

On the very edge: faunal and functional responses to the interface between benthic seagrass and unvegetated sand assemblages

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ABSTRACT: Changes in macrobenthic spatial structure were investigated across the precise 0.5 m wide boundary zone between intertidal seagrass and unvegetated sand in Moreton Bay, Queensland, Australia. Faunal abundance and species density in the marginal seagrass were only slightly reduced relative to local non-boundary areas. Although gradual diminution in seagrass faunal abundance occurred towards the interface and a few locally dominant species were absent from the boundary zone, most transition was far from gradual, instead being exactly coincident with the specific 0.1 m interface between the 2 habitats. Over this distance, faunal abundance and species density fell by 56 to 60 % (from 1412 to 625 m⁻² and from an estimated 42 species per sampling horizon to 17, respectively). Dominant seagrass species were abundant right up to the interface itself, but their densities had fallen by 82 % a further 0.1 m into the adjacent sand. Functional-group density and diversity mirrored these changes, decreasing over the same distance by 30 to 36 %. Spatial analysis showed that adjacent cores along lattice sampling horizons, although spaced further apart, were more similar to each other than were those oriented across horizons, even though these were contiguous. Characteristic high animal species richness in the seagrass relative to adjacent sand appears to be not so much related to characteristics of the seagrass habitat as a whole rather than to the presence or absence of individual plants. Asymmetrically, distributions of species characteristic of the sand stopped somewhat in advance of the interface, leaving a marginal sand zone dominated by generalists occurring at equal (low) species and population density across both habitats.

KEY WORDS: Benthos · Biodiversity · Ecotone · Edge effects · Sandflat · Seagrass

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INTRODUCTION

Edge effects in ecology are much studied but are as difficult to generalise today as they were 20 yr ago (see e.g. Donovan et al. 1997), not least because ecotonal changes may be dependent on the precise situation and species concerned (Walker et al. 2003) and be 'idiosyncratic' (Warman et al. 2013). This is the case in seagrass (Boström et al. 2006, Macreadie et al. 2010), where edge effects vary in magnitude and nature across both space and time (Vonk et al. 2010, Włodarska-Kowalczyk et al. 2014). In general, how-

ever, macrofaunal biodiversity and abundance change from the centre of meadows towards their margins (Bologna & Heck 2002, Tanner 2005, Moore & Hovel 2010, Wong & Dowd 2015) and such change continues across the interface into adjacent unvegetated regions (O'Gower & Wacasey 1967, Boström & Bonsdorff 1997, Berkenbusch et al. 2007, Siebert & Branch 2007, Barnes & Barnes 2012). The actual boundary zone between the 2 abutting systems, though, is not necessarily intermediate in its assemblage metrics (Bologna & Heck 2002, Wong & Dowd 2015), not least because of the potential operation of

'mass effects' (Kunin 1998) and the consequences of relative resource availability (Ries & Sisk 2004).

Nevertheless, 'virtually without exception' according to Hemminga & Duarte (2000, p. 200), areas of seagrass and of adjacent unvegetated sandflat support macrobenthic assemblages differing markedly in biodiversity and/or abundance, with the seagrass supporting the larger values. Several reasons have been suggested for this difference, most revolving around the notion that seagrass beds are the more favourable habitat for benthic macrofauna by virtue of their provision of greater refuge from predation, greater availability of food, enhanced larval entrainment, and more habitat structure (Reise 1978, Fonseca et al. 1982, Edgar 1999, Boström et al. 2006, Heck & Orth 2006, Berkenbusch et al. 2007, Siebert & Branch 2007). Exceptions to this paradigm are more common than seems generally appreciated, however, with some systems showing no such effect and others even displaying the converse (Wolff et al. 1993, Asmus & Asmus 2000, van Houte-Howes et al. 2004, Polte et al. 2005, Hewitt 2007). This has suggested the alternative hypothesis that, where such differentials do occur, they are due not to any supposed greater favourability of the vegetated condition but to local unfavourability of the bare sediment (Barnes & Barnes 2014), especially where impacted by sediment turnover produced by animals such as axiidean sand-prawns that can dominate unvegetated sandflats (Pillay & Branch 2011) and mobilise >10 kg sand $m^{-2} d^{-1}$ (Branch & Pringle 1987). Pillay et al. (2012) also showed that another consequence of axiidean-induced bioturbation is suppression of surface microphytobenthic production, which may further negatively impact the other bare-sediment fauna (although cf. Ktrak & Bird 2003). The soldier crab *Mictyris* can have the same effect (Webb & Eyre 2004). Seagrasses and, where they occur, axiideans and equivalent bioturbators act as opposing ecosystem engineers (Berkenbusch & Rowden 2007, Siebert & Branch 2007, Kneer et al. 2013); the 2 alternative habitat states they induce being dynamic and interchangeable, each capable of expanding into territory dominated by the other (e.g. Yamakita et al. 2005, Berkenbusch et al. 2007, Carr et al. 2010).

The intertidal zone of the ca. 1500 km², shallow, subtropical, lagoon-like Moreton Bay in Queensland, Australia, conforms to this classic model. There, seagrass dominated by the dwarf-eelgrass *Zosterella capricorni*, and adjacent bare sandflat structured by the axiidean *Trypaea australiensis* and by *Mictyris longicarpus*, have been shown to display a Bray-Curtis faunal similarity of only 2%, with the seagrass

supporting some 2.5× the number of individuals and twice the number of species present in the unvegetated sand (Barnes & Barnes 2012). Barnes & Hamylton (2013) investigated the transition from one of these macrofaunal assemblages to the other by sampling at 0.25, 0.5 and 0.75 m on either side of the interface, and contrary to expectation (e.g. Dangerfield et al. 2003), found the change from one to the other to be abrupt. At a distance of 0.25 m from its margin, the seagrass supported 115 species at an overall density of >2100 m^{-2} . In contrast, 0.25 m from the interface in the other direction, the bare sand supported only 45 species at an overall density of <700 m^{-2} . In each case, 7 species contributed 54% of the total individuals, but there was no overlap in the identity of these dominants. Indeed, of the 128 species present across the 2 horizons, only 25% occurred in both, and 40% of those only as a single individual in one of them. Effectively, the entire change-over was accomplished within the intervening distance of 0.5 m.

The nature of Barnes & Hamylton's (2013) sampling regime, however, did not permit resolution of the marked changes taking place within that critical 0.5 m. The purpose of the present work was to extend the earlier study by examining in detail the nature and spatial ecology of benthic assemblages within this zone — as previously, in terms both of the component species of the 2 contrasting macrofaunas and, in addition, of the arguably more ecologically relevant 'functional groups' they comprise (McGill et al. 2006, Violle et al. 2007), since such groups may respond to habitat change in a contrasting manner to taxonomically defined assemblages (Törnroos et al. 2013, Wong & Dowd 2015). The null hypotheses that change occurs gradually from one assemblage to the other across the 0.5 m boundary zone, that the 2 assemblages react symmetrically to the interface and that functional changes mirror taxonomic changes were investigated.

MATERIALS AND METHODS

Study area, sample collection and processing

Macrofaunal sampling was conducted over a period of 11 wk during the 2015 austral spring (October to early December) along the same stretch of the sheltered Rainbow Channel coast of the North Stradbroke barrier island in Moreton Bay, Queensland, Australia, that supported the earlier studies of faunal differences between adjacent seagrass and bare sand (Barnes & Barnes 2012), the nature of faunal transitions across

1.5 m boundary zones (Barnes & Hamylton 2013), and spatial variation of functional groups within the seagrass (Barnes & Hamylton 2015). New data were collected from 2 of the former localities—Deanbilla ($27^{\circ}30'27''$ S, $153^{\circ}24'30''$ E) and Polka ($27^{\circ}29'32''$ S, $153^{\circ}23'54''$ E), 2 km apart (Fig. 1)—with, as earlier, precise sampling sites being located where the margins of seagrass beds appeared neither to be advancing nor retreating to avoid possible complications resulting from temporally transitional states. Advancing seagrass was identified by lines of young plants extending out from the bed and retreating seagrass by the occurrence of extensive dead root-rhizome mats beneath the surface of the bare sand.

As advocated by Fortin (1994), in all cases data were collected from 2-dimensional lattices set across and along the bare sand/seagrass interface. Four replicate lattices were worked at 2 sites, 150 to 200 m apart at mean low water–low water spring (MLW–

LWS) level at each locality, having been shown earlier (Barnes & Hamylton 2013) that the same critical 0.5 m zone applied at both localities across that tidal level. Each lattice (see Fig. 1) comprised a grid of 56 individual core samples, extending over a 0.6×1.8 m area, i.e. a line of 7 cores together forming a belt transect perpendicular to the interface, replicated 8 times at intervals of 0.25 m. Rows of 8 adjacent cores running parallel to the interface at unit distances from it formed sample 'horizons'. All 4 lattices were located in areas where large continuous blocks (>0.5 ha) of the 2 habitat types met to avoid the potentially confounding variable of patch size (Bowden et al. 2001, Mills & Berkenbusch 2009). Coordinates of each lattice were taken by means of a hand-held GPS+GLONASS unit (with a stated accuracy of 3 m). Individual samples were collected by means of 8.3 cm diameter core tubes, and hence 7 contiguous cores (taken by 2 leapfrogging tubes) sampled the entire critical 0.5 m zone, one core straddling the interface itself and 3 extending a further total distance of 0.26 m away from that interface in each direction. Allowing for the thickness of the core tube walls, the 7 sampling horizons (Fig. 1) were therefore:

- +3 \approx +27 cm (+22.2 to +30.5 cm)
- +2 \approx +18 cm (+13.4 to +21.7 cm)
- +1 \approx +9 cm (+4.6 to +12.9 cm)
- 0 \approx the boundary line (+4.1 to -4.1 cm)
- 1 \approx -9 cm (-4.6 to -12.9 cm)
- 2 \approx -18 cm (-13.4 to -21.7 cm)
- 3 \approx -27 cm (-22.2 to -30.5 cm)

where positive distances and horizons were in the seagrass (*Zosterella capricorni* together with some *Halodule uninervis* and less commonly *Halophila ovalis*), and negative ones in immediately adjacent unvegetated fine- to medium-grained tidal-delta quartz sand. This sampling regime also made possible investigation at considerably smaller spatial lag than earlier lattices worked in the habitats concerned, i.e. the lags of 8×9 m and 0.25×1.0 m of Barnes & Hamylton (2013, 2015).

Since most seagrass macrofauna occurs in the top few mm of sediment (e.g. 98% in the top ≤ 50 mm in the studies of Lewis & Stoner 1981 and Klumpp & Kwak 2005), each core was taken to a depth of 100 mm. This procedure collects the smaller and most numerous species that constitute the large majority of invertebrate biodiversity (Gaudêncio & Cabral 2007, Albano et al. 2011), but not the scarcer megafauna (e.g. *Holothuria*) or deeply burrowing forms (e.g. *Marphysa*). Collection and treatment of core samples followed the same procedure as the earlier studies of the

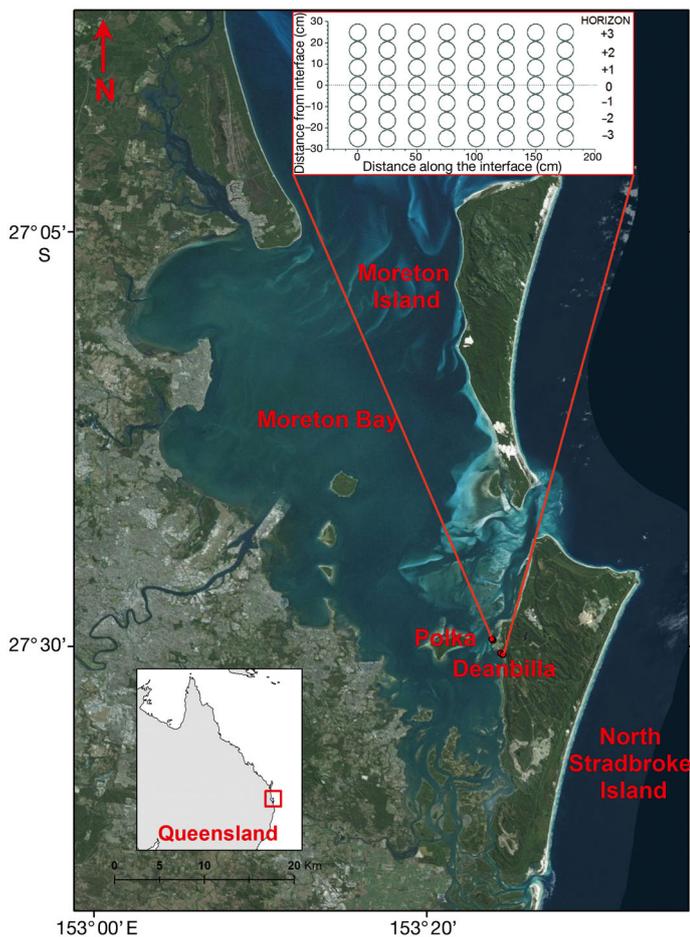


Fig. 1. Study sites along the Queensland coastline (inset, lower left) and in Moreton Bay, Australia, with an inset diagrammatic representation of each sampling lattice (note the 2 axes are not to the same scale)

North Stradbroke intertidal macrofaunal assemblages cited above. Cores were taken at low tide, soon after tidal ebb from the sites concerned, and were gently sieved through 710 μm mesh on site. Contained animals were identified to species level wherever possible, with nomenclature as listed in the World Register of Marine Species (www.marinespecies.org, accessed December 2015). Several taxa, although relatively important in Moreton Bay, have not yet been investigated systematically in southern Queensland (Davie & Phillips 2008) and their identification to named species poses 'enormous problems' (Davie et al. 2011, p. 8). Such animals were treated as morphospecies, an operationally appropriate procedure to detect spatial patterns of numbers of species and their differential abundance (Dethier & Schoch 2006, Albano et al. 2011). Number of seagrass shoots in each sample was also recorded, but as previously, sessile macrofauna attached to the seagrass leaves was not. *Mictyris longicarpus* (individuals of which were present at one of the 4 sites) was also excluded. These soldier crabs do not inhabit a fixed location but bury beneath the surface for the duration of high water and then emerge to wander over the surface, travelling up to 450 m before reburying again some 4 h later (Cameron 1966, Dittmann 1998). By chance, some samples can be overwhelmingly dominated by these wandering crabs (e.g. up to 50 juveniles 0.01 m^{-2} in the present study), whereas at another point in time or space they might contain none. In such circumstances, exclusion of the crab from the dataset seemed most appropriate. Although information on which biological traits really correlate with benthic ecosystem properties and processes is scarce (Murray et al. 2014), species were allocated to a working system of 29 'functional groups' based with minor modification on that used earlier for the local fauna (Barnes & Hamylton 2015, Barnes & Hendy 2015).

Statistical analyses

Raw data on numbers of each component species and of individuals within each functional group in the various sampling horizons were subjected to similarity analysis, and assemblage metrics were derived and compared across the same horizons. Assessments of faunal-assemblage and functional-group similarity and calculation of biodiversity metrics were carried out via EstimateS v.9.1.0 (Colwell 2013, Colwell & Elsensohn 2014). Metrics assessed were (1) overall abundance, (2) number of groups per unit area, (3) α -diversity, and (4) compositional similarity. Given the

high proportion of rare species in the local fauna (in the present study, 48% of the 147 species obtained from the 0.5 m wide boundary zone were each represented by <3 individuals), number of species per unit area (i.e. species density sensu Gotelli & Colwell 2001) was assessed both as those observed (S_{obs}) and as abundance-based coverage estimates of likely numbers (S_{ace}) (see Gotelli & Colwell 2010). Alpha-diversities were estimated by Hill's (1973) N_2 —a probability of intra- or interspecific encounter (PIE) metric (Hurlbert 1971) expressed as the equivalent number of species (ENS) or functional groups (i.e. the number that, if equally abundant, would yield the same value of the metric). It is generally insensitive to both spatial grain/extent and size of species pool, and for that reason was recommended by Dauby & Hardy (2012) and Chase & Knight (2013). Also, because of the high probability of absence from any given sample of species present at low population density, changes in quantitative faunal composition (β -diversity) across adjacent sampling horizons were estimated by both the Bray-Curtis statistic and the abundance-based Sørensen similarity statistic of Chao et al. (2005, 2006) corrected for undersampling bias, with a set upper abundance limit for rare species of 5 per sampling horizon (referred to below as Chao-Sørensen estimated similarity, CSE). This modification substantially reduces the negative bias of indices such as the Bray-Curtis, especially when samples from species-rich assemblages are likely to be incomplete (Chao et al. 2005), but can give spuriously high values for comparisons involving relatively barren habitats supporting only few rare species. Changes in relative functional-group composition were quantified by the Morisita-Horn index (Gotelli & Chao 2013), and the relative importance of individual species within the various macrofaunal assemblages was assessed by Barnes' (2014a) index of numerical importance, which combines data from both abundance and occupancy. As the pattern of relative importance of individual species in an assemblage (whether measured as abundance, occupancy or a composite of the two) can yield information on factors structuring different ecological assemblages when displayed in rank order as a Whittaker Plot (e.g. Magurran 2004, Jenkins 2011), such plots were constructed for each sampling horizon.

Spatial analyses undertaken included the calculation of (1) spatial autocorrelation, (2) spatial interpolation of samples of faunal abundance and density metrics for species and functional groups in each lattice, (3) anisotropy across the sample lattices, and (4) a spatial regression of sample metrics against seagrass shoot density. Positive spatial autocorrelation is

a statistically quantifiable property expressing the idea of near things being more alike than far things with respect to a single variable. It is commonly detected in assemblage metrics calculated from population data because of a pervasive continuity and structure to ecological phenomena, which rarely change dramatically over short distances. Univariate measures of spatial autocorrelation were calculated as the Moran's I statistic for adjacent pairs of sampling horizons. This employed the same methodology as Barnes & Hamylton (2013, 2015) on an iterative basis (999 permutations) to enable calculation of p-values for each statistic, and it enabled patterns in spatial autocorrelation to be examined relative to the seagrass/sand interface. In each case, Moran's I was calculated for observed species densities and overall faunal abundance on a subset of cores representing 2 adjacent sampling horizons at the 4 sites. Resulting patterns in autocorrelation were plotted across the lattice horizons.

Spatial interpolation is the process of estimating unknown values of a variable on the basis of sampled point values. It is often used as a tool for visualising the spatial distribution of sampled populations because it enables a transition from a dataset composed of a collection of disparate point samples to a continuous dataset (Burrough & McDonnell 2011). Faunal abundance and density metrics for species and functional groups in each core sample were interpolated to a continuous surface to allow their trends to be visualised alongside seagrass shoot density in a 3-dimensional plot. Given previous observations of spatial autocorrelation in assemblages at these sites (Barnes & Hamylton 2013), a simple kriging interpolator was used to capture spatial variability of each metric and to account for both deterministic and autocorrelated assemblage variation, as well as uncorrelated noise (Burrough & McDonnell 2011). Interpolated raster data surfaces were then plotted side by side in 3 dimensions using ArcScene v.10.2 (ESRI) to aid interpretation and comparison of spatial distributions.

Anisotropy is the property of a given phenomenon exhibiting different values when measured along axes in different directions, arising for example because of directionally dependent environmental or ecological drivers that influence an assemblage. It is commonly investigated by calculating statistical functions that describe spatial structure by comparing the value of each point to all other points within a dataset. These functions include the semivariogram or covariance function, from which ecologically meaningful features can be extracted. For example, the range

represents the distance of separation, discernible from the levelling out of plotted points on a semivariogram, at which paired point samples are no longer autocorrelated. This is a useful indicator of the spatial dimensions of potentially influencing ecological processes, e.g. predation, competition or reproduction (Hamilton 2013), and may be detectable as the statistically significant presence (or absence) of similarity between point samples of population data. To elucidate directional influences within populations, semivariograms can be constructed in which point samples of assemblage metrics (e.g. faunal abundance, species density or functional group density) are compared along different directional axes (i.e. 0 to 359°). Comparisons proceed through calculation of the major (longest) range (d_1), the minor (shortest) range (d_2) measured from the different directions, and an anisotropic factor (the ratio of the major to minor range, g) to indicate the strength of the directional influence. By using such a dense lattice of core samples, localised directionality can be investigated by quantifying the major and minor ranges as a measure of the dimensions of autocorrelation, alongside the angles at which these occurred (θ). Lattices were mapped in such a way that the directional angle of 0° (or 180°) was perpendicular to the interface, and 90° (or 270°) was parallel to it.

Spatially explicit regression uses the location information of each data case to incorporate an additional, geographically weighted term into a standard regression equation. This characterises the structured component of variation in the data cases (or core samples), that would otherwise be unexplained by a classic regression model. For example, a spatially lagged dependent variable incorporates a term that represents the value of the dependent variable itself at a given distance away from the location for which the variable is being modelled (i.e. a spatial lag). Because most population data exhibit spatial structure (Koenig 1999), this has the effect of improving the explanatory power of the regression model, as well as making it more statistically rigorous (Haining 2003). Spatial regression was used to explore the relationship between the overall assemblage metrics and the potential ecological driver of seagrass shoot density. A spatially lagged autoregression was employed to overcome some of the statistical violations associated with spatially dependent datasets, including reduced independence of observations and autocorrelation of residuals (see Eq. 4 in Hamylton 2013). Diagnostics reported include the coefficient of variation (R^2), p-value and z-score associated with each regression.

RESULTS

Nature of boundary zone assemblages

Faunal assemblage metrics (abundance, species density and diversity) of the adjacent 0.26 m wide boundary zones on either side of the actual 0.08 m interface between seagrass and unvegetated sand at each site all showed marked differences (Wilcoxon matched pairs test; $p < 0.005$), indeed almost no overlap in values. Overall, the marginal strip of seagrass supported a total of 126 taxa at an abundance of 2093 ind. m^{-2} and an N_2 diversity of 20.8; in contrast, the abutting marginal strip of sand supported only 56 taxa, 628 ind. m^{-2} , and an N_2 diversity of 11.4 (values very similar to those recorded from points further apart across the boundary zone by Barnes & Hamylton 2013). Even though < 0.1 m apart, the 2 assemblages shared only 30% of their observed total fauna. The 0.08 m wide interface itself supported intermediate values of 1418 ind. m^{-2} and N_2 diversity of 16.9. The boundary fauna was dominated by just 9 of the 29 functional groups present, contributing 81% of the total individuals in that zone.

Each site supported a somewhat different subset of the local species pool, which in the seagrass was dominated by the crab *Enigmaplax littoralis*, gastropod *Calopia imitata* and amphipod *Limnoporeia yarrague* (together comprising 32% of total individuals), a total of 8 species contributing to 50% of the total. The seagrass of Deanbilla 1, for example, was also dominated by the tanaid *Longiflagrum caeruleus*, whilst the spionid *Malacoceros ?reductus* was also prominent there in both seagrass and sand; at Deanbilla 2, however, *L. caeruleus* was rare and *M. reductus* was absent. At Deanbilla 2 the most abundant seagrass species included the gastropod *Tricolia fordiana*. At Polka 2, however, the otherwise ubiquitous *C. imitata* was relatively uncommon, whilst *Goniada ?tripartita* was particularly abundant and the gastropod *Alaba difformis* was one of the dominants. The bare sand was dominated by infaunal polychaetes at all sites (especially by *G. ?tripartita*), *Dasybranchus caducus* and other capitellids at Deanbilla, and by *Spio pacifica* at Polka.

There was no variation from site to site in species density per core within any horizon (Kruskal-Wallis test; $p > 0.2$), nor in faunal abundance (Kruskal-Wallis; $p > 0.1$). Excluding relative rarities (< 5 ind. in total), 12 species (6 polychaetes, 2 bivalves, 3 peracaridans and a gastropod) occurred with equal abundance in both habitats (within ratios of 0.67 to 1.25:1), their combined abundance and species den-

sity being a relatively uniform 287 ± 14 ind. m^{-2} and 9.4 ± 0.4 species horizon $^{-1}$. With one exception, each polychaete species that dominated the sand fauna occurred at a very similar density in both seagrass and sand (ratios of $< 1.09:1$; Pearson's r : -0.1 to $+0.3$; $p > 0.5$). The exception, *S. pacifica*, was 20× more abundant in the unvegetated sand.

There were 2 notable absentees from the boundary fauna. The third most abundant animal within the Deanbilla seagrass the previous year (Barnes & Hamylton 2015) and also across the seagrass of the whole region in 2011 (Barnes & Barnes 2012) was the tornid microgastropod *Pseudoliotia* (present as 3 species), and together with related genera (e.g. *Circulus*), tornids formed the second most abundant taxon away from the boundary zone; whilst the local unvegetated sand was dominated by the amphipod *Urohaustorius mertungi* (Barnes & Barnes 2012, Barnes & Hamylton 2013). Yet neither animal showed more than a token presence in these interface samples, and only one species of *Pseudoliotia* occurred (*P. speciosa*). Excluding the tornids and the gastropod *Velacumantus australis* (that occurs across the whole area very patchily), however, comparison of the species assemblage in the main body of the seagrass at Deanbilla (data of Barnes & Hamylton 2015) with the equivalent groups in the marginal Deanbilla seagrass zone, for example, yielded a very high Morisita-Horn similarity of 0.86 for the remaining fauna.

Univariate analyses

In spite of inter-site variation, all 4 lattices displayed a similar pattern of distribution of both assemblage similarity between adjacent sampling horizons and changes in overall abundance and species density across the boundary zone. Fig. 2A displays similarity between the faunal assemblages of adjacent horizons across the zone, and Table 1 shows the effect of increasing distance away from the actual interface on similarity between the seagrass and unvegetated sand assemblages. The equivalent effects of distance on assemblage metrics are shown in Fig. 3A–C and Table 2. Seagrass shoot density decreased significantly across the marginal seagrass horizons towards the interface (Pearson's $r = -0.66$; $p < 0.0001$); however, this is not necessarily indicative of a general marginal decrease in that the average local densities further towards the interior of the bed were of the same magnitude as those of horizon +1 (Fig. 3D). Faunal abundance within the seagrass horizons also decreased towards the interface (Pear-

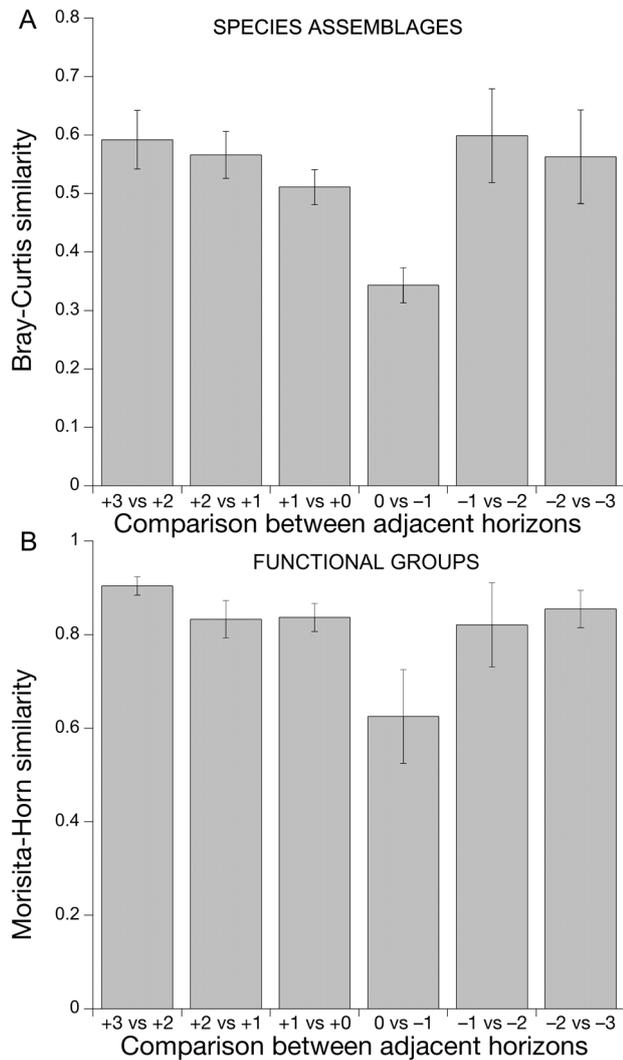


Fig. 2. Changes in similarity of adjacent sampling horizons across the boundary zone between seagrass (+) and unvegetated sand (-) (means \pm SE): (A) Bray-Curtis similarity of assemblage taxonomic composition; and (B) Morisita-Horn similarity of relative functional-group composition

son's $r = -0.94$; $p < 0.0001$), with differences between the horizons in species density per core being significant (Friedman $p < 0.01$); and those per horizon being marginally so (Friedman $p = 0.05$). No significant changes occurred across the unvegetated sand horizons in either faunal abundance or species density (Friedman $p > 0.5$ in both cases).

Although these results provide evidence of a gradual change in seagrass faunal abundance towards the interface, the majority of the transition in species density and species diversity, and in much of that in abundance, from the seagrass to the bare sand state clearly occurred abruptly, immediately after the seagrass cover ended. Not only was there a marked and highly

Table 1. Differences in assemblage species composition across paired sampling horizons at various distances from the seagrass/unvegetated sand interface, presented as Bray-Curtis (BC) similarities and as those estimated by the Chao-Sørensen Estimated (CSE) similarity statistic (in each case estimated complete dissimilarity = 0; estimated complete similarity = 1). All similarities are significantly less than levels displayed between horizons within each habitat type (i.e. mean BC = 0.561 ± 0.028 ; mean CSE = 0.844 ± 0.023) (Mann-Whitney test; $p < 0.0001$)

Site	Distance apart of centres of sampling horizons		
	0.54 m (+3 vs. -3)	0.36 m (+2 vs. -2)	0.18 m (+1 vs. -1)
Deanbilla 1			
BC	0.132	0.188	0.316
CSE	0.329	0.219	0.639
Deanbilla 2			
BC	0.115	0.123	0.272
CSE	0.362	0.462	0.724
Polka 1			
BC	0.156	0.240	0.220
CSE	0.178	0.375	0.471
Polka 2			
BC	0.180	0.241	0.235
CSE	0.316	0.436	0.598

significant decrease in similarity between those horizons that contained seagrass (+3 to 0) and those that did not (-1 to -3) (similarity levels between horizons 0 and -1 being significantly lower than for any other adjacent horizons; Mann-Whitney $p < 0.005$), but the core samples of horizon 0 straddling the boundary (and therefore containing approximately half seagrass and half bare sand habitat) possessed a fauna much more similar to the seagrass cores than to those of the sand (Bray-Curtis similarities: average seagrass horizon vs. horizon 0 = 0.62; average bare sand horizon vs. horizon 0 = 0.40; Wilcoxon matched pairs test $p < 0.005$). Indeed, horizon 0 supported fauna dominated by the same taxa listed above as dominating the seagrass. Over the critical distance of < 0.1 m between horizon 0 and horizon -1, average overall faunal abundance dropped from 1412 to 625 m^{-2} , observed species density from 23 to 11, estimated species density from 42 to 17, and species diversity from 10.5 to 6.3. Abundance of the seagrass-associated species (i.e. those not equally abundant in seagrass and sand) showed an 82% fall from horizon 0 to horizon -1, more than 3 \times the greatest proportional drop in those species across any other pair of adjacent seagrass horizons (Fig. 4A). Some 50 to 75% of the total decrease in species density and diversity from horizon +3 to horizon -3 therefore occurred within the < 0.1 m between horizon 0 and horizon -1.

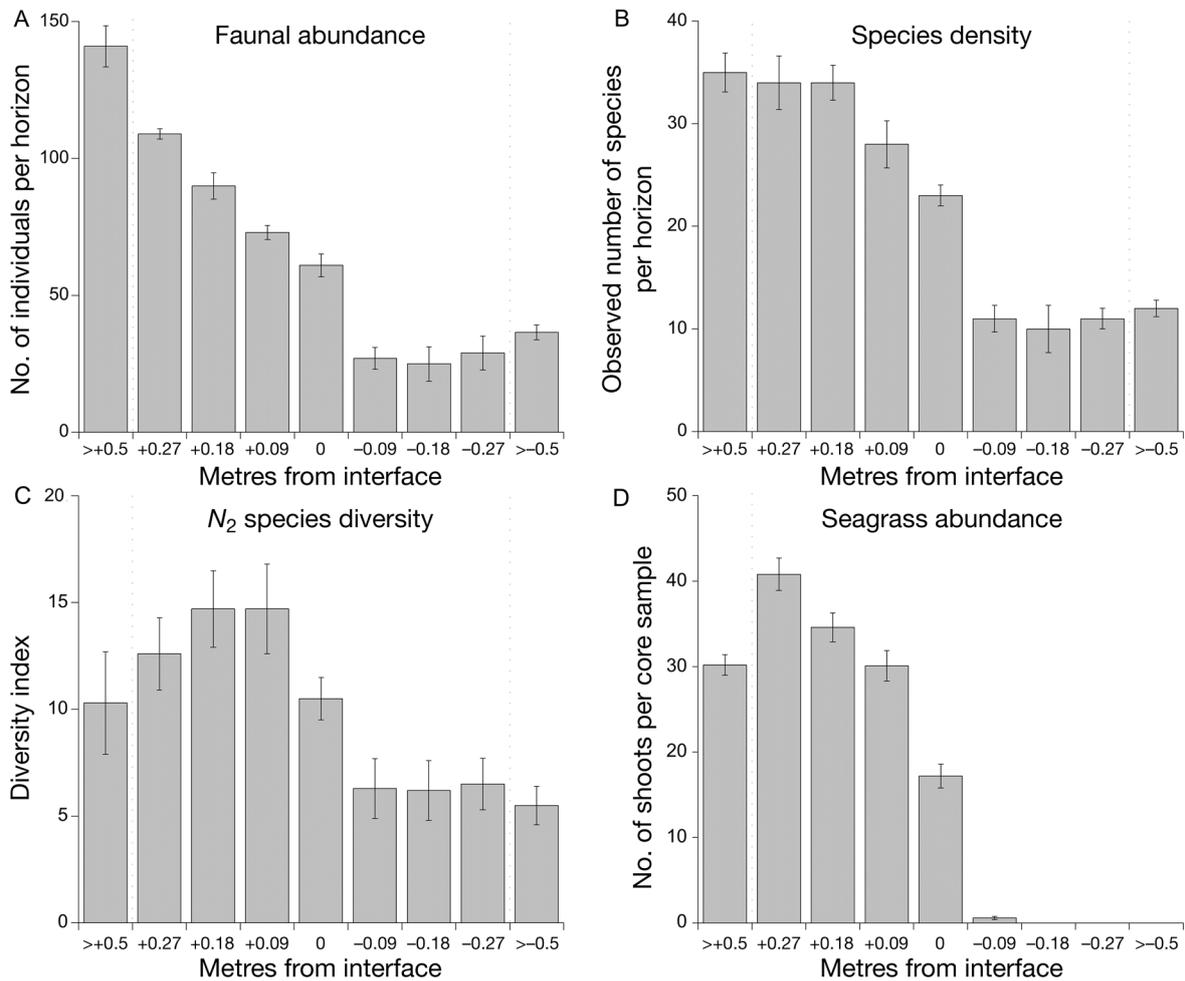


Fig. 3. Distribution of macrofaunal species-assembly metrics across the boundary zone between seagrass (+) and unvegetated sand (-): (A) abundance; (B) observed numbers of species; and (C) N_2 α -diversity; together with (D) number of seagrass shoots per core sample (mean values per sampling horizon \pm SE). Earlier data for horizons further away from the interface at the 2 localities, adjusted to the equivalent sampled area, are included for comparison (data of Barnes & Hamylton 2013). Note the large standard errors associated with α -diversity

Table 2. Mean differences in various macrofaunal assemblage and functional-group metrics across paired horizons at various distances from the seagrass/unvegetated sand interface. S_{obs} : observed number of species; S_{ace} : abundance-based coverage estimator. Significant values are indicated in **bold** (Wilcoxon patched pairs $p < 0.05$)

	Distance apart of centres of sampling horizons		
	0.54 m (+3 vs. -3)	0.36 m (+2 vs. -2)	0.18 m (+1 vs. -1)
Species assemblages			
Faunal abundance	80	65	46
S_{obs} species density	23	24	17
S_{ace} species density	34	39	34
Faunal α -diversity	6.1	8.5	8.4
Observed % species shared	15	16	22
Functional groups			
Functional-group density	7.7	11.2	6.0
Functional α -diversity	2.9	4.3	2.9

The ranked relative importance distributions of the component species in each horizon are displayed in Fig. 5. It is evident that whilst abundance, species density and faunal composition changed markedly across the 0.5 m boundary zone, structural attributes of the assemblages remained virtually unaffected by the presence or absence of vegetation cover, without any indication of segregation of seagrass or bare sand horizons.

Functional-group metrics and patterns of similarity across the boundary zone closely matched those of the taxonomically based assemblages (cf. Fig. 2A & B, Figs. 3B,C & 6, and Tables 1

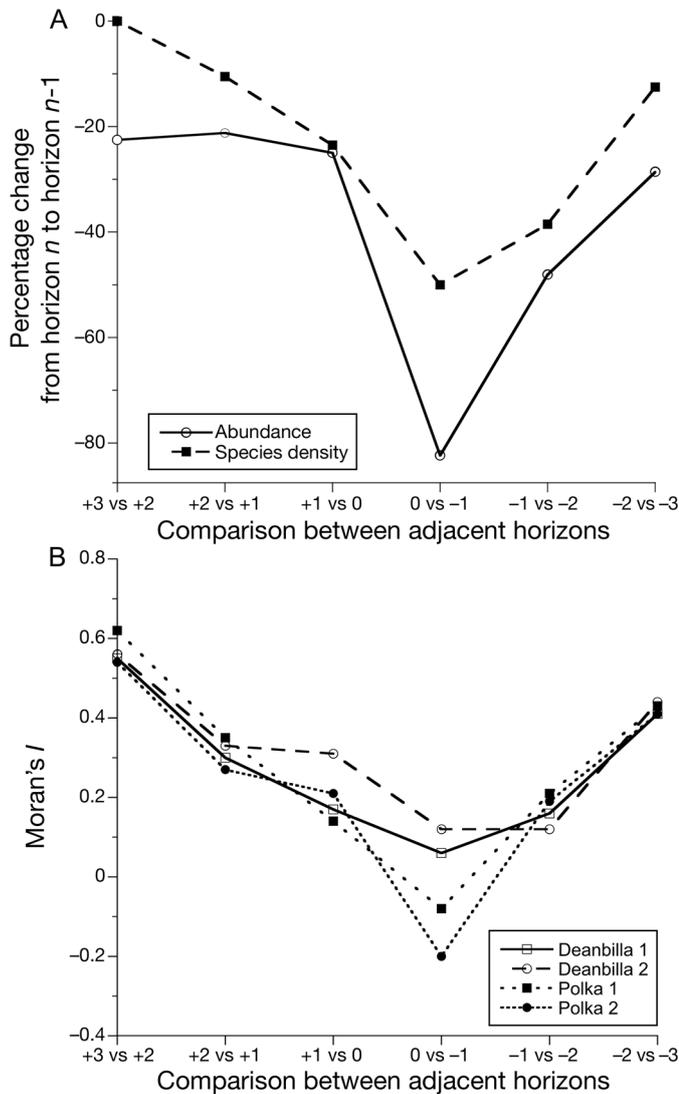


Fig. 4. The <0.1 m distance between horizons 0 and -1 as the location of most faunal transition. (A) Proportional decrease between adjacent horizons in the abundance and species density of the more important specialist seagrass species (i.e. those 41 species $>4\times$ more abundant in the seagrass than in the unvegetated sand, and each represented by ≥ 5 ind. in total). (B) Values of Moran's I for comparisons between the observed species densities across adjacent horizons at the 4 sites; Moran's I for comparisons involving over all faunal abundance showed the same pattern

& 3). Over the <0.1 m from horizon 0 to horizon -1 , the number of functional groups fell from 14 to 9, and functional diversity from >8 to <6 . Most functional groups occurred right across the zone, however. Some did so at relatively uniform abundance but increased in relative importance in the sand purely by virtue of the decreased abundance of other groups (e.g. the infaunal predatory and deposit-feeding worms, and bivalved suspension-feeders). Omnivorous and meio-

fauna-consuming peracaridan crustaceans and surface-feeding infaunal worms (e.g. nemertines) also occurred across the whole boundary zone but in reduced numbers in the sand, a pattern seen in extreme form in the 2 dominant groups within the seagrass plus interface region (biofilm-consuming microgastropods and omnivorous small crabs). The tentaculate-feeding worm group was the only one to show the converse distribution, increasing in numbers in the sand (see the Supplement at www.int-res.com/articles/suppl/m553p033_supp.pdf). Whichever similarity index was used, the seagrass and unvegetated sand were more similar to each other functionally than taxonomically (e.g. Morisita-Horn; taxonomically 0.27, functionally 0.65).

Spatial analyses

Equivalent to the analyses above, levels of spatial autocorrelation between the species densities and the faunal abundances of adjacent pairs of sampling horizons were at a minimum between horizons 0 and -1 at all 4 sites (Fig. 4B).

Fig. 7 shows the interpolated data surfaces for spatially referenced seagrass shoot density, faunal abundance, and observed species and functional-group densities within each lattice, plotted in 3 dimensions to facilitate interpretation and comparison of spatial patterns, both along and across horizons. As expected from univariate analyses of mean data across horizons (Figs. 3 & 6), all sites displayed elevated faunal abundances and species and functional-group densities in association with higher densities of seagrass shoots, although this general tendency for larger values of metrics to occur within the seagrass was not quantitatively consistent along the sampling horizons. Rather, individual core samples displayed marked peaks in assemblage metrics, particularly across Deanbilla 2 and both Polka sites.

Semivariograms detected anisotropy for 11 of the 16 lattice-metrics tests, with anisotropic factors ranging from 1.59 to 2.98 (Table 4). In all cases, major ranges were aligned along the sampling horizons (major range angles ranged from 83.3 to 91.9), and minor ranges fell across them. Autocorrelation dimensions indicated that benthic assemblages were no longer detectably influencing each other statistically across relatively short distances, with minor ranges typically around only 0.2 to 0.3 m. Major ranges were more variable, reaching a maximum of 0.74 m for the functional-group densities observed at Polka 1. Across all sites, the minor anisotropic range

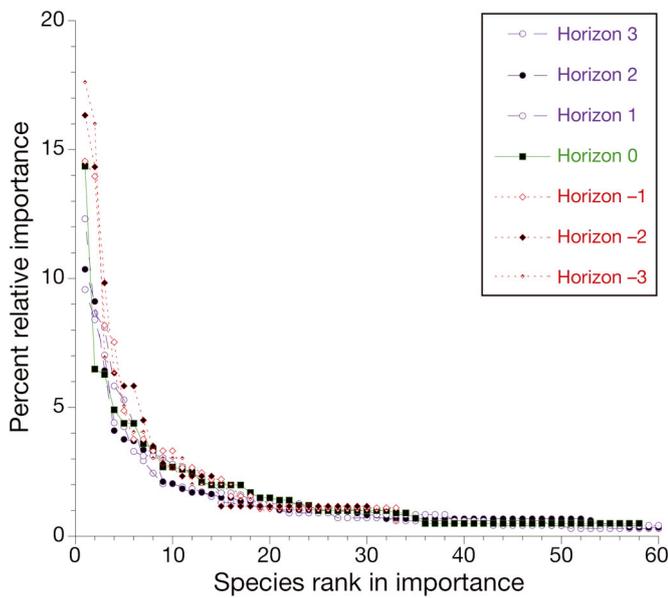


Fig. 5. Whittaker Plot of assemblage structure across the 7 sampling horizons (ranked species importance sensu Barnes 2014a)

traversing the boundary zone was larger for functional-group density than for either species density or faunal abundance.

Regression diagnostics indicated moderately strong relationships between the bivariate function composed of seagrass shoot density and the various assemblage metrics (R^2 ranged from 0.43 to 0.72; Table 5). In general, stronger relationships were observed at Deanbilla, with the strongest association noted for faunal abundance. Of the 12 regressions run, 8 were found to be significant at $p < 0.05$, as indicated in bold in Table 5. In all cases, a positive relationship was observed between density of seagrass and assemblage metrics.

DISCUSSION

At all 4 sites and for all assemblage metrics tested, spatially referenced analyses showed that adjacent cores, although spaced further apart along the sampling horizons (i.e. 0.25 m), were more similar to each other than were those oriented across the horizons even though these were actually touching. There must therefore be very strong directional environmental heterogeneity across the seagrass–sand boundary zone. Notably, the dimensions of the anisotropic minor ranges oriented across the sampling horizons were typically only 0.2 to 0.3 m. Spatially explicit regressions revealed moderately strong

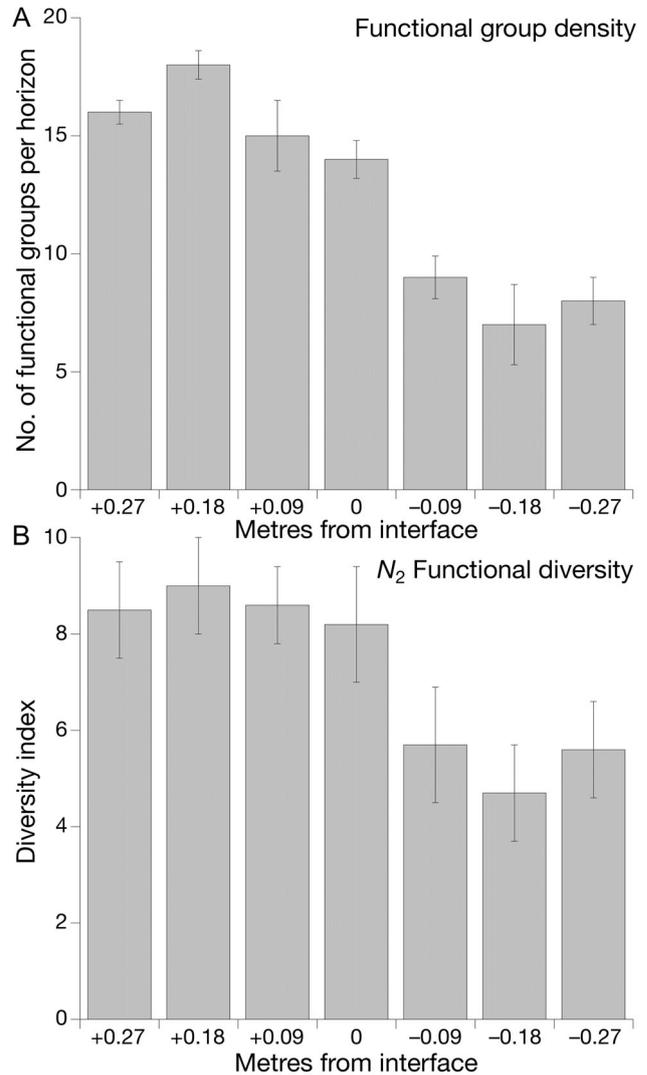


Fig. 6. Distribution of mean functional-group metrics (\pm SE) per sampling horizon on either side of the interface between seagrass (+) and unvegetated sand (-): (A) functional-group density; (B) functional-group N_2 α -diversity

Table 3. Differences in relative functional-group importance across paired sampling horizons at various distances from the seagrass/unvegetated sand interface, as estimated by the Morisita-Horn statistic (no overlap = 0; proportional composition of functional groups identical = 1). All values of the Morisita-Horn statistic are significantly less than those displayed between horizons within each habitat type (mean within-seagrass value = 0.874 ± 0.02 ; mean within-sand value = 0.815 ± 0.05) (Mann-Whitney test; $p < 0.01$)

Site	Distance apart of centres of sampling horizons		
	0.54 m (+3 vs. -3)	0.36 m (+2 vs. -2)	0.18 m (+1 vs. -1)
Deanbilla 1	0.297	0.309	0.654
Deanbilla 2	0.373	0.473	0.745
Polka 1	0.626	0.607	0.607
Polka 2	0.222	0.309	0.313

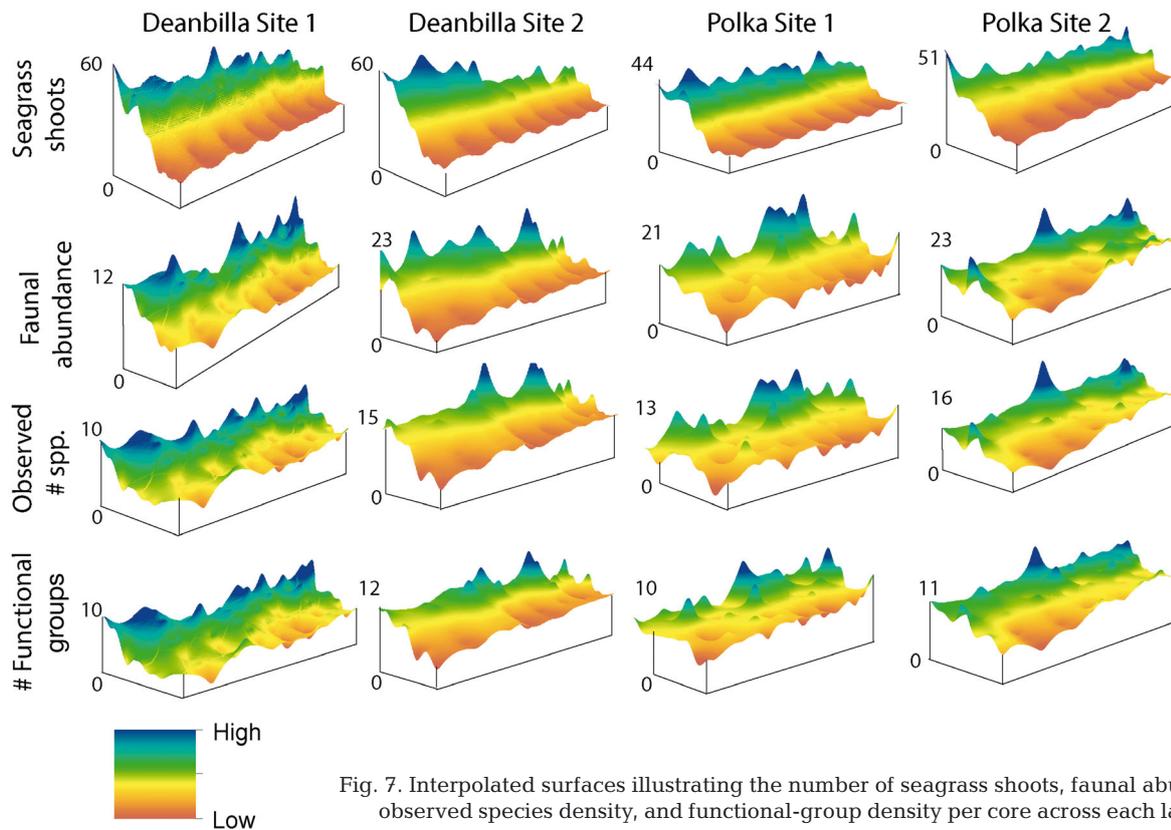


Fig. 7. Interpolated surfaces illustrating the number of seagrass shoots, faunal abundance, observed species density, and functional-group density per core across each lattice

Table 4. Anisotropic dimensions and directions for core metrics at each site: major range distance (d_1), angle direction of major range (θ), minor range distance (d_2) and anisotropy factor (g). Distance units are m; angle units are degrees. Direction angle values, shown in *italics*, are only specified for major range distances where the anisotropic factor exceeds 1

Site	Faunal abundance			Species density			Seagrass shoot density			Functional group density		
	d_1 (θ)	d_2	g	d_1 (θ)	d_2	g	d_1 (θ)	d_2	g	d_1 (θ)	d_2	g
Deanbilla 1	0.63 (<i>91.9</i>)	0.28	2.27	0.27	0.27	1.00	0.27	0.27	1.00	0.64 (<i>88.9</i>)	0.31	2.11
Deanbilla 2	0.53 (<i>88.9</i>)	0.33	1.63	0.53 (<i>89.8</i>)	0.33	1.61	0.53 (<i>89.2</i>)	0.34	1.59	0.64 (<i>89.8</i>)	0.33	1.98
Polka 1	0.27	0.27	1.00	0.27	0.27	1.00	0.27	0.27	1.00	0.74 (<i>89.1</i>)	0.36	2.03
Polka 2	0.63 (<i>83.3</i>)	0.25	2.52	0.63 (<i>84.6</i>)	0.23	2.80	0.61 (<i>86.8</i>)	0.20	2.98	0.56 (<i>90.4</i>)	0.30	1.87

Table 5. Diagnostics of spatially lagged regression relationships tested to explore the association between number of seagrass shoots per core and benthic invertebrate assemblage characteristics (faunal abundance, species and functional-group density). Diagnostics are coefficient of determination (R^2), p-value and z-scores (z). Significant regressions are indicated in **bold**

Site	Faunal abundance			Species density			Functional group density		
	R^2	p	z	R^2	p	z	R^2	p	z
Deanbilla 1	0.72	0.001	9.72	0.66	0.001	8.40	0.67	0.02	12.13
Deanbilla 2	0.71	0.001	6.14	0.70	0.001	22.06	0.68	0.01	15.23
Polka 1	0.55	0.07	9.13	0.50	0.19	8.82	0.43	0.31	10.22
Polka 2	0.53	0.01	7.33	0.57	0.03	9.22	0.55	0.20	9.11

relationships between assemblage metrics and seagrass shoot density, particularly at Deanbilla 1. This provides clear empirical evidence to support the notion of the critical importance of the presence of seagrass in permitting high levels of faunal abundance and biodiversity in a type of habitat otherwise structured by bioturbation, even around the margins of beds. Further research that incorporates other potential drivers of benthic faunal assemblage metrics, including physical environmental parameters such as current speed, and associated sediment properties (grain size, composition, organic matter) might expand and improve these relationships. This, however, was beyond the scope of the present study.

Earlier studies of the intertidal Rainbow Channel seagrass fauna have shown a consistent picture of local pools of some 150 species occurring at a density of 2200 to 2600 ind. m⁻², to which 4 or 5 numerically dominant species contribute 50% of the total, and in which >33% of species are present as only singletons or doubletons (Barnes 2014b, Barnes & Hamylton 2015). Rank order of these dominants vary from site to site, but are drawn from a common pool of species (especially the microgastropods *Calopia* and *Pseudoliotia*, minute crab *Enigmaplax* and peracaridan crustaceans *Limnoporeia* and *Longiflagrum*, with the larger gastropods *Velacumantus* and *Nassarius* and spionid *Malacoceros* being locally important, and with the polychaetes *Goniada*, *Armandia* and *Dasybranchus*, and the gastropods *Tricolia*, *Smaragdia* and *Calthalotia* being sub-dominant). The present results from the extreme margins of the same seagrass system only appear to depart from this picture in minor respects. The boundary assemblage was less dominated by a very small number of species than has been observed within the beds; i.e. 8 species between them comprised 50% of the total individuals, rather than 4 or 5. Overall assemblage density was slightly lower at some 2100 m⁻² and the size of the local seagrass-boundary species pool was also slightly smaller at 126, a value commensurate with that observed by Barnes & Hamylton (2013) across the wider boundary zone of 1.5 m. Except for the scarcity of *Pseudoliotia*, the faunal assemblage of the extreme marginal seagrass zone was in essence little changed from that nearer the centre. The magnitude of the differentials in faunal abundance, species density and species diversity between seagrass and unvegetated sand—some 3.4, 3.1 and 2.2×, respectively—were also equivalent to those demonstrated earlier for areas further away from the interface (Barnes & Barnes 2012). If context is indeed everything in understanding ecotonal changes (Warman et

al. 2013), there is nothing in the present case to suggest that there is any particular faunal distinctiveness of the seagrass edge except its close proximity to the unvegetated sand.

To convert from the levels of faunal abundance, species density and species diversity displayed within the seagrass horizons to those characterising the bare sand required an overall decrease in the 2 former metrics of >65% and in the latter metric of 50% over a distance of 0.5 m. There was little sign of any gradual transition across that distance, however, especially in species density and diversity. Although spatial analyses revealed variation between individual transects, on average >50% and up to 75% of the change occurred abruptly from the horizon that still contained some seagrass (horizon 0) to the one that did not (horizon -1), involving within 0.1 m the reduction of a suite of species that had occurred at an average density of >1000 m⁻² down to 80 ind. m⁻². We are unaware of any other such dramatic ecological transition taking place over such a small distance that does not also involve a complete change in type of substratum (as from rock to sand). Confinement of the majority of the faunal change to such a minute zone suggests that the relative richness of the seagrass is not a faunal reaction to broad-scale characteristics of the seagrass-bed habitat, e.g. greater safety from predation or enhanced larval entrainment. Seagrass edges are likely to be much more exposed to predators (Tuya et al. 2010, Smith et al. 2011), and subject to considerably greater water velocities (Peterson et al. 2004), yet high biodiversity was maintained across them. An immediate response to the presence or absence of seagrass plants appears more likely. This must obviously be the case for leaf-associated microgastropods (e.g. *Tricolia*, *Alaba*, *Smaragdia*), although such biofilm-consumers elsewhere can segue seamlessly from seagrass to bare sediment (Barnes & Barnes 2014), but it seemingly applies equally to non-leaf-associated and more mobile crustaceans from a variety of functional groups, such as *Enigmaplax*, *Limnoporeia* and *Longiflagrum*, which on the basis of work on equivalent animals (e.g. Eggleston et al. 1999, Arponen & Boström 2012) are likely to be capable of reacting to small-scale heterogeneity and of moving between even relatively isolated interface plants.

Data from the earlier study of changes within the 3× wider boundary region of 1.5 m suggest that the abundance of sand-specialist species fell particularly and increasingly rapidly as the interface was approached (see e.g. Barnes & Hamylton 2013, their Fig. 5). By 0.25 m from the interface, numbers of the dominant *Urohaustorius mertungi*, for example, had

already fallen by 75% (authors' unpubl. data). The asymmetrical relative barrenness of the marginal sand zone in the present study is almost entirely a consequence of (1) the effective absence of *U. mertungi* from the region even closer to the interface than 0.25 m (only 4 individuals being encountered) and (2) omission of *Mictyris* from the dataset. In that earlier survey, apart from *Urohaustorius* and *Mictyris*, the most abundant animals in the bare sand were the bivalves *Mysella* and *Eumarcia*, the polychaetes *Goniada* and *Spio* and the gastropod *Nassarivus* (together contributing 46 to 58% of the remaining individuals). These taxa were also among those most abundant in the sand in the present study. Of them, however, all except *Spio* (which is particularly characteristic of bare sand elsewhere along the eastern Australian coast; Dexter 1983) were equally abundant in the seagrass, and although their contribution to the total numbers there was small (<15%), it was 70% within the sand fringe.

The overall picture at these Moreton Bay sites is therefore one in which the seagrass specialists extend right to the actual interface, whilst the sand specialists have largely disappeared by 0.25 m from it in the other direction (except sporadically for *Mictyris*); leaving that section of the boundary zone to *Spio* and to the infaunal (mainly polychaete and bivalve) species that are present at similar population densities across both habitats. According to Ries & Sisk's (2004) edge-effects model based on relative resource availability, if resources are predominantly located in 1 of 2 interfacing habitats, a decrease in faunal abundance would be predicted towards its margin but an increase in numbers in the marginal zone of the resource-poor habitat. If, as is likely to be the case here (Bologna & Heck 1999, Macreadie et al. 2010), the seagrass is the more resource-rich habitat, their model correctly predicts the decline in seagrass-associated abundance and diversity across the interface, but not the poverty of the unvegetated sand margin. None of the outcomes of the Ries & Sisk (2004) model accounts for a decrease in both habitats towards their interface, however, suggesting that there is more than just resource availability at issue. But why species such as *Urohaustorius* do not extend to the interface is not obvious, although there were visible indications on the sediment surface at both localities of peak *Mictyris* bioturbatory activity along the sand side of the interface (even when no soldier crab individuals were present at the time), and *M. longicarpus* can reduce the chlorophyll and organic carbon available to other species by up to 95% (Webb & Eyre 2004). It is therefore quite possible that

the relative bare marginal sand zone observed at these study sites is only a local phenomenon. The observation that the ranked relative importance distributions of the component species across the boundary zone are unchanging despite the marked differences in the 2 interfacing ecological systems is puzzling and emphasises the need to gain a better understanding of the form and meaning of such patterns (McGill et al. 2007).

Working at 3 sites in Nova Scotia, Canada, Wong & Dowd (2015) also compared bare sand, seagrass and their interface from the viewpoint of functional ecology. At 2 of their sites, taxonomic diversity and species richness increased from sand to seagrass, whilst functional diversity showed less change or none, though both increased along the gradient at the third. Equivalent work carried out in the northern Baltic (Törnroos et al. 2013) showed seagrass and bare sand there to be more similar to each other functionally than taxonomically, as was the case in the present Moreton Bay study. No consistent pattern in differential abundance was found across the different habitat types at the sites in Wong & Dowd's (2015) study, although at one of the 3 sites it was maximal at the interface. In Moreton Bay, both functional and taxonomic approaches displayed a very similar pattern, increasing from sandflat to seagrass, although functional-group density and diversity increased less than those of the species assemblages. No suggestion of increased abundance or diversity at the interface occurred. The change in functionality occurring across the interface was largely as might be expected: infaunal animals mainly active beneath the surface or with only retractable feeding organs positioned at the surface (e.g. bivalve molluscs and subsurface feeding polychaetes) were unaffected, whilst epibenthic species and those intimately associated with seagrass leaves (e.g. surface-active polychaetes, microgastropods and many crustaceans) decreased markedly. The only unexpected change in a functional component was the increase in surface-feeding canalipatan polychaetes away from the seagrass. These, like the unaffected functional component, have bodies hidden beneath the surface of the sediment and have interface-feeding tentacular systems that can be withdrawn for safety. Possibly *Spio*, in particular, has a preference for suspension feeding in areas of relatively dynamic water movement (see e.g. Dauer 2000). As yet, however, there is insufficient information on changes in functional systems across seagrass boundaries to permit explanation of the variation that is displayed across the few studies so far undertaken.

It must be stressed that the present results apply only to what appeared to be stable interfaces between seagrass and unvegetated sand, and there is no reason to predict that the same features will also be shown by retreating or, even less likely, by advancing seagrass systems. They do, however, provide a baseline against which such temporal habitat change can be compared. Seagrass, which is being allowed to disappear at a mean global rate of $>100 \text{ km}^2$ (i.e. some 7% of the total) yr^{-1} (Waycott et al. 2009), provides a wide range of ecosystem services with an estimated value of \$19000 (USD) $\text{ha}^{-1} \text{yr}^{-1}$ (Costanza et al. 1997, Barbier et al. 2011), some 3 times that of coral reefs (Costanza et al. 1997, Duarte et al. 2008). When seagrass cover disappears, what is left is (usually) much less valuable bare sediment—less valuable in some measure because of the loss of the small invertebrates that are the food of several larger species using seagrass as a nursery area (Luczkovich et al. 2002, Nagelkerken & van der Velde 2004, Verweij et al. 2006). Hence, comparisons of local vegetated and unvegetated areas of substratum and the transition from one state to the other are of considerably more than just academic interest. This is particularly so in Moreton Bay, where the 189 km^2 of seagrass is a regionally significant habitat for juvenile prawns (Young 1978) and fish (Burfeind et al. 2009), but where there is also a long and complex history of seagrass loss (Kirkman 1978, Cuttriss et al. 2013, Roelfsema et al. 2013, Hanington et al. 2015), providing serious cause for concern of potential future loss of productivity (Gibbes et al. 2014).

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