seagrass macrobenthic biodiversity in the warm-temperate Knysna estuarine bay, Western Cape: a review

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Abstract Knysna estuarine bay in South Africa's Garden Route National Park is that country's most significant estuarine system for biodiversity and conservation value. One outstanding feature is support of 40% of South Africa's—and maybe 20% of the world's—remaining vulnerable and decreasing dwarf-eelgrass, *Zostera capensis*, whose associated benthic macrofauna has been studied since 2009. For these invertebrates, Knysna comprises several significantly different compartments: sandy mouth; well-flushed marine embayment; poorly flushed central sea-water 'lagoon'; and two disjunct but faunistically similar peripheral regions—marine backwater channels, and low-salinity upper estuary. Although macrofauna ranges from dilute brackish to fully marine, its abundance, local patchiness, and over considerable stretches, species density remains remarkably

constant; further, one-third of species occur throughout. Intertidally, all but peripheral compartments are low density and infaunally dominated, while some peripheral areas, and much of the subtidal, are higher density and epifaunally dominated. Overall, seagrass macrobenthos appears maintained below carrying capacity (e.g., by abundant juvenile fish) and of random species composition within a site. Two further characteristics are notable: Unusually, seagrass supports fewer animals than adjacent unvegetated areas, probably because of lack of bioturbatory disturbance in them, and the vegetation cover may ameliorate ambient habitat conditions. Unfortunately, continual heavy and effectively unpreventable exploitation for bait occurs, and chlorophyte blooms have developed because of high nutrient input. Knysna presents a microcosm of problems facing biodiverse and high-value habitats set within areas of high unemployment where subsistence fishing provides the main source of protein and seagrass provides the only source of bait.

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Introduction

The permanently open Knysna estuarine bay (34°03'S, 23°03'E) is a drowned river valley in South Africa's

Western Cape separated from the adjacent Indian Ocean by a narrow gorge (300 m wide, 700 m long, and 4 m deep at low tide) carved through the coastal quartzite ridge by the Knysna River during times of lower sea level. The bay forms part of the open-access Garden Route National Park, and on a basket of criteria, including its size, diversity of habitat, zonal rarity, and biodiversity, is ranked South Africa's most significant estuarine system in terms of conservation importance (Turpie and Clark 2007; van Niekerk et al. 2019). Known locally as the Knysna Lagoon, the system has an area of some 10 km² at low tide and 16 km² at high tide and receives the inflow of the Knysna River at its head and a large number of smaller streams along its northern and eastern shores. Nevertheless, it is marine-dominated, consequent on low average rates of freshwater inflow and a very large tidal prism, during spring tides equaling $19 \times 10^6 \text{ m}^3$ [the largest of any South African estuary (Grindley 1985)], causing semi-diurnal flushing of its main channel. The estuarine bay can be divided hydrologically into three linear compartments, which vary in areal extent and precise geographical position with the tidal cycle and magnitude of river flow: An outer marine bay tidally flushed with cool water from the Indian Ocean and with salinities usually > 34; a middle, more isolated lagoonal water body also of high salinity (30–34) but with long residence times (c. 4 weeks); and an inner, stratified and well-flushed estuarine region with low and variable salinity (0–30) as a result of freshwater input from the Knysna River (Largier et al. 2000).

This system is also one of the most thoroughly researched of any South African estuary with more than 100 published articles (Russell et al. 2012; Whitfield and Baliwe 2013), work there beginning in 1947 (Day et al. 1951) (see the summaries of Day 1967; Grindley 1985; Russell et al. 2012; and the articles in Hodgson and Allanson 2000). Among other important features, Knysna supports 40% of South Africa's dwarf-eelgrass, *Zostera (Zosterella) capensis* [or *Nanozostera capensis* in the recent revision of the Zosteraceae of Coyer et al. (2013)] which may equate to 20% of its world area (Adams 2016; Wasserman et al. 2020). It also forms the only known African locality of the unusual marine valvatoidean gastropod *Cornirostra* (GBIF 2020), as well as being the main habitat of several other rare seagrass-associated species, including the endangered Knysna seahorse

(*Hippocampus capensis*), and it is one of the only two localities that support the critically endangered seagrass false-limpet (*Siphonaria compressa*) and a seagrass population of the dwarf cushion-star *Parvulastra exigua*. Except in the immediate vicinity of the mouth, *Z. capensis*, together with some mixed *Halophila ovalis*, occurs virtually throughout the intertidal zone of the system as one continuous bed (Maree 2000), and it also occurs subtidally though more patchily (Wasserman et al. 2020; Barnes and Claassens 2020). Such meadows support well-developed invertebrate macrofaunas that serve the vital functions of consuming epiphytic algal growths and providing the trophic link between microphytobenthic production and that of the larger, more mobile nekton (Murphy et al. 2021). This article synthesizes the main findings of the disparate series of researches conducted on these invertebrate faunal assemblages at Knysna since 2009, re-analyzing the original data where appropriate, with particular emphasis on patterns of macrofaunal assemblage composition, abundance, species richness, and patchiness along the bay's main axial transitional gradient, as well as along the gradient of shelter, located perpendicular to that axis across its eastern section.

General methodology

Patterns described in this review are based mainly on a series of 23 sites positioned to represent the whole area over which *Zostera capensis* is present intertidally (Fig. 1), with additional comparison between the macrofaunal eelgrass assemblages at some of those sites and the equivalent assemblages in immediately adjacent areas of bare sediment and/or in subtidal seagrass. Sampling was conducted each year between 2009 and 2020 during the austral summer, the research being approved by SANParks and conducted in accordance with their scientific research regulations and requirements. A standard procedure was used, involving series of core samples, each of 0.0027 m² diameter prior to 2013 and of 0.0054 m² diameter thereafter and of 100 mm depth, taken from continuous stretches of seagrass while still covered by > 10 cm of water. Cores were gently sieved ('puddled') through 710-μm mesh on site. This sampling procedure collects the smaller and more numerous members of the benthic and epibenthic macrofauna that

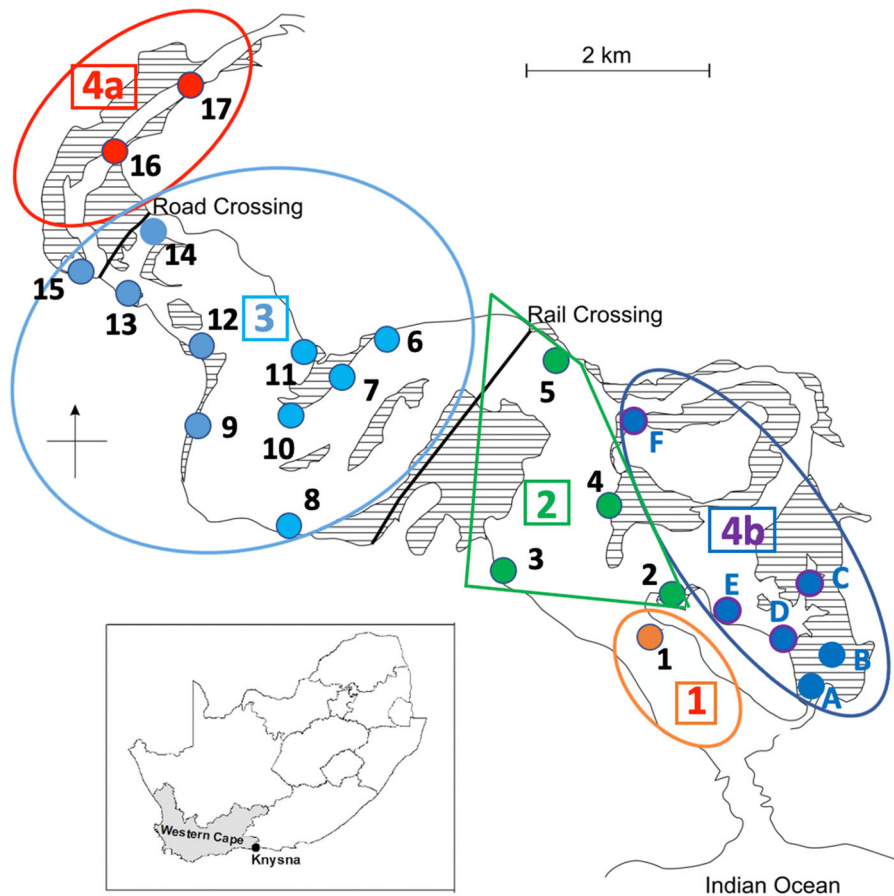


Fig. 1 Knysna estuarine bay, showing location of the linear chain of 17 sampling sites along its longitudinal axis and of the six sites **a–f** set within the backwaters of the Ashmead and

Steenbok Channels separating the two large bay islands from the mainland. The approximate geographical extents of the faunally distinct regions suggested in Fig. 2 are also indicated

constitute the large majority of invertebrate biodiversity (Bouchet et al. 2002; Albano et al. 2011), though not the meiofauna nor much scarcer megafauna nor sessile animals attached to the seagrass leaves.

In the laboratory, retained animals from each core were identified to species level wherever possible, with all organismal nomenclature here being as listed in the World Register of Marine Species (www.marinespecies.org), accessed November 2020, except in respect of the currently genus-less microgastropods '*Assiminea*' *capensis* and '*A.* *globulus*' (see Barnes 2017). It should be noted, however, that the specific identity of several animals, especially among the Polychaeta, is questionable because of lack of recent revision; those of South African taxa of Polycladida, Oligochaeta, and Nemertini, and many members of other groups less than 3 mm–4 mm in largest

dimension are virtually unknown. Such animals were treated as morphospecies, an operationally appropriate procedure to detect spatial patterns of numbers of species and their differential abundance (Dethier and Schoch 2006; Gerwing et al. 2020).

All calculations were carried out in Microsoft Excel for Mac 16.37 with the StatPlus:mac Pro 7.1.1 add-on or via PAST 3.24 (Hammer et al. 2019). Numbers of each component zoobenthic species at each site were subjected to similarity analysis, and assemblage metrics were derived and compared. Univariate metrics assessed included: (i) overall faunal numbers per unit area, (ii) observed numbers of species per unit sample, N_0 [i.e., 'species density' sensu (Gotelli and Colwell 2001)], and (iii) patchiness in spatial abundance of the macrofaunal assemblages as estimated by the 'index of patchiness' (I_p) of Lloyd (1967), with

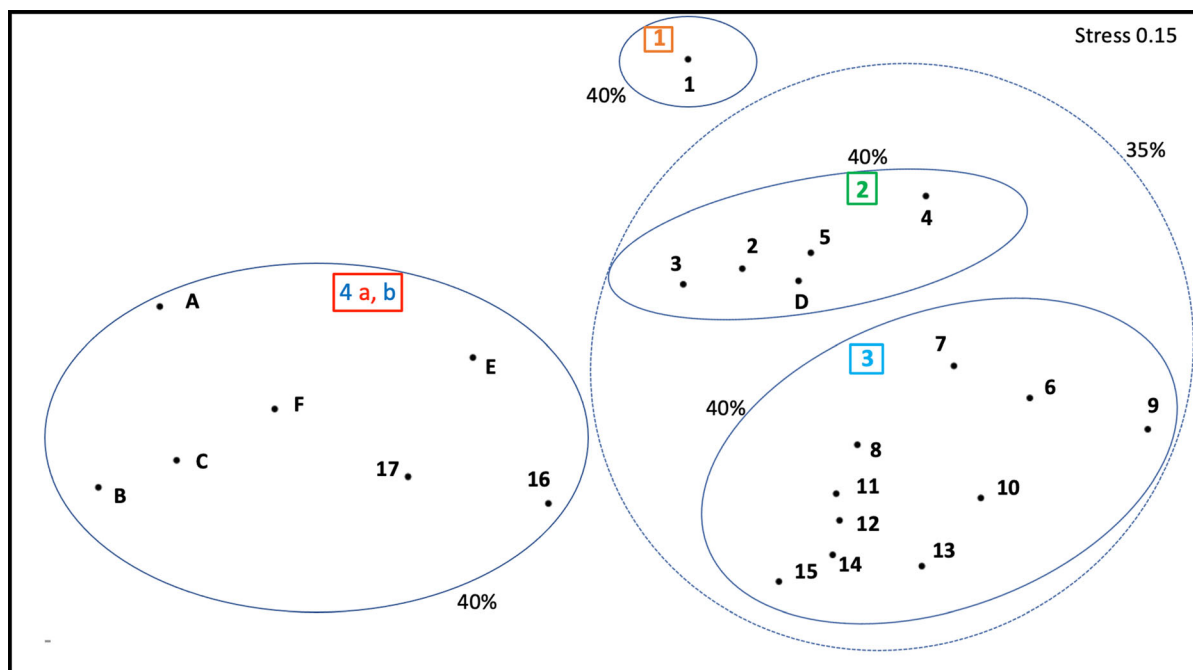


Fig. 2 nMDS plot based on Bray–Curtis similarities between percentage species composition data at the 23 sites, showing the four groups of seagrass macrofaunal assemblage types, i.e., those in: **a** the sandy mouth region; **b** the marine bay; **c** the lagoon and lower estuary; and **d** the upper estuary and the marine-basin backwater channels. The boundary between

backwaters and axial channel conditions in the marine section would appear to lie along the Steenbok Channel in that site D falls within one grouping and E in the other. Envelopes enclose sites with the stated levels of Bray–Curtis similarity, for which the approximate geographical locations are shown in Fig. 1

statistically significant departures from random being determined by Monte Carlo simulation using 9999 iterations. Correlations were assessed using Spearman's rank coefficient S_p or the Pearson product-moment coefficient P_p as appropriate; number of species per site unit of 30 cores and per region unit of 180 cores was determined by Mao tau rarefaction; curves were fitted using KaleidaGraph 4.5.4; and, where not known, information on life style of individual species was derived from that of close relatives in compendia such as Macdonald et al. (2010).

Multivariate comparison of macrofaunal assemblage composition used hierarchical clustering analysis of S_{17} Bray–Curtis similarity, ANOSIM, ANCOVA, SIMPER, and ordination by non-metric multidimensional scaling (nMDS), with 9999 permutations. For such comparison, all data sets were standardized for overall species density (by dividing all ranks by the total number of species in the set) and for sample size (by dividing each species total by the overall number of individuals in the set) to reflect

solely differential taxonomic composition and to permit comparison of curve slopes (Passy 2016), a measure of equitability in individual species contribution to the total (Whittaker 1972). Overlaps in quantitative assemblage composition between adjacent regions were measured by the Bray–Curtis similarity index. All multivariate analyses were based on sample sizes of > 250 animals, well above the minimum number recommended by Forcino et al. (2015).

Principal findings

Patterns in assemblage composition

In total, some 67,000 individual macrofauna, representing 160 species, were examined in 2,100 core samples from the *Zostera* beds during the study. These ranged from typical freshwater/dilute-brackish species such as *Afrochiltonia capensis*, *Corallana africana* and *Melanoides tuberculata* through to fully marine

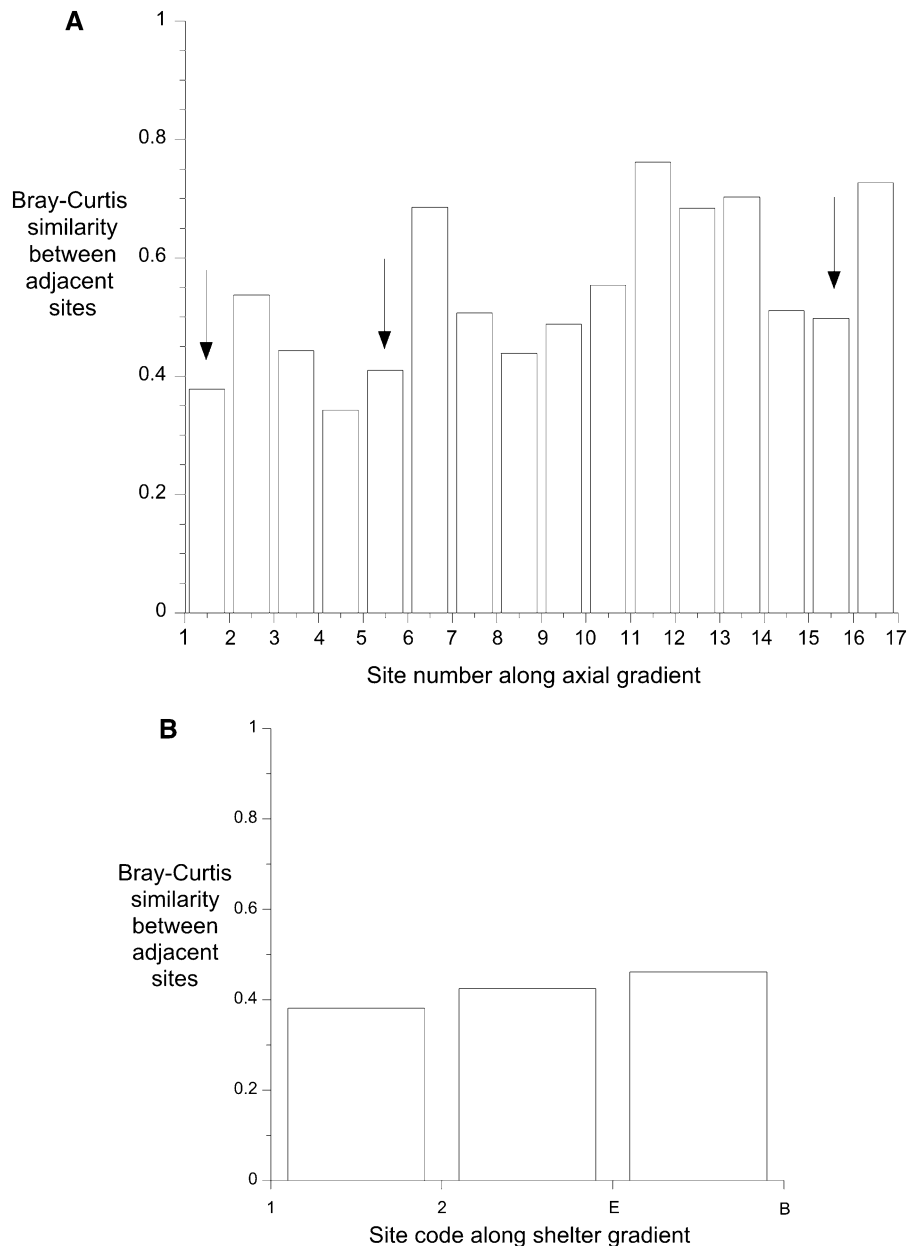


Fig. 3 Levels of Bray–Curtis similarity between the seagrass macrofaunal assemblages of adjacent sites: **a** along the longitudinal axis of the estuarine bay (arrows indicating points of transition between adjacent faunal assemblage types shown in

Fig. 2), and **b** along the axis of shelter perpendicular to 'A' from the main channel into the fringing backwaters of the marine embayment

forms such as *Gibbula cicer*, *Limaria tuberculata*, *Nebalia capensis* and *Parechinus angulosus*. Ordination by nMDS of Bray–Curtis similarity data from the 23 intertidal sites suggested that four significantly different faunal clusters occurred in the system (ANOSIM $R = 0.88$; $P < 0.0001$) (Figs. 1 and 2), an

essentially similar pattern to that derived earlier using non-standardized (but fourth-root transformed) abundance data (Barnes 2013a). These represented: (i) the sandy mouth region immediately adjacent to the true mouth, (ii) the outer marine embayment, and (iii) the lagoon plus lower-estuary divisions of the main axial

Table 1 The more dominant members of the Knysna intertidal seagrass macrofauna present in all four significantly different compartments of the system. These 21 species together comprise 70% of the total macrofaunal individuals sampled

GASTROPODA	<i>Capitella</i> sp.
' <i>Assimineae</i> ' <i>capensis</i>	<i>Orbinia angrapequensis</i>
<i>Nassarius kraussianus</i>	<i>Cirriformia</i> sp.
<i>Alaba pinnae</i>	<i>Paradoneis lyra capensis</i>
<i>Turritella capensis</i>	PERACARIDA
BIVALVIA	<i>Exosphaeroma hylecoetes</i>
<i>Arcuatula capensis</i>	<i>Melita zeylanica</i>
<i>Salmacoma litoralis</i>	<i>Grandidierella lutosa</i>
OLIGOCHAETA	<i>Cymadusa filosa</i>
tubificid sp.	BRACHYURA
POLYCHAETA	<i>Danielella edwardsii</i>
<i>Simplisetia erythraeensis</i>	<i>Hymenosoma orbiculare</i>
<i>Prionospio sexoculata</i>	OSTRACODA
<i>Caulleriella capensis</i>	? <i>Cylindroleberis</i> sp.

channel, and (iv) the fringing backwater-creek system of the smaller, saltmarsh-enclosed creeks and channels that separate the bay's two large islands (each c. 82–84 ha) from the mainland, together with sites in the upper estuary. Separation of the backwaters/upper-estuary sites from those along the main axial channel was the most marked, with a Bray–Curtis similarity between the two blocks of sites of only 20%, and the mouth region was an outlier within the axial channel. The three points of change along the longitudinal axis of the bay, however, were not marked by sharp faunal contrasts (Fig. 3). Indeed, SIMPER indicates that most (> 50%) of the differences are brought about by the relative abundances of just eight common and widespread species, the gastropod molluscs *Hydrobia knysnaensis* and '*Assimineae*' *capensis* (dominant in region iv), *Turritella* and *Alaba* (dominant in i), and *Nassarius* (dominant in iii), and the polychaetes *Prionospio* (dominant in iii), and *Caulleriella* and *Simplisetia* (dominant in ii). Despite statistically significant regionalization, 32% of the species (representing > 75% of the total individuals) occurred in all four regions in more than token quantities (Table 1 lists the more numerous of these shared taxa, and Table 2 displays those characteristic of each region). Patterns of relative species abundance within the four regions did not differ (ANCOVA equality of means $F = 0.17$, $P = 0.92$; equality of slopes $F = 0.59$,

$P = 0.62$) (Fig. 4), further indicating similarity between the different local assemblages. Number of species per sample did not vary across test areas of up to 1.5 ha at a given site, whether in the bay or in the lagoon (Table 3). The observation that the seagrass macrofauna of the brackish upper estuary did not differ from that in the fully saline, saltmarsh-enclosed backwater channels of the marine embayment is noteworthy and reinforces the earlier comments of Day (1959) and Barnes (1989) that so-called estuarine faunas may be as characteristic of sheltered areas of fully marine soft sediment as they are of regions subject to low salinity.

Major differences, however, did occur in the relative importance of infauna versus epifauna. Except at the lagoonal site 9, where the small biofilm-feeding cushion star *Parvulastra exigua* occurs in large numbers, the intertidal zone of the whole axial channel apart from the upper estuary is dominated by infaunal species (Fig. 5a), principally by polychaetes. From sites 1 to 15, the infauna comprised 68% (SE 3.7) of animals with no significant trend in their relative importance along the gradient ($S_p = 0.31$; $P = 0.26$) (Fig. 5B). In contrast, the shores of the upper estuary and the marine backwater channels were dominated by epifaunal truncatelloid microgastropods, especially by '*Assimineae*' *capensis* and *Hydrobia knysnaensis*, epifauna here comprising 64.4% of individuals. Only a few subtidal *Z. capensis* sites have so far been examined, but such areas are also overwhelmingly dominated by an epifaunal microgastropod, here by the cerithioid *Alaba pinnae*, although the importance of this species and hence of the subtidal epifauna in general decreases upstream so that epifauna and infauna contribute equally in the upper estuary (Fig. 5a). Thus in the bay region there is a transition at some LWS between a burrowing polychaete infauna and a seagrass-leaf-associated gastropod epifauna, and although upstream sub- and intertidal faunas are relatively similar, downstream in the bay they are markedly different (Fig. 6a). Few data are available to help explain the great downstream subtidal abundance of the epifaunal *Alaba* (a mean density of 28,000 m⁻²), although various studies have suggested that few fish consume significant numbers of shelled gastropods, even relatively small ones (McCormick 1998; Reynolds et al. 2018), not least because of their low nutritive value per unit intake (Vinson and Baker 2008). It is known that in South Africa, mugilids will

Table 2 Characteristic intertidal seagrass macrofauna (i.e., those together comprising 75% of the faunal individuals) of the four significantly different faunal regions of the Knysna estuarine bay

Species	%	Species	%
Mouth sandflats		Marine bay	
<i>Alaba pinnae</i>	21.4	<i>Simplisetia erythraeensis</i>	17.8
<i>Turritella capensis</i>	13.5	<i>Prionospio sexoculata</i>	11.1
<i>Simplisetia erythraeensis</i>	9.8	<i>Caulleriella capensis</i>	8.9
? <i>Cylindroleberis</i> sp	7.1	<i>Exosphaeroma hylecoetes</i>	4.5
<i>Orbinia angrapequensis</i>	4.3	<i>Nassarius kraussianus</i>	3.6
<i>Paradoneis lyra capensis</i>	3.6	<i>Melita zeylanica</i>	3.5
<i>Pseudopolydora ?kempi</i>	2.9	<i>Hymenosoma orbiculare</i>	3.4
<i>Diogenes brevirostris</i>	2.9	<i>Danielella edwardsii</i>	3.4
<i>Caulleriella capensis</i>	2.7	<i>Cyathura estuaria</i>	3.1
<i>Nassarius kraussianus</i>	2.6	<i>Grandidierella lutosa</i>	2.4
<i>Paridotea unguata</i>	1.9	<i>Cymadusa filosa</i>	2.4
<i>Grandidierella lutosa</i>	1.8	<i>Arcuatula capensis</i>	2.3
Lagoon + lower estuary		tubificid sp.	2.1
<i>Prionospio sexoculata</i>	27.3	? <i>Cylindroleberis</i> sp.	2.0
<i>Nassarius kraussianus</i>	15.6	<i>Paramoera capensis</i>	1.9
<i>Arcuatula capensis</i>	10.7	' <i>Assiminea</i> ' <i>capensis</i>	1.6
<i>Parvulastra exigua</i>	6.0	<i>Alaba pinnae</i>	1.5
<i>Simplisetia erythraeensis</i>	5.3	Backwater channels + upper estuary	
<i>Salmacoma litoralis</i>	5.2	' <i>Assiminea</i> ' <i>capensis</i>	40.0
<i>Cirriformia</i> sp.	2.9	<i>Hydrobia knysnaensis</i>	27.3
<i>Dosinia hepatica</i>	2.7	<i>Halmyrapseudes cooperi</i>	4.1
		<i>Simplisetia erythraeensis</i>	3.7

take microgastropods (Whitfield and Blaber 1978; Whitfield 1988), but at Knysna mugilids do not characterize the dense sublittoral eelgrass beds favored by *Alaba* (Pollard et al. 2017). Several equivalent subtidal areas of seagrass in other continents are also dominated by species of *Alaba*, although Knysna is the only known such locality outside the tropics (Barnes and Claassens 2020). These other areas are of relatively high salinity which may help to account for the lesser importance of this gastropod in and near the upper estuary. Why the same suite of truncatelloid microgastropods dominates the otherwise contrasting habitats of the intertidal backwaters and upper estuary is not known for certain, but their common shelter (see paragraph above) is likely to be an important component.

With one exception, no evidence of any strong species interactions within any given site was forthcoming. The exception was the positive correlation between numbers of the ectoparasitic pyramidellid snail *Sayella* sp. and those of its probable host

Hydrobia at the backwater site 'A' in Fig. 1 ($R_s = 0.78$; $P < 0.00001$). Such a parasite/host association is known from the western Atlantic (e.g., Hershler and Davis 1980), but although the pyramidellid concerned is a widely distributed animal, it is otherwise not recorded from Africa (GBIF 2020). That exception apart, however, in a large sample (325 cores) from the Kingfisher Creek seagrass (site 2 in Fig. 1), for example, Barnes (2013b) recorded 75 macrofaunal species at overall and mean densities of 2581 and 34 m⁻², respectively. Considering the 34 relatively common species there that each attained a mean density of at least 10 m⁻² (and together comprised 96% of the total individuals), all pairwise correlations of species abundance were very weak to non-existent (sensu Moore et al. 2018), positives averaging only $P_p = 0.069$ (± 0.060 SD) and negatives $P_p = 0.047$ (± 0.035 SD); and allowing for the familywise errors inherent in such a large correlation matrix (via Bonferroni correction), no negative correlations and only three positive ones were significant at

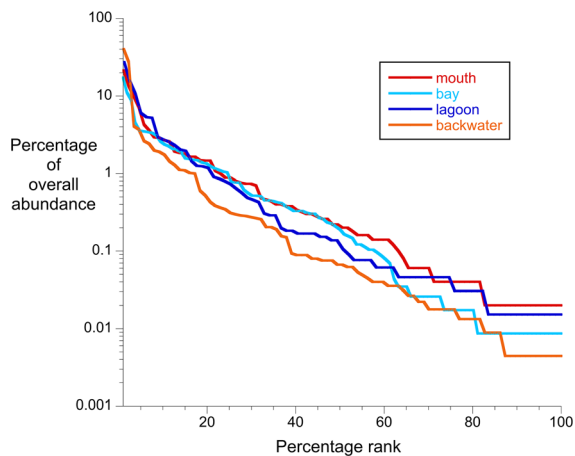


Fig. 4 Species abundance diagrams (Whittaker plots) for each of the four faunistically distinct assemblage types

Table 3 Uniformity of number of intertidal species per sample at different scales across test areas of (A) 0.2 ha and (B) 1.5 ha at Site 2 and (C) along a 350 m transect at site 9, as assessed by Lloyd's index of patchiness (I_p) and the Azovsky et al. (2000)

index of spatial homogeneity (I_a), with significance of I_p tested by Monte Carlo simulation (data from Barnes, 2013b, 2016 and Barnes and Hendy, 2015a)

Unit sample size	Lloyd's I_p	Azovsky et al.'s I_a	Significance of uniformity
A			
0.0015 m ²	0.948	0.977	$P = 0.1$
0.0027 m ²	0.938	0.988	$P = 0.03$
0.0054 m ²	0.933	0.995	$P = 0.004$
0.0095	0.962	0.995	$P = 0.009$
B			
0.0054 m ²	0.974	0.997	$P = 0.005$
C			
0.0054 m ²	0.929	0.994	$P = 0.01$

a critical α of < 0.05 (between the polychaetes *Simplisetia* and *Caulleriella*, *Glycera* and *Cirriformia*, and between the polychaete *Prionospio* and the gastropod *Nassarius*). Equivalently, although qualitative co-occurrence patterns across the whole of the marine-influenced embayment at Knysna show deterministic structuring (Barnes and Elwood 2011), as indeed might be expected granted the location of the sampled sites in three distinct faunal regions (sandy mouth, marine bay, and backwater system), syntopic species within a single one of those regions did not differ from random co-occurrences (Barnes and Barnes 2014b).

In the absence of strong bioturbators such as *Kraussillichirus kraussi* (*Callianassa kraussi* in the

older literature) from the majority of the system, faunal relationships between seagrass and bare sediment at Knysna are not the classic one of seagrass supporting the greater number of species and of individuals per unit area (Hemminga and Duarte 2000; Pillay et al. 2011; Hyman et al. 2019, etc.). To date studies have only concerned the outer marine embayment, but there seagrass macrofauna at a given site is more similar to those occurring in adjacent areas of bare sediment than either habitat is to other areas of the same type in the general region [Bray–Curtis faunal similarity between the two contiguous habitat types being a mean 0.58, whereas within-habitat-type similarity averaged 0.26 for the seagrass and 0.25 for the bare sediment (ANOVA $F_{1,14} = 5.05$; $P < 0.05$)] (see

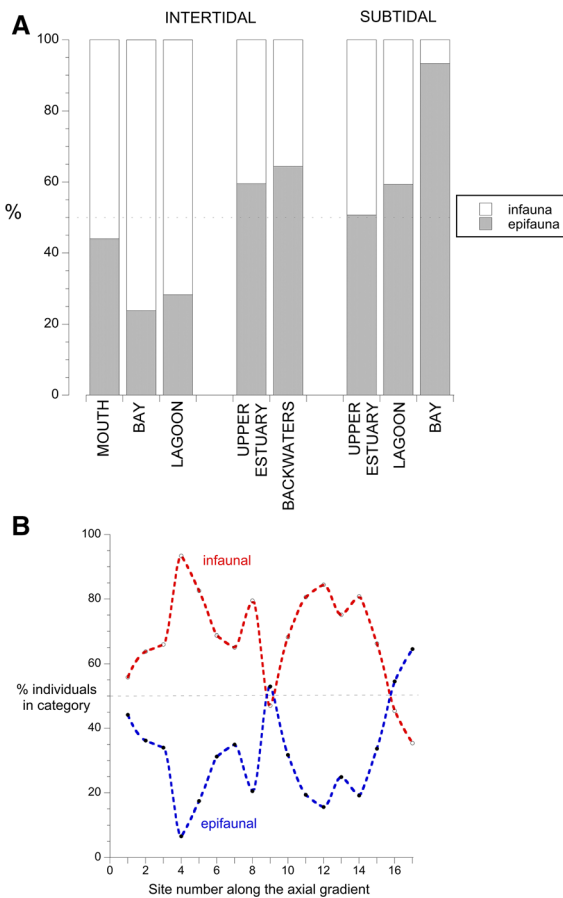


Fig. 5 Relative importance of infauna and epifauna in **a** the different intertidal and subtidal regions of the estuarine bay and **b** at each of the sites along the longitudinal axial channel

Fig. 6b). In general, seagrass beds supported lower, not higher, levels in half the metric comparisons in which there was a significant difference (Barnes and Barnes 2014a). Overall, faunal abundance was lower in seagrass in the ratio of 0.64: 1, while species density was indeed higher, but only by 1.13 to 1, with in large measure the higher numbers in the unvegetated sediments resulting from a quadrupled abundance of infaunal polychaetes, maybe because of the greater volume of available sedimentary habitat in the absence of eelgrass rootmass, although numbers of epifaunal crustaceans were 15 times less there (from a much smaller base). The same overall effect was not the case, however, in bare areas created by the death of seagrass following blanketing by the chlorophyte blooms described by Allanson et al. (2016) and

Human et al. (2016). In these circumstances, the former seagrass sites clustered together, as did the same areas when de-vegetated, although macrofaunal abundance was again significantly lower in the former seagrass than it was in the replacement bare sediment (in a ratio of 0.62: 1) and again largely because of an increased number of polychaetes and decreased number of crustaceans in the unvegetated sediment (Barnes 2019a).

Knysna's marine embayment forms a natural harbor, has been in the past a busy port (Grindley 1985), and today supports several marinas, and hence it is one of the centers of ship-borne alien immigrant species in South Africa (Griffiths et al. 2009). Alien species of *Boccardia*, *Polydora*, *Dipolydora*, *Pseudopolydora*, *Diopatra*, *Capitella*, *Desdemona*, *Erichthonius*, *Jassa*, *Monocorophium*, *Paracerceis*, *Elysia*, *Favorinus* and *Indothais* all form part of its seagrass fauna, as do amphipods such as *Cymadusa filosa*, *Melita zeylanica* and *Americorophium triaenonyx* that are regarded by Robinson et al. (2005) and Mead et al. (2011) as being cryptogenic—to which could presumably be added *Victoriopisa chilensis*. Relatively recently, these aliens have been joined by more northerly species spreading southward probably as a result of global warming. *Smaragdia souverbiana*, for example, is now a member of the subtidal seagrass fauna (Barnes and Claassens 2020). In the Knysna intertidal, *Melanoides tuberculata* has arrived and joined *Cerithidea decollata* (Hodgson and Dickens 2012) and *Austruca occidentalis* (formerly *Uca annulipes*) (Peer et al. 2015), the latter two in the adjacent saltmarsh or at the seagrass/saltmarsh interface.

Patterns in assemblage metrics along the axial gradient

As would be expected, the number of species at the 17 sites that were spaced along the system's longitudinal axis decreased with distance upstream ($S_p = -0.82$; $P < 0.0001$; Fig. 7a), but the form of the decrease in species density suggests the occurrence of a step change within the general area of the lower estuary, with the downstream sites showing a considerable degree of uniformity of species density (Fig. 7b; Table 4). The points in Fig. 7 are based on the whole available 12-year dataset, and hence, the location of faunal and regional boundaries will have been blurred

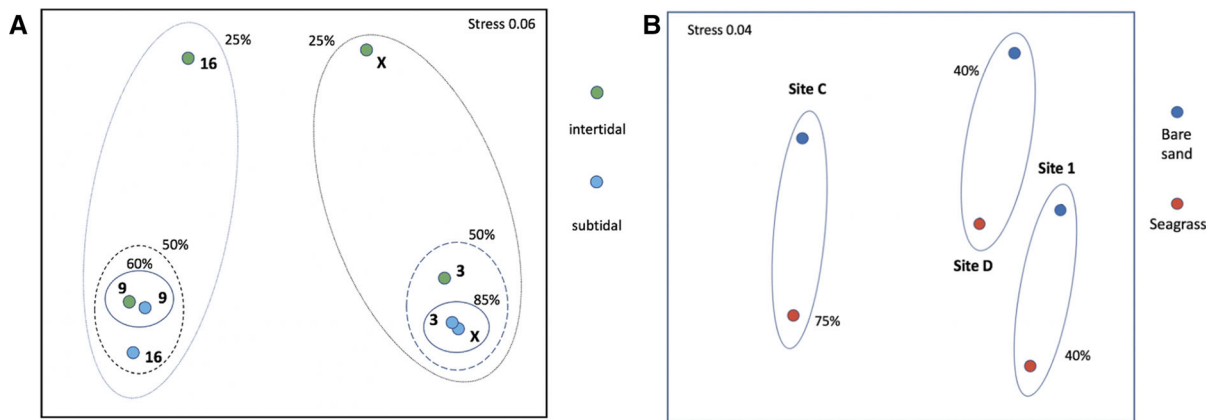


Fig. 6 nMDS plots based on Bray–Curtis similarities between percentage species composition data: **a** at four sites in the Knysna estuarine bay, one in each faunal compartment, showing the similarity between macrofaunal assemblages of seagrass at LWS in the intertidal zone and in the adjacent subtidal area (from data in Barnes and Claassens 2020), and **b** at three sites in the marine embayment forming a transect from the main

channel (site 1) into the backwater Steenbok Channel and its tributaries, showing similarity between macrofaunal assemblages in seagrass and in adjacent areas of bare sediment (from data in Barnes and Barnes 2014a). Envelopes enclose sites at the stated levels of Bray–Curtis similarity, and site codes are those given in Fig. 1, plus in (A) an additional site, 'X', located between sites 1 and 2

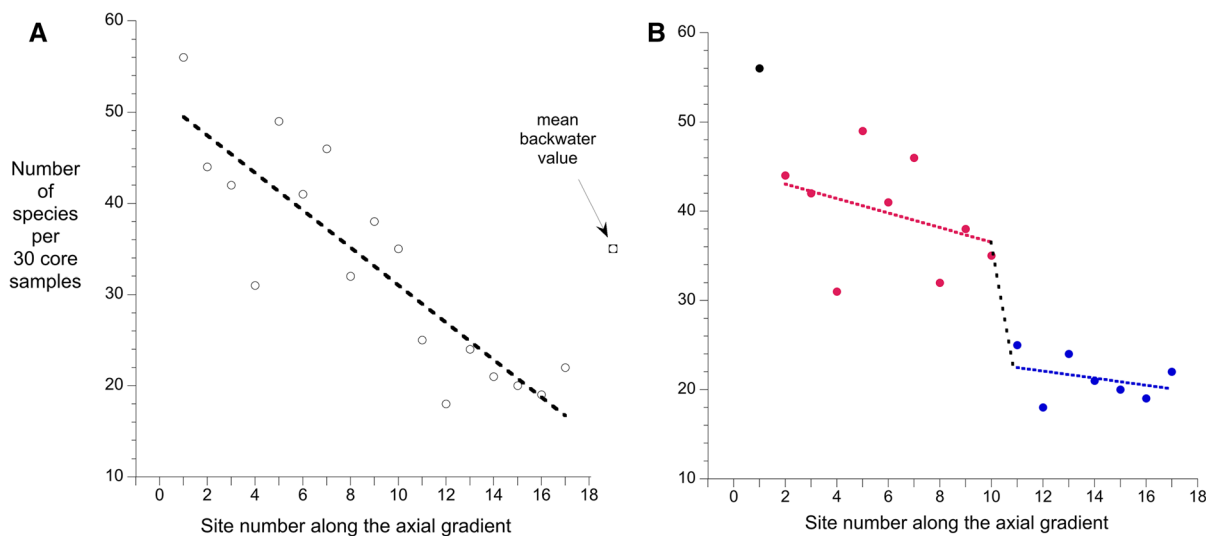


Fig. 7 Change in number of seagrass macrofaunal species along the longitudinal axis of the estuarine bay **a**. Note in **b** the apparent break between sites 10 and 11, corresponding to the one in the same area shown by Barnes and Ellwood (2012)

by temporal shifts, but an individual survey of macrofaunal animals along the axial channel in 2012 showed an almost identical (and sharper) feature (Barnes and Ellwood 2012) in the same general location. Comparison of data across different spatial scales shows that decline upstream in number of species when assessed per site (Fig. 7) is greater than when assessed per region (Table 4): Clearly, the bay and lagoon + lower-estuary regions are large and, as

also would be expected, the total fauna contained in each is considerably in excess of that at any individual site.

Assemblage abundance per unit area ($S_p = -0.35$; $P = 0.16$; Fig. 8a) and patchiness in assemblage abundance ($S_p = -0.20$; $P = 0.45$; Fig. 8b), however, showed no significant change with distance upstream; indeed, degree of patchiness along the axial gradient was significantly unchanging (Barnes 2019b). Neither

Table 4 Biodiversity metrics of the various intertidal faunal regions of Knysna estuarine bay: Mao tau species density (N_0), with Chao 2 estimations; N_1 and N_2 species diversity; equitability of species abundance (J); taxonomic diversity (Δ) and distinctness (Δ^*); and N_2 functional diversity (F_d) [withfunctional categories as per Macdonald et al. (2010) and Barnes and Hendy (2015a)]. Each axial regional metric is based on the common sample size of $180 \times 0.0054 \text{ m}^2$ cores, yielding some 90% of the likely total species; backwaters metric based on $148 \times 0.0054 \text{ m}^2$ samples. Peak values in bold

	Mouth	Bay	Lagoon + lower estuary	Upper estuary	Backwaters
Mao tau N_0 density	94	78	72	34	59
Chao 2 N_0	104	84	76	38	63
N_1 diversity	21.3	23.5	14.8	9.8	5.5
N_2 diversity	10.9	13.1	8.1	7.8	3.1
J equitability	0.68	0.73	0.61	0.65	0.42
Δ diversity	4.09	4.25	3.89	3.75	2.45
Δ^* distinctness	4.54	4.50	4.72	4.32	3.61
F_d diversity	7.56	8.38	5.13	4.77	1.64

was there any significant relationship between number of species per site and overall assemblage abundance there ($S_p = 0.43$; $P = 0.08$). However, significant relationships have been found between how patchy an individual species is and its occupancy and, to a lesser extent, its abundance: The more abundant and widespread the species, the less its patchiness, both in subtidal and in intertidal seagrass (Barnes 2019c, 2020), and both in interspecific comparisons (Barnes 2020) and intraspecifically (Barnes, in prep.) (Fig. 9). This suggests that the well-known macroecological abundance-occupancy pattern (e.g., He and Gaston 2003) can be extended into a patchiness-abundance-occupancy one, at least in this habitat type. As can be seen in Fig. 9, the slopes of the power laws relating logit occupancy to log patchiness in individual species are much more variable than those interspecifically in the different faunal regions; thus, while the interspecific occupancy-patchiness slopes representing different regions do not differ (ANCOVA $F = 1.3$, $P = 0.3$), the equivalent intraspecific slopes are heterogeneous (ANCOVA $F = 4.9$, $P < 0.0001$) with a further six of the dominants (including the epifaunal *Alaba* and *Cymadusa*, and infaunal *Caulleriella* and *Salmacoma*) not showing significant occupancy-patchiness relationships at all. This also indicates that disparate species together form assemblages with similar properties in the various regions. There were no discernable trends in either metric upstream, although the upper estuary did display the largest value of both β and R^2 .

General discussion and conclusions

The most striking feature of the Knysna intertidal seagrass-associated macrobenthos is its relative spatial uniformity. Macrofaunal abundance does not vary markedly along the longitudinal axis, neither does patchiness of macrofaunal density. Number of species per unit area at a given site is a constant, while species density along whole sections of the gradient can be relatively uniform, and its fauna appears to form a single assemblage with only local variation in relative frequency of its dominant components. Even the subtidal fauna does not differ qualitatively from the intertidal one, although there are marked quantitative differences and overall it is much more abundant especially in the most marine-influenced regions where *Alaba* dominates (Barnes and Claassens 2020). Admittedly, being a marine-dominated system with under normal circumstances relatively little freshwater input (Day et al. 1951), for an estuarine system salinity is relatively constant; however, occasional episodes of severe freshwater flooding do occur once every 10–12 years or so, rendering most or all of the system temporarily fresh (see, e.g., Korrington 1956; Blake and Chimboza 2010). But, although sea water may penetrate far upstream and dominate most areas, there is much change along the Knysna axis in other features of direct relevance to macrobenthos, as in transitional paralic systems in general (Tagliapietra et al. 2012; Pérez-Ruzafa et al. 2019). Sediment changes from clean sand at the mouth, to soft organic mud in the lagoonal and lower estuarine regions, and

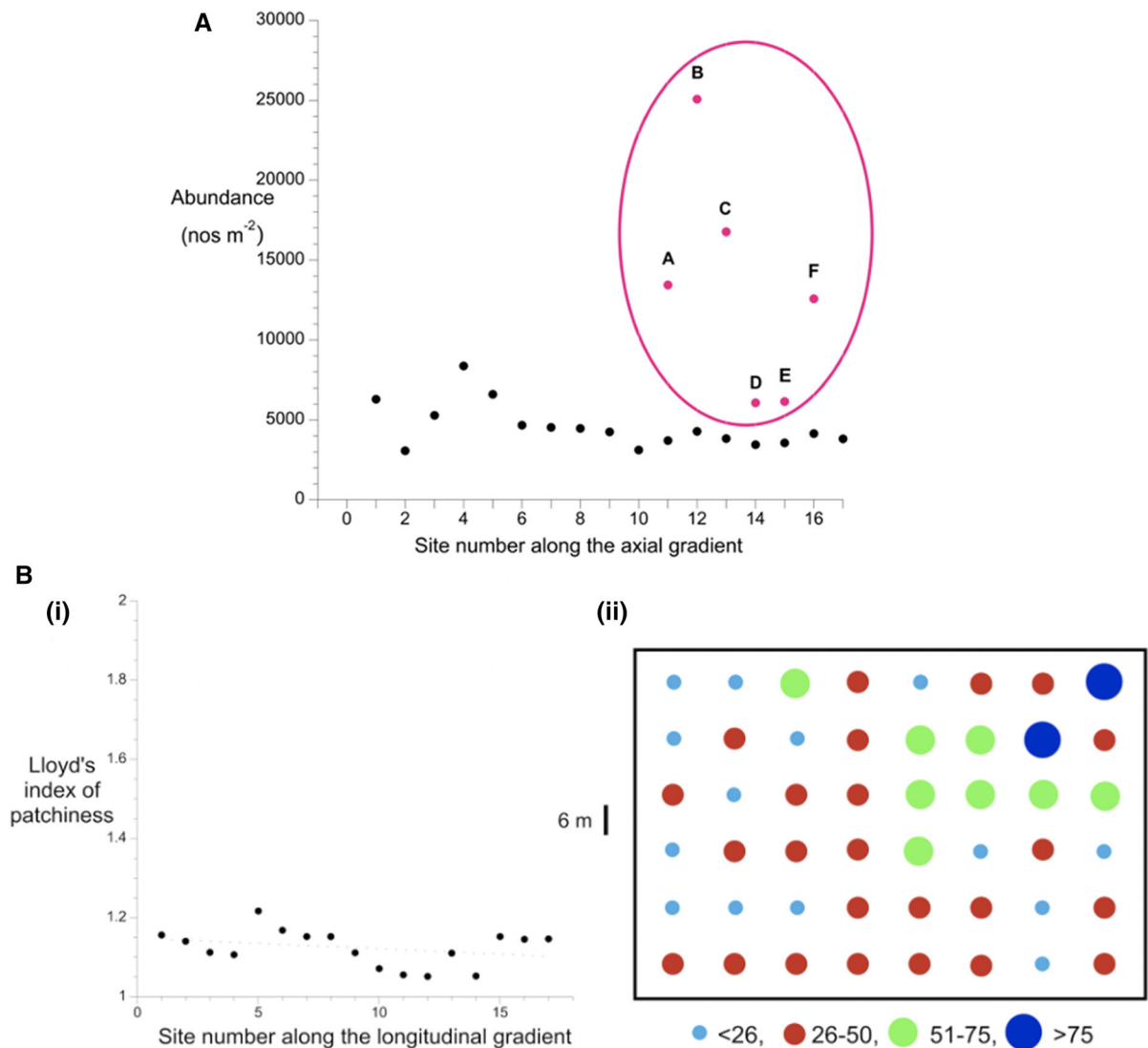


Fig. 8 Relative constancy of intertidal seagrass macrofaunal assemblage metrics along the longitudinal axis of the estuarine bay: **a** assemblage abundance, with an inset showing abundances at the six backwater-channel sites; and **b(i)** assemblage

patchiness (data from Barnes 2019b). **b(ii)** illustrates spatial variation in macrofaunal density 0.01 m^{-2} across an area of site 2 (from data in Barnes 2016)

to mud with admixed riverine gravel in the upper estuary (Day et al. 1951); shelter changes both as the estuary narrows and on transition from axial channel into backwater creeks (Day 1967); and shore profiles change from extensive tidal flats near the mouth to narrow steep slopes in the estuary supporting only linear strips of seagrass (Day 1967; Maree 2000). Rates of water exchange vary along the channel (Largier et al. 2000); characteristic density and shoot length of the eelgrass change with shore height and

exposure (den Hartog 1970; Adams and Talbot 1992); and so on.

Being located at 34°S , Knysna lies within the narrow mid-latitude belt recently identified by Whalen et al. (2020) as that displaying peak intensity of animal food consumption and hence potential top-down control of prey species. Like other South African estuarine areas supporting dwarf-eelgrass (Whitfield et al. 1989; Nel et al. 2018), it is a nursery area for many nektonic species (Whitfield and Kok 1992),

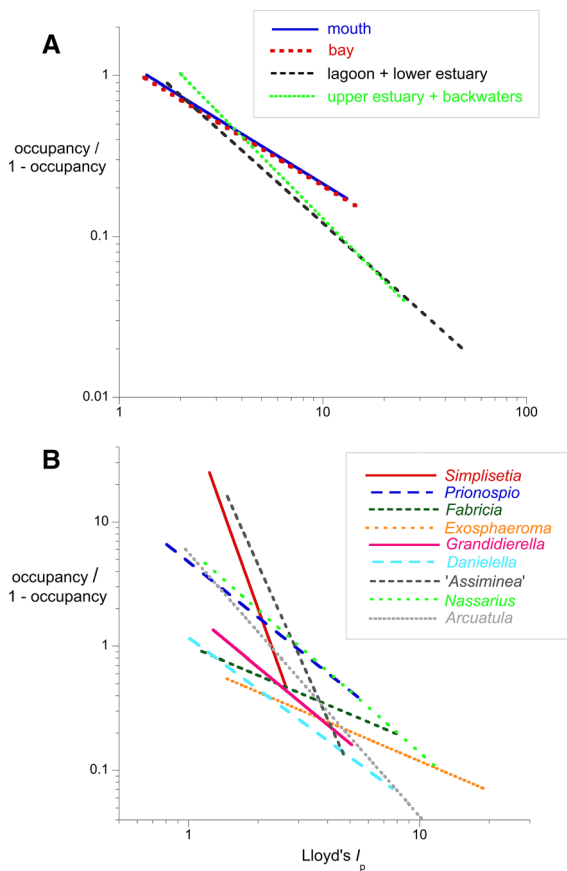


Fig. 9 The power laws ($y = \alpha x^\beta$) describing significant relationships between log Lloyd's I_p patchiness and logit occupancy in the seagrass macrofauna of Knysna estuarine bay, both **a** interspecifically in the different assemblage types and **b** intraspecifically in individual dominant species

schools of juvenile fish being a common sight in its seagrass beds. Indeed, seagrass beds have been regarded as one of the most important types of coastal nursery (Whitfield 2017; Lefcheck et al. 2019), both because of the food they provide (Whitfield 2017) and as refuge from larger fish predators (Whitfield 2020a). If, as is generally held to be the case in seagrass (Moksnes et al. 2008; Lewis and Anderson 2012; Duffey et al. 2015, etc.), the effect of this consumption, together with that exerted by adult fish (Pollard et al. 2017) and predatory members of the invertebrate macrobenthos, is top-down control of the seagrass microphytobenthic-biofilm consumers that dominate both epifauna and infauna, then many of features of

Knysna's seagrass macrobenthos become more understandable.

Three lines of evidence suggest that across the whole system seagrass macrofaunal abundance is below carrying capacity and not structured by density-dependent factors. First, the prevailing intertidal density along the longitudinal axis of some $4,000 \text{ m}^{-2}$ is very low compared to the $> 40,000 \text{ m}^{-2}$ animals occurring in similar intertidal dwarf-eelgrass beds in cool-temperate Europe (Blanchet et al. 2004; Barnes and Ellwood 2011; etc.) where predator rates are almost certainly lower on a fauna of similarly sized animals that are often members of the same families as represented at Knysna (Barnes and Hendy 2015b). Secondly, constancy of number of species per unit area, as demonstrated at the Kingfisher Creek site at Knysna (Barnes 2013b), is exactly what would be expected were the various species to be distributed independently of each other (granted their overall frequencies of occurrence) (Barnes and Barnes 2014b). Such independence of distribution is likely only if the whole assemblage is being maintained below the level at which species would otherwise interact. Thirdly, the large quantitative dataset of Barnes (2013b) from the same Kingfisher Creek site also showed that there were very few significant correlations (0.5%) between the abundances of pairs of species and all those were very weak. Moreover, as seen elsewhere, for example within Pacific Canadian *Zostera marina* meadows (Stark et al. 2020), weak and very weak positive relationships greatly outnumbered negative ones, further suggesting the lack of competitive interspecific interactions. In such overall circumstances of low and unpredictable density of potential invertebrate prey species, predators could thus be expected to have to forage optimally (Beseres and Feller 2007) and to graze down local prey stocks to threshold levels before moving and repeating the process elsewhere, and having reduced their food stocks to low levels over wide areas could themselves then experience food limitation (Saulnier et al. 2000). The actions of such predators roaming widely over the surface might also help explain the uniform levels of macrofaunal patchiness characterizing large areas (Barnes and Hamylton 2019).

A second process that could help account for the observed features of the Knysna macrobenthic assemblages, and particularly their relative uniformity along the longitudinal axis, is if the presence of the seagrass



Fig. 10 Destructive effects of bait-collecting activities on intertidal seagrass habitat in the 'no-take bait sanctuary' section of the Knysna estuarine bay: **a** The hole and jettisoned plug created by pushing for mudprawn; **b**, a substratum pock-marked

by such mudprawn pushing; and **c**, the resultant plugs scattered over the seagrass surface; **d**, an area of seagrass destroyed by trenching for bait worms (from Barnes and Claassens 2020)

ameliorates variation in the local ambient microclimatic conditions, as a macro-algal cover has been shown to do (Scrosati 2017; Monteiro et al. 2017). Within the relatively uniform and stable conditions provided by the *Z. capensis* bed, species can penetrate upstream further than they might otherwise be able to do (Barnes and Ellwood 2012). Seagrass beds and other structurally complex systems (Hyman et al. 2019) generally appear to support macrofaunal assemblages that display spatial and temporal stability of abundance and composition, and high levels of resilience (Whanpetch et al. 2010; Blake et al. 2014; Gartner et al. 2015), and this may have important knock-on effects on the whole local coastal food web (Jankowska et al. 2019).

Granted the current high loss rates of seagrass throughout the world (Waycott et al. 2009; Short et al. 2011) and of *Zostera capensis* in southern Africa (Adams 2016), an important question is the implication of the operation of such potential structuring factors at Knysna for the future of its important seagrass system. Threats to the health of Knysna estuarine bay have recently been reviewed by

Claassens et al. (2020), and the two that might particularly affect the seagrass and its inhabitants are uncontrolled bait harvesting by destructive means and chlorophyte blooms. Bait harvesting by 'pushing' for mudprawns (*Upogebia capensis*) and trenching for worms (*Marphysa*, *Polybrachiorhynchus* and *Arenicola* spp.) is rife in Knysna (Simon et al. 2019), even (and arguably especially) in the formally protected bait-reserve area (Fig. 10) that also supports 79% of the estuarine bay's seagrass-associated species. Unfortunately, there are immense logistic and social problems associated with preventing illegal and restricting legal bait harvesting in southern Africa, especially in areas of high unemployment where subsistence fishing provides the main or only source of protein (Bandeira and Gell 2003; Napier et al. 2009) and the local intertidal provides the only source of bait (Barnes and Claassens 2020). Subsistence harvesting at Knysna is worth some ZAR 1×10^6 (Turpie 2007). Its precise effect on the seagrass macrofauna is unknown; however, basically because the extent of harvesting means that a like-with-like, harvested versus unharvested, comparison is not possible: No area of

intertidal seagrass remains un-pushed or un-pumped. At other localities, however, it and the associated trampling are known to have severe consequences (e.g., Pillay et al. 2010; Garmendia et al. 2017; Short et al. 2011; Adams 2016). Nevertheless, the inherent resilience and spatial uniformity of the Knysna seagrass beds referred to above, together with the fact that they form one large interconnected system with dispersal possible between all sections, does offer hope.

In respect of the second major threat, at the moment the problems of eutrophication, to which *Z. capensis* is known to be sensitive (Mvungi and Pillay 2019), and consequent algal blooms are only local, affecting mainly the backwater channels into which the municipal sewage treatment plant discharges and in which there is a legacy of organic matter retention (Human et al. 2020). Knysna's large tidal prism proves invaluable insofar as minimizing blooms in the main axial channel is concerned. But the local effect of the chlorophyte blanket is dramatic and destructive. Animal numbers may increase on its seasonal dieback, except in the very local areas of anoxia, although this increase is almost entirely confined to densities of the dominant polychaete groups (except, for some reason, cirratulids) (Barnes 2019a). Crustaceans do not bounce back so readily, and as they provide the food for most fish in the nearby Swartvlei Estuary (Whitfield 1988, 2020b) and presumably therefore do so at Knysna, the fish populations may suffer the consequences: There is some evidence that this is indeed the case (Pollard et al. 2018). The chlorophyte problem is soluble (no pun intended) but at considerable cost (see Human et al. 2020). The financial reward, however, might also be large, not least because such blooms impact on tourism (Boesch et al. 1996) and tourists contribute some ZAR 1×10^9 per annum to the Knysna economy (Turpie 2007).

Knysna is perhaps not a typical South African estuary in being permanently open (see van Niekerk et al. 2020), without a significant presence of *Kraussillichirus*, and with a subtidal dominated by the little-known *Alaba pinnae*, but nevertheless its fauna generally appears to be the classic Cape estuarine one (Day 1981; de Villiers et al. 1999); indeed, it supports > 40% of South African estuarine biodiversity. It also seems a microcosm of the country's estuarine problems, both environmental and socio-economic, including loss of area to reclamation

(> 30% of the saltmarsh has already gone, and 25% of that remaining is under threat). Thus far, at least, it has managed to fare better than many other South African estuarine systems (van Niekerk et al. 2013), and it may yet continue to do so.

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Data availability and material Datasets on which these analyses are based have been lodged in electronic format in the Rondevlei Office of SANParks Scientific Services (<http://dataknp.sanparks.org/sanparks/metacat/Nerinak.23.11/sanparks>) and are available on request.

Compliance with ethical standards

Conflict of interest The author declares no conflict of interest.

Consent for publication The author consents to publication.

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.

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