CHAPTER 9
Exposed sandy beaches and macrofaunal community structure in eastern Australia: biogeography and synopsis

9.1 Introduction

Given that the data collected in the present survey represent different localities along a geographically continuous coastline, it is possible that differences in the current results compared to beaches sampled on a global spatial scale, are partly due to inherent evolutionary differences in the taxonomic and physiological characteristics of the local macrofaunal community members (ie. as a result of contrasting temporal effects on separated coastlines, macrofaunal species of beaches across the planet may have developed varying tolerances to swash climate as represented by BSI at particular locales). This would affect the numerical composition of the communities when plotted against beach state, raising or lowering the values on the Y-axis[1]. This type of influence on within-region plots of macrofaunal/BSI relations may thus account for some of the differences in between-region regressions on a global scale.

However, there are no known biogeographical accounts of sandy beach macrofauna for eastern Australia and it is possible that the three geographic localities selected (mainly based on rocky shore data, refer section 1.1.4) do not actually represent separate biogeographical sections for the intertidal sandy shore. It could be that the common responses of species number with BSI within the regional macrofaunal communities of this study reflect the presence of a largely common eastern Australian macrofaunal species "pool". Hence the macrofaunal communities, as combinations of "common" species, relate to BSI in a similar manner across the defined "regions". This possibility, and the effectiveness of BSI in relating biogeographically discrete macrofaunal communities, cannot be further elucidated without awareness of the actual degree of biological distinctness of the present beaches. Thus, the aim of this chapter is to:

i) determine the extent of faunal similarity (in terms of species composition) between all the sampled beaches; and accordingly

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[1] - accepting that it is a conservative feature of beaches across the globe to broadly increase in species, abundance and biomass with increasing dissipativeness (refer Chapters 4-8).

ii) summarise conclusions for exposed sandy beach macrofaunal communities of eastern Australian, with reference to the combined results so far.

9.2 Materials and Methods

9.2.1 Selected analysis

The raw species/abundance data for each beach in the present study were combined to form a common matrix. This matrix was then analysed for faunal similarities between sites in two main ways:

a) Hierarchical clustering

Hierarchical clustering methods take a similarity matrix (common data table) as a beginning and successively fuse the samples (sites) into groups starting with the highest mutual similarities and gradually decreasing the similarities in which the groups form. At the lowest similarity a single cluster contains all groups. Thus, groups of sites with distinct semblances in community structure can be determined. The graphical result of this type of analysis is a dendogram (or tree-diagram): the x-axis showing the full set of samples under consideration and the y-axis defining the similarity level at which two groups are accepted to have coalesced (Clarke and Warwick, 1994). Biogeographical "regionalisation" of the present macrofaunal data was investigated in this way in terms of clusters of faunally similar beaches across the latitudinal spectrum. Similarities between beaches were calculated and expressed as a dendogram using group-average linking provided by the Bray-Curtis Similarity Coefficient (Field et al., 1982) and as determined by Primer v3.1 (PRIMER, 1991).

b) Ordination analysis

Cluster analysis, by its hierarchical nature, dictates that, once a sample is grouped with another, it will not be separated from it at a later stage of the process. Thus, dendograms do not display sample inter-relationships on a continuous scale. Cluster analysis may also become misleading where there is a gradation in community structure across the samples (as might be exhibited by the continuum[2] in morphodynamic states of the combined beaches in this study). As an alternative, ordination analysis maps "distances" of dis-similarities between samples in a 2-dimensional plot: nearby points having very similar communities and distant points with few species in common or with distinctly different levels of abundance (Clarke and Warwick, 1984).

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[2] The beach type "continuum" refers to beaches in order of ascending BSI values (ie. meso-tidal reflective → intermediate → dissipative → macro-tidal low tide terrace → towards tidal flats).

Beaches of the present study were subject to ordination in two dimensions using Multi-Dimensional Scaling (MDS) based on the Bray-Curtis Similarity Coefficient as generated for cluster analysis by Primer v3.1 (PRIMER, 1991). The resulting MDS ordination plots represent configurations of the samples which, as far as possible, have been successively refined to satisfy the similarity relations between them. Thus communities with similar structure can be determined as groups of closely plotted sample points.

The adequacy of the MDS plot, however, decreases with reducing dimensionality of the ordination and/or with increasing quantity of data. Associated "stress values' are therefore calculated to indicate the acceptability of the plot as a useable summary of the data. These stress values and their meanings are summarised as follows (Clarke and Warwick, 1994):

Stress<0.05 - an excellent representation with no prospect of misinterpretation.

Stress<0.1 - a good ordination with no real prospect of a misleading interpretation

Stress<0.2 - a potentially useful 2-dimensional picture which can be cross-checked for conclusions with an alternative technique (eg, cluster analysis).

Stress>0.2 - the points are close to being arbitrarily placed in 2-dimensional space and higher-dimensional ordinations should be considered as an alternative.

9.2.2 Data transformations in cluster and ordination analysis

Successive transformations of the data in the above analyses can be of use in focusing attention on patterns within the whole community; progressively decreasing the contributions of numerically common species to the similarity analysis. Data transformations provide a range of effect from: untransformed (for which only the most common species contribute to similarity), through to square-root and 4th root transformations (which take intermediate and rarer species into considerations of similarity), to simple species presence/absence data (which takes into account only species types, with no considerations towards relative abundances) (Clarke and Warwick, 1994).

Beaches of this study have been previously shown to significantly fluctuate in abundance with BSI (refer Chapters 4-7). Thus, regional differences in species composition may be masked by some numerically dominant animals if the data were to be analysed in a raw form. Consequently the present data are investigated in: i) 4th root transformation (which places a very slight emphasis on relative abundances); and ii) presence/absence form (which analyses species residence alone).

9.3 Results

Fourth root transformation of the data resulted in almost succinct clusters of "provinces" within the dendogram - tropical beaches showing only 15% faunal similarity to temperate beaches which, in turn, became more-or-less separate groups at 22% similarity (Fig. 9.1a). However, there was a small overlap in the dendogram of warm and cool-temperate beaches; the most reflective warm-temperate beach classed as more similar to cool-temperate beaches than to its geographically surrounding kind. Nevertheless, MDS ordination of 4th root transformed data produced three distinct regional groupings of beaches with an acceptable stress value (Fig. 9.1b).

Analysis of species presence/absence data resulted in more discrete clusters of beaches within regions, with no similarity overlap between locales (Fig. 9.2a). Tropical beaches separated from temperate beaches at 17% faunal similarity, the latter beaches separating into "warm-" and "cool-temperate" groups at 24%. MDS ordination of species presence/absence data also produced obviously divided arrangements of beaches into regions (Fig. 9.2b). The stress values in this case again indicate that the MDS plot is a usable two-dimensional summary of the data. Supported by dendogram clusters, this strongly suggests that the present beaches represent three distinct beach macrofaunal assemblages related to location/latitude.

9.4 Discussion

9.4.1 Effect of regional differences in macrofaunal species composition on species number/BSI relationships.

It might have been expected that tropical beaches would group separately in the above analyses purely due to the higher BSI values for beaches in the region and hence a larger species richness overall for the area. Indeed, tropical beaches of this study become a distinct entity from temperate beaches at a low level of similarity using both 4th root and presence/absence data transformations; while the beaches within the region showed upwards of 40-45% similarity to each other across the range of morphodynamic types.

Warm temperate and cool temperate beaches were more similar to each other than to the tropical beaches, yet could be delineated as separate regions at 24% similarity using presence/absence data (Fig. 9.2). Although the beach morphodynamic types in the two areas showed a similar range of BSI values, the species numbers increased in the same mathematical manner across the beach type continuum. The present results

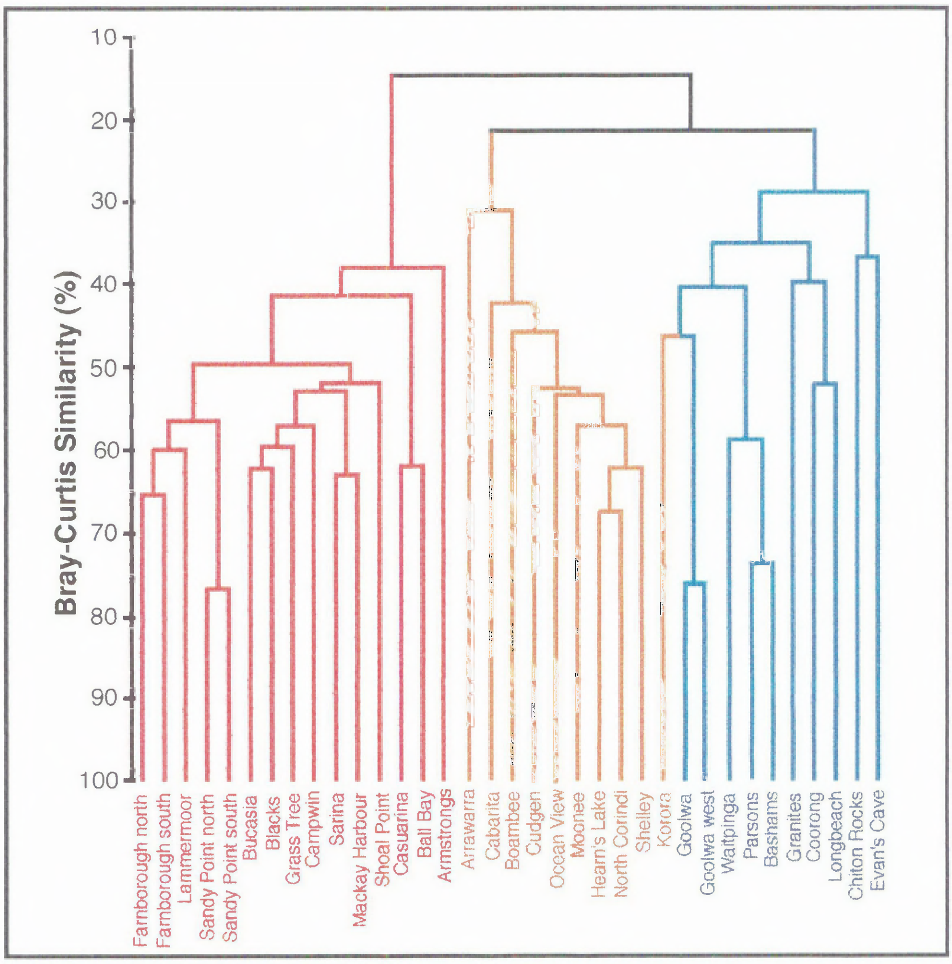
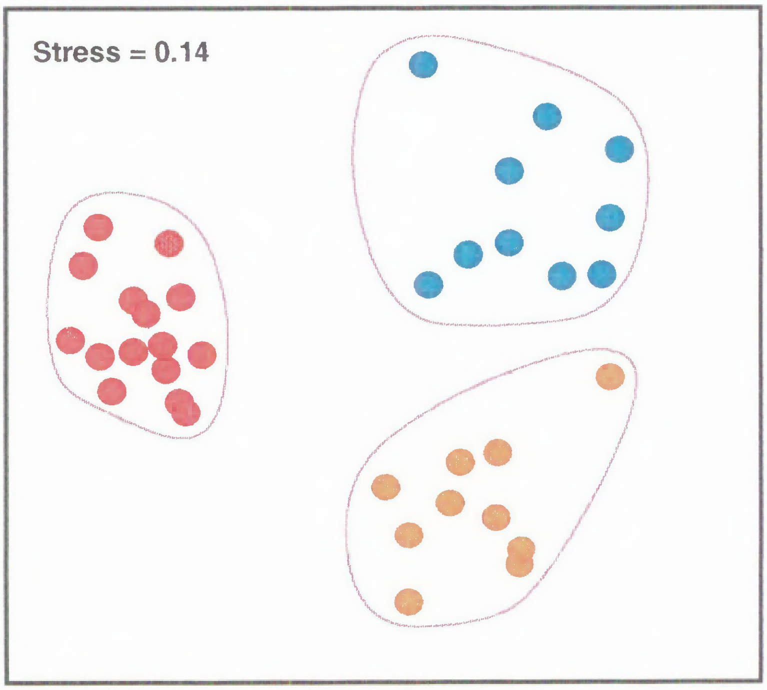


Figure 9.1a: Dendogram of cluster analysis for all beaches; 4th root transformation

Key: ● -Tropical beaches ● -Warm Temperate beaches ● -Cool Temperate beaches

Figure 9.1b: MDS ordination of all beaches in two dimensions; 4th root transformation



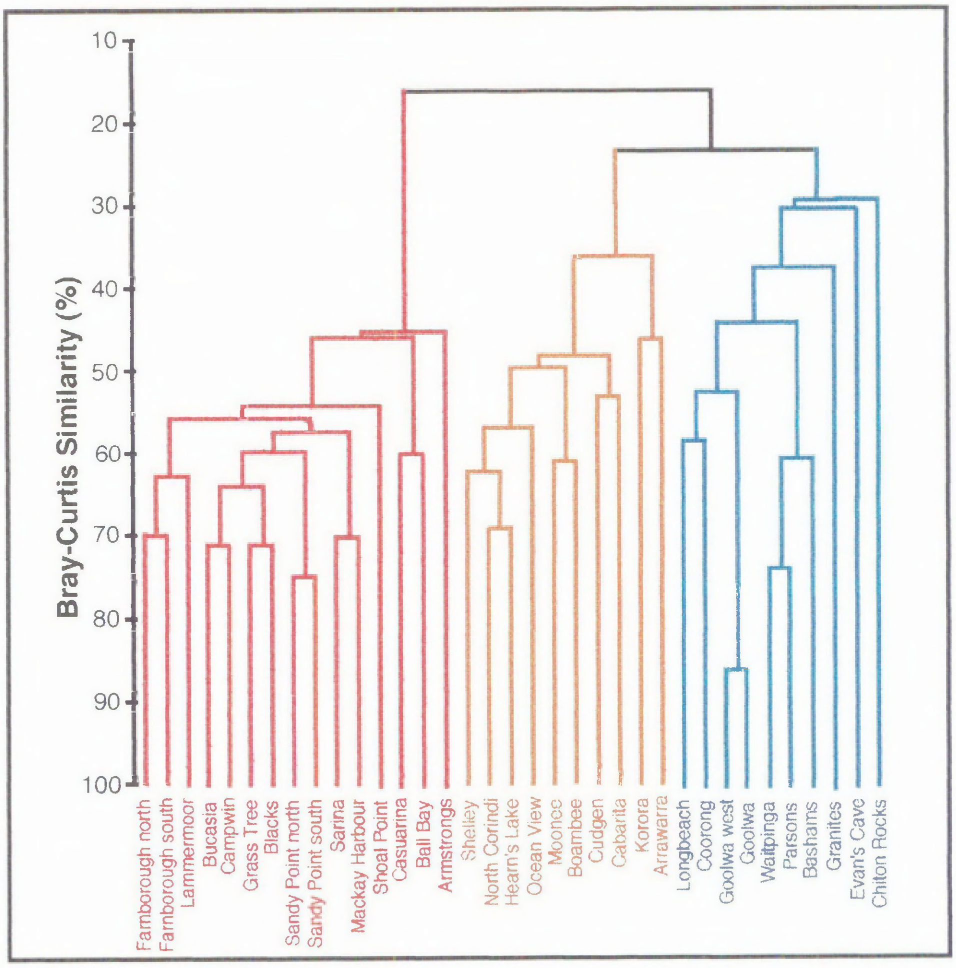
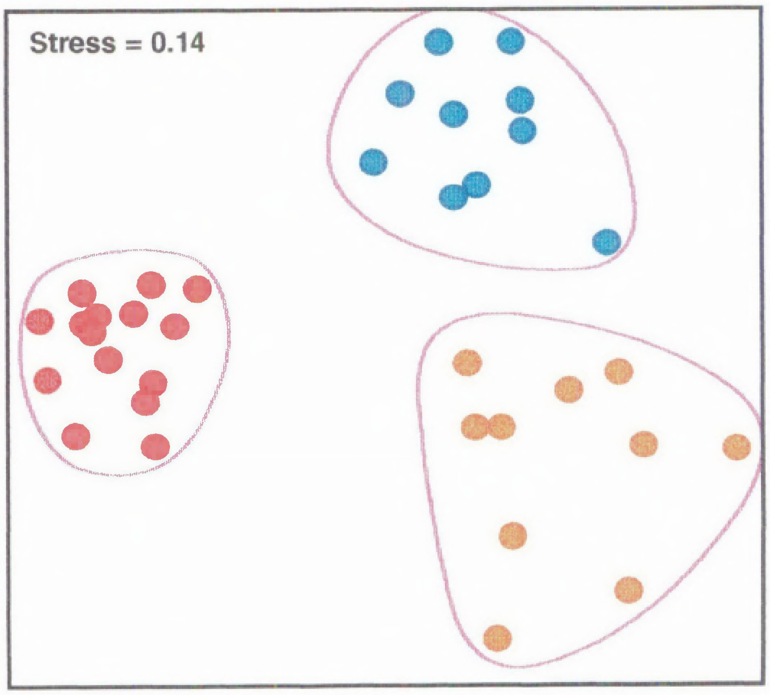


Figure 9.2a: Dendogram representing cluster analysis; species presence/absence

Key: -Tropical beaches -Warm Temperate beaches -Cool Temperate beaches

Figure 9.2b: MDS ordination of all beaches in two dimensions; species presence/absence



suggest that this is a common reaction to beach state by two faunally distinct sand-dwelling assemblages. Similarly, and despite the lack of overlap with beach types from other regions, tropical beach communities as a distinctive macrofaunal group also exhibit the same numerical dependence on morphodynamic beach state. This is demonstrated by non-significant differences in the species number/BSI regressions between tropical and temperate regions and the subsequent calculation of a common regression equation (refer Chapter 7).

Accepting that the regional communities are quite distinct, whilst still exhibiting statistically significant common relationships of macrofaunal species number to BSI, it seems that latitudinal or geographic location is of minor importance in shaping the species composition of beach communities of eastern Australia.

Further, regardless of beach state, it appears that biogeographical regions of sandy shores can be effectively defined simply by the presence of particular species (i.e. with no potentially confounding abundance considerations really necessary).

9.4.2 General biogeography of eastern Australian beach macrofauna (according to the present data).

Given that the macrofaunal communities of the presently defined "tropical', "warm temperate" and "cool temperate" beaches are distinct in over 75% of their species composition, it should be possible to characterise these regions according to specific types of animal fauna present. At present, it appears that the "warm temperate" area of this study is not simply a transition area for temperate and tropical species (as indicated for molluscs by Wilson and Gillette (1971) - refer Fig. 1.8). Rather, this province contains a distinctive species assemblage which may include some "tropical" and/or "cool temperate" representatives from within the small range of regionally "shared" fauna. In fact, the warm temperate beaches in this study contain species assemblages which are as "distant" (in MDS ordination) from cool temperate and tropical assemblages as the latter communities are from each other. This is demonstrated by the "circular" ordination of the provincial groups in Figure 9.2b (ie. there is no "middle" assemblage which might suggest an overlap zone consisting primarily of species from both adjacent regions).

The present sampling method would very likely have overlooked some representatives of species within beaches. Nevertheless, broad-scale trends in species connections within and between regions can be defined using the dendograms and MDS plots as a guide to the raw data.

9.4.3 Cosmopolitan eastern Australian beach macrofauna.

Species found in the cool temperate, warm temperate and tropical provinces are listed in Tables 4.1, 5.1 and 6.1 respectively. Thirteen of the 107 species collected were found in more than one province, with eight of these present across all the sampling regions:

a) *Pseudolana concinna* (isopod) - though appearing most abundant in the warm temperate area, these isopods were found in relatively large numbers across the complete range of beach types and regions.

b) *Urohaustoriius halei* and *U. metungi* (amphipods) - appearing throughout the geographical range from micro-tidal intermediate beach types through the continuum to tide dominated sand flats.

c) *Nephtys longipes, Sigalion cf. oviger* (polychaete worms) and Nemertean - present throughout the geographical range of beaches from micro-tidal intermediate states to tidal sand flats.

d) Diptera larvae and Staphylinid beetles (insects) - insects were only identified to family level, which may have confounded any potential regional separations. Generally, however, Diptera or "fly" larvae and "clicker" beetles were found within each province from micro-tidal intermediate beaches through to macro-tidal low-tide terrace systems.

a) Common species of the cool temperate and tropical regions

The following species represent an anomaly in terms of their residence in non-adjacent regions which contrast in beach morphodynamic processes. It is thus likely that these species can (and do) exist in the warm temperate area and were missed during sampling due to patchy distribution and/or low numbers. Although all beaches were sampled during the summer months of December/January, the warm temperate beaches of this study were sampled a year earlier than the cool temperate and tropical regions. Thus, the detection of particular species in only the cool temperate and tropical provinces may reflect a large scale temporal effect in nutrient availability (or other parameter essential to abundance). This would in turn influence the subsequent "ease of detection" of the species with respect to the sampling method. These fauna include:

i) *Talorchestia quadrimana* (amphipod) and *Dispio glabrilamellata* (polychaete worm) - present across the range of beach types within the cool temperate and tropical regions.

ii) *Paphies elongata* (bivalve mollusc: "pipi") - this species was present from intermediate beaches through to sand flats, often forming copious patches of juveniles in the tropics.

Although only found in the cool temperate and tropical beaches during the present sampling, the polychaete *Scolelepis carunculata* has, in fact, been detected in northern N.S.W beaches as part of a separate study (see chapter 11). It is thus a confirmed example of an animal that was too low in abundance to be detected in the warm temperate region during this study. Alternatively, *Orbiinia papillosa* (polychaete) may be capable of existing at warm temperate latitudes, though only in fully dissipative conditions (a beach type not present in northern N.S.W). These were collected at the most dissipative of the micro-tidal beaches (Granites Beach, South Australia) and across the spectrum of macro-tidal beach states. Nevertheless, *Orbiinia papillosa* has been collected by Dexter (1983b) in beaches near Sydney, N.S.W.

b) Common species of the "cool" and "warm" temperate regions

The following species were present throughout the temperate regions:

i) *Arabella iricolor iricolor* and *Hemipodus australiensis* (polychaetes) - present across the temperate regions from reflective to dissipative beach states.

ii) *Notomastus cf. torquatus* (polychaete) - located in low numbers on intermediate beaches within the temperate areas.

iii) *Donax deltoides* (bivalve mollusc: "bait pipi") - present in the temperate latitudes towards high energy intermediate and dissipative beach conditions.

c) Common species of the warm temperate and tropical regions

The following species were common to both the tropical and warm temperate localities:

i) *Ocypode cordimana* ("ghost" crab); *Scopimera inflata* ("sand-bubbler" crab); and *Neverita incei* (gastropod mollusc: "sand-plough" or "moon" snail) - present across the range of beach states studied in the warm temperate and tropical regions.

ii) *Hirsutonuphis mariahursuta* (polychaete) - present within the tropical and warm temperate latitudes from high energy intermediate to low tide terrace conditions.

Although the isopod *Actaecia pallida* (detected in the present tropical beaches) was not found in the warm temperate region of this study, it has been detected in beaches near Sydney, N.S.W by Dexter (1983b) and James and Fairweather (1996).

9.4.4 Macrofauna of "cool temperate" eastern Australian beaches.

The macrofauna of beaches defined as "cool temperate" in this study may represent part of the Western Warm Temperate and/or Flindersian biogeographical provinces currently proposed for eastern Australian marine communities (refer Chapter 1.1.4, Figures 1.6 and 1.7). In any case, there are many species that are notably found only in the "cool temperate" area (refer also Table 4.1):

a) *Actaecia thomsoni* (isopod: "beach pill bug") and *Exoediceroides latrans* (amphipod) - except for the most reflective sites, these species were encountered across the spectrum of cool temperate beach types, often in relatively large numbers.

b) Insects and arachnids: Coleoptera 1-4 (beetles); Coleoptera larvae; Curculionidae ("snout" beetle or "weevil"); Largidae ("bug"); Lygaeidae ("seed" bug); Lepidoptera larvae (caterpillar); and Arenaea (spider) - except for the most reflective site, these species were present as an arthropod group across the range of beach types.

c) *Aenigmathura sp.* (isopod) - this species was located at only the most reflective beaches of the cool temperate region.

As well as being characterised by the presence of the above species, cool temperate beaches also exhibited a distinct *absence* of large crustaceans (eg. crabs and shrimps) at the time of sampling. The heavy wave action afforded by the Southern Ocean may be the reason for the lack of large crustaceans - although this may also be related to latitudinal differences in climate. It seems that the numerous scavenging beetles, bugs and larvae have assumed the role of the crabs of warmer areas on the upper shore (see also Part C - across-shore distributions of beach macrofauna). The insect species present on the South Australian shores are most likely adapted to the extensive dune system that backs most of the beaches in the sampling area, the upper inter-tidal beach being the seaward limit of their distribution. Use of beach habitat niches by these other animal types most likely explains the common species number relationships with BSI (i.e. statistically similar data sets) between the study regions despite differences in local taxonomic compositions.

9.4.5 Macrofauna of "warm temperate" eastern Australian beaches

The macrofauna of the "warm temperate" study region may represent part of the Eastern Warm Temperate and/or Peronian biogeographical provinces. The beach species primarily characterising the "warm temperate" area include:

i) *Pseudolana elegans* (isopod); *Urohaustoriius gunni* (amphipod); *Scolelepis normalis* and Nepthys *australiensis* (polychaetes); and *Donax veruinus* (bivalve mollusc) - located across the range of warm temperate beaches

ii) *Eurylana arcuata* (isopod); *Exoediceroides cf. maculosus* and *Tittakunara katoa* (amphipods); *Mictyrus platycheles* ("soldier" crab) and *Lobochesis longiseta* (polychaete) - scattered presence among the lower energy intermediate beaches types within the warm temperate region

iii) *Zobracho canguro* (amphipod); *Ocypode ceratopthalma* ("spiney-eyed" ghost crab); *Diogenes custos* (hermit crab); *Haplostylus indicus* (mysid shrimp); *Australosquilla vercoi* (stomatopod); and *Lumbrinereis cf. latrielli* and *Scoploplos sp.* (polychaetes) - these species were located among the most dissipative beaches of the warm temperate region (ie. high-energy intermediate states).

9.4.6 Macrofauna of "tropical" eastern Australian beaches

The northern-most beaches of this study form part of the tropical and/or Solanderian marine provinces. The beaches here were characterised by:

i) *Matuta sp.* (crab); *Callianassa australiensis* (ghost shrimp or 'yabby"); *Haplostylus sp.* (mysid shrimp); Coleoptera 1-2 (beetles); Gerridae (insect: water strider); and *Scolelepis sp., Axiothella sp., Drilonereis sp., Hemipodus sp.* and *Lobochesis bibranchia* (polychaetes) - present across the morphodynamic spectrum of beach types studied in the tropical region.

b) *Actaecea pallida* (isopod); *Platyschnopis mirablis* (amphipod); *Notomastus annulus, Ophelia multibranchiata* (polychaetes); *Conuber conicus* (gastropod mollusc); and *Donax brazieri, Mactra pusilla* and *Strigilla euronia* (bivalve molluscs) - all found primarily among the more wave dominated low-tide-terrace beach systems.

c) *Quadrivisio sp.* (amphipod); *Diogenes ovarus* and *Diogenes sp.* (hermit crabs); *Macropthalmus setosus, Hymenosomatidae, Mictyrus longicarpus* and *Albunaea symnista* (crabs); Botroiidae (cumacean); *Peneaus plebejus* ("eastern king" prawn); Blattodea (cockroach); Forminicidae ("green" ant); *Arenicola bombayensis, Armandia sp.* 1-2, *Barantolla lepte, Diopatra dentata* (polychaetes); *Anisodonta caledonica* (bivalve mollusc); Amphiuridae (brittle star); *Australopectin vappa* (starfish); Clypeasteroidea ("sand dollar"); Spatangoidea ("heart" urchin); and Anemones 1-3. -

these species were mostly located in the more tidally dominated "sand flat" beaches of the tropical region.

It must be noted that the above species distributions reflect a generalisation based on sampling conducted once, in summer and within communities acknowledged to be locally patchy in distribution. Thus wider application of the observed trends must be viewed with caution.

9.4.7 A synopsis of eastern Australian beach macrofaunal communities and morphodynamics

Combining conclusions from all the previous chapters, it appears that, for the eastern Australian coastline:

i) Species numbers of intertidal exposed sandy beaches in eastern Australia are predominantly controlled by the nature of the physical beach system. This is most effectively expressed as BSI over regions with differing tidal influence. Although species increase with beach dissipativeness appears to be linear, larger sampling areas in future research may reveal a logarithmic relationship.

ii) Faunally distinct macrofaunal communities distributed over a large latitudinal gradient of common coastline may exhibit common numerical responses to beach morphodynamic state; increasing in species number, abundance and biomass along the continuum of BSI. Species number is the most significantly related macrofaunal community parameter to beach state (expressed as either Ω or BSI); however, it is likely that the common responses of macrofaunal abundance and biomass to BSI in eastern Australia is an artefact of a high correlation between BSI and latitude. If a multiple regression is performed, these community parameters appear more strongly related to the combination of dimensionless fall velocity (Ω) and latitude. Abundance and biomass values may thus be more indirectly related to beach processes by the associated generation and distribution of nutrients.

iii) Faunal increases with dissipativeness of beach type are most likely to be related to the corresponding decrease in "harshness" of the intertidal climate in terms of the swash processes associated with beach morphodynamics. In other words, fauna seem less subject to "exclusion" by the physical environment, with the increasing hospitality of intertidal swash conditions as beaches move from low to high BSI values. Although no actual measurements of swash intensity were made, results of the present research support the "swash exclusion hypothesis" of McArdle and McLachlan (1992).

iv) Micro-tidal, wave dominated beaches of eastern Australia contain mostly very mobile macrofaunal animals such as specially adapted crustaceans (including isopods, amphipods, crabs, shrimps, and stomatopods), bivalve and gastropod molluscs, insects, polychaetes and nemertean worms. In "cool temperate" areas, insects appear to fill the niche of the high-shore crabs of other regions.

v) Macro-tidal, tide-dominated beaches support the largest species collections containing all the above animals along with other less motile and more fragile sand-dwelling fauna. These fauna include more permanent burrowers (such as tube-dwelling polychaetes, yabbies and prawns) as well as relatively slow-moving echinoderms (sand dollars, heart urchins, starfish and brittle stars) and burrowing anemones. These additional species are able to survive and utilise the increasing stability of the intertidal area as tides replace waves as the major force of water movement over the exposed sandy shore.

vi) Relationships between macrofaunal communities, beach state and latitude around the world can not be confidently compared and a ubiquitous model ascertained without standardisation of the sampling procedure.

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The present study so far has considered the "forest before the trees" in terms of attempting to define broad scale community patterns over a range of beach types rather than within a singular beach. Part C (following) examines some aspects of the contributing "trees", with investigations into the intertidal distributions of populations of macrofaunal species within each beach and region.