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Abrupt transitions between macrobenthic faunal assemblages across seagrass bed margins

Abstract

The nature of the transition from one contrasting macrobenthic assemblage to another across interfaces between intertidal seagrass and unvegetated sand was investigated in the subtropical Moreton Bay Marine Park, eastern Australia, via six two-dimensional core lattices. The same pattern of transition was manifested in each lattice. Macrofaunal abundance, species density (both observed and estimated total) and assemblage composition did not vary with distance away from the interface within the 0.75 m wide marginal bands of each habitat type. Neither were there significant differences in assemblage metrics or composition between the marginal and non-edge regions of either habitat. There were, however, very marked differences in assemblage composition, abundance and species density across the 25 cm wide strip on either side of the actual interface, the interacting assemblages reacting symmetrically. All these differences therefore took place over an ecotone distance of only 0.5 m at most. Spatial trends in assemblage metrics across the boundary zone were captured accurately by second and third order polynomial regression models. It also appeared that edge effects on individual species within the seagrass were a variable local response not a consistent effect of closeness to the bare sand.

Keywords

bed, seagrass, across, assemblages, margins, faunal, abrupt, macrobenthic, between, transitions

Disciplines

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1 **Abrupt transitions between macrobenthic faunal assemblages across**
2 **seagrass bed margins**

3

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13

14 **ABSTRACT**

15 The nature of the transition from one contrasting macrobenthic assemblage
16 to another across interfaces between intertidal seagrass and unvegetated
17 sand was investigated in the subtropical Moreton Bay Marine Park, eastern
18 Australia, via six two-dimensional core lattices. The same pattern of
19 transition was manifested in each lattice. Macrofaunal abundance, species
20 density (both observed and estimated total) and assemblage composition did
21 not vary within the 0.75 m wide marginal bands of each habitat type with

1 distance away from the interface. Neither were there significant differences
2 in assemblage metrics or composition between the marginal and non-edge
3 regions of either habitat. There were, however, very marked differences
4 across the 25 cm wide strip on either side of the actual interface, the
5 interacting assemblages reacting symmetrically. All these differences in
6 composition, abundance and species density therefore took place over an
7 ecotone distance of only 0.5 m at most. Spatial trends in assemblage
8 metrics across the boundary zone were captured accurately by second and
9 third order polynomial regression models. It also appeared that edge effects
10 on individual species within the seagrass were a variable local response not
11 a consistent effect of closeness to the bare sand.

12

13 **Key words**

14 Benthos, biodiversity, ecotone, edge effects, sandflat, seagrass

15

16 **1. INTRODUCTION**

17 Most natural environments, including coastal marine ones (Eyre et al.,
18 2011), are mosaics of different habitat patches and the transitional zones
19 between these patches are increasingly being recognised as ecologically
20 important, not least because landscape structure affects habitat quality
21 (Levin et al., 2001; Zajac et al., 2003; Ries et al., 2004; etc.). The quality of
22 seagrass habitats is of particular current concern because of their recent
23 worldwide decline and fragmentation (Lotze et al., 2006; Waycott et al., 2009;

1 Fourqurean et al., 2012), because of concerns that the resultant denuded
2 habitat may support lesser animal abundance and biodiversity (e.g. Pillay et
3 al., 2010), and because seagrass beds provide economically important
4 ecosystem services, including not only physically protective habitat for the
5 juveniles of commercially-significant fish and crustaceans but also food for
6 those juveniles in the form of the smaller benthic macrofauna that
7 seagrasses support in abundance (Duarte, 2000; Unsworth and Cullen,
8 2010; Coles et al., 2011; Barbier et al., 2011).

9 Throughout much of the world, sheltered intertidal and shallow
10 subtidal sandflats occur in one of two characteristically alternative patch
11 states: one being seagrass beds, the other unvegetated sediment. These two
12 alternatives are dynamic and interchangeable, with each member of the pair
13 expanding into territory held by the other in one area or another of shared
14 sandflats (e.g. Yamakita et al., 2005; Berkenbusch et al., 2007; Carr et al.,
15 2010). Although not always the case in vegetated versus unvegetated
16 comparisons, especially in high latitude areas subject only to *Arenicola*
17 bioturbation (see e.g. Asmus and Asmus, 2000; Polte et al., 2005), wherever
18 the bare sediment is structured by the bioturbation of burrowing
19 thalassinidean crustaceans (Pillay and Branch, 2011) benthic macrofaunal
20 assemblages supported by the two alternative habitat types may be very
21 different, as, for example, in the *Nanozostera capensis* versus *Callichirus*
22 *kraussi* system in Langebaan, South Africa (Siebert and Branch, 2007) and
23 in the *Nanozostera muelleri* versus *Trypaea australiensis* system in Moreton
24 Bay, Australia (Barnes and Barnes, 2012). At these localities, as well as at

1 others (Boström and Bonsdorff, 1997), areas of bare sediment are dominated
2 by burrowing species whilst the seagrass supports a large epifaunal
3 component. Such faunal contrasts can often be linked to the marked
4 change in nature and stability of the substratum induced by the contrasting
5 ecosystem bioengineers (Berkenbusch and Rowden, 2007; Siebert and
6 Branch, 2007; etc.).

7 Some aspects of the boundary zone between seagrass and adjacent
8 habitat types have received detailed attention. In particular, edge effects
9 within blocks of seagrass have been extensively studied in both the Atlantic
10 and the Pacific (Bologna and Heck, 2002; Tanner, 2005, 2006; Warry et al.,
11 2009; Murphy et al., 2010; etc), with, somewhat paradoxically, it often being
12 reported that densities of seagrass-associated animals were higher on the
13 margins of the bed than nearer its centre. Equivalent work on edge effects in
14 unvegetated sediment is much rarer, however. The studies by van Houte-
15 Howes et al. (2004) and Tanner (2005) are two of the very few that have
16 extended right across an interface to examine both two habitat types. Van
17 Houte-Howes et al. (2004) explored the boundary between mid-intertidal
18 unvegetated sand and *Nanozostera muelleri* in North Island, New Zealand,
19 and they reported evidence that distinctive assemblages were present at the
20 edges of the seagrass (at least under conditions of abundant seagrass
21 shoots). These authors investigated the transitional zone via a series of
22 sampling points relatively far apart and spanning the relatively large total
23 distance of 100 m (at -50, -10, -1, +1 and +50 m, where zero is the interface
24 itself). Tanner (2005), from the perspective of the abundance of certain

1 seagrass-associated species in fragmented systems, narrowed the zone of
2 investigation to the 2 m on either side of the bare sand/seagrass boundary
3 and showed marked changes in population density of various seagrass
4 polychaetes, crustaceans and bivalves across this zone in a *N. muelleri*
5 meadow at LWS in South Australia.

6 In order to examine in detail the actual transition from seagrass faunal
7 assemblage to that of the adjacent unvegetated sediment, the present study
8 was designed to investigate the precise interface between the two. Further,
9 this was conducted at a locality for which recent data on the contrasting
10 faunal assemblages of the seagrass and unvegetated sediment away from the
11 interfaces were also available (Barnes and Barnes, 2012), permitting each
12 marginal habitat zone to be placed in context. Three specific questions were
13 addressed. (i) Do faunal transitions between seagrass and bare sediment
14 take the form of sharp ecotones or of more gradual ecoclines (*sensu* Attrill
15 and Rundle, 2002; Yarrow and Marín, 2007)? (ii) Do the two interacting
16 faunal assemblages react symmetrically to habitat change across the
17 interface? (iii) What is the effect of the transition on the magnitude and
18 spatial variation of local benthic abundance and biodiversity?

19

20 **2. METHODS**

21 *2.1. STUDY AREA, SAMPLE COLLECTION AND PROCESSING*

22 Macrofaunal sampling was conducted over a period of 11 weeks during
23 the 2012 austral spring along the sheltered Rainbow Channel western coast

1 of North Stradbroke, a large (27,400 ha) sand-dune barrier island in the
2 relatively pristine Eastern Banks region of the oligohaline, sub-tropical
3 Moreton Bay Marine Park, Queensland (Dennison and Abal, 1999). The
4 Eastern Banks contain the majority of the Bay's 190 km² of seagrass
5 (Roelfsema et al., 2009) and support its greatest numbers of animal
6 species, including many southern outliers of the tropical Great Barrier Reef
7 fauna (Davie and Hooper, 1998). Here, for example, the seagrass is the
8 refuge and feeding ground for juveniles of many species of penaeid prawns
9 and fish as well as for green turtle and dugong (Weng, 1990; Davie et al.,
10 2011). In the specific area sampled, the beds are predominantly of the
11 dwarf-eelgrass *Nanozostera muelleri capricorni* (= *Zostera capricorni* =
12 *Zosterella capricorni*) with some *Halodule uninervis* (especially at lower shore
13 levels) and *Halophila ovalis*, and the seagrass extends from the sublittoral
14 right up into the mangrove zone amongst the seaward pneumatophores of
15 *Avicennia marina*, i.e. over an intertidal vertical height of half the tidal range
16 (i.e. over c. 1 m) and in places for a distance of >500 m. Typically, the
17 seagrass plants are of the smaller morphological forms characteristic of
18 shallow areas (Young and Kirkman, 1975). Also within the seagrass zone
19 are unvegetated areas of the fine- to medium-grained quartz sand that
20 comprises the island (Laycock, 1978), often occurring as a series of large
21 patches from about LWN to MSL. Such areas are structured by two
22 bioturbating decapods, the thalassinidean *Trypaea australiensis* and soldier
23 crab *Mictyris longicarpus*, both dependent on sedimentary diatoms
24 (Spilmont et al., 2009). The same sand, with or without a surface coating of
25 mud, underlies the upper-shore mangroves.

1 Data on the macrobenthic assemblages were collected from three sites
2 over a distance of 2.5 km centred on the Moreton Bay Research Station at
3 Dunwich — (a) Deanbilla, (b) Polka, and (c) Yerrol (Fig. 1) — roughly in the
4 middle of a virtually uninterrupted 25+ km long belt of seagrass. Precise
5 sampling sites were located where the margins of the seagrass beds
6 appeared neither to be advancing nor retreating to avoid possible
7 complications resulting from temporally transitional states. Advancing
8 seagrass was identified by lines of young plants extending out from the bed
9 and retreating seagrass by the occurrence of dead root-rhizome mats
10 beneath the surface of the adjacent bare sand. As advocated by Fortin
11 (1994), in all cases data were collected from two-dimensional lattices across
12 and along the bare sand/seagrass interface (see Fig. 1). Six replicate
13 lattices were worked, each comprising 60 core samples in the form of 6
14 transects ('rows') worked parallel to the interface, at +0.75, +0.5, +0.25, -
15 0.25, -0.5 and -0.75 m from it (where '+' indicates seagrass and '-' indicates
16 unvegetated sand), and 10 core samples ('columns') taken at 1 m intervals
17 along each transect; this interval allowed for the high level of small-scale
18 spatial variability previously seen in such systems (Winberg et al., 2007;
19 Barnes and Ellwood, 2012). Interfaces were sampled at three intertidal
20 heights, near LWS, LWN and MSL, each replicated at two different sites
21 (LWS and LWN at both Deanbilla and Polka; MSL at Deanbilla and Yerrol).
22 At LWS and LWN the interfaces were between seagrass and unvegetated
23 open sandflat, and near MSL they were between seagrass and the sand
24 adjacent to the seaward zone of *Avicennia* pneumatophores. As noted at
25 other localities (e.g. Bryan et al., 2007; Carr et al., 2010), the boundary

1 between *N. m. capricorni* beds and blocks of unvegetated sand can be very
2 sharp, and the sites near LWS and LWN had such sharp boundaries (Fig.
3 2). The seagrass/ pneumatophore-field interface near MSL, however, was
4 mostly more diffuse, broken up into small patches, and with an extensive
5 overlap of up to 20 m, although in places the seagrass had its upper limit
6 as a sharp boundary immediately below the pneumatophore-zone edge and
7 it was in these areas that the two upper-shore lattices were located. With
8 one exception, all lattices were located in areas where large continuous
9 blocks (>0.5 ha) of the two habitat types met to avoid the potentially
10 confounding variable of patch size (Bowden et al., 2001; Mills and
11 Berkenbusch, 2009). However, as previously (Barnes and Barnes, 2012),
12 the core samples near MSL at Yerrol had to be located on the margin of a
13 patch of seagrass isolated from the lower shore bed by an intervening
14 stretch of bare sand. Coordinates of each lattice were taken by means of a
15 hand-held GPS+GLONASS unit (with a stated accuracy of 3 m). To
16 compare transitional zone assemblages and those from within the main
17 blocks of the relevant habitat types, equivalent data on the nature of faunal
18 assemblages at each locality >4 m away from any boundary zone were
19 extracted from the earlier database of Barnes and Barnes (2012). These
20 data were from samples taken 12 months previously, also from transects of
21 10 replicate cores.

22 All core samples were of 54 cm² area and 10 cm depth on the basis
23 that (a) most benthic macrofauna in seagrass is known to occur in the top
24 few mm of sediment (e.g. 98% in the top 5 mm in the study by Klumpp and

1 Kwak, 2005), and (b) earlier work (Barnes and Ellwood, 2012) had
2 suggested that 10 replicates of that surface area would yield an acceptable
3 standard error <17.5% of the arithmetic mean in estimation of local
4 macrofaunal abundance. This sampling procedure collects the smaller and
5 most numerous members of the macrofauna that constitute the large
6 majority both of invertebrate biodiversity (Albano et al., 2011) and of the
7 food of the commercially-significant juvenile nekton (O'Brien, 1994), but not
8 the scarcer megafauna or the deeply-burrowing species that include the
9 ecosystem bioengineers *Trypaea* (that burrows down to depths of 1m) and
10 *Mictyris* (that vacates its burrow during the first part of low tide), although
11 juveniles of both species were frequently obtained. Trampling adversely
12 impinges on seagrass systems (e.g. Eckrich and Holmquist, 2000) and
13 hence great care was taken to cause minimal disturbance to the site,
14 particularly to areas to be sampled on future occasions.

15 Collection and treatment of these core samples essentially followed the
16 same standard procedure as earlier studies of macrofaunal assemblages
17 associated with *Nanozostera* beds both within the North Stradbroke
18 intertidal (e.g. Barnes and Barnes, 2011, 2012) and elsewhere (e.g. Barnes
19 and Ellwood, 2011; Barnes, 2013). Cores were collected at low tide, soon
20 after tidal ebb from the sites, and these were gently sieved through 710 μm
21 mesh on site. All sieved samples were immediately transported to a local
22 laboratory, where each was placed in a 30 x 25 cm white tray in which the
23 living fauna was located by visual inspection and was counted; the time
24 interval between collection and analysis of any given batch of samples never

1 exceeding 24 hours. This continued until no further animal could be seen
2 during a 3-minute period. Animals were identified to species level wherever
3 possible, with nomenclature as listed in the World Register of Marine
4 Species (WoRMS, www.marinespecies.org). Several taxa, however, although
5 relatively important in Moreton Bay, have not yet been investigated
6 systematically in southern Queensland (Davie and Phillips, 2008) and their
7 identification to named species poses 'enormous problems' (Davie et al.,
8 2011, p. 8). Such animals were treated as morphospecies, an operationally
9 appropriate procedure to detect spatial patterns of numbers of species and
10 their differential abundance (Dethier and Schoch, 2006; Albano et al.,
11 2011). The number of seagrass shoots in each sample was also recorded,
12 but sessile macrofauna attached to the seagrass leaves was not.

13 2.2. STATISTICAL ANALYSES

14 Raw data on numbers of each component species in the various
15 sampling horizons at different distances from the actual interface were
16 subjected to similarity analysis and various assemblage metrics were
17 derived and compared across the same distances, both univariately by
18 ANOVA and via spatial analyses. Assessment of faunal similarity and of
19 univariate changes in biodiversity metrics were carried out via *EstimateS*
20 8.2.0 (Colwell, 2011; Colwell et al., 2012). Given the high proportion of rare
21 species in the local seagrass fauna [29% of the 184 species obtained from
22 the boundary zone were represented by single individuals, and a further
23 14% by doubletons], estimates of total numbers of species (S_{max}) per unit
24 area (i.e. of species density *sensu* Gotelli and Colwell, 2001) were derived

1 from the observed numbers of species (S_{obs}) and their differential
2 abundance. Different estimators of true species density yield different
3 results, hence each value of S_{max} was obtained by taking the mean of three
4 disparate *EstimateS* measures: Chao-2, Michaelis Menten Means, and
5 Abundance-based Coverage, using, where appropriate, the bias-correction
6 formula for Chao-2 and an upper abundance limit of 5 for infrequent
7 species for the Abundance-based Coverage estimator. To permit
8 quantitative comparison (Jost, 2006), both α and γ species diversities were
9 assessed as the linear 'effective number of species' by the reciprocal of the
10 Hill (1973) N_2 . Also because of the high probability of absence of species
11 present at low population density from any given sample, changes in
12 quantitative faunal composition (β -diversity) across adjacent transitional
13 horizons were estimated by the Chao et al. (2005; 2006) abundance-based
14 Sørensen (Bray-Curtis) (dis)similarity statistic, as modified to correct for
15 undersampling bias, again with a set upper abundance limit per sample for
16 rare species of 5. This modification substantially reduces the negative bias
17 of traditional similarity indices, especially when samples from species-rich
18 assemblages are likely to be incomplete (Chao et al., 2005). Estimated
19 numbers of shared species between different assemblages were likewise
20 obtained from Chao et al.'s (2000) coverage-based estimator. Univariate
21 comparison of these assemblage metrics at various distances from the
22 interface, i.e. species density, total faunal abundance and dissimilarity,
23 used one-way or two-way ANOVA after $\ln[x+1]$ transformation of data,
24 followed by post-hoc Tukey HSD tests where applicable.

1 Spatial analyses were executed using a combination of GeoDa
2 software and the Geostatistical Analyst tools within ArcGIS10. Spatial
3 statistical techniques employed were cross-scale trend analysis, calculation
4 of the global Moran's *I* statistic at both local and regional scales, and
5 calculation of a semivariogram and associated semivariogram surface for
6 each lattice. Trend analysis was undertaken to ascertain whether
7 transitions in the four assemblage metrics could accurately and
8 consistently be captured in a simple spatial model. Trends were explored at
9 both local (lattice) and regional (all sites) scales by plotting values of the
10 metrics along an axis representing distance from the bare sand/seagrass
11 interface. Local scale analysis examined mean values from all sites along
12 the transition axis, whilst regional scale analysis retained the relative
13 geographical positions of each site. A series of models was developed
14 (linear, first, second and third order polynomial) to express the observed
15 changes in each metric at both regional and local scales. The accuracy of
16 each model was expressed as the percentage of variation of the observed
17 distribution explained by the model (R^2). To assess cross-scale consistency
18 in models, the most accurate model type was recorded at both local and
19 regional scales.

20 To assess the strength of spatial relationships between the
21 macrofaunal assemblages, the global Moran's *I* statistic was calculated on
22 each of the four metrics as a measure of spatial autocorrelation between
23 point sample locations. This was calculated for specified distance classes
24 as the cross product for a given assemblage metric at points across a

1 defined neighbourhood such that only the pairs of points within a specified
2 distance class of each point location were taken into account (Hamylton,
3 2013). This yields a large positive I in the presence of positive spatial
4 dependence, a large negative I in the presence of negative spatial
5 dependence, and values close to zero with a random assemblage
6 distribution. Spatial autocorrelation was also assessed at the local scale by
7 generating a semivariogram for each lattice. This calculated Geary's C
8 statistic on the total number of individuals sampled to assess similarity for
9 every possible combination of pairs of sample points across each lattice grid
10 (Hamylton, 2013). Geary's C measures correspondence for a given distance
11 class on the basis of the squared difference of a particular characteristic
12 between pairs of point locations, and ranged from 0 to some unspecified
13 value larger than 1. Values of Geary's C were then plotted against the
14 distance between points to generate a semivariogram exploring the
15 magnitude and spatial configuration of locally-measured autocorrelation
16 plotted across the map. The distance at which Geary's C levelled off and no
17 further increase in the statistic was observed as the distance between point
18 pairs increased, the sill point, was recorded for each semivariogram. This
19 corresponds to a given distance range beyond which there was no spatial
20 autocorrelation. Finally, a semivariogram surface was generated to map
21 the value of the Geary's C across each lattice as a localized measure of
22 assemblage metric similarity in geographical space. To account for the
23 anisotropic effect across the tidal axis, a search direction of 90° was used to
24 define the neighbourhood of each point. The surface was generated using
25 an interpolation technique that combined values in the semivariogram plot

1 into bins based on the direction and distance between pairs of point sample
2 locations. Binned values were then averaged and smoothed to produce the
3 semivariogram surface.

4

5 **3. RESULTS**

6 Faunal assemblages of the adjacent 0.75 m wide boundary zones on
7 either side of the interface between seagrass and unvegetated sand at each
8 lattice showed markedly different abundance and species density (all one-
9 way ANOVA $F_{1,34} > 60$; $P < 0.0001$). Overall, the marginal strip of seagrass
10 supported an observed total of 168 species (estimated true total 220) at an
11 overall abundance of 2,430 ind. m⁻² and a γ -diversity of 16.0. The abutting
12 marginal strip of sand, in contrast, supported only 61 observed species
13 (estimated true total 78), 750 ind. m⁻², and a γ -diversity of 11.6. Even
14 though contiguous, the two assemblages shared only 24% of their observed
15 total fauna and only 44% of their higher-level taxa (at the level of
16 suborder/superfamily). The relative richness of the seagrass assemblage
17 was not a consequence of its greater abundance (Gotelli and Colwell, 2001)
18 since the number of species per macrobenthic individual within the seagrass
19 was always considerably larger than that in the unvegetated sand (at a ratio
20 of 1 : >1.5) (Fig. 3a). Per unit area the ratio was close to 1 : 2.7. The
21 seagrass-edge assemblage was dominated numerically by the rissoiid
22 *Calopia imitata* (434 m⁻²), grapsoid *Enigmaplax littoralis* (300 m⁻²),
23 phoxocephaloid *Limnoporeia* sp. (191 m⁻²), buccinoid *Nassarius burchardi*
24 (109 m⁻²) and apseudoid *Longiflagrum caeruleus* (100 m⁻²), which were the

1 only species to contribute $\geq 4\%$ of the total individuals. In the unvegetated
2 sand the same percentage was contributed by each of the haustorioid
3 *Urohaustorius mertungi* (174 m^{-2}), grapsoid *Mictyris longicarpus* (65 m^{-2}),
4 galeommatoid *Mysella vitrea* (61 m^{-2}), cerithioid *Finella fabrica* (47 m^{-2}),
5 veneroid *Eumarcia fumigata* (42 m^{-2}), phyllodocidan and scolecidan *Goniada*
6 *?tripartita* (39 m^{-2}), *Leitoscoloplos ?normalis* (34 m^{-2}) and *Nephtys* spp (33 m^{-2}).
7 2), oedicerotoid *Doowia dexterae* (32 m^{-2}) and spionidan *Spio pacifica* (31 m^{-2}).
8 The rank-abundance curves of both assemblages, but particularly of that in
9 the seagrass, were of the concave form (Fig. 3b) characteristic of a number of
10 benthic marine systems (Hughes, 1984; and see Hubbell, 1997).

11 One-way ANOVA comparisons of the abundance of the dominant
12 species in the marginal and in the non-edge areas of their respective habitat
13 types did not show any significant differences in unvegetated areas of sand,
14 except in respect of *Finella* which was more abundant in the marginal sand
15 zone than in the main sandflat (ANOVA $F_{1,22} = 4.9$; $P = 0.04$). In the seagrass
16 beds, several animals (including *Calopia*, *Limnoporeia*, *Longiflagrum* and the
17 paratanaoid *Leptochelia*) showed greater abundance at the seagrass edge at
18 some sites but were less abundant marginally at others. Tanaids, for
19 example, were five times more abundant near some edges, but only half as
20 dense at others. Overall, the 25 peracaridan species present were more
21 abundant at the edge at half the sites but were less abundant at the other
22 half. The most numerous seagrass inhabitant, *Calopia*, was also more
23 abundant near edges at two sites, but was less so at two others. On average,
24 the locality's 33 rissoid and other microgastropod species were less

1 abundant at the edge at two-thirds of the sites and overall were only half as
2 abundant marginally, although the effect was not statistically significant.
3 Only in respect of the rissoid *Pseudoliotia* was there a significant difference
4 overall (ANOVA $F_{1,22} = 13.1$; $P = 0.001$), this microgastropod being less
5 abundant near the seagrass margins.

6 Regardless of site and of shore height, all six lattices displayed the
7 same pattern of distribution of both assemblage dissimilarity between
8 adjacent sampling horizons and changes in overall abundance and species
9 density across the boundary zone. Variation in quantitative assemblage
10 composition between adjacent sampling horizons (i.e. β -diversity) is shown in
11 Table 1. There was effectively no change between horizons within each of
12 the two marginal habitat blocks and no interactions with shore height (two-
13 way ANOVA all $F_{2,2,4} < 2.5$; $P > 0.1$), but a marked and highly significant
14 increase in dissimilarity occurred across the 25 cm wide strip on either side
15 of the actual interface. The mean value of the dissimilarity statistic within
16 each habitat block was 0.10 (SE 0.02) and between the main body of the
17 habitat type and its margin was 0.19 (SE 0.04), with in each case no
18 difference between the values within seagrass and within the sand (within
19 marginal zone ANOVA $F_{1,22} = 0.22$, $P > 0.6$; marginal *vs* non-marginal ANOVA
20 $F_{1,10} = 0.21$, $P > 0.6$). On either side of the interface the mean dissimilarity
21 statistic rose to 0.56 (SE 0.04).

22 Variation across the boundary zone in faunal abundance, observed
23 and estimated true species density, and levels of α -diversity is shown in
24 Figure 4a-c. Two-way ANOVA tests of these features in the seagrass

1 marginal horizons and in the unvegetated sand margins indicated no
2 significant effect of distance of the sampling horizon from the interface on
3 any assemblage metric, and no significant interaction between this distance
4 and position on the shore (All seagrass $F_{3,2,6} < 1.2$, $P > 0.3$. All unvegetated
5 sand $F_{3,2,6}$, except α -diversity, ≤ 0.6 , $P > 0.6$; α -diversity $F = 3.3$, $P = 0.06$). In
6 each case, this included comparisons between the marginal zone and the
7 non-edge area of the habitat concerned. As previously noted at these sites
8 (Barnes and Barnes, 2012), values of the $1/N_2$ α -diversity metric were very
9 variable (see Fig. 4c).

10 In marked contrast to the constancy within each of the marginal
11 habitat zones, however, and as seen above in assemblage composition (Table
12 1), there were highly significant differences in faunal abundance and
13 observed and estimated true species density (though not α -diversity) between
14 adjacent horizons across the 25 cm wide strip on either side of the actual
15 interface (Table 2), where a very sharp change in seagrass abundance also
16 occurred (Fig. 4d). Each of the four seagrass horizons was significantly
17 different from each of the four unvegetated-sand horizons in both faunal
18 abundance and species density (all Tukey HSD test statistics ≥ 6 ; $P \leq 0.003$).
19 Therefore, effectively all the dramatic change in composition, abundance and
20 species density between the faunal assemblages of seagrass and of adjacent
21 unvegetated sand took place over the very small distance of 0.5 m at most.
22 Categorising the component assemblage species as either 'seagrass
23 specialist', 'unvegetated-sand specialist' or 'generalist', on the basis of
24 whether their abundance in the two habitat types was greater or less than a

1 ratio of 1 : 2.5, and removing all rare species (those with ≤ 5 individuals in
2 total) from the analysis, the two assemblages reacted symmetrically to the
3 interface (Fig. 5). Total abundance of the generalist category (principally
4 *Nephtys*, *Goniada*, *Spio* and *Mysella*) was unaffected by the transition. As a
5 result of the difference in overall abundance, however, these four taxa were
6 significant elements in the fauna of the unvegetated sand (see above) but not
7 in that of the seagrass.

8 Figure 6 illustrates a plot of the four assemblage metrics at the local
9 and regional scales. Spatial trends in the metrics were captured accurately
10 at both scales (local $R^2 = 0.87-0.93$; regional $R^2 = 0.71-0.74$) using second
11 and third order polynomial regression models, although local-scale models
12 consistently performed better than regional-scale ones. In terms of cross-
13 scale comparisons, the highest performing model type remained consistent
14 transitioning from the local to the regional scale. The metric modelled with
15 the highest accuracy at each scale was α species diversity.

16 Global Moran's I statistics calculated for all sites together and for each
17 individual lattice are shown in Table 3. Three of the four metrics (faunal
18 abundance and the two species density measures) exhibited significant
19 positive spatial autocorrelation of moderate strength ($I = 0.16$ to 0.44),
20 although α species diversity mostly showed weaker levels of autocorrelation
21 that approximated a randomly distributed community ($I = -0.18$ to 0.11).
22 The semivariogram surfaces (Fig. 7) indicate a symmetrical pattern of
23 autocorrelation about the bare-sand/seagrass interface at all sites. With the
24 exception of the Polka LWS site that showed by far the smallest maximum

1 sill points (30 cm) and most uniform distribution of spatial autocorrelation
2 values, lattices displayed low levels of autocorrelation close to the interface
3 (i.e. sill points of c. 30 cm – less than the distance apart of sampling points
4 across the interface) and higher levels within each of the two abutting
5 habitat types (i.e. sill points of c. 40-75 cm, *c.f.* the interval between
6 sampling points of 25 cm there) (Fig. 7).

7 Since the potential effect of positive spatial autocorrelation on the
8 reliability of the ANOVAs above will be to increase the chance of Type I errors
9 (Legendre, 1993; Dale and Fortin, 2002), its only effective occurrence in the
10 data nested within each of the abutting habitat types will result in it having
11 no adverse influence on our statistical conclusions. No relevant null
12 hypotheses involving within-habitat comparisons were rejected, and the
13 rejected cross-habitat null hypotheses were all based on data lacking
14 significant spatial autocorrelation.

15

16 **4. DISCUSSION**

17 Although the precise faunal assemblages present in the seagrass and
18 bare sand near Dunwich vary significantly from location to location and
19 those in the seagrass also vary up the shore (Barnes and Barnes, 2012), the
20 same three features of interfaces between these two habitat types stand out
21 regardless of site and shore height, i.e. occurred in all six lattices. First, the
22 faunal assemblages of the marginal zone of both seagrass and unvegetated
23 sand in each lattice not only did not vary with closeness to the actual

1 interface but were not significantly different from those present locally away
2 from the edges of their respective habitat types. Secondly, as in the main
3 habitat areas (Barnes and Barnes, 2012), the assemblages immediately on
4 either side of the interface were very different, with the seagrass supporting
5 both greater animal numbers (>3 x) and species densities (>2.5 x). Only a
6 few generalist species were common to both (some 10% of the total). All
7 marginal seagrass horizons were significantly different from all marginal
8 sandflat ones in composition, faunal abundance and species density. Hence
9 there must be a very abrupt change from one assemblage type to the other
10 across the interface. Thirdly, that this was accomplished over a distance of
11 only 0.5 m at most is unexpected; although Warry et al. (2009) have shown
12 that 0.5 m is a large distance for seagrass harpacticoids and other
13 meiofauna. Local ecological changes over small distances are commonplace
14 in seagrass systems (Thrush et al., 2001; Barnes and Ellwood, 2012) but the
15 changes taking place over 0.5 m here are far from local, occurring at all
16 shore heights investigated and at all localities. Attrill and Rundle (2002, p.
17 929) define an ecotone (as distinct from an ecocline) as ‘an area of relatively
18 rapid change, producing a narrow ecological zone between two different and
19 relatively homogeneous community types’: the boundary zone and
20 assemblage types studied here exactly fit this definition. Although Hansen
21 and di Castri (1992) consider that ecotones can range in width from
22 distances measured in centimetres to those measured in kilometres, the
23 dimension of this ecotone must be one of the smallest ever recorded in
24 association with a major change from one ecosystem bioengineer to another
25 in what is otherwise essentially the same substratum type. Walker et al.

1 (2003), for example, considered an ecotone width of 4 m to be a ‘sharp’
2 boundary, and to Kingston and Morris (2000) one less than 20 m is ‘abrupt’.
3 Unlike most other transitional zones (Rand et al., 2006; Kark, 2013), that
4 between seagrass and unvegetated sand on Stradbroke certainly does not
5 appear to support mixed faunal assemblages enriched by elements from both
6 juxtaposed habitat types and to display peak local species density and
7 faunal abundance. Mean species diversity was indeed largest in this region
8 (Fig. 6d), although here this indicates a more even allocation of total
9 individuals between the few species present rather than increased numbers
10 of faunal elements (Magurran, 2004; Barnes and Barnes, 2012).

11 There are a number of potential reasons why the Stradbroke
12 seagrass/sandflat ecotone might be of such particularly small width. The
13 interfaces chosen for study were deliberately those that appeared stable, and
14 therefore those in actively advancing or retreating boundary zones may well
15 be more extensive. Much may also depend on the precise habitat provided
16 by the marginal seagrass areas (van Houte-Howes et al., 2004; Tuya et al.,
17 2011). At the sites investigated, there was no diminution in the number of
18 seagrass shoots per unit area as the interface was approached (see Figure
19 4d), and maintenance of a relatively constant habitat framework — water
20 velocities excepted (see below) — right up to the interface itself may well aid
21 continuation of relatively constant assemblage characteristics until that
22 point. Thirdly, the two assemblages are dominated by organisms of
23 contrasting biology: the seagrass fauna being largely epifaunal and that of
24 the unvegetated sand being mainly infaunal (Barnes and Barnes, 2012). It is

1 well established (Orth et al., 1984; van Houte-Howes et al., 2004; etc) that
2 seagrass root/rhizome systems inhibit burrowing, whilst the lack of a plant
3 cover can expose surface-dwelling species to heavy predation. Such
4 contrasting assemblages are not universal, however. Differences between
5 seagrass and adjacent sand assemblages, and hence changes across
6 seagrass/sand boundaries, in high-latitude, high-abundance but low
7 biodiversity regions such as the north-west Atlantic, for example, have in
8 contrast been shown to be less significant (Asmus and Asmus, 2000; Polte et
9 al., 2005; Barnes, 2010). Bray-Curtis similarity between seagrass (*N. noltii*)
10 and muddy-sand assemblages at a 52°N site that supported a combined
11 fauna of 33 species at overall densities of >50,000 ind. m⁻², for example, was
12 >0.8 (RSK Barnes, unpubl.); *c.f.* the equivalent Stradbroke value of 0.13. In
13 temperate *N. m. capricorni* systems at 36°-37°S in New Zealand, van Houte-
14 Howes et al. (2004) also found little difference between overall faunal
15 abundance, species density and species diversity in the seagrass and in the
16 unvegetated sediment, and noted that differences in assemblage composition
17 between the two were due mainly to differential abundance.

18 Thrush (1991) noted that spatial autocorrelation in variables that
19 capture the biodiversity of macrobenthic assemblages has the potential to
20 confound experimental designs and to affect the reliability of inferential
21 statistics that may be used to assess distribution patterns. For example, the
22 presence of spatial dependence can result in a violation of the statistical
23 assumption of independence of observations. Tobler's (1970) First Law of
24 Geography, that objects closer together tend to be more similar than those

1 further apart, has repeatedly been found to apply to point sample datasets of
2 ecological communities (Fortin and Dale, 205), although critically not here
3 across the seagrass/bare-sand interface. Granted the considerable
4 differences between values of the studied assemblage metrics in seagrass
5 and in unvegetated sand, it is hence no surprise that moderate
6 autocorrelation was detected within each boundary zone in three of the four
7 metrics (i.e. in faunal abundance and both species density measures). In
8 contrast to the other metrics, however, α species diversity showed
9 remarkable and generally consistent resistance to autocorrelation at all sites.
10 This might be taken to suggest that $1/N_2$ could potentially be a good
11 resistant measure of biodiversity for benthic studies, albeit one strongly
12 biassed towards the evenness component. That this is not so, however, is
13 suggested by the very large degree of scatter in this metric seen in both this
14 (Fig. 4c) and the earlier study of the sites by Barnes and Barnes (2012).
15 Indeed, despite the very marked changes in habitat type, in assemblage
16 composition, in overall faunal abundance and in species density across the
17 interface, the $1/N_2$ metric failed to detect any significant change in
18 biodiversity there. Its resistance could simply be a measure of its
19 insensitivity (see Magurran and Henderson, 2010).

20 It is also noteworthy that the results of this study do not show large
21 straight-forward and consistent edge effects. Earlier work on the response of
22 benthic animals to the edges of seagrass beds has produced a complicated
23 picture (Ries and Sisk, 2004), reactions seemingly varying from group to
24 group (Murphy et al., 2010) and from study to study (Tuya et al., 2011) or

1 not even occurring at all (Nakaoka & Toyohara, 2000). The most consistent
2 effect has been claimed to be the greater densities of peracaridan
3 crustaceans (including tanaids) found at edges than away from them
4 (Boström et al., 2006). Nevertheless, in Port Phillip Bay, Victoria, tanaids
5 increased in abundance away from the edge, and the effect in other
6 peracaridans was dependent on size of patch investigated (Murphy et al.,
7 2010). In the present study, tanaids were more abundant near the edge at
8 some sites but were less so at others, as indeed were peracaridan
9 crustaceans in general, and microgastropod species displayed the same
10 pattern although overall they were only half as abundant marginally. In the
11 Stradbroke intertidal, only one animal (the microgastropod *Pseudoliotia*)
12 showed a consistent reaction. Little previous work has concerned small,
13 fragile, epibenthic microgastropods such as *Calopia* and *Pseudoliotia* —
14 forms that dominate the Stradbroke seagrass patches away from edges
15 (Barnes and Barnes, 2011, 2012; Barnes and Ellwood, 2012). But as water
16 velocities are known to be higher near seagrass margins (Peterson et al.,
17 2004; Murphy et al., 2010), it is perhaps not surprising that some species,
18 such as *Pseudoliotia*, should be less abundant and widespread under the
19 more turbulent conditions near the interface, maybe via effects on their
20 recruitment (Bologna and Heck, 2002; Matias et al., 2013) or because of
21 dislodgement (Tuya et al., 2011). In addition, small, fragile animals may be
22 at greater risk from predators when relatively exposed (Kark and van
23 Rensburg, 2006; Barnes, 2010). Generally, however, it would appear that
24 edge effects are a variable local response to specific habitat conditions within

1 patch margins rather than a consistent effect of closeness to an interface
2 with a different habitat type.

3 Winberg et al. (2007) have highlighted the value of examining multiple
4 measures of macrobenthic biodiversity across a variety of spatial scales. The
5 present study has examined spatial patterning in quantitative assemblage
6 composition and in four assemblage metrics at the local (lattice) and regional
7 (all sites) scales traversing spatial dimensions ranging over 5 orders of
8 magnitude from 0.25 m to 2.5 km. Significantly, the emergent assemblage
9 features captured in each of the four metrics could accurately and
10 consistently be characterised across scales as second and third order
11 polynomial regression models. Such models further our understanding of
12 how communities are organised in space (Peres-Neto and Legendre, 2010)
13 and can be used as a basis for predicting community composition at
14 unsampled locations within the spatial extent of the sample lattice, for
15 example, underpinning interpolation techniques such as kriging. As is the
16 case with all interpolation (as opposed to extrapolation) methods, predictive
17 values should not be generated outside the geographical area within which
18 the model parameters were defined by the trend analysis.

19 Overall, we conclude that faunal transitions across stable bare
20 sand/seagrass boundaries in Moreton Bay take the form of very narrow
21 ecotones indeed, across which the two assemblages react symmetrically,
22 with the actual interface being the location of the entire change in faunal
23 abundance and biodiversity observed between the contrasting patch types.
24 However, this state seems unlikely to be a necessary response to changes in

1 the prevailing habitat conditions *per se* and more likely to be a specific
2 consequence of the two low-latitude, low-abundance but high-biodiversity
3 faunal assemblages that are interacting here (or of the key members of those
4 assemblages), in that such marked quantitative and/or qualitative changes
5 in assemblages do not necessarily occur across intertidal bare
6 sediment/*Nanozostera* bed boundaries elsewhere, e.g. in lower latitudes.

7

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- 7

1 Table 1. Changes in assemblage composition across adjacent sampling
 2 horizons on either side of seagrass/unvegetated-sand interfaces, as
 3 estimated by the Chao/Sørensen abundance-based dissimilarity statistic,
 4 corrected for undersampling bias (estimated complete similarity = 0;
 5 estimated complete dissimilarity = 1). Positive horizon distances are in
 6 seagrass, negative ones in unvegetated sand, the interface itself being zero.
 7 The sharp change between +0.25 and -0.25 m from the interface (in bold) is
 8 highly significant (post-hoc Tukey HSD statistic >12; $P < 0.0001$).

9

10 Sampling horizons being compared (in metres from interface)

11 >+4 to +0.75 to +0.5 to +0.25 to -0.25 to -0.5 to -0.75 to
 12 Site +0.75 +0.5 +0.25 -0.25 -0.5 -0.75 >-4

13

14 Deanbilla MSL 0.03 0.03 0.08 **0.70** 0.01 0.19 0.43

15 Yerrol MSL 0.18 0.10 0.10 **0.56** 0.23 0.25 0.08

16 Polka LWN 0.34 0.00 0.18 **0.50** 0.12 0.04 0.04

17 Deanbilla LWN 0.16 0.00 0.08 **0.51** 0.09 0.05 0.19

18 Polka LWS 0.16 0.00 0.04 **0.43** 0.07 0.02 0.09

19 Deanbilla LWS 0.35 0.28 0.20 **0.67** 0.00 0.23 0.18

20

1 Table 2. Summary of post-hoc Tukey HSD tests on various macrofaunal
 2 assemblage metrics immediately on either side of the unvegetated sand/ seagrass
 3 interface (i.e. 0.5 m apart). Significant effects are indicated in bold.

4

5	Emergent property	test statistic	<i>P</i>
7	Faunal abundance	6.87	<0.001
8	Observed species density	9.62	<0.0001
9	Estimated true species density	6.49	<0.001
10	α -diversity	0.16	1

11

12

13

1 Table 3. Global Moran's I statistic calculated on mean assemblage metrics at
 2 the local (individual sites) and regional (all sites) scales. Significant effects (at
 3 $P < 0.05$) are indicated in bold.

4

5	Site	Abundance	S_{max}	S_{obs}	α -diversity
7	Deanbilla MSL	0.37	0.22	0.26	-0.18
8	Yerroil MSL	0.29	0.16	0.35	0.05
9	Polka LWN	0.21	0.41	0.44	0.11
10	Deanbilla LWN	0.37	0.29	0.37	0.04
11	Polka LWS	0.42	0.41	0.43	-0.2
12	Deanbilla LWS	0.26	0.29	0.37	-0.0009
13	All sites	0.44	0.38	0.43	0.26
14					
15					

1 Legends for Figures

2 1. Sampling locations, with inset showing the structure of the individual
3 core lattices.

4 2. Interface between intertidal seagrass and unvegetated sandflat at Polka.
5 Foreground width some 2 m.

6 3. (A) Mao Tau numbers of macrofaunal species in marginal areas of
7 seagrass and of unvegetated sandflat in relation to (a) cumulative number of
8 individuals sampled (squares) [i.e. species richness] and (b) cumulative area
9 sampled, as number of cores (circles) [i.e. species density]. (Sample
10 accumulation orders randomised 50 times.) (B) Ranked species abundance
11 curves.

12 4. The distribution of assemblage metrics across the sampling horizons on
13 either side of the interface between unvegetated sand (-) and seagrass (+) in
14 the six lattices: (A) mean macrofaunal abundance (\pm SE); (B) mean observed
15 (S_{obs}) and estimated true (S_{max}) species density (\pm SE); (C) macrofaunal α
16 diversity values; and (D) mean number of seagrass shoots per core sample (\pm
17 SE; $n = 60$). Values of macrofaunal abundance and species density away
18 from the transitional zone ($>+4$ and >-4) are shown for comparison in A and
19 B.

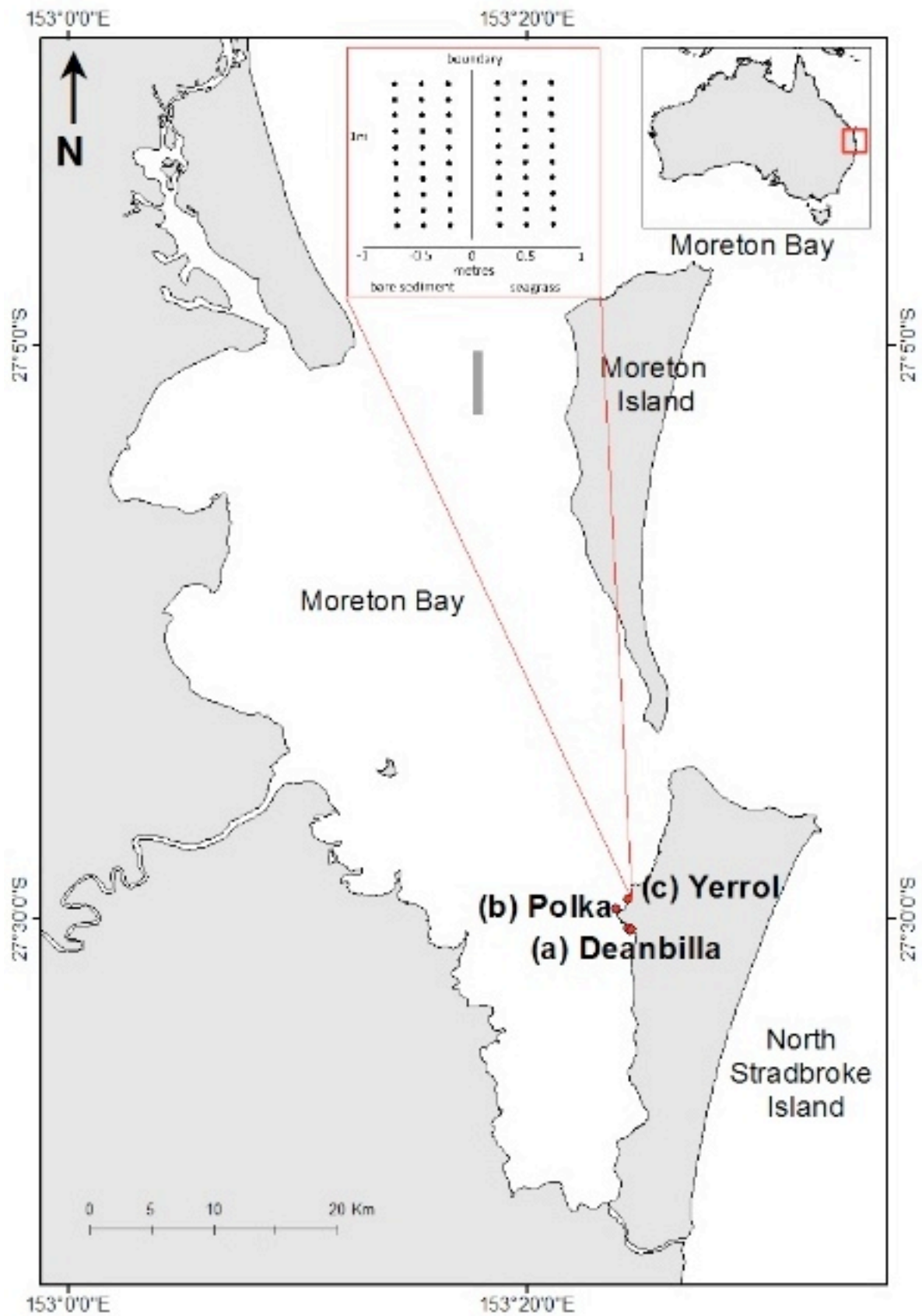
20 5. Percentage of maximum total abundance of seagrass specialist ($n = 55$),
21 bare-sand specialist ($n = 10$) and generalist ($n = 8$) macrofaunal species (as
22 judged by their local distributions) in each sampling horizon on either side of
23 the intertidal interface between unvegetated sand (-) and seagrass (+).

- 1 6. Spatial trend analysis plot of the assemblage metrics at the local (lattice)
2 and regional (all sites) scales. Mean values for each lattice are shown on the
3 left hand side and values are plotted in their geographical (x,y) locations on
4 the right hand side with the z axis depicting the value of the metric. The x
5 axis on both the local and regional plot is a proxy for distance from the
6 seagrass/bare-sand interface.

- 7 7. Semivariogram plots and surfaces constructed for the lattices at each site.
8 Stated sill points for each lattice are the maximum values at that site.

- 9

1 Figure 1



2

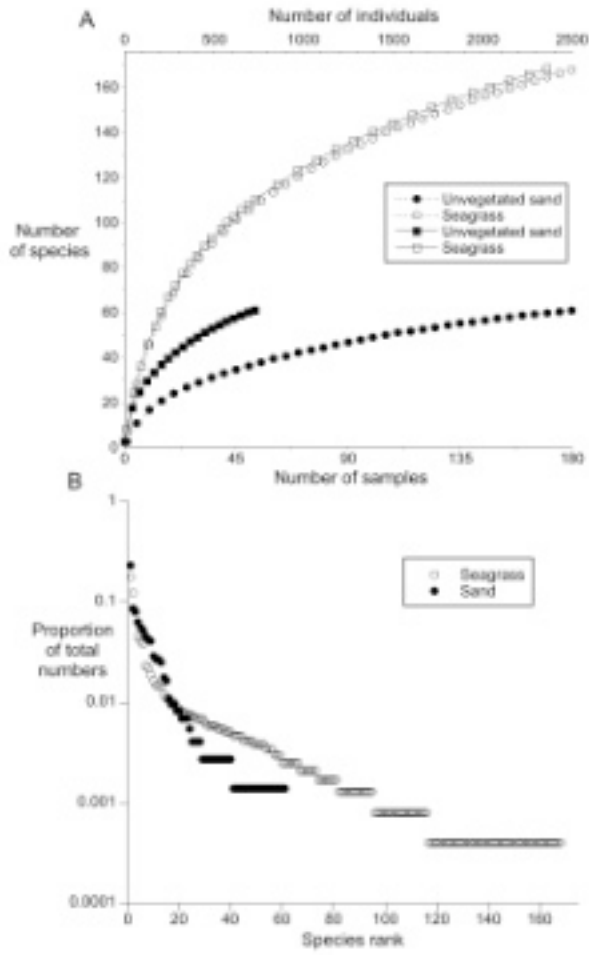
1 Figure 2



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3

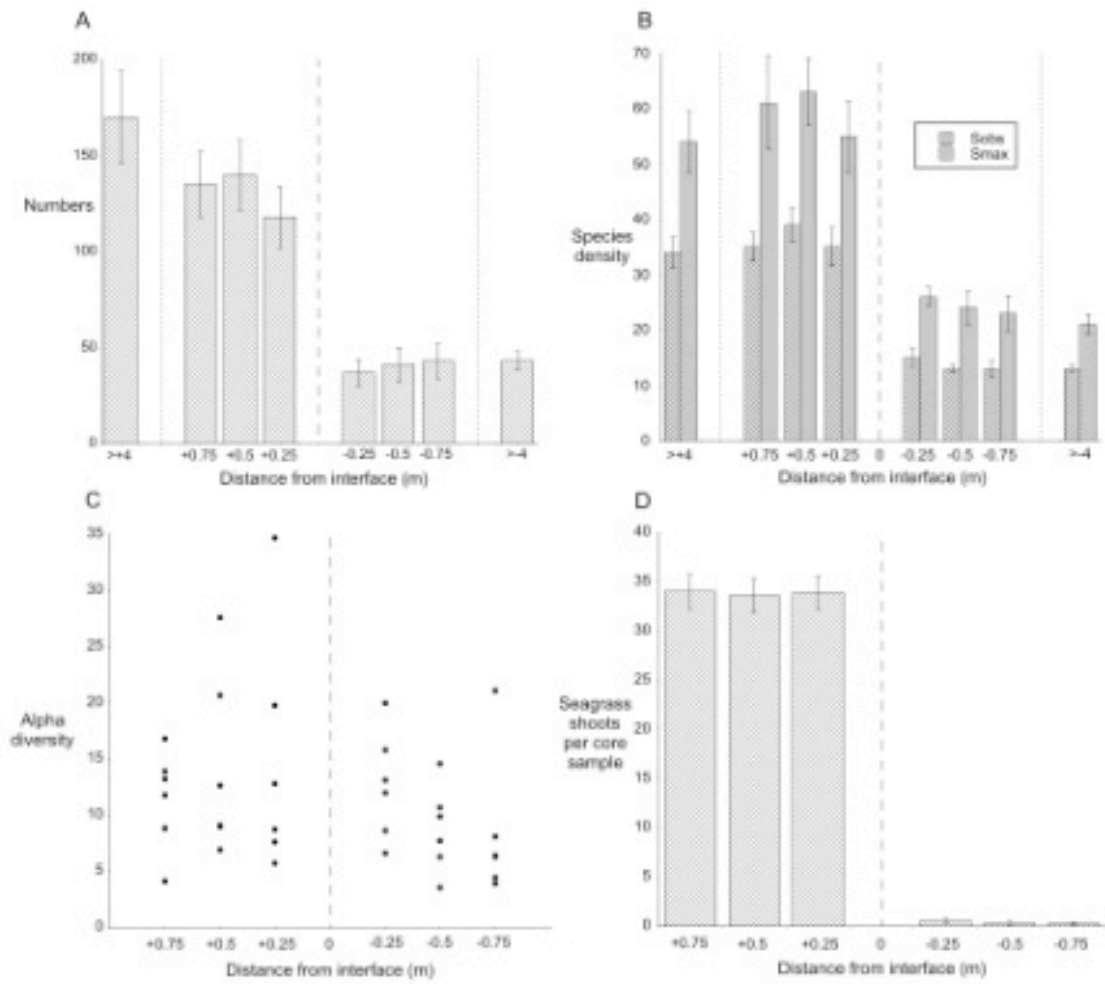
1 Figure 3



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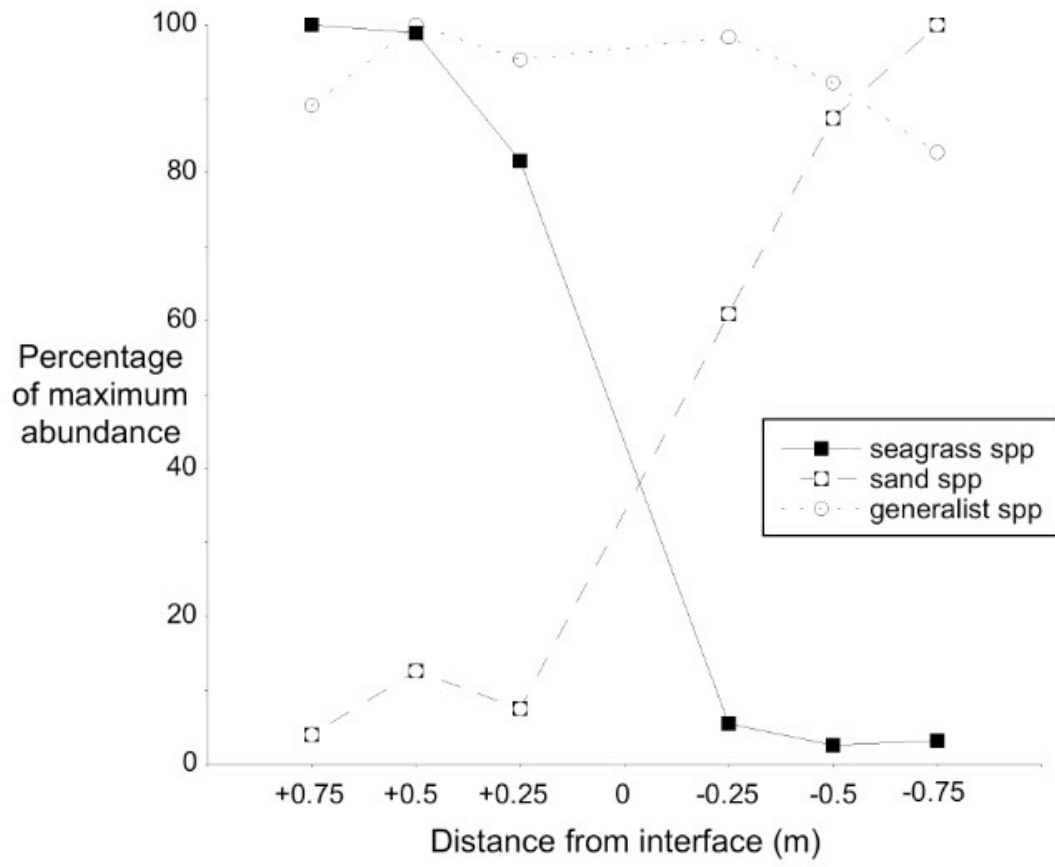
1 Figure 4



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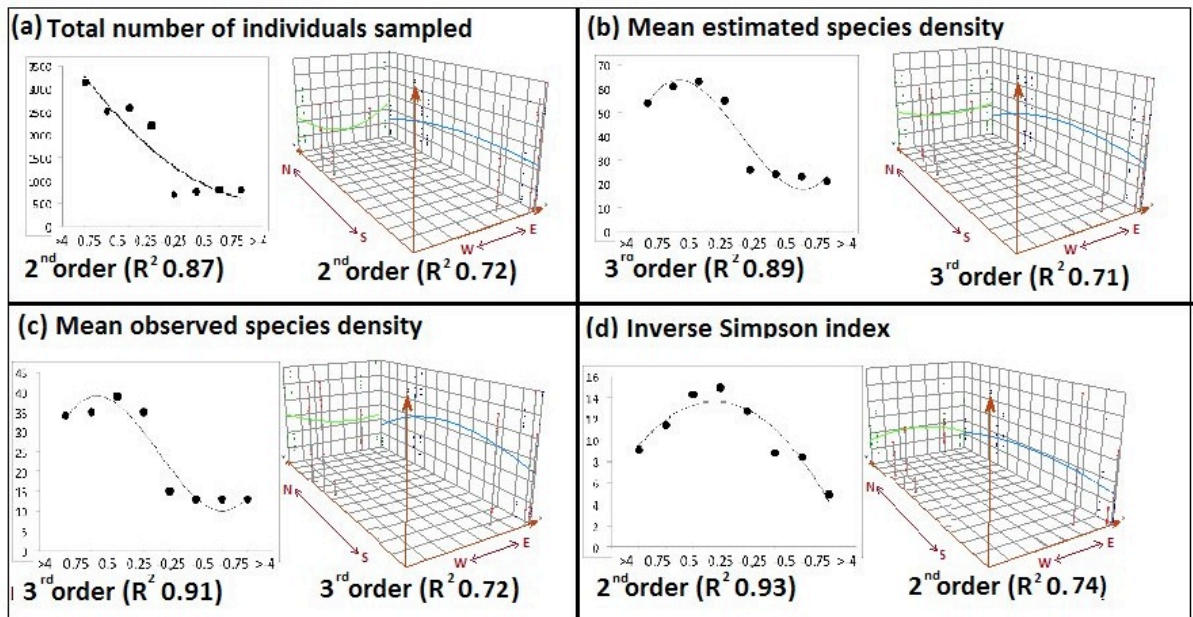
1 Figure 5



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1 Figure 6



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1 Figure 7

