

# CHAPTER 12

## **Across-shore distribution of eastern Australian beach macrofauna**

### **12.1 Introduction and aim**

Chapters 10 and 11 have examined some of the discrepancies and controversies currently associated with defining a ubiquitous zonation scheme for sandy beach macrofauna. However, despite possessing a wide range of physiological tolerances, some beach species appear to show characteristic low-tide distribution patterns. The data for the beaches in Part B are broadly applicable to the examination of animal distributions from high to low tide over a range of physical beach types. Using these data the current aim is thus to: i) identify any consistencies in macrofaunal distribution across the tidal gradient for eastern Australian beaches; ii) relate faunal distributions to morphodynamic state and/or biogeography; and iii) relate faunal groupings to the sandy beach zonation schemes of Dahl (1952), Salvat (1964) and/or Brown (Brown and McLachlan, 1990).

### **12.2 Materials and Methods**

For each beach of Part B, at each of the ten tidal levels, the three 35x35x35cm faunal samples were pooled and plotted as kite diagrams of distributions against the beach profile. Using the cluster and MDS ordination techniques described in chapters 9.2 and 11.2, the data were then analysed for “zonation” in terms of clusters of species across the beach slope. In order to classify the inter-tidal distributions of eastern Australian sandy beach species and relate the results to existing schemes, the data were investigated in two forms:

#### **a) Total community**

Inter-tidal distribution of the total beach community (as characterised by populations of different species) was analysed using the complete data set (ie. containing all fauna). In order to define the contributions of common and rarer species to potential zonation (in terms of faunal similarities between levels) these data were also approached in two forms:

**i) Untransformed** - this transformation describes faunal similarities between beach levels based on the most common species (ie. large abundances are heeded and may characterise a level of the beach),

**ii) Presence/absence** - this transformation describes faunal similarities between beach levels based on occupancy of species. That is, abundance (or dominance in terms of numbers) is disregarded in defining similarities between beach levels.

## **b) Crustacea**

In an attempt to directly apply the present beach faunal data to the zonation scheme of Dahl (1952), the complete data set (used above) was reduced to contain only the crustacean species. The resulting data were then fourth-root transformed<sup>1</sup> and investigated for similarities among beach levels using the cluster and ordination technique earlier described.

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Because it will always produce groupings even if assemblages grade into one another, cluster analysis alone should be viewed with caution in describing community patterns (Rafaelli *et al.*, 1991). Thus cluster analysis is performed only as a supplement to MDS ordinations in this study. Ordination techniques have been shown to successfully distinguish zones as representative of all inter-sample similarities and, where there is little association between dendograms and MDS plots, ordination is a more illustrative technique.

Faunal "groupings" (clusters of levels of similar faunal composition) in the MDS plots were discerned by eye (ie. are subjective) and circled. It is emphasised that the drawing of these envelopes may be instructive in outlining groups but is not a test of significance (Dorfman and Hochuli, 1995). Levels in numerical order (ie. 1,2,3,...10) across one MDS axis suggests that the fauna are graded according to similar factors ("seriated") and this is represented on the plot by an arrow from high to low shore. This is also subjective. It must also be stressed that no direct causal factors have been investigated; this chapter is simply an attempt to describe intertidal beach faunal patterns for potential use in future Australian beach research.

<sup>1</sup> Dahl's zonation scheme is the only scheme relating beach zonation to faunal indices on a global scale. In formulating his scheme, Dahl (1952) examined a wide geographic range of beach macrofaunal data from combined literary records as well as his own observations. Although it appears that his inter-tidal zones are characterised by a degree of dominance of particular crustacean species (ie. not simply by the presence/absence of animals), the format of his data is unclear. Because of this, the present crustacean data were fourth root transformed to allow contributions to similarity from rarer species while still acknowledging the numerical dominants.

## 12.3 Results

Kite diagrams for each beach and associated cluster and ordination analyses are presented in Figures 12.4-12.38 (located at the end of this chapter). The number of apparent faunal groupings for each beach and data transformation are summarised in Table 12.1. Generally faunal groupings across the shore were difficult to distinguish. Although two to three groupings were common, many of these could be further separated into four or more.

Community data often ordinated differently with transformation, numbers of apparent groupings and/or their “boundaries” changing with the form of the data. Because species numerically dominating a level are often found across the whole shore it might be expected that presence/absence transformation would confound detection of any discrete assemblages. However, groupings with both untransformed and presence/absence data were equally ambiguous, suggesting that neither transformation is “best” for describing “zonation” of beach fauna. The descriptions are merely different. “Middle” transformations (square- and fourth-root) were subsequently investigated; however these showed no clarification and are thus not presented or further discussed.

Of the zonation schemes currently published, these eastern Australian data broadly support the ideas of Dahl (1952) in terms of the types of crustacean fauna present at broad levels of the beach. Generally the upper beach seems to separate into an assemblage, with the lower shore separating into two assemblages at different points on different beaches and/or with different data transformations. Consequently, no “universal” boundaries can be inferred. A seriation/gradation of the beach fauna across the shore is often a more appropriate description than discrete faunal assemblages.

Additionally, the number of apparent faunal groupings appears unrelated to beach morphodynamic state (BSI). Although in agreement with Jaramillo *et al.* (1993) that lower-shore fauna is sparse on more reflective beaches (eg. Bashams beach, Fig. 12.4; Chiton Rocks beach, Fig. 12.5), there is no real suggestion of an increase in “zones” (or any other distributional trend) from reflective to dissipative along the morphodynamic continuum of the present data. Nevertheless, there seems to be some broad consistencies in the distributions of species within regions (for example, the usual detection of the isopod *Pseudolana concinna* in the upper shore area - see Figs 12.1, 12.2 and 12.3). Comparisons between beaches have also been considered most meaningful when made within a single biogeographic region by Tarr *et al.* (1985). Thus, in the next section, the beaches will be discussed and related to existing zonation schemes according to their geographic locality.

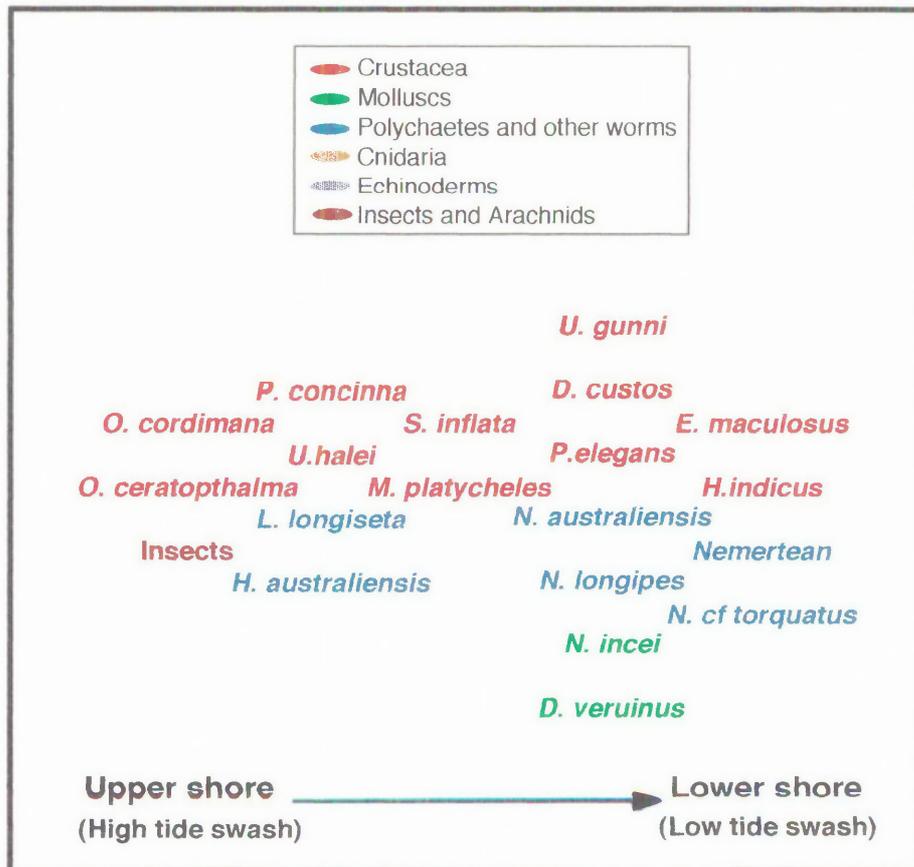
**Table 12.1:** Apparent number of macrofaunal groupings across the shore for each of the selected analyses.

This table highlights differences in apparent "zonations" (in terms of numbers of faunal groupings discerned by cluster/ordination analysis) with data transformation and/or reduction. There is also no apparent trend in number of "zones" with increasing BSI.

Beach	BSI	Community: Untransformed data	Community: Presence/ absence data	Crustacea: 4th root transformed	Figure
Bashams	0.563	3	3	1-3	12.4
Chiton Rocks	0.599	2-3	3	2	12.5
Korora	0.701	3-4	3	2 (cluster analysis only)	12.6
Evans Cave	0.712	2	2-3	3	12.7
Goolwa (west)	0.816	2	2-4 or seriation	2	12.8
Waitpinga	0.850	3	3	3-4 or seriation	12.9
Longbeach	0.859	2	2	2-3	12.10
Nth Corindi	0.860	3	3	3	12.11
Goolwa	0.879	no pattern	no pattern	3	12.12
Parsons	0.911	3	3	3	12.13
Arrawarra	0.933	3 or seriation	3 or seriation	2	12.14
Shelley	0.944	3	3-4	3	12.15
Coorong	0.957	2-3	2	3-4 or seriation	12.16
Ocean View	1.011	3	3-4	3-4	12.17
Cabarita	1.025	3	2-3 or seriation	4	12.18
Hearn's Lake	1.068	seriation	2-3 or seriation	3-4 or seriation	12.19
Cudgen	1.072	2	3-4	3	12.20
Boambee	1.083	2-4 or seriation	2-3 or seriation	2	12.21
Moonee	1.083	2	3-4	2-3	12.22
Granites	1.110	3	seriation	2	12.23
Lammermoor	1.120	2	3-4	2	12.24
Farnborough (sth)	1.180	3-4	3	3	12.25
Blacks	1.280	3 or seriation	3 or seriation	3	12.26
Mackay Harbour	1.280	3	3-4	3	12.27
Sandy Point (nth)	1.310	2-3	2 or seriation	3-4 or seriation	12.28
Sandy Point (sth)	1.310	3	2-3 or seriation	3-4 or seriation	12.29
Farnborough (nth)	1.330	3-4	3 or seriation	3 or seriation	12.30
Sarina	1.360	2-3	2-3	2-4	12.31
Campwin	1.280	2	2	2+	12.32
Grass Tree	1.450	3	3	2	12.33
Shoal Point	1.460	seriation	seriation	3	12.34
Armstrongs	1.490	2	3	2-4	12.35
Bucasia	1.490	3 or seriation	3 or seriation	3-4	12.36
Ball Bay	1.600	2-3	3	2 or seriation	12.37
Casuarina	1.620	2-3	3-4	2	12.38

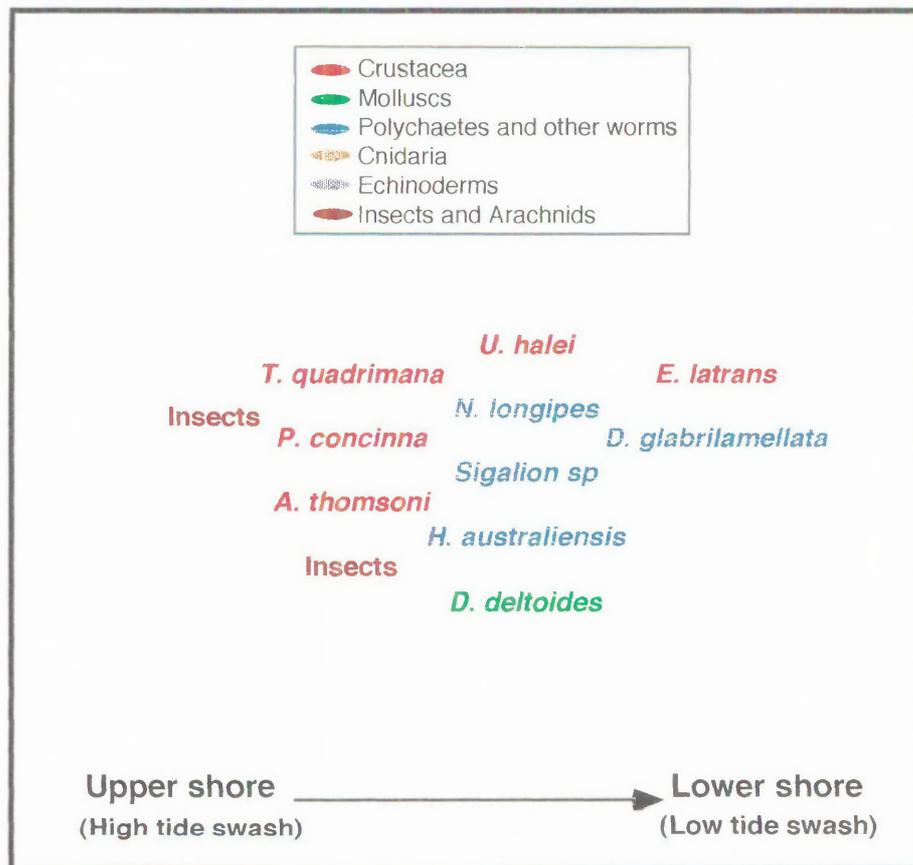
**Figure 12.1:** Generalised distribution ("regional seriation") of sandy beach macrofauna in warm temperate Australia.

This figure represents the seriation of warm temperate species down the shore based on the present data. No boundaries or limits to distribution are inferred and distributions of species may expand or compress at any point in response to local factors.



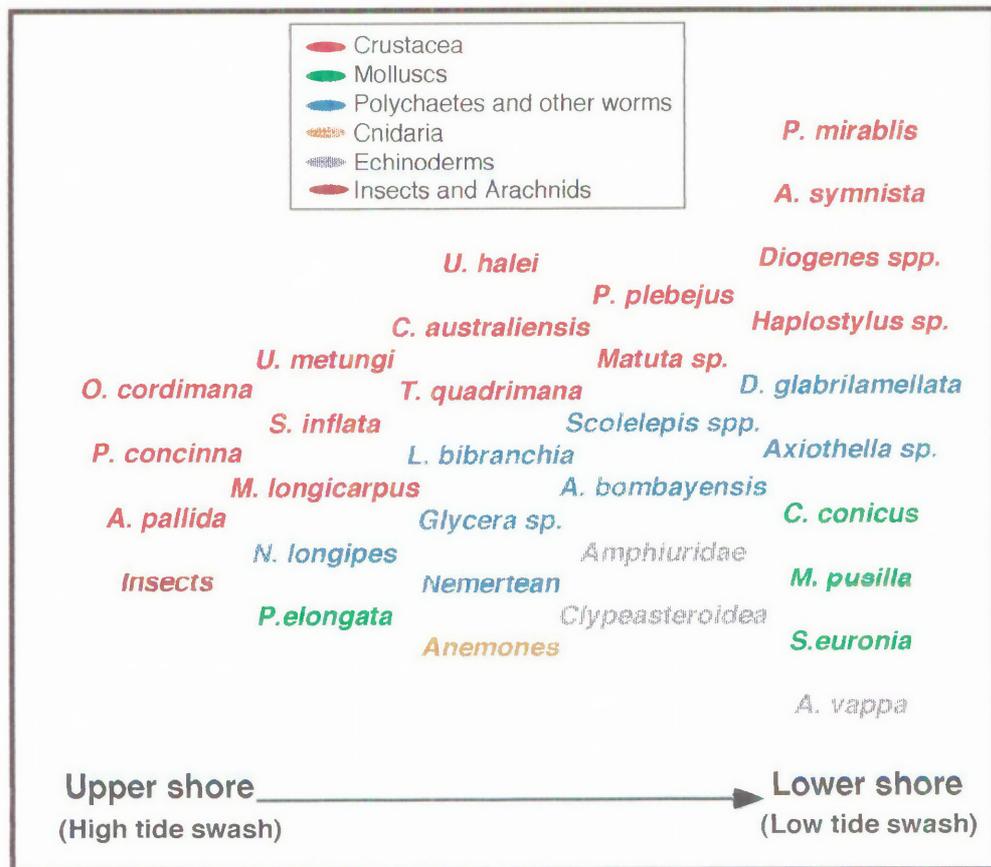
**Figure 12.2:** Generalised distribution ("regional seriation") of sandy beach macrofauna in cool temperate Australia.

This figure represents the seriation of cool temperate species down the shore based on the present data. No boundaries or limits to distribution are inferred and distributions of species may expand or compress at any point in response to local factors.



**Figure 12.3:** Generalised distribution ("regional seriation") of sandy beach macrofauna in tropical Australia.

This figure represents the seriation of tropical species down the shore based on the present data. No boundaries or limits to distribution are inferred and distributions of species may expand or compress at any point in response to local factors.



## 12.4 Discussion

Whether the data are analysed in untransformed, presence/absence or crustacean format, no consistent groupings or boundaries to faunal distribution (in terms of repeatedly demonstrated faunal associations or areas of dominance on the shore) have been indicated across the beaches studied. On rocky shores integrated physical and biological factors give rise to more-or-less consistent ecological positions of the biota. Although the “boundaries” vary in location between shores in response to local factors, they are usually quite distinguishable. This type of obvious sectioning of the fauna is not apparent for the sandy beaches of this study and is very likely related to the active mobility of the fauna within and between daily tidal cycles. Nevertheless, some fauna within geographic regions appear to “prefer” a certain broad area of the shore at low tide. Faunal associations may arise from similar responses to a condition by a suite of species (Racocinski *et al.*, 1991). Similarly these associations may diminish with a change in a causal factor. It thus appears that the exact distribution pattern of macrofauna down-shore on a given beach will depend on the species present (as largely pre-determined by beach type/BSI) and their individual reactions to local inter-tidal factors at the time.

Given the high mobility of many beach animals and the constantly changing nature of the beach system, the only real “zonation scheme” that can be consistently applied for Australian beaches (at least with the current sampling method) is a loose contiguity of local species. For the present data, a series for each region has been drawn from a combination of the kite diagrams and cluster/ordination analyses (see figures 12.1, 12.2, 12.3). This series may compress or expand at any point or for individual species, depending on localised limits and the physical nature of the beach at the time of sampling. Consequently, at a given time or locality, this seriation and any apparent faunal groupings within it may be associated with the schemes of Dahl (1952), Salvat (1964) and/or Brown (Brown and McLachlan, 1990). This idea of a consistent “**regional seriation**” at low tide (as opposed to discrete, repeatable, ubiquitous “zones”) broadly encompasses much of the present discord in the literature (see also section 12.4.5).

### 12.4.1 Macrofaunal distribution for warm temperate beaches of eastern Australia

The faunal seriation of the warm temperate beaches of this study can be broadly connected with the scheme of Dahl (1952) in that ghost crabs (*Ocypode cordimana* and *O. ceratophthalma*) are a feature of the upper shore. These are followed by the Cirolanid isopods *Psuedolana concinna* and *P. elegans*, and the Urohaustoriid amphipods

*Urohaustoriuss halei* and *U. gunni* (Fig. 12.1). The distributions of these and other animals on the intertidal shore usually grade into one another; hence it has proven difficult to separate discrete assemblages or areas of dominance using the present sampling and statistical methods.

In accordance with Dahl (1952), the “warm temperate” beaches of this study might be better considered “sub-tropical”; owing to the presence of ghost crabs rather than Talitrid amphipods on the upper shore. Ghost crabs are considered representative of warmer climates because of their greater resistance to drought and heat. This is demonstrated by their reproductive biology; ghost crabs utilise pelagic larvae in order for vulnerable juveniles to avoid potential conditions of heat stress on the upper shore (Dahl, 1952). However, on the warm temperate beaches of this study other members of the family Ocypodidae were consistently found around mid-shore: the sand-bubbler crab, *Scopimera inflata*. These crabs have been described in Australia as occurring on sheltered or protected sandy ocean beaches at high tidal levels (Bennett, 1992; Jones and Morgan, 1994); however, the present data for exposed beaches show this not solely to be the case. Also usually associated with more sheltered estuarine conditions, the soldier crab *Mictyrus platycheles*, was also common in some mid-shore areas of the present exposed beaches.

Consistent with Dahl's (1952) scheme in terms of tidal positions, the warm temperate beaches showed a presence of Cirolanid isopods across the intertidal area. This has also been described for many beaches elsewhere (Wendt and McLachlan, 1985). Contrary to Dahl (1952) however, the present Cirolanid isopod and Urohaustoriid amphipod fauna do not show separate dominances at the mid- or lower-shore respectively (“mid-littoral” zone or “sub-littoral fringe”). Rather, where they are found in northern NSW, species of these groups may occur together across the tidal gradient. For example, of the present species, *P. concinna* and *U. halei* are most consistently found in the upper shore sediments, with *P. elegans* and *U. gunni* most common lower down (Fig. 12.1). So, although not necessarily associated with each other, Cirolanid and Urohaustoriid macrofauna seem to be able to occupy any position below the drift line. Thus, although the con-generic species appear to broadly separate in their distributions, positioning of these collective groups seems more supportive of the two-part macrofaunal distribution pattern suggested by Brown (Brown and McLachlan, 1990). That is, these genera appear to occupy the intertidal area where the sediment is moist. They do not usually occur above the drift line where “air-breathers” may reside. However, the separation of the individual species into “upper” and “lower” assemblages indicates a greater complexity in distribution than a simple division of the shore into air- and water-breathers.

Jones (1979) has also reported the separation of Cirolanid species across the tidal gradient on a sandy beach. The present data support his idea that: where a single Cirolanid species exists it is most likely to inhabit the upper shore; where multiple Cirolanid species exist they separate across the shore. This has been attributed to competition (Jones, 1979). For perhaps the same reason, *Psuedolana elegans* was constantly distributed lower on the shore than the more common *P. concinna* where these species were found together (*P. concinna* usually inhabiting the upper shore when found alone). Nevertheless, these distributions could also reflect their preferred physical setting in the shore (i.e. the zones of "retention" and "resurgence" originally described by Salvat (1964)).

Some warm temperate Australian fauna also suggest a continuous distribution at the lower tidal area. For example, hermit crabs (*Diogenes custos*) and gastropod and bivalve molluscs (*Neverita incei* and *Donax veruinus*) appear to be consistently distributed in the lower half of the shore. Additionally, mysid shrimps (*Haplostylus indicus*), amphipods (*Exoediceroides maculosus*) and various polychaete species seem to consistently reside even further towards the low tide limit. It has been shown that macrofaunal trophic relationships and migratory patterns largely overlap between intertidal and sub-tidal assemblages (Leber, 1982; Borzone *et al.*, 1996). Therefore the present low shore "extremists" may represent a transition to a benthic surf-zone community.

#### **12.4.2 Macrofaunal distributions for cool temperate beaches of eastern Australia**

Although containing a different suite of species, beach animals of South Australia are also somewhat characteristically distributed on the shore at low tide (Fig. 12.2). Consistent with the scheme of Dahl (1952), Talitrid amphipods (*Talorchestia quadrimana*) are a feature of the upper shore. The presence of these amphipods here has been associated with temperate climates and, possibly owing to lesser heat stress than for warmer climes, they are able to persist using brood protection mechanisms as a means of reproduction (Dahl, 1952).

It is unfortunate that insects have been little considered in sandy beach zonation schemes or other research. Many insect species have adapted to the high tide area and can survive immersion periods or actively avoid drowning by temporarily displacing towards the dunes (Chelazzi *et al.*, 1983). Perhaps the most obvious feature of the South Australian upper shore is the wide variety of insect fauna inhabiting the area. These, along with Talitrid amphipods, may occupy the same niche as the ghost crabs of

warmer climates. However, unlike Dahl's scheme, Cirolanid and Scyphid isopods (*Psuedolana concinna* and *Actaecea thomsoni*) are also broadly consistent with this area (Fig. 12.2). Thus, Dahl's "Talitrid-" and "Cirolana-" belts appear to be combined on the southern Australian coastline.

Where found in this region, the lower shore is consistently occupied by polychaetes, bivalves, Urohaustoriids and other amphipods. Here the Exoedicerotid amphipod (*Exoediceroides latrans*) may be allied with the Oedicerotid group typified by Dahl (1952) for the low-shore of cool temperate beaches by Dahl (1952). Additionally, and in contrast to their usual positions in the warm temperate area, *Urohaustorrius halei* and the Glycerid polychaete *Hemipodus australiensis* also loosely appear to show a preference for the lower shore in this region.

The data for the South Australian beaches of this study are comparable with that of Haynes and Quinn (1996) for Cape Patterson, Victoria. They also believe that insects are confined to the upper beach and polychaetes to the lower beach, with various crustacea spanning the entire intertidal area. Using MDS methods Haynes and Quinn (1996) likewise found difficulty distinguishing distinct zones; their results also more suggestive of a gradation down the shore.

### **12.4.3 Macrofaunal distribution for tropical beaches of eastern Australia**

The tropical assemblages of fauna from high to low tide seemed especially ambiguous using the present methods. This is likely to be the result of the increased spectrum of species and their associated "tolerances" to the various intertidal beach conditions (ie. there are more species on these macro-tidal beaches which, as a result of individual reactions to conditions, further obscures any "zones"). Polychaetes seem especially various on these beaches as might be related to the lower wave intensity (Knott *et al.*, 1983). It is also likely that faunal patterns on these macro-tidal beaches were blurred by under-sampling across the shore (Jaramillo *et al.*, 1995) which might obscure the precise definition of patterns. Nevertheless, a generalised contiguity of species can still be constructed for the area (Fig. 12.3).

Consistent with Dahl (1952), Ocypodid crabs are feature of the high shore (*Ocypode cordimana*). Like the warm and cool temperate beaches of this study, insects and isopods (*Psuedolana concinna* and *Acteacea pallida*) also occupy this area. These species often grouped as an upper shore assemblage in the present analyses - especially on the beaches with a steep, reflective upper shore (for example:

Lammermoor beach, Fig. 12.24; Sandy Point (south), Fig. 12.29; Armstrongs beach, Fig. 12.35; and Casuarina beach, Fig. 12.38). High tide levels of macro-tidal beaches present the harshest conditions of atmospheric exposure and thus might be expected to contain a more specialised and distinct faunal assemblage than the collective lower shore (Schottler, 1991; Dexter, 1992). On these beaches, the lower levels could be often grouped together as one cluster on the MDS plot. However, this does not mean that the faunal composition of these levels is greatly similar; rather, as a proportion of similarity, they are simply more similar to each other than to the upper levels. Although this appears to wholly support the zonation theory of Brown (Brown and McLachlan, 1990), the lower shore groupings of these beaches could often be further sub-divided relative to each other.

Consistent with the idea that, because of heat/drought stress, Talitrid amphipods do not live on the high shore in warm climates, *Talorchestia quadrimana* was found in the middle beach for the tropical sites of this study. Very large abundances of juvenile bivalves (*Paphies elongata*) were also often found in this area. Where they were found, the slower moving animals and/or those inhabiting more permanent burrows appeared to favour the mid to lower shore (for example, the yabby, *Callinassa australiensis*; eastern king prawn, *Penaeus plebejus*; anemones; brittle star, F:Amphiuridae; sand dollars, F:Clypeasteroidea; polychaetes, *Arenicola bombayensis* and *Diopatra dentata*; starfish, *Australopectin vappa*). This may be partly due to the more constant water content of the sediments here (Salvat, 1964; Pollock and Hummon, 1971).

Although not abundant, the presence of the mole crab, *Albunaea symnista* and hermit crabs, *Diogenes spp* ("Decapod crustacea") in the lower shore is concordant with Dahl's (1952) tropical scheme. However, within this broad area these and other species also appear to alter their intertidal position between beaches; thus no "universal" areas of dominance can be inferred. Indeed, as for the temperate beaches, most of the species distributions appear to grade into one another with potential groupings superficial at best.

#### **12.4.4 Synopsis - Does "zonation" exist on sandy beaches?**

Any local area of species dominance along a gradient can be considered a "zone". In this respect some sandy beach animals can be considered to be "zoned" on the eastern Australian beaches at the time of sampling. However, assemblages or dominances of fauna which have common positions across the tidal gradient for all the beaches (or even within a region or range of similar BSI values) have not been demonstrated. Thus,

a “universal zonation” appears non-existent for these macrofaunal communities. Rather, a “**regional seriation**” is suggested as a more accurate description.

It is recognised that the data on which the above discussion is based are of limited use in providing conclusive answers to the question of zonation on sandy shores. The beaches were sampled only once, at low tide, during summer months. Additionally, or as a result, the MDS analyses failed to consistently separate beach heights into consistent biological “zones” across the beaches. Thus, although the present species are apparently usually distributed as 2-3 loose faunal assemblages, these were not repeated units and it is difficult to support, refute or even suggest an alternative to the previously published “zonation” schemes.

Nevertheless, this study does have the advantage of a constant sampling method across a selection of 35 beaches. From this collection, it appears that the limits to distribution of intertidal beach animals in eastern Australia are more complex than suggested by Dahl (1952) or Brown (1990); yet species assemblages based directly on the physical factors of Salvat (1964) and Pollock and Hummon (1971) are also not evident.

Many authors who have managed to fit their faunal data to the above schemes also acknowledge that the apparent boundaries are rarely clear or static. This has likewise been noted where attempts have been made to relate faunal assemblages to potential causal factors such as tidal height and stage (springs versus neaps), exposure, grades of sediment, competition/predation or food availability<sup>2</sup>. Indeed, it has been suggested that many macrofaunal species distribute themselves lower on the shore in the summer months to escape desiccation (Jaramillo *et al.*, 1996). If this is the case then the present “regional seriation” patterns may be lower on the shore than the temporal “average”.

Compounding this, the short-lived opportunistic nature of many beach species causes wide fluctuations in numbers according to various environmental conditions (Dexter, 1972; McLachlan *et al.*, 1979). Within a population, intra-specific interactions in recruitment and growth may also influence across-shore distribution and survival (Dugan and Hubbard, 1996). Additionally confounding, it seems that most of the dominant beach species can handle environmental extremes greater than they experience in nature (Newell, 1970) and may actively change inter-tidal positions according to intrinsic rhythms, sun/moon-orientations or other cues (Branch and Barkai, 1988; Naylor, 1988; Ugolini *et al.*, 1988; Scapini *et al.*, 1996). These determinants need

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<sup>2</sup> For example: Weiser, 1959; Fincham, 1971; Eleftheriou and Nicholson, 1975; Holland and Dean, 1977; McLachlan, 1977; McLachlan and Hesp, 1984; Ansell, 1988; McLachlan, 1988; Jaramillo and Gonzalez, 1991; Bamber, 1993; Jaramillo *et al.*, 1993; Lastra and McLachlan, 1996.

to be more fully understood in order to explain the distributions of the present local species at even a single low tide.

Constantly changing environments such as beaches promote learning and plasticity in their inhabitants; the large degree of behavioural plasticity demonstrated for many beach animals means that the response of a species to a condition at one time may not necessarily be adhered to at another (Dauer and Simon, 1975; Hazlett, 1988; Brown, 1996). Indeed it seems that animals must be able to modify their behaviour in order to be able to exist at all on sandy beaches - especially to survive environmental "crises" such as storm events (Ong and Krishnan, 1995; Brown, 1996). An example of a potential response to such as "crisis" might be observed from the data of Goolwa beach (South Australia, figure 12.12). This beach is modally dissipative (A. Short, pers. comm.), yet was steep and coarse grained at the time of sampling. As described by local residents, this was possibly due to the effects of a "summer storm" the day before. As a likely result of this event, some species were distributed lower on the shore than "usual" (most notably the isopod *P. concinna*) and no pattern could be discerned by MDS for the community data. Notwithstanding, some species remained "characteristically" distributed (eg. insects, *A. thomsoni*, *E. latrans*). This suggests individual responses of species to prevailing environmental conditions.

Although macrofauna appear physically controlled between beaches (by compound influences expressed as BSI; refer to chapters 4-8), if the distribution of species was similarly controlled by physical factors on a within beach scale, their arrangement would be more concordant with the description of Salvat (1964). This has not been the case and macrofaunal or crustacean community distribution does not appear directly related to any critical tidal or other physical level. Given the many added variables and potential combinations in space and time, it seems impractical to expect consistent separations of beach height into macrofaunal sub-communities. Thus, even with very extensive standardised sampling on all scales, an acceptable universal "zonation" scheme for sandy beach macrofauna may never be demonstrable, or indeed exist.

The MDS analyses and consequent description of patterns in this study, however, are not end points to the question of sandy beach "zonation". No hypothesis has been statistically tested and the descriptions simply indicate directions for future research. The present series of "snapshot" surveys supports the general idea that beach animals are distributed in a characteristic "regional seriation" from high to low shore, within which groups of animals may or may not dominate or statistically cluster according to the local physical and biological conditions. Broadly consistent low-tide seriations, such as those described here, endorse the **autecological hypothesis** of Noy-Meir (1979). This conjecture states that: *in physically controlled environments, communities are*

*structured by the independent responses of individual species to that environment.* This idea has also been maintained by McLachlan (1990) and Dugan and Hubbard (1996).

It also appears that zoogeographical considerations are necessary in defining even a "seriation" for a beach as species may distribute themselves in different intertidal areas depending on the climatic locality. As demonstrated in chapter 11, distributions of animals may also alter with the rise and fall of the tide; thus, at this stage, it is essential to specify that the regional seriations of this study refer only to low tide distributions. Within habitat diversity at low tide is not always similar even at homogeneous latitudes (Dexter, 1992) and multiple transects repeated over time would be required to accurately characterise the distributions of even the dominant local animals (Borzone *et al.*, 1996). Nevertheless, a consistent "regional seriation" at low tide appears less difficult to demonstrate than a "universal zonation" for sandy beach macrofauna.