Spatial structure on ocean-exposed sandy beaches: faunal zonation metrics and their variability

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ABSTRACT: Spatial ecological structure is expected to be amplified at interface regions, such as sandy beaches, which form the globe's largest ecotone between the oceans and the land. Yet, the dynamic and unstable nature of sandy shore habitats, coupled with the great mobility and behavioural plasticity of beach species, theoretically counteract the development and maintenance of stable spatial structure, such as faunal zonation across the intertidal. We examined spatial structure across the non-vegetated beach-face, using a large data set (3120 replicate samples distributed across 260 cross-shore transects) of intertidal macrobenthos distribution from eastern Australia. Most (94 %) distribution data of the benthic assemblage contained distinct spatial structure, evident as faunal zonation across the shore from the swash to the dunes. A general model recognised a tripartite biological division of the shore, but variability in the number of zones was pronounced. This variability implies that designs employing low temporal replication may fail to accurately describe the spatial structure on many ocean-exposed sandy beaches. Overall, our data support the prediction of distinct spatial structure based on the prominent interface traits of beach systems as well as the prediction of heterogeneity in spatial structure based on the mobility of beach species and instability of their habitat.

KEY WORDS: Spatial structure · Sandy shores · Zonation · Ecotones · Community dispersion

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INTRODUCTION

Detection, description and mechanistic understanding of spatial patterns lie at the heart of ecology, both historical and contemporary (Elton 1927, Brown 1995). Spatial heterogeneity in the distribution of genes, organisms, populations, and communities relates to a wide range of ecological and evolutionary processes; hence, the analysis of spatial patterns is integral to population biology and epidemics, food-web interactions, community dynamics, biodiversity studies, landscape ecology, and conservation biology (Legendre & Fortin 1989). Perhaps most fundamentally, theories of how ecosystems and communities are organized pivot on discovering predictable spatial patterns within and among systems, and these patterns can be a product of, and influence, evolutionary processes at multiple scales (Levin 1992).

Spatial patterns are amplified at ecotones, where steep gradients in environmental conditions and geo-biochemical processes promote the development of strong spatial structure at comparatively small scales (McClain et al. 2003, Ries et al. 2004). The largest interface regions between the biosphere's 2 largest domains—the oceans and continents—are marine shorelines. These coastal ecosystems, particularly rocky shores, have played a central role in understanding ecotone structures (Colman 1933, Stephenson & Stephenson 1949). 'Zonation', the sequence of bands across the rocky shore gradient where each band is biologically distinct (e.g. structure, colour, and species composition), is a prime example of spatial structure in ecology (Grosberg 1982, Foster 1990, Peterson 1991, Harley & Helmuth 2003). Identifying the mechanisms that determine this zonation has greatly influenced our conceptual and theoretical under-

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standing of fundamental ecological interactions, such as competition (Underwood 1984, Iveša et al. 2010) and predation (Paine 1974). This type of analysis examining patterns and drivers of spatial heterogeneity on intertidal shores continues unabated (Meager et al. 2011, Mislán et al. 2011, Valdivia et al. 2011).

Ocean-exposed sandy beaches form over 70% of ice-free coastlines, making them the geographically longest ecological interface region between marine and terrestrial biomes globally (Bascom 1980). Theoretically, sandy beach ecosystems have detectable spatial structure across the land-sea gradient. There has, however, been some debate about whether biological zonation on beaches is less distinct than on rocky shores (Brazeiro & Defeo 1996). Several properties of beach habitats and organisms can, arguably, make spatial structure less distinct and more variable than on rocky shores: (1) beaches are dynamic, malleable, and unstable habitats; (2) sandy beach organisms are mobile, continually re-adjusting their vertical and horizontal position; and (3) behavioural plasticity is a key trait of sandy beach organisms, and such plastic behaviour can result in variable distributions (McLachlan & Jaramillo 1995, Brown 1996, Schlacher et al. 2008b).

Expectations are that the unique features of beach systems—instability and variability of habitats combined with the plastic behaviour and mobility of organisms—result in indistinct, or at least variable, zonation structures: this is the core predictive hypothesis and justification for the present study. Specifically, we examined the zonation structure of sandy beaches in terms of 3 interrelated, thematic areas, set out in detail in Table 1: (1) 'zone metrics': the existence, number, and variability of biological zones and the species characterising such zones; (2) 'boundaries and consistency': the distinctiveness of faunal discontinuities and heterogeneity within faunal bands; and (3) 'environmental drivers': links between the spatial structure of habitat properties and species distributions.

MATERIALS AND METHODS

Study sites and field collections

The distribution of benthic invertebrates across the intertidal zone was quantified on 4 exposed sandy beaches located on the east coast of Australia (Fig. 1). The beaches are described in detail by Schlacher et al. (2008a). Briefly, they are typically of the intermediate morphodynamic type (Dean's parameter: 1.6 to

3.8), the intertidal zone spans 57 to 75 m from the base of the dunes to the swash and slopes relatively gently (2.1 to 2.6°), the sediments are composed mostly of medium-grained sands (272 to $371\ \mu\text{m}$), and all sites are fronted by 100 to 200 m wide surf zones with typical waves being 0.8 to 1.8 m high and breaking at a period of 12 to 20 s (Schlacher et al. 2008a). All 4 beaches are fully exposed to the predominant SE swell (Fig. 1). The driftline (i.e. band of accumulated wrack, carrion, and flotsam) is commonly located at the base of the dunes. However, all beaches receive only very small amounts of stranded material, usually making the driftline much less distinct than on beaches with large deposits of drift algae or seagrass.

Field collections

Biological distribution patterns were recorded by sampling the benthic fauna from 12 levels spread across 5 replicate transect lines (30 m apart along the shore) that ran from the base of the foredunes to the swash. The distance between the 12 sampling levels was adjusted to cover the entire intertidal zone, but was usually 5 to 7 m. At each level, 5 core samples (inner diameter: 15.4 cm; depth: 30 cm) were taken and pooled. Placement of the 5 cores was at the same elevation, and shore-parallel positions of cores were haphazard within 5 m of the centre of the transect line. Pooled core samples were sieved in the swash zone through mesh bags (1 mm aperture size) to separate the fauna from the sediment.

At the same levels where fauna cores were extracted, triplicate sediment cores were collected (30 mm diameter, 100 mm deep) and pooled per level. In the laboratory, sand moisture was measured as the weight loss after drying to constant weight (65°C , 48 h). Granulometry was determined by dry-sieving, using a nested series of sieves with mesh sizes of 4000, 2000, 1000, 500, 250, 125, and $63\ \mu\text{m}$. Sediment statistics (e.g. mean grain size, sorting, skewness, kurtosis, etc.) were calculated with the GRADISTAT software, using the Folk & Ward method (Blott & Pye 2001).

All sites were sampled 13 times over 4 years from August 2005 to June 2009 (Fig. 1C). Per event, the 4 sites were sampled on 4 consecutive days (sequence of sites randomised per event) around spring tides, with the frequency and interval between sampling events largely determined by resource availability. The total sampling effort was 3120 replicates (i.e. 12 samples per transect, $\times$ 5 transects per site, $\times$ 4 sites, $\times$ 13 times).

Table 1. Summary of the key questions tested, the statistical techniques and approaches matched to each question, and the main conclusions drawn

Key question	Numerical analysis	Main conclusions	Tables, Figs.
Faunal zones: number, variability, properties, and 'typical' species			
1 How many faunal zones can be identified on ocean-exposed beaches?	Cluster analysis and similarity profiles (SIMPROF) ^a	Biological zonation evident in 94 % of cases (49 of 52 cross-shore fauna data sets). The median number of zones is 3 but can vary between no distinct zonation and 4 zones	Figs. 2 & 3
2 Is the number of zones related to habitat dimensions, sediment properties, or beach morphodynamic state?	Rank correlation ^b between physical habitat metrics and the number of biological zones	NO significant ($p > 0.05$) correlations between any habitat metric and the number of faunal zones	Table 2
3 Notwithstanding variability in the number of zones, what is the 'typical' zonation pattern for the local situation?	SIMPROF based on the frequency at which individual levels were allocated to zones	Three zones is the 'modal' pattern, with biologically defined bands partitioning the intertidal into (1) swash and lower shore (spionid polychaetes, several species of amphipods, cirrolanid isopod), (2) 'middle shore' (cirrolanid isopod, urohaus-toriid amphipod, glycerid polychaete), and (3) upper beach (dominated by a single species of cirrolanid isopod)	Figs. 3 & 4, Table 3
4 How many species characterise each biological zone?	Species accumulation curves based on similarity percentage (SIMPER) ^c analysis	There was a marked intertidal gradient in the number of species 'typical' of each zone: 8 species make up 90 % of assemblage-wide similarity on the lower shore, 6 in the middle zone, and 3 on the upper shore	Fig. 5
Consistency of zones and boundaries			
5 Is community structure equally consistent within each of the biological zones identified?	Comparison (GLM) ^d of mean assemblage-wide similarity (i.e. average of all Bray Curtis similarity values among all levels comprising a zone) among the 3 biologically defined zones	Partially : some evidence that mean biological similarity among levels contained in the upper zones is lower compared to more homogenous zones further downshore	Fig. 6
6 Are biological discontinuities between abutting zones more distinct on the upper part of the beach?	Contrast (t -test) of dissimilarities (derived from SIMPER ^c analysis) between abutting zones on the upper and lower part of the beach	Mostly : there was stronger separation of upper-shore zone from the next zone seawards compared with smaller dissimilarities between the lowest zone and the middle beach	Table 4
Environmental drivers			
7 Which environmental factors influence the distribution patterns of fauna across the intertidal?	Distance-based linear models (DISTLM) ^e	All commonly measured environmental factors that vary monotonically from the swash to the dunes explain similar (32 to 40 %) proportions of spatial variation in the fauna across the intertidal gradient	Table 5
8 Do boundaries of zones based on faunal community structure coincide with major discontinuities in environmental conditions across the shore?	(1) Planned contrasts (ANOVA and SNK post-hoc test) ^d of differences in environmental variables between adjacent levels, comparing the mean change across a boundary with the change between abutting levels downshore and upshore of the boundary (2) Map position of the effluent line to that of faunal boundaries between zones	(1) NO : slope, mean grain size, sorting, or sediment moisture do not change more at faunal boundaries than between adjacent levels within a biologically defined zone outside that boundary (2) NO : in only 16 % of cases where biological zones were evident across the intertidal did the location of the effluent coincide spatially with a zone boundary	Fig. 7

^aClarke & Gorley (2006); ^bZar (1996); ^cClarke & Warwick (2001); ^dUnderwood (1997); ^eMcCordle & Anderson (2001)

Fig. 1. Study area showing 4 beach sites sampled (red and green dots: sites with and without vehicles, respectively). (a) Location of the study site in Eastern Australia. (b) Spatial layout of the fauna collections; 5 core samples were taken from each of 12 levels arranged on 5 transects (A to E) that extended from the base of the dunes to the swash zone (photo: T. A. Schlacher). (c) Timing of 13 sampling events (▼) in relation to variation in wave height from 2005 to 2009 (wave data courtesy of the Queensland Environmental Protection Agency)

Data analyses

We addressed a series of questions listed, together with their corresponding statistical techniques, in Table 1.

A central question was whether zonation can be objectively identified using the full set of community data available; this was tested with cluster analysis,

followed by similarity profiles (SIMPROF) to determine whether clusters (i.e. zones) represent patterns in community structure that are significantly ($p < 0.05$) different from random spatial structure among the 12 levels sampled across the intertidal gradient (Clarke & Gorley 2006). The cluster analysis and other multivariate methods used were based on Bray-Curtis resemblance coefficients on square-root

transformed species abundance data. Because we found considerable variation in the number of zones between the 52 sets of cross-shore data sets (i.e. 4 sites $\times$ 13 times), the 'modal' pattern of zonation was identified by first tabulating the frequency at which a level was assigned to a zone in individual SIMPROF tests run separately for each of the 52 independent sets and then subjecting this 'frequency matrix' to a further cluster/SIMPROF analysis.

It has been hypothesized that communities on the lower shore are more variable than those on the upper shore (McLachlan & Jaramillo 1995). We tested this prediction by comparing community-wide similarity (i.e. 'internal' similarity) within biologically defined zones between the lower and upper shore. Replicate values of community-wide similarity for this test came from similarity percentage (SIMPER) analyses (Clarke & Warwick 2001) run independently for each site $\times$ time combination. Group membership in the SIMPER analysis was defined by clusters identified in preceding SIMPROF analyses. A complementary analysis tested whether boundaries between abutting zones are more clearly defined on the upper or lower part of the beach; this test was based on contrasting dissimilarities between abutting zones, using SIMPER outputs for individual data sets.

We assessed which environmental variables influence the across-shore spatial patterns in community structure with distance-based linear models (McArdle & Anderson 2001). Because all habitat metrics change in a similar way across the intertidal gradient, all predictors in these models are collinear. Consequently, we only used the statistics from marginal tests for individual variables. Marginal tests were run for each replicate data set of across-shore distributions independently, and the statistics (i.e. F statistics and R^2) were averaged for each predictor variable in the models.

To test whether faunal boundaries occur at pronounced environmental 'step' changes across the intertidal, we compared the magnitude of change in key habitat descriptors (e.g. grain size and sediment moisture) between adjacent sampling levels at biologically defined boundaries and next to such boundaries. If biological boundaries are primarily defined by environmental discontinuities, the expectation is that mean environmental gradients are steeper at biological boundaries (i.e. differences in the value of environmental variables between 2 levels that fall either side of a biological boundary are expected to be larger than those between the next pair of adjacent levels not falling on a boundary).

The position of the water table outcrop on the beach face, the 'effluent line' (EL), presents a prominent and clearly defined environmental boundary on the beach face. Whether this boundary also biologically partitions the shore was tested by calculating how often the EL coincided with a faunal zone boundary.

RESULTS

Faunal zones: number, variability, and typical species

We found distinct biological zones across the intertidal gradient in 94 % of cases (49 of 52 cross-shore fauna data sets). However, there was considerable variation in both the number of zones and how they were distributed across the intertidal gradient (Figs. 2 & 3). In a few instances, there were no distinct biological zones (Fig. 2a). When zones could be recognized, the intertidal was sub-divided into 2, 3, or 4 bands (Fig. 2). The mean number of zones was 2.56 (SE = 0.10) compared with a global average of 2.94 (SE = 2.56; Fig. 3). The number of zones was not correlated with beach dimensions, sediment properties, or commonly used indices of morphodynamic beach state (e.g. Dean's parameter; Table 2).

Notwithstanding variability in the number of zones, a modal zonation pattern could be derived from analysing the frequency at which levels were assigned to different zones across all replicate data sets of across-shore distributions (Fig. 4); this analysis identified 3 zones:

(1) The 'lower shore and swash' is the most seaward biological zone on a relatively flat part of the beach (mean slope: 1.85°) that is composed of comparatively coarse (mean diameter: $414\ \mu\text{m}$) and saturated (mean moisture: 19.6 %) sands. Biologically, this zone is characterised by the spionid polychaete *Sciolelepis* sp. 1, 3 species of amphipods from the families Urohaustoriidae, Exoedicerotidae, and Platyischnopidae, and the cirrolanid isopod *Pseudolana elegans*. Other commonly found taxa in this zone are clams, *Donax deltoideus* and *Paphies elongata*, and the polychaete *Glycera* sp. 1 (Table 3).

(2) The 'middle shore' is a biologically defined zone landward of the swash and lower shore. Its gradient (2.32°) and grain size ($378\ \mu\text{m}$) are intermediate between the upper and lower parts of the beach, and the sands remain for the most part well-saturated (17.4 %). The polychaete *Glycera* sp. 1, the amphipod *Urohaustorius halei*, and the cirrolanid isopod

Fig. 2. Examples of faunal zonation patterns on ocean-exposed beaches found in the present study, ranging from (a) no distinct bands of faunal communities across the intertidal to (d) 4 bands. Zones were numerically defined by similarity profile (SIMPROF) analysis. Shading shows the mean level of the water table and the position of the effluent line (EL) on the beach face. LWST: Low Water Spring Tide

Fig. 3. Frequency distribution of the number of biological zones identified in 78 sandy beach studies in (open bars) the global literature compared with (shaded bars) the present study. Data sources for literature values: Defeo et al. (1992), Haynes & Quinn (1995), McLachlan & Jaramillo (1995), Souza & Gianuca (1995), Brazeiro & Defeo (1996), Jaramillo et al. (1996), McLachlan et al. (1996, 1998), Giménez & Yannicelli (1997), Degraer et al. (1999, 2003), Aerts et al. (2004), Gheskiere et al. (2004), Janssen & Mulder (2005), Kotwicki et al. (2005), Fernandes & Soares-Gomes (2006), Rodil et al. (2006), Alves & Pezzuto (2009)

Pseudolana concinna are typical of this zone, complemented by a single species of spionid polychaete and a donacid clam (Table 3).

(3) The 'upper shore' comprises the topmost biological zone of the intertidal, where it occupies the steepest gradient of the beach face (4.24°), composed of the finest ($331\ \mu\text{m}$) and driest (7.14%) sands. The fauna of this zone is dominated by a single species of cirolanid isopod *Pseudolana concinna* that makes up 86% of the total invertebrate abundance and contributes 72% of the community-wide similarity (Table 3).

Table 2. Correlations (Spearman rank) between sediment properties, wave characteristics, beach dimensions, and beach morphodynamic indices and the number of biological zones across the shore; all $r_s p > 0.05$

Variable	r_s
Grain size (μm)	-0.09
Coarse sand (%)	-0.17
Sand moisture (%)	0.14
Max. beach elevation (m)	0.04
Slope ($^\circ$)	0.01
Beach width (m)	-0.01
Wave height (m)	0.03
Wave period (s)	0.02
Beach index (BI)	0.06
Beach deposit index (BDI)	0.05
Dean's parameter (Ω)	-0.01
Beach state index (BSI)	-0.01

Fig. 4. Modal zonation pattern of fauna across the shore based on cluster/SIMPROF analyses of frequency distributions of levels allocated to zones across replicate data sets (top panel). Profile and gradient in sand moisture based on mean values for individual sampling levels

Overall, the number of species which characterise each zone decreases from the swash to the dunes: 4 species make up 50% of the community-wide similarity on the lower shore, 2 species in the middle zone, and a single species (*Pseudolana concinna*) on the upper shore (Fig. 5). Similarly, 8 species contribute collectively 90% of the similarity on the lower shores, whereas the same level of similarity is made up by only 6 species in the middle zone and by 3 species on the upper beach (Fig. 5).

Table 3. Summary of (A) physical properties, (B) macrobenthos density and species diversity, and (C) species (parentheses: Family) 'typical' of each zone. Indicator species marked with * in (C) are those which collectively contribute a minimum of 90 % to community-wide similarity within a zone

	Lower shore & swash		Middle shore		Upper shore	
	Mean	SE	Mean	SE	Mean	SE
(A) Physical characteristics						
Elevation (m)	0.25	0.03	0.90	0.06	2.02	0.06
Distance upshore (m)	8.61	0.78	28.10	1.27	48.56	1.32
Slope (°)	1.85	0.09	2.32	0.09	4.24	0.18
Sediment grain size (µm)	414.52	9.00	378.22	8.76	331.08	6.11
Moisture (%)	19.62	0.11	17.37	0.25	7.14	0.50
(B) Density and diversity						
No. total individuals (ind. m ⁻²)	118.33	10.03	138.81	13.58	408.58	56.87
No. species per sample (S)	7.26	0.19	5.91	0.23	3.24	0.15
Species diversity (I – λ)	0.67	0.02	0.57	0.02	0.27	0.02
(C) Indicator species						
	Mean density (ind. m ⁻²)	Sim. contrib. (%)	Mean density (ind. m ⁻²)	Sim. contrib. (%)	Mean density (ind. m ⁻²)	Sim. contrib. (%)
Polychaetes						
<i>Scolecopsis</i> sp. 1 (Spionidae)	37	20*	16	6*	1	<1
<i>Glycera</i> sp. 1 (Glyceridae)	6	8*	11	21*	7	11*
Crustacea: amphipods						
<i>Urohaustorius halei</i> (Urohaustoriidae)	25	10*	50	21*	29	9*
<i>Exoedicerus maculosus</i> (Exoedicerotidae)	12	13*	13	3	<1	<1
<i>Tittakunara katoa</i> (Platyischnopidae)	6	10*	<1	<1	<1	<1
Crustacea: isopods						
<i>Pseudolana concinna</i> (Cirolanidae)	10	7*	31	28*	353	72*
<i>Pseudolana elegans</i> (Cirolanidae)	8	12*	1	1	<1	<1
Mollusca: bivalves						
<i>Donax deltoides</i> (Donacidae)	4	9*	4	6*	<1	<1
<i>Paphies elongata</i> (Mesodesmatidae)	3	5*	5	10*	2	1

Fig. 5. Cumulative contribution of species to total, community-wide similarity within each zone. Vertical dotted lines indicate the number of species that collectively make up 90 % of the similarity within a zone

Consistency of zones and boundaries

Consistency in community structure within a zone (i.e. the mean value of Bray-Curtis similarity among all levels assigned to zone) varied to some degree across the intertidal (Fig. 6). For shores where 3 dis-

tinct zones could be identified, assemblages on the upper shore were significantly (ANOVA $p < 0.001$) less consistent from level to level ($\bar{x} = 52.79 \pm 4.41$, mean $\pm$ SE) compared with assemblage in the middle and lower part of the shore (middle: $\bar{x} = 66.18 \pm 2.76$, lower: $\bar{x} = 66.86 \pm 6.13$; Fig. 6). In contrast, no differences in assemblage heterogeneity amongst levels were evident for data sets in which 2 or 4 zones were evident (Fig. 6). The central part of the beach was more strongly separated (in terms of differences in community structure) from the upper beach than it was from the lowest zone; this difference in biological boundary distinctiveness was more pronounced for shores with 3 biological zones (Table 4).

Environmental drivers

Not surprisingly, all environmental factors that change monotonically from the swash zone to the dunes explained a similar amount of the total variation in the faunal distribution patterns across the intertidal gradient (Table 5). Between 32 % (slope) and 40 % (elevation) of spatial variation in assemblage

Fig. 6. Comparison of within-zone similarity (Bray-Curtis) between zones for data sets with 2, 3, and 4 biologically distinct zones across the intertidal gradient. The p-values relate to main effect in ANOVA comparing means among groups, and letters (a and b) denote homogenous groups defined by SNK tests

Table 4. Bray-Curtis dissimilarities between abutting zones across the intertidal gradient for beaches where 3 and 4 distinct biological zones could be identified

	Lower vs. middle zone		Middle vs. upper zone		$t_{(df)}$	p
	Mean	SE	Mean	SE		
Three zones	58.62	2.507	74.79	1.99	5.06, 22	<0.001
Four zones	57.33	6.35	66.85	4.71	1.46, 6	0.200

Table 5. Summary statistics for marginal tests in distance-based linear models (DISTLM) relating the distribution of intertidal invertebrates to 5 commonly measured environmental predictors

	Pseudo- F		Proportion of variance explained	
	Mean	SE	Mean	SE
Elevation	6.94	2.10	0.40	0.07
Sediment moisture	6.77	2.85	0.39	0.10
Position relative to effluent line	5.66	1.89	0.35	0.08
Grain size (mean diameter)	5.65	2.36	0.35	0.10
Beach-face slope	5.15	2.44	0.32	0.11

structure was accounted for by environmental variability (Table 5). However, boundaries between biologically defined zones (cf. Fig. 4) did not coincide with major and abrupt changes in environmental conditions (Fig. 7). For example, changes in grain size between adjacent levels were similar at the boundary of the lower to the middle zone ($\Delta 13 \mu\text{m}$) to those between abutting levels immediately downshore ($\Delta 22 \mu\text{m}$) and upshore ($\Delta 14 \mu\text{m}$) of that boundary

(Fig. 7b). Only sediment moisture showed a larger mean gradient at the boundary between the upper and middle shore compared to level-to-level variation further downslope (Fig. 7d). However, within the uppermost zone, changes in moisture were markedly more pronounced than at the boundary (Fig. 7d). In the majority of cases (84 %), the position of the effluent line did not match a faunal boundary on the lower and middle part of the beach.

DISCUSSION

Spatial structure of macrobenthos across the intertidal: metrics and variability of zonation

Macrobenthic assemblages on ocean-exposed sandy beaches had distinct spatial structure (sensu Legendre & Fortin 1989, Levin 1992). This spatial structure was expressed as faunal zonation across the intertidal gradient, where bands of assemblages were separated from other bands by differences in the occurrence and density of species suites (sensu Colman 1933, Stephenson & Stephenson 1949). Yet, metrics of zonation and zonation itself appear variable on sandy shores, for both our data set and previously published accounts of zonation (Table 6).

Our general zonation classification, derived from a cluster analysis of the frequency distribution of shore levels assigned to zones, contains 3 bands (Fig. 4). A synopsis of the global literature shows

that most studies also recognize a tripartite biological division of the shore (Fig. 3, Table 6): out of 78 studies in which zonation was explicitly analysed, or in which an account or description of zonation could be found, 48 (62%) have recognized 3 biological zones. The presence of 2 or 4 zones has been less frequently identified (12 and 18 %, respectively), and 5 zones are described in a single study only (Table 6).

Fig. 7. Change in the values of key habitat descriptors between adjacent levels across the intertidal gradient. Shaded boxes denote zone boundaries (level 4 to level 5 and level 7 to level 8). The p-values refer to *t*-tests for differences in means between changes at zone boundaries and changes within zones abutting these boundaries. If boundaries of biological zones are primarily determined by steep gradients in environmental conditions, the expectation is that mean contrasts (shaded boxes) at boundaries are greater than (open boxes) outside of the boundaries. Boxes represent the interquartile range, whiskers the 10th and 90th percentiles, and dots are values smaller or larger than these percentiles

Some of the debates about the existence of biological zonation on sandy beaches, the consistency and distinctiveness of zones, and the number of recognized zones can be traced to inadequacies of temporal aspects in study designs. Various authors have recognized that lack of temporal replication (or low replication) can lower the accuracy and precision at which the spatial structure of macrobenthos across the intertidal is described (Haynes & Quinn 1995). For example, working on microtidal Uruguyan beaches, Giménez & Yannicelli (1997) demonstrate remarkably high temporal variability in the number of cross-shore zones that could be identified in successive monthly samples, ranging from no distinct faunal zonation at a site to 4 zones at the same site. Our study suggests that lack of replication may bias the number of zones described as 'typical' for a beach. Based on the full data set, we identified a general zonation scheme that recognizes a tripartite faunal division of the shore (Fig. 4). There were, how-

ever, instances when fewer or more than 3 zones occurred during individual surveys; single surveys may therefore not accurately represent zonation on a shore. Yet, of 21 studies that have analysed zonation and were published after the seminal review of beach zonation by McLachlan & Jaramillo (1995), just under half ($n = 10$, 48%) were based on 'spot measurements', using designs lacking in temporal replication.

It has been asserted that biological heterogeneity increases toward the swash (i.e. 'zones are clearest at the top of the shore and become increasingly blurred, moving downshore', McLachlan & Jaramillo 1995, p. 325). We have explicitly tested this prediction and found the opposite for cross-shore data sets with a tripartite biological division of the shore: here, similarities among samples classified to form part of the upper beach were significantly lower than the observed similarities among samples further downshore (Fig. 6).

General model of zonation and characteristic species

In their comprehensive review of sandy beach zonation, McLachlan & Jaramillo (1995) provide a general model of beach zonation based on a thorough, qualitative synthesis of species distribution patterns from a large number of published studies. Their model contains a tripartite biological division of the shore: (1) a 'supralittoral zone' situated at and above the drift line and characterised by air-breathing crustaceans, (2) a 'littoral zone' between the drift line to around the effluent line with a more diverse mix of fauna of true intertidal species (e.g. cirolanid isopods, several families of amphipods, and spionid polychaetes), and (3) a 'sublittoral zone' extending from near the effluent line into the swash/sublittoral and characterised by the most species-rich communities composed of crabs, mysids, clams, and several families of amphipods and polychaetes.

Our data lend broad support to the McLachlan & Jaramillo (1995) model in terms of the faunistic identity of zones. Burrowing amphipods and polychaetes are abundant on the lower ('sublittoral') and middle ('littoral') shore, complemented by bivalves and cirolanid isopods (Table 3). Cirolanid isopods were abundant across the entire beach, their distribution showing a distinct bipartite zonation between 2

species: *Pseudolana elegans* occurred mainly on the lower beach, whereas *Pseudolana concinna* dominated the assemblages of the upper shore (Fig. 4).

Ocypodid crabs are common around the drift line of the warm-temperate beaches of Eastern Australia and should therefore be considered a 'typical' species of the supralittoral zone (Barros 2001, Moss & McPhee 2006, Lucrezi et al. 2009). However, because the crabs tunnel deeply (>0.5 m) into the sediment, they are not routinely captured in reliable numbers by standard coring techniques that sample the macrobenthos to a depth of ≤0.3 m (Lucrezi & Schlacher 2010, Schlacher & Lucrezi 2010).

Environmental drivers of zonation

The range and distribution of intertidal species are in many cases set by tolerances to environmental conditions, most notably temperature, moisture, emersion time, and UV exposure (Valdivia et al. 2011). Physiological tolerances and preferences for temperature, moisture, and emersion are not uniform amongst the suite of sandy beach species (Brown 1983) and are therefore expected to shape spatial structure across the intertidal. Similarly, sediment properties (e.g. grain size) determine the burrowing performance of beach species (Nel et al. 1999, 2001, de la Huz et al. 2002) and may therefore further modify cross-shore patterns.

We found, however, no conclusive evidence that biological zones are closely matched to physical subdivisions of the habitat (e.g. above or below the water-table outcrop) or that biological zone boundaries correspond to sharp step-changes in environmental conditions across the shore (Fig. 7). Our findings are similar to previous attempts to determine the position of biological boundaries based on abiotic variables, such as moisture levels and tidal inundation (reviewed by McLachlan & Jaramillo 1995; but see Wendt & McLachlan 1985). However, there are no data on environmental tolerances or preferences for any sandy beach species from Australia, making interpretations about the response of individual species to environmental gradients on sandy beaches speculative at best.

Table 6. Synopsis of the number of biological zones identified for the cross-shore distribution of benthic invertebrate assemblages on exposed sandy beaches. Data sources for literature values: Defeo et al. (1992), Haynes & Quinn (1995), McLachlan & Jaramillo (1995), Souza & Gianuca (1995), Brazeiro & Defeo (1996), Jaramillo et al. (1996), McLachlan et al. (1996, 1998), Giménez & Yannicelli (1997), Degraer et al. (1999, 2003), Aerts et al. (2004), Gheschiere et al. (2004), Janssen & Mulder (2005), Kotwicki et al. (2005), Fernandes & Soares-Gomes (2006), Rodil et al. (2006), Alves & Pezzuto (2009)

Published global studies (n = 78)	No. of zones				
	1	2	3	4	5
Africa	0	0	9	4	0
Asia/Arabia	0	1	4	1	0
Australia, New Zealand, Pacific	1	2	10	1	0
Caribbean, Central America, North America	0	0	6	1	1
Europe	3	2	5	4	0
South America	2	4	14	3	0
	6	9	48	14	1
	8 %	12 %	62 %	18 %	1 %
Present study (n = 52)	No. of zones				
	1	2	3	4	5
	3	22	22	5	0
	6 %	42 %	42 %	10 %	0

CONCLUSIONS

Spatial structure is generally distinct at interfaces. Exposed sandy shores form prominent interfaces and are therefore predicted to contain distinct spatial structure across the intertidal. In contrast, unstable and variable habitats that favour highly mobile species are expected to lead to less distinct or more variable spatial structure in these ecosystems. The present study lends support to both predictions: faunal distribution patterns across the intertidal gradient display distinct spatial structure in most cases, but this structure can also be variable.

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