The significance of shore height in intertidal macrobenthic seagrass ecology and conservation

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ABSTRACT

1. Benthic faunal assemblages of an intertidal seagrass bed were sampled at three shore heights (LWN, MLW, LWS) at the mouth, mid-point and head of the Steenbok Channel in South Africa's premier seagrass site, the warm-temperate Knysna estuarine bay, Garden Route National Park.

2. Faunal abundance, species richness, species diversity, and proportion of rare species were relatively uniform along the Channel, as were faunal abundance, species diversity and proportion of rare species down the shore. Overall species richness per station, however, was significantly lower at LWN than at either MLW or LWS, although the distribution of species richness over the shore did not depart from random at one of the three sites. Overall faunal abundance and those of individual component species were dispersed patchily through the bed.

3. The nature of the faunal assemblages present, however, varied significantly throughout the bed, both along the Channel at each shore-height horizon, and down the shore at each site. LWN assemblages formed a unit distinct from those at MLW and LWS. Overall, the shore-height axis accounted for 47% and the along-shore axis 28% of total assemblage variation.

4. Faunal assemblages were randomly structured at each nodal intersection point of the down-shore and along-shore axes, but were significantly non-randomly assembled down the shore at each site and along the Channel at each shore-height horizon except at the LWN level.

5. Components of total assemblage variance were largest at the smallest scale investigated (1 m).

6. Higher seagrass horizons are not just progressively more impoverished versions of lower ones and although macrofaunal assemblage composition is heavily influenced by shore height much of the ecological structure of faunal assemblages seems little affected by tidal horizon. These findings are discussed in relation to conservation of the vulnerable seagrass *Nanozostera capensis* at Knysna, a system affected by subsistence exploitation of its intertidal benthic invertebrates.
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INTRODUCTION

Both seagrass meadows and coral reefs are shallow-water centres of great biodiversity, are highly productive, and are currently disappearing from the planet at a similarly fast rate (some 7% or >100 km² year⁻¹). However, it is coral reefs that occupy most of the media headlines, receive the themed injection of major research funding and command the wider scientific attention (Duarte *et al.*, 2008; Waycott *et al.*, 2009; Unsworth and Cullen, 2010), leaving much seagrass ecology poorly understood (Holmer and Marba, 2010). Some of this may reflect the overt economic importance of tourist revenues attracted by coral reefs (Spalding *et al.*, 2001; Conservation International, 2008), although seagrasses also have a huge – albeit largely hidden – economic value, at an estimated US$ 1.9 trillion year⁻¹ (Waycott *et al.*, 2009). Some of the disparity may also be a reflection of the visually obvious richness and diversity of reefs, whereas many seagrass meadows appear uniform, monotonous and apparently lacking individual features of interest, turtles and dugong aside.

This, however, is an illusion: in reality seagrass beds are far from uniform. Studies conducted in small, semi-enclosed,

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eelgrass-dominated bays have shown great spatial variation in faunal assemblages even within systems structured by essentially a single seagrass species (Blanchet *et al.*, 2004; Barnes, 2010a). The Knysna estuarine bay on the Indian Ocean coast of the Western Cape is one such example: it is also South Africa's most important seagrass site. The 355–420 ha of Cape dwarf-eelgrass *Nanozostera capensis* estimated to be present there (Maree, 2000; Bandeira and Gell, 2003; CES, 2009) comprises over half the total national area of seagrass. Over just the landwards margins of the *N. capensis* beds in the marine Outer Basin of the bay, five significantly different clusters of macrofaunal species, corresponding to various degrees of exposure to water movement, have been identified (Barnes, 2010a). These ranged from assemblages dominated by suspension feeders near the mouth to those dominated by deposit-feeding microgastropods under conditions of maximum shelter, via communities of small polychaetes where semi-sheltered. At two sites <500 m apart, only 13 out of a total of 57 species were held in common. A comparable situation occurs in the *N. noltii* beds of the Bassin d'Arcachon in Atlantic France (Blanchet *et al.*, 2004).

The Knysna estuarine bay is also a microcosm of the current problems facing seagrass. Over the last century, the area of the bay — and hence of seagrass — has been reduced by causeway construction isolating its shallow fringes, by infilling and excavation for rail and road crossings, harbours, housing, commerce, industry and an aircraft landing strip, and more recently by marina developments and an enhanced peripheral road system (Russell *et al.*, 2009). Water quality has also been reduced by influxes of sediment (Cabaço *et al.*, 2008; Cyrus *et al.*, 2008) from activities in its catchment, including the laying out of golf courses. Since March 2009, the estuarine bay has formed part of the Garden Route National Park and hence is a Protected Area under the South African Natural Environment Management: Protected Areas Act 57 of 2003, although it has not been designated a MPA. Protection is therefore far from total; indeed <50 of the >1600 ha of the Knysna aquatic system nominally have complete formal protection from disturbance (Knysna Municipality, 2009), and in many areas including the formally protected ones the intertidal seagrass beds are heavily impacted by digging and pumping for bait worms and mud-prawns, including subsistence collecting, a practice that has increased over recent decades (Hodgson *et al.*, 2000; Napier *et al.*, 2009). Such activities have been implicated in the loss of almost 40% of the seagrass at its other major Western Cape site, Langebaan (Wynberg and Branch, 1994, 1997; Pillay *et al.*, 2010a), once the fourth-most important South African area of seagrass.

The classic and effectively unchallenged paradigm for intertidal seagrass faunas – and indeed for much shore biodiversity – is well illustrated by Day's diagram of the intertidal *Nanozostera* fauna of Knysna's marine Outer Basin (Day, 1967, Figure 5). It portrays species penetrating from the sublittoral up the shore to differing degrees, but species richness continually decreasing with increasing shore height as individual species reach their desiccation or other tolerance limit and drop out of the fauna. This exactly parallels equally classic paradigms for other intertidal systems, such as rocky shores (Hawkins and Hartnoll, 1980) and sandy beaches (see Raffaelli and Hawkins, 1996 for a review), as well as the other major axis dominating estuarine systems: the reduction in numbers of marine species on progression from the sea into increasingly brackish waters (Barnes, 1989; Attrill, 2002; Yamada *et al.*, 2007). Such a paradigm has reassuring conservation implications for shores exploited by gleaning: it would appear that damage to intertidal populations can always be made good by immigration from the unaffected sublittoral pools. But even if the sublittoral pools are indeed unaffected, how valid is the model and is damage to the exploited populations the real ecological and conservation problem? In the light of the globally threatened state of seagrass systems (Orth *et al.*, 2006; Waycott *et al.*, 2009) and their fragility in the face of human disturbance (Airoldi *et al.*, 2008), and specifically of the increased importance of Knysna as the major location of South African seagrass, we present a univariate and multivariate investigation of the ecological and conservation significance of shore height, including in relation to the shelter gradients documented previously (Barnes, 2010a). We specifically assessed vertical trends in faunal abundance, species richness and diversity, assemblage composition and structure, and the relative contribution of uncommon species to the fauna.

METHODS

Given the disparate nature of the seagrass fauna in different areas of the Knysna Outer Basin (Barnes, 2010a) and therefore the need to eliminate as much regional variation as possible, this study was confined to one local area and to the shores of one specific short creek system: the Steenbok Channel separating the north-eastern shore of Leisure Isle from the heavily saltmarshed eastern mainland shore before joining the larger Ashmead Channel that isolates Thesen's Island (Figure 1). Conditions along this creek range from semi-sheltered at its mouth to highly sheltered at its head, as it narrows, shallows and becomes more enclosed by saltmarsh. From February to April 2011, samples were taken along the southern (Leisure Isle) shore of the Steenbok Channel in a manner permitting them to be spatially nested in two different sets, one along the shore (i.e. within given tidal height horizons), the other down the shore (i.e. within different transects), permitting the significance of the tidal height axis to be assessed in relation to that along the creek. The Outer Basin seagrass beds are known to extend from just above MSL (i.e. from some 1.2 m above datum) down to and below that of ELWS (0.1 m) and over a horizontal intertidal distance of up to 500 m. Three tidal height horizons (= 'locations') distributed over this vertical range, at >0.8 m ('upper' ≈ LWN), 0.6–0.5 m ('mid' ≈ MLW), and <0.3 m ('lower' ≈ LWS), were each investigated along three replicate transects (= 'sites') that were run out perpendicular to the shoreline across the intertidal seagrass bed at intervals of some 500 m. The landwards limits of these transects were located between 34°03′43″S, 23°03′06″E and 34°03′56″S, 23°03′47″E at (i) the mouth of the Channel, (ii) at its mid point, and (iii) at its head (Figure 1). Each of the nine intersection 'nodes' of the location versus site axes was represented by three 'stations' 75 m apart in a line parallel to the shore, and each station comprised ten core 'samples' separated by intervals of 1 m also in a line parallel to the shore. Although the distance between each set of three nodes as measured along the Channel was fixed at 500 m, the distance between each set of three as measured down the
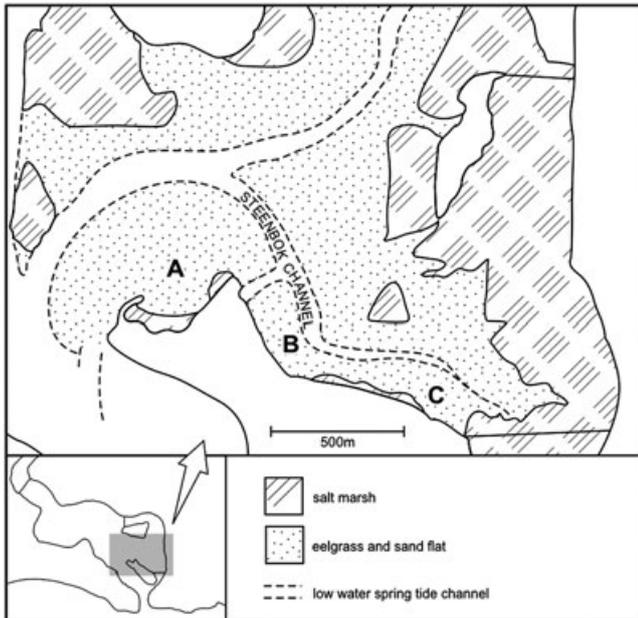
Figure 1. Sketch map of the Knysna estuarine bay showing the location of the site transects along the Steenbok Channel; A = Channel mouth; B = mid-point; C = Channel head.

shore of necessity varied with beach slope: it approximated 240 m at the mouth but <100 m at the Channel's mid-point and head.

Thus 270 core samples were taken, each being of 27 cm^2 area and 50 mm depth, earlier studies in the Knysna Outer Basin (Barnes, 2010a, b) having indicated that 10 cores of that area would yield an acceptable standard error <10% of the arithmetic mean in estimation of animal numbers. A 50 mm depth was selected because most benthic macrofauna in seagrass beds occur in the top few millimetres of sediment (e.g. 98% in the top 5 mm in the study by Klumpp and Kwak, 2005). All samples were taken in areas of 100% seagrass cover, comprised exclusively by *Nanozostera capensis* at higher tidal levels but with co-dominant *Halophila ovalis* in some places at LWS, and all were taken in areas free of blanket green-algal cover to avoid its effects on fauna (Soulsby et al., 1982; Raffaelli et al., 1998). Each core sample was collected at low tide, soon after tidal ebb from the area of shore concerned, and was gently sieved through 710 μm mesh. All retained material (i) was placed in a large polythene bag of sea water and all seagrass was shaken vigorously to dislodge all but sessile animals and then discarded (earlier testing having shown that no motile species remained within the seagrass after such treatment); (ii) was then re-sieved and transported to a local field laboratory, where (iii) it was placed in a large white tray from which the living fauna was extracted by eye, extraction continuing until no further animal could be seen after a 3 min search, which preliminary trial runs had indicated was sufficient to permit the removal of all live individuals. Other fauna present that were too large or too deeply burrowing to be taken by the core included the epifaunal sea-anemone *Pseudactinia flagellifera* and sea-hare *Bursatella leachii*, and the infaunal bait worms *Marphysa* spp. and *Polybrachiorhynchus dayi*.

With the exception of two nereid polychaete species, all collected fauna were identified to species and counted, excluding any sessile or semi-sessile animals that had become detached from the seagrass leaves during sorting (e.g. the pulmonate limpet *Siphonaria compressa* and the anemone *Halianthella annularis*). The nereid fauna of the Knysna Outer Basin seagrass beds is overwhelmingly dominated by *Ceratonereis erythraeensis* (Day et al., 1952; Day, 1967) but several other species are also present in small numbers. As the juveniles of *C. erythraeensis* and *Perinereis namibia* (Barnes, 2010a as *Perinereis nuntia vallata*) do not easily evert their pharynges and thereby display the features needed for their accurate separation, as previously (Barnes, 2010a) the two were lumped together as a single taxonomic unit and are reported below as *Ceratonereis erythraeensis*. Other nereids, however, could if necessary be distinguished on non-paragnath criteria and were identified to species. All animal generic and specific names are as listed in the World Register of Marine Species (WoRMS <www.marinespecies.org>), except for the unlisted species *Hydrobia knysnaensis* (Krauss) (Barnes, 2004), *Alaba pinnae* (Krauss) (Kilburn and Ripley, 1982), *Perinereis namibia* Wilson and Glasby (Wilson and Glasby, 1993), and the microgastropod originally described (and referred to earlier (Barnes, 2010a, b)) as *Rissoa capensis* Sowerby. On the basis of its anatomical and molecular taxonomy, this gastropod is not a rissoid but instead is related to *Assiminea globulus* (W.F. Ponder, pers. comm.) and is referred to below as *(Assiminea) capensis* pending the publication of a taxonomic revision of the group (n.b. *nec Assiminea capensis* Bartsch which is a synonym of *Assiminea ovata*: see Kilburn and Ripley, 1982).

Faunal assemblages were compared multivariately via: (i) ordination by non-metric multidimensional scaling (nMDS), hierarchical clustering analysis using S17 Bray–Curtis similarity, similarity percentage analysis (SIMPER), permutational analysis of variance (PERMANOVA), including partitioning of variance components, and permutational analysis of multivariate dispersions (PERMDISP), including as a test for variability in between-group species composition (i.e. in β diversity) (Anderson et al., 2006), carried out using PRIMER 6 (PrimerE Ltd: Plymouth Routines in Multivariate Ecological Research, Version 6); and (ii) canonical correspondence analysis (CCA), using CANOCO for Windows 4.5 (Microcomputer Power, Ithaca NY). PERMANOVA and nMDS were carried out on Bray–Curtis similarity matrices with fourth-root transformed versions of the data, PERMANOVA using 9999 permutations. Observed patterns of species co-occurrence were compared with statistical randomizations of the original species occurrence data using ECOSIM simulations (Gotelli and Entsminger, 2010). As recommended by Fayle and Manica (2010), 30 000 random matrices were simulated for each analysis to avoid Type 1 errors. ECOSIM's randomization algorithm maintains fixed sums for row and column totals so each matrix generated had the same number of species and core samples as the original. Differences between simulated and observed co-occurrence patterns were tested using the Stone and Roberts (1990) checkerboard score (*C*-) index which indicates: random assemblage structuring if C_{obs} is not significantly different from C_{sim}; non-random structure by virtue of more than expected negative co-occurrences if C_{obs} is significantly larger than C_{sim}; and non-randomness by virtue of excess positive co-occurrences if C_{obs} is significantly smaller than C_{sim}.

Bivariate or univariate relationships between shore height horizon and/or distance up the channel and faunal abundance, species diversity, species richness and proportion

of rare species per station used two- and one-way ANOVA, with, where appropriate, $\log(n+1)$ transformation to achieve homoscedasticity of variances. Departures of dispersion patterns from random were tested using Morisita's Index of Dispersion χ^2 statistic (Morisita, 1959). Species diversity was assessed as Simpson's Index of Diversity, $1 - \lambda$; constancy indices are percentage frequencies of occurrence in core samples; and categories of faunal rarity are *sensu* Colwell and Coddington (1994). Potential area effects on diversity and other parameters were avoided because the same total area was sampled at each locality, site and station.

RESULTS

The 270 core samples yielded 4438 individuals of 90 species (including *Perinereis namibia*) with an overall species diversity of 0.91, and revealed a Steenbok Channel seagrass fauna dominated by a suite of species usually considered to be estuarine or brackish-water in nature (Day, 1981; Branch *et al.*, 2010), notwithstanding the fully marine local salinity regime (Largier *et al.*, 2000). Of these, only the gastropod *Hydrobia knysnaensis* and the polychaetes *Ceratonereis erythraeensis* and *Caulleriella capensis* comprised >10% of total individuals and only the two polychaetes occurred in >40% of core samples (see Appendix A). Most species were rare, >75% of them each comprising <1% of the assemblage individuals, 16% being represented by only a single individual, and >40% occurring in <2% of the samples (Table 1).

Variation across the nine nodes in overall levels of the assemblage features of faunal abundance, species richness, species diversity, and proportion of rare species are shown in Figures 2 and 3 in relation to shore height horizon within the seagrass bed and to distance along the axis of the channel. On the basis of the values at each of the 27 component stations sampled, there were no significant differences in any of the four assemblage features along the channel (two-way ANOVA F <3.67; P ≥0.05), although both faunal abundance and species richness did verge on significance ($P = 0.05–0.06$), nor in three of them (faunal abundance, species diversity, and proportion of rare species) down the shore (two-way ANOVA F <1.94; P >0.17). Only in respect of species richness down the shore was there a clear significant difference (two-way ANOVA F 16.4; P <0.0001), consequent on a smaller number of species per station at the LWN horizon than at either of the two lower shore stations (Tukey's HSD post-hoc test P <0.003) which did not themselves differ in species

richness (Tukey's HSD post-hoc test P >0.2). Within each of the three sites individually, however, the difference in richness down the shore was not significant at the mid-point of the creek (one-way ANOVA F 3.0; $P = 0.12$), only at the two ends (one-way ANOVA F >7.5; P <0.02). Total faunal abundance per station was very patchily distributed through the seagrass bed (χ^2 >117; df = 8; P <0.00001).

Most members of the total Steenbok Channel seagrass fauna occurred at the LWS level (66 species = 74% of the total) (Figure 2(C)). But many of these (47 species) also occurred at MLW and the majority (36) extended right across the bed to its upper horizon at LWN. The absence of 30 of the lower-shore species from the upper part of the seagrass bed was in part balanced by the presence of 23 species that were found only at the upper- and mid-horizons. The same phenomenon was displayed along the Channel from mouth to head: of the 65 species present at the mouth, 56 also extended to the mid-region but only 36 reached the head. Absent species were there partly replaced, however, by 24 species that occurred only in the mid-region and head region. As the fauna includes many rare species (see above and Table 1), numbers quoted above are of course minimum estimates: Barnes and Ellwood (2011) presented data suggesting that the real numbers of species present in the Knysna seagrass beds were 40% higher than such estimates.

The nature of the faunal assemblages present varied significantly across the nine nodes sampled (PERMANOVA pseudo-$F = 18.7$; P <0.0001), as did their β-diversities (PERMDISP $F_{(8,261)}$ 4.8; $P = 0.0001$). Indeed, pairwise PERMANOVA indicated that each node was significantly different from all others (P <0.003), on average a given node sharing only 40% of its species with another. Nevertheless, the assemblages of the three transect sites spaced along the Channel axis did not differ (PERMANOVA pseudo-$F = 1.2$; $P = 0.3$), and while those of the three tidal height horizons did differ, the difference was only marginally significant (PERMANOVA pseudo-$F = 2.3$; $P = 0.04$). In marked contrast, however, faunal assemblages of nodes and stations nested within a given height horizon did vary along the Channel, and those of nodes and stations nested within a given transect did vary down the shore (PERMANOVA pseudo-F >2.9; P < 0.0001) (Table 2). SIMPER analysis showed that variation in the abundance of *C. erythraeensis*, *C. capensis*, *Nassarius kraussianus*, *H. knysnaensis* and *Prionospio sexoculata* was most responsible for differences between nodes along the Channel axis, and that of the first four named above together with *Arabella iricolor*, *Danielita edwardsii* and *Paratylodiplax algoensis* (Table 3) was most responsible for differences between nodes down the shore. Canonical correspondence analysis showed that altogether the down-shore axis accounted for 46.7% of assemblage variation and distance along the Channel axis accounted for 28.4%, leaving only 25% unexplained. This residual may represent small-scale patchiness although there are several other possibilities (Palmer, 1993).

The fact that four of the same species are among the top five in respect of changes along each axis suggests interaction between the two. This was indeed partly the case. In respect of the two-way ANOVA data presented above there were no significant interactions between the two axes in species richness, species diversity or proportion of rare species per station (F <1.72; P >0.19), but a significant interaction did

Table 1. Percentage of species contributing by different degrees to the total faunal numbers and to faunal occurrences by site and by locality

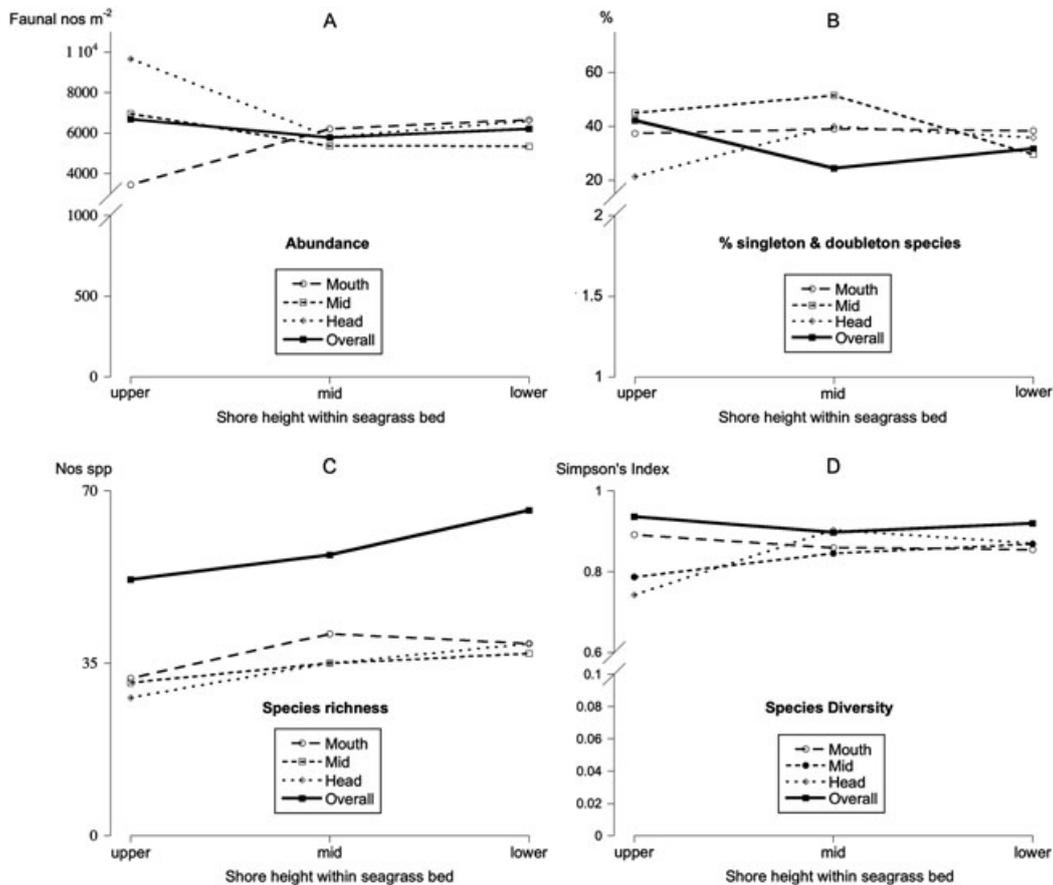|	Percentage of total numbers			Constancy indices		
	≥10%	≥5%	≤1%	≥40%	≥10%	≤2%
Sites						
mouth	1.5	4.5	69.7	3.0	33.3	36.4
mid-point	6.6	8.2	72.1	6.6	34.4	36.1
head	2.3	9.6	65.3	7.7	38.5	26.9
Seagrass localities						
upper	5.8	9.6	75.0	7.7	30.8	42.3
middle	3.5	8.8	68.4	8.8	38.6	26.3
lower	4.5	7.6	68.2	9.1	40.9	34.8
Overall	3.4	4.5	76.4	2.2	24.7	42.7

Figure 2. Relationship between shore-height horizon within the dwarf-eelgrass bed and (A) faunal abundance, (B) percentage of singleton and doubleton species within the fauna, (C) species richness, and (D) species diversity at the three sites along the Steenbok Channel. The difference in upper horizon (LWN) faunal abundance between the three sites in (A) is solely due to the gastropod *Hydrobia knysnaensis*, which at that height increased markedly in density along the Channel (see Figure 4).

occur with faunal abundance (F 4.51; $P = 0.01$). In terms of individual faunal components, numbers of the most widely distributed and most numerous of the species, *C. erythraeensis* (which occurred in >70% of samples and comprised 20% of the total faunal individuals) and *C. capensis* (which was the second-most widely dispersed species) were dispersed very unevenly ($\chi^2 > 1000$; df = 269; $P < 0.00001$; negative binomial constant $k \approx 1$). The patchy abundance per station of *C. capensis*, however, showed no effect of either shore height or position along the channel nor was there any significant interaction between the two (two-way ANOVA $F < 2.30$; $P \geq 0.1$), whereas that of *C. erythraeensis* showed no relationship with shore height (two-way ANOVA F 1.84; $P > 0.1$) but did so with position along the channel (F 5.14; $P < 0.02$) and there was a significant interaction (F 7.73; $P = 0.001$). The effects of both environmental axes on distribution, however, was clearly exemplified by *H. knysnaensis* (occurring at the LWN horizon and at the channel head, Figure 4) and by the two camptandriid crabs present – *P. algoensis* occurred through the middle to lower seagrass horizons from the mouth to the mid- section of the channel while *D. edwardsii* effectively replaced it in the upper horizon of the seagrass bed and at the channel head. Bray–Curtis analysis and non-metric multidimensional scaling of the faunal assemblage data (Figure 5) showed that the primary division was between the LWN nodes and the rest, all nine upper-shore stations clustering together separately from the other 18. The MLW and LWS stations then separated into two

clusters not on the basis of shore height but on their position along the channel; those at the mouth of the channel clustering separately from those of the mid-region plus head region (Figure 5).

Components of total variance were greatest at the smallest spatial scale sampled (1 m) both when nested in down-shore sites and in along-shore locations, but they did not uniformly decrease as spatial scale increased. In both nestings, the variance component at the scale of node was greater than at that of station (Table 2). Faunal assemblages were randomly organized at each of the nine nodes (Table 4), but within groups of nodes nested both down the shore and along it assemblage organization was largely significantly deterministic. All three *C*-score analyses of the down-shore gradient at the Channel head were significantly non-random, as were two of the three analyses at each of the other two sites (Table 5); and all three *C*-score analyses of both the mid- and lower-seagrass horizons along the Channel axis were significantly non-random in contrast to all those along the upper-seagrass horizon (Table 6). All non-randomly structured assemblages showed greater than expected negative co-occurrences.

The occurrence or abundance of a few members of the Steenbok Channel fauna also merits specific comment. The presence in the samples of an α-morph male of the alien sphaeromatid isopod *Paracerceis sculpta* (Shuster, 1987) is noteworthy in that it is the first time that this animal has been recorded in South Africa from outside Port Elizabeth harbour
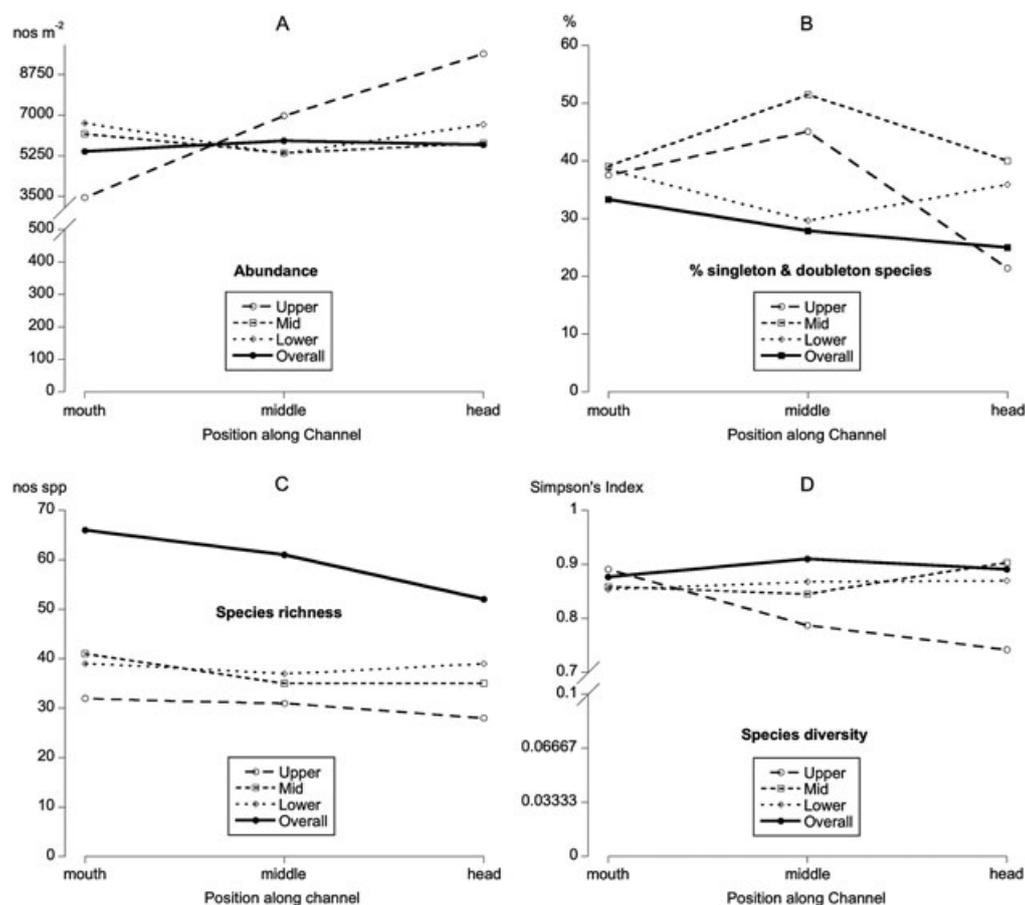
Figure 3. Relationship between distance along the length axis of the Steenbok Channel and (A) faunal abundance, (B) percentage of singleton and doubleton species within the fauna, (C) species richness, and (D) species diversity at three shore-height horizons (= locations) within the dwarf-eelgrass bed.

where it was first observed in 2006 (Griffiths *et al*., 2009). Also of interest are the occurrence of: (i) the small nudibranch *Favorinus ghanensis*, of which only a single South African specimen was previously known (Gosliner, 1987; GBIF, 2011) (also from Knysna, but from a rocky shore, whereas it was locally common in the Steenbok Channel seagrass occurring at 50 m^{-2} at LWS in the mid-channel region), (ii) *Polydora* cf *nuchalis*, one of five species of free-living 'polydorid' polychaete present (at mean densities of up to 400 m^{-2} at LWN) but otherwise previously known only from intertidal mudflats in the eastern Pacific and Brazil, and (iii) a high

diversity of pyramidelloidean microgastropods (four sympatric genera). A member of the Knysna seagrass fauna of national conservation concern is the small starfish *Parvulastra exigua*, which, although common on rocky shores, otherwise occurs in seagrass only in the Langebaan Lagoon (Pillay *et al*., 2010a, b) (if indeed the rocky-shore and seagrass forms are the same species – see Hart *et al*., 2006). Pillay *et al*. (2010a) expressed fears that following reduction of the *N. capensis* beds there (see above), *P. exigua* had 'declined almost to extinction'. Fortunately, in contrast the Knysna population appears to remain very healthy,

Table 2. Partitioning of variance components by nested PERMANOVA in the Steenbok Channel data at the levels of (a) site = transect (Si), node (No), station (St) and core sample (Co), and (b) locality = height horizon (Lo), node (No), station (St) and core sample (Co) using fourth-root transformed data. (MS mean square; UP unique permutable units, EV estimate of variance, V variance component as percentage of total.)

Scale	df	MS	pseudo-*F*	*P*	UP	√EV	V
Si	2	42646	1.22	0.33	280	9.2	9.1%
No(Si)	6	34980	6.74	<0.0001	9895	31.5	31.2%
St(No(Si))	18	5190	2.98	<0.0001	9718	18.6	18.4%
Co(St(No(Si)))	243	1739				41.7	41.3%
Total	269						
Lo	2	64331	2.32	0.04	280	20.2	18.7%
No(Lo)	6	27751	5.35	<0.0001	9868	27.4	25.4%
St(No(Lo))	18	5190	2.98	<0.0001	9772	18.6	17.2%
Co(St(No(Lo)))	243	1739				41.7	38.7%
Total	269						

Table 3. Species collectively responsible for 50% of the dissimilarity between the macrofaunal assemblages of the various shore height horizons within the seagrass (SIMPER)

Species	Percentage contribution	Cumulative percentage
1. Upper (LWN) and middle (MLW) horizons (average dissimilarity 78.6)		
Hydrobia knysnaensis	8.9	8.9
Ceratonereis erythraeensis	6.6	15.5
Caulleriella capensis	6.3	21.8
Danielita edwardsii	5.5	27.3
Nassarius kraussianus	5.4	32.6
Arabella iricolor	4.1	36.7
Prionospio sexoculata	3.7	40.4
(Assiminea) capensis	3.5	43.9
Exosphaeroma hylecoetes	3.3	47.2
Orbinia angrapequensis	3.2	50.4
2. Upper (LWN) and lower (LWS) horizons (average dissimilarity 82.9)		
Hydrobia knysnaensis	7.8	7.8
Nassarius kraussianus	6.6	14.4
Ceratonereis erythraeensis	5.7	20.2
Caulleriella capensis	5.6	25.7
Danielita edwardsii	5.0	30.7
Paratylodiplax algoensis	4.3	35.0
Arabella iricolor	4.2	39.2
Exosphaeroma hylocoetes	3.1	42.3
Grandidierella lutosa	2.9	45.2
Orbinia angrapequensis	2.8	48.0
Prionospio sexoculata	2.7	50.8
3. Middle (MLW) and lower (LWS) horizons (average dissimilarity 69.5)		
Ceratonereis erythraeensis	7.4	7.4
Caulleriella capensis	6.2	13.6
Nassarius kraussianus	5.7	19.3
Arabella iricolor	5.1	24.4
Paratylodiplax algoensis	4.3	28.7
Grandidierella lutosa	3.9	32.6
Prionospio sexoculata	3.8	36.4
Orbinia angrapequensis	3.7	40.1
Aricidea capensis	3.6	43.7
Timarete tentaculata	2.9	46.6
Alaba pinnae	2.8	49.4
Paridotea ungulata	2.6	52.0

Figure 5. Non-metric multidimensional scaling plot of the superimposed group-average S17 Bray–Curtis similarity clusters of fourth-root transformed abundances of the faunal assemblages at the nine nodes, each with three replicate stations, within the Steenbok Channel dwarf-eelgrass bed. The envelopes of 40% and 50% are Bray–Curtis similarities. Location (height horizon within the seagrass) codes – U upper (LWN), M mid (MLW), L lower (LWS); Channel site codes – H head, Mi mid-point, Mo mouth.

Channel rissooidean microgastropods. In 2010, total faunal abundance at the upper mid-channel node was nearly 17 000 m^{-2} of which rissooideans comprised 86% (Barnes, 2010a). Almost exactly one year later, those microgastropod species had declined dramatically to a total of only 3,600 m^{-2}, *Hydrobia knysnaensis* numbers having fallen by 64% and those of *(Assiminea) capensis* by 87%. Overall faunal abundance reflected this decrease, being only <7000 m^{-2} in 2011. Such fluctuations in microgastropod populations are a well known phenomenon (Barnes, 1991, 2010a) although their causes are still not understood.

occurring at the middle and lower shore stations at the head of the channel at a mean density of 220 m^{-2} (more than ever recorded at Langebaan), and being present in one third of the core samples. The same cannot be said for the Steenbok
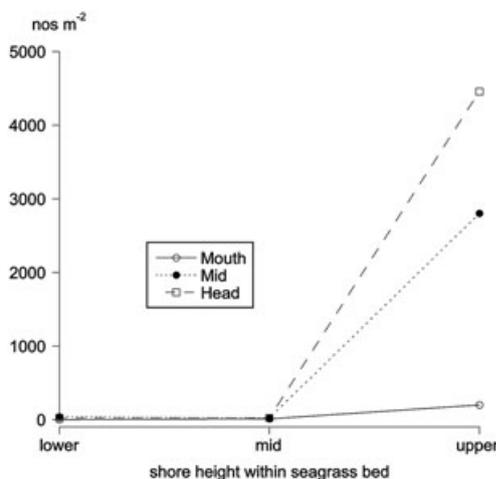

Figure 4. Effects of the down-shore and along-shore axes on the abundance of the microgastropod *Hydrobia knysnaensis*.
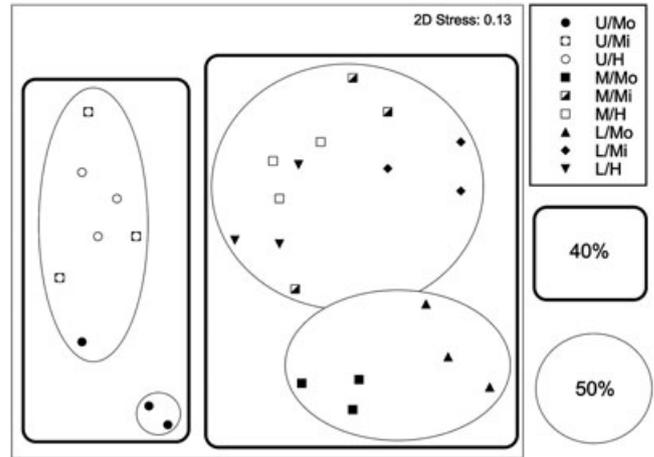
DISCUSSION

Studies of *N. capensis* beds at Knysna (Barnes, 2010a; and the present paper) and those of equivalent intertidal *Nanozostera* systems in Moreton Bay, Australia (Barnes and Barnes,

Table 4. Stochasticity of macrofaunal assemblage structure within each of the nine sampled nodes: C-scores derived from the observed pattern of species co-occurrence (C_{obs}) and the mean expected C-score from randomized versions of the data (C_{sim}). Where $C_{obs} > C_{sim}$ is not significant, as in all the cases presented here, assemblage structure is random. Each node was represented by 30 core samples

	Position along channel		
	Mouth	Mid-point	Head
upper horizon (LWN)	$C_{obs} = 11.48$ $C_{sim} = 11.26$ $P = 0.07$	$C_{obs} = 10.61$ $C_{sim} = 10.62$ $P = 0.48$	$C_{obs} = 12.54$ $C_{sim} = 12.49$ $P = 0.33$
middle horizon (MLW)	$C_{obs} = 22.08$ $C_{sim} = 21.92$ $P = 0.20$	$C_{obs} = 11.80$ $C_{sim} = 11.76$ $P = 0.39$	$C_{obs} = 19.22$ $C_{sim} = 19.42$ $P = 0.91$
lower horizon (LWS)	$C_{obs} = 23.78$ $C_{sim} = 23.64$ $P = 0.20$	$C_{obs} = 19.03$ $C_{sim} = 19.09$ $P = 0.63$	$C_{obs} = 21.29$ $C_{sim} = 21.71$ $P = 0.52$

Table 5. Deterministic macrofaunal assemblage structure along the down-shore gradient from upper to lower seagrass horizons: C-scores derived from the observed pattern of species co-occurrence (C_{obs}) and the mean expected C-score from randomized versions of the data (C_{sim}). Each of the three replicate C-scores was represented by 10 core samples (one third of the total) drawn from each of the three height horizons, and therefore by 30 cores in total. Where $C_{obs} > C_{sim}$ is significant, as in all but two of the replicates (one at each of the mouth and mid- channel), assemblage structure is non-random

| | Position along channel | | |
	Mouth	Mid-point	Head
replicate 1	C_{obs} =27.34 C_{sim} =26.95 $P = 0.03$	C_{obs} =21.98 C_{sim} =21.12 $P < 0.001$	C_{obs} =20.66 C_{sim} = 20.29 $P = 0.006$
replicate 2	C_{obs} =27.04 C_{sim} =26.42 $P = 0.004$	C_{obs} =20.45 C_{sim} =20.15 $P = 0.06$	C_{obs} =27.25 C_{sim} =26.55 $P < 0.001$
replicate 3	C_{obs} =20.80 C_{sim} =20.61 $P = 0.13$	C_{obs} =20.09 C_{sim} =19.23 $P < 0.001$	C_{obs} =25.04 C_{sim} =24.63 $P = 0.02$

2011), and in the North Sea, UK (Barnes and Ellwood, 2011), are beginning to reveal a consistent picture. Within a given bed general ecological features such as benthic faunal density and species richness and species diversity are relatively uniform across space (at least over distances <5 km) whereas the actual assemblages yielding these uniform values are highly variable in both species composition and relative abundances of shared species. Adjacent areas only a few tens of metres apart have significantly different faunas; variance components are maximal at very small spatial scales (≈1 m); and at those scales assemblage structure does not depart from random. At somewhat larger spatial scales, however, assemblage organization changes from random to deterministic. In the 1 km long, fully marine Steenbok Channel at Knysna, this change in structure occurs in association with clear environmental gradients, both that along the creek axis and that down the shore across the seagrass bed, although no such obvious environmental gradients were evident at sites in Moreton Bay (Barnes and Barnes, 2011) or the North Sea (Barnes and Ellwood, 2011).

Table 6. Stochastic and deterministic macrofaunal assemblage structure along the axis of the Steenbok Channel from mouth to head: C-scores derived from the observed pattern of species co-occurrence (C_{obs}) and the mean expected C-score from randomized versions of the data (C_{sim}). Each of the three replicate C-scores was represented by 10 core samples (one third of the total) drawn from each of the three sites, and therefore by 30 cores in total. Where $C_{obs} > C_{sim}$ is significant, as at the mid- and lower-seagrass horizons, assemblage structure is non-random; in the case of the upper-seagrass horizon, C_{obs} was < C_{sim} in all three replicates but not significantly so ($P > 0.2$)

Horizon	Replicate 1	Replicate 2	Replicate 3
upper	C_{obs} =14.94 C_{sim} =15.07 $P = 0.76$	C_{obs} =13.51 C_{sim} =13.63 $P = 0.72$	C_{obs} =9.65 C_{sim} =9.72 $P = 0.60$
middle	C_{obs} =22.16 C_{sim} =21.55 $P = 0.001$	C_{obs} =27.58 C_{sim} =26.93 $P < 0.001$	C_{obs} =21.94 C_{sim} =21.40 $P < 0.001$
lower	C_{obs} =26.17 C_{sim} =25.83 $P = 0.04$	C_{obs} =30.66 C_{sim} =30.26 $P = 0.02$	C_{obs} =35.35 C_{sim} =34.51 $P < 0.001$

What specific (small-scale) spatial scales are critical to such changes in assemblage variance and structure are as yet unknown. It may be significant, however, that the only gradient along which there was no departure from random organization was that along the Channel axis at the upper (LWN) seagrass level. This zone also supported faunal assemblages that differed significantly from those occurring lower down the shore both in terms of species richness and assemblage composition. A simplistic explanation based on physical structuring at this tidal height, close to the upper limit of the *N. capensis*, versus biological structuring lower down the shore (Tomanek and Helmuth, 2002), is rendered unlikely, however, by the equivalent zone along the axis of the Channel, the more physically influenced, shallow and most tidally-exposed head region, being in marked contrast the most deterministically structured of the three regions of the creek sampled.

Thus, as would be expected in an intertidal aquatic fauna (Raffaelli and Hawkins, 1996), the shore height axis did influence the Steenbok Channel seagrass macrobenthos. A number of numerically important components, for example the polychaetes *Orbinia* and *Arabella*, the gastropod *Hydrobia*, the amphipod *Grandidierella* and the decapods *Paratylodiplax* and *Danielita*, were clearly so influenced. Nevertheless, although shore height was the major determinant of the faunal assemblages present, accounting for almost half of the total variation, its broad ecological effects were in several respects surprisingly minor. Numbers of individuals per station of the dominant *Ceratonereis erythraeensis* and *Caulleriella capensis* were unaffected; and of the 44 species represented by at least 10 individuals in total, 73% occurred throughout the entire bed from LWN to LWS. There was no significant variation with shore height in overall faunal abundance, species diversity or the contribution of rare species to the total fauna; and although the upper shore horizon around LWN did support a significantly smaller number of species per station than the mid and lower horizons across the Steenbok Channel bed as a whole, the difference in richness was not so marked as to be significant at each individual site. The absence of the clear reduction in abundance or diversity with increasing shore height that would be expected on the basis of earlier broader brush-stroke studies (Day, 1967) is likely to be in part at least a consequence of the effect of the seagrass cover in retaining a high water content within and over the surface of the sediment during low tide (Leduc and Probert, 2011), and therefore in mitigating the usual effect of decreasing tidal cover on sediment-dwelling marine animals (cf. distributions in unvegetated intertidal soft sediments; Edwards *et al.*, 1992).

Further, faunal assemblages present in the transects at the mouth, mid-point and head of the Channel did not differ significantly and the difference between those within each of the three shore height horizons within the seagrass bed was only marginally significant. Yet within any given shore-height horizon assemblages did differ markedly along the Channel and likewise within any given transect down the shore they did differ markedly with respect to shore height. This paradoxical situation is likely to be consequent on the patchy distributions of many of the species, local variation in abundance of the few widespread species, and the interactions between the effects of the shore-height and along-shore axes.

Although sampling did yield several small individuals of the exploited mud-prawn *Upogebia africana*, the fauna encountered was not that targeted by local invertebrate harvesters, which tends to occur at deeper levels in the sediment. Nevertheless, a clear implication of these results for conservation is that the upper, more accessible, regions of seagrass beds are not resources that can safely be disturbed on the basis that they will continually be made good from lower less-exploited horizons. Several upper-horizon species may not occur at lower levels at all and the pattern of distribution of most of the fauna is a system of patches determined by a complex set of interactions between the shore height, shelter and other environmental axes. *N. capensis* has IUCN Red List status of 'vulnerable' and 'declining', and destructive invertebrate harvesting is one of the major threats to its survival (Short *et al.*, 2007, 2011). Since 1990 the entire Steenbok Channel area has been included in a declared Marine (Bait) Reserve within which the collection of invertebrates is forbidden. Such no-take zones are seen as an important part of management for sustainable exploitation by subsistence fishers (Cockcroft *et al.*, 2002) but nevertheless, especially near its mouth, the Steenbok Channel intertidal zone showed very clear signs of illicit pumping for mud-prawns (e.g. discarded sods from tin-can pumps strewn over the surface) and, more seriously, of being trenched for worms (large – up to 7×2 m – rectangular seagrass-less depressions surrounded by raised banks of spoil). As in many parts of the world, it is simple to declare areas to be reserves but enforcement is a completely different matter. However, irrespective of the reality or magnitude of the effects of bait collection on populations of the exploited invertebrates (Olive, 1993; Hodgson *et al.*, 2000) and of others incidentally affected (Skilleter *et al.*, 2005, 2006), experience from equivalent dwarf-eelgrass beds elsewhere (not least at the Langebaan example cited above, and see Coetzee *et al.*, 1997 and Short *et al.*, 2007) suggests that bait-collection pressure of this magnitude and the associated trampling to which eelgrass is particularly susceptible (Fonseca, 1993; Short *et al.*, 2011) leads inevitably to loss of the habitat itself, particularly when the collection techniques are so environmentally unfriendly. In this context, it is particularly unfortunate that most bait collectors questioned at Knysna did not believe that their activities had any adverse effect on the environment (Hodgson *et al.*, 2000). For socio-economic reasons subsistence bait-collection is unlikely to diminish at Knysna, nor indeed at other South African seagrass sites (Bluepebble, 2010), and so it would appear that innovative conservation measures will have to be designed and implemented if the country's remaining seagrass resource is to be prevented from becoming degraded. Napier *et al.* (2009) suggest targeting the buyers and traders of bait worms rather than the collectors of them to discourage trenching, but any action likely to diminish the immediate income of subsistence fishers will be resisted by their communities despite any potential long-term advantages that might accrue (Bluepebble, 2010).

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APPENDIX A

The most numerous and widespread members of the Steenbok Channel seagrass fauna by position along the creek and by height horizon on the shore.

Species comprising ≥10% of total faunal numbers	Species with a Constancy Index ≥40%
Sites	
Channel mouth	
Ceratonereis erythraeensis (32.0%)	*Ceratonereis erythraeensis* (87.8%)
	Orbinia angrapequensis (42.2%)
Mid-point	
Hydrobia knysnaensis (16.2%)	*Ceratonereis erythraeensis* (55.6%)
Nassarius kraussianus (14.9%)	*Caulleriella capensis* (54.4%)
Ceratonereis erythraeensis (13.9%)	*Nassarius kraussianus* (54.4%)
Caulleriella capensis (11.4%)	*Arabella iricolor* (45.6%)
Channel head	
Hydrobia knysnaensis (20.4%)	*Ceratonereis erythraeensis* (71.1%)
Ceratonereis erythraeensis (17.1%)	*Caulleriella capensis* (62.2%)
Caulleriella capensis (14.9%)	*Prionospio sexoculata* (50.0%)
	Danielita edwardsii (40.0%)
Seagrass height horizons	
Upper horizon (LWN)	
Hydrobia knysnaensis (37.0%)	*Ceratonereis erythraeensis* (84.4%)
Ceratonereis erythraeensis (16.6%)	*Hydrobia knysnaensis* (67.8%)
Caulleriella capensis (11.5%)	*Danielita edwardsii* (61.1%)
	Caulleriella capensis (58.9%)
Middle horizon (MLW)	
Ceratonereis erythraeensis (25.4%)	*Ceratonereis erythraeensis* (70.0%)
Caulleriella capensis (12.6%)	*Caulleriella capensis* (53.3%)
	Nassarius kraussianus (47.8%)
	Arabella iricolor (46.7%)
	Prionospio sexoculata (40.0%)
Lower horizon (LWS)	
Ceratonereis erythraeensis (19.8%)	*Nassarius kraussianus* (64.4%)
Nassarius kraussianus (12.7%)	*Ceratonereis erythraeensis* (60.0%)
Caulleriella capensis (10.9%)	*Arabella iricolor* (53.3%)
	Paratylodiplax algoensis (46.7%)
	Grandidierella lutosa (44.4%)
	Caulleriella capensis (40.0%)
Overall	
Ceratonereis erythraeensis (20.4%)	*Ceratonereis erythraeensis* (71.5%)
Hydrobia knysnaensis (13.5%)	*Caulleriella capensis* (50.7%)
Caulleriella capensis (11.6%)	