

Part C

Across-shore distribution of sandy beach macrofauna



Across-shore view of Shoal Point beach/sand flat, central Queensland

[Photo: N. Hacking]

CHAPTER 10

Across-shore distribution of beach macrofauna - a review

In chapters 4-9 it was shown shown that, per beach, macrofaunal species numbers and abundances are related to the combined characteristics of the physical environment. The degree of harshness of the swash climate associated with morphodynamic state (expressed as BSI) appeared to be the limiting factor for many species. Severity of swash processes also varies *within* beaches along the gradient of tidal exposure. Thus beach species might additionally be expected to restrict their within-beach distributions according to a preferred degree of tidal inundation (and related physical processes). This chapter introduces the concept of faunal “zonation” within a sandy beach environment. Chapters 11 and 12 investigate this idea in relation to morphodynamic beach state.

10.1 What is “zonation”?

Major *zones* can be identified in any community if abundances of species cluster and dominate at a particular section of an environmental gradient (Rafaelli et al., 1991). Such clusters have been attributed to physiological tolerances of species to environmental *stress* (in terms of surviving the particular conditions)(Newell, 1976). Physical conditions which exceed the physiological tolerances of particular animal groups have been proposed as limiting factors. Nevertheless, the concept of “zonation” is not simple. Animals may still appear to “zone” themselves when their physiological tolerances are broader than the physical conditions. This implies that physical limits are not crucial in determining the distributions of many animals; rather, combinations of factors (both physical and biological) act to place an animal in space and time (Underwood, 1985).

Although assemblages of species may occur at all scales and habitats, the phenomenon is particularly striking over the short inter-tidal span of rocky shores. Indeed, it has been proposed that universal vertical zones (or ‘bands’) can be recognised from the distribution of rocky shore biota (Stephenson and Stephenson, 1949). The theory behind this zonation scheme was that animal distribution is related to the air-water interface and its associated gradients. Lewis (1955) later re-defined a

universal scheme into three major components based solely on biological parameters¹, tides emphasizing rather than creating the faunal distributions (Carefoot and Simpson, 1985). Accompanying these schemes was the parallel idea that *critical tidal levels* (sharp changes in the tidal emmersion curves) set the boundaries to the characteristic assemblages (Colman, 1933). Although some influence of physical environmental factors is undisputed, in a re-examination of critical tidal levels as sole determinants of biological "boundaries", Underwood (1978) rejected the concept. Models of distribution based on biological interactions within the confines of the physical gradient have since been favoured for rocky shore environments, particularly for the lower shore (Underwood, 1985).

Rocky shore zonation appears ubiquitous as it is based on ecological species analogues across the globe. That is, closely related species with wide geographic ranges usually characterise the "bands". Even where a particular indicator species is absent, an ecological "equivalent" takes its place within comparable boundaries (eg. particular forms of algae may replace barnacles in the Eulittoral zone at high latitudes)(Simpson, 1976). Nevertheless, although the intertidal boundaries to these distributions appear similar, different combinations of processes are almost certainly responsible.

Animals of a sandy beach must also withstand tidal fluctuations and may physically "zone" themselves according to individual tolerances. However, tidal processes are manifested differently on sandy shores so that parallel references to rocky shore patterns past this point are likely to be misleading. Nevertheless, contrasting the two systems may assist in understanding the forces behind potential sandy beach zonation.

10.1.1 Direct effects of tidal fluctuations in water level

Exposure to atmospheric conditions at low tide demands a number of adaptations for survival by intertidal marine invertebrates. In order to persist in the intertidal area, these animals must withstand the changes in temperature, desiccation, ultraviolet radiation and osmotic balance that accompany each tidal ebb and flow. To rocky shore animals these effects are direct and potentially severe - especially as many species are of sedentary lifestyle and cannot move to escape extreme conditions. However, animals in inter-tidal sedimentary environments are buffered against some of this physical stress;

¹ Lewis (1955) considered rocky shores to consist of:

- a) a Littoral Fringe - characterised by the dominance of littorinid molluscs and lichens.
- b) a Eulittoral Zone - characterised by the dominance of barnacles, and
- c) a Sublittoral Zone (or Sublittoral Fringe) - characterised by the dominance of Laminarian or Coralline algae.

overlying particles blocking UV radiation, retaining capillary moisture and hindering temperature changes (Peterson, 1991). Nevertheless, beach macrofauna still widely experience the limitations of tidal exposure on respiration, burrowing and feeding activities.

In terms of stress experienced during exposure, the high tide region of the intertidal area presents the most harsh conditions to marine macrofauna. This area experiences the least "wetting" during a tidal cycle and thus is most exposed to the extremes of atmospheric weather (ie. rain, wind, sun and frost). Upper shore faunal limits of marine animals are defined within a beach by the degree of physiological tolerance and/or adaptations to these conditions (or lack of) of the fauna present. For example, many species of Ocypodid crabs and Cirolanid isopods have developed specific adaptations to the "almost terrestrial" high tide beach (eg. special respiratory membranes, methods of heat and salt balance, reproductive methods). Where they are found, these animals may exhibit a characteristic dominance ("zonation") of the upper shore (Dahl, 1952; Dexter, 1984; Jaramillo, 1994). However, because of the special adaptations required, the high tide region of sandy beaches usually displays a low diversity of species .

In a similar manner, but with opposite implications, truly air-breathing macrofauna (such as insects) are limited in their down-shore distribution by the amount of tidal inundation they can endure. However, as outlined in Chapter 1.2, most beach animals are very mobile and can actively escape unfavourable conditions of the tide by burrowing or moving across the shore. In fact, active movement of beach animals towards more favourable surrounds contributes greatly to their observed distributions down the shore over time, masking some of the effects of physical zoning of the environment (see also chapter 11).

10.1.2 Competition for space and food

Inter-specific competition for space on rocky shores is a strong organisational force in patterns of invertebrate distribution, especially for sessile organisms. In contrast, lack of space is not such a major feature of sedimentary environments owing to the availability of a third dimension for avoidance of contact (burial depth).

However, though beach animals are not primarily subject to overgrowth or dislodgment by aggressive competitors, interference competition may exist for food supply. This too is mostly limited because the effects of food depletion are not localised or long-lasting on a sandy beach. Each tidal influx potentially precipitates new nutrients through the

sand as well as suspending and redistributing previously deposited particles (Peterson, 1991).

As a function of their total environment, densities of beach species are generally low (see previous chapters). This additionally removes the need for resource competition between individuals and hence creates more subtle "zonations" where they exist. However, beach species often exhibit an unfixed patchiness in their intertidal distributions due to food concentrations or breeding aggregations (McLachlan, 1988).

10.1.3 Predation

Although not as obvious or plentiful as animals of the rocky shore, beach invertebrates may also face predation from the land or sea depending on the level of the tide. When the tide is low, predatory shore-birds utilise the sandy expanse to forage for animals as food. Indeed, many birds have evolved bills adapted for digging in the sediments and/or behaviours to extract molluscs from their shells. Avian predators are mobile enough to effect the whole inter-tidal shore at low tide; however, the migratory behaviour of many birds dictates that predation impact and potential influence on animal distribution is more-or-less a seasonal pressure.

Nevertheless, beach invertebrates are constantly subject to predators making their way into the intertidal from the sea. At high tide, water levels are sufficient for swimming crabs, rays and other predatory fishes to enter the sub-aerial beach and utilise the abundance of near-surface sand fauna for food. Pressures of this activity are obviously greater in the low-tide area of the beach which is inundated to the greatest extent. This may set distributional boundaries of the preferred prey. As shown in the previous chapters, however, there is strong evidence indicating that predatory and competitive intimidations are over-riden by physical factors in determining overall abundances on a beach. Where predation does occur, it is only likely to affect abundances at predator densities higher than those normally found in the natural environment (Henry and Jenkins, 1995).

10.1.4 Disturbance

In direct contrast to rocky shores, perhaps the major process influencing the distribution of sandy beach animals is the degree of wave induced substrate movement at various levels of the tide. Owing to varying strengths, this type of water action may create a gradient of sediment sizes across the intertidal area which can have a fundamental

influence on the distributions of beach invertebrates (McLachlan, 1996). Wieser (1959) believes that benthic fauna are primarily distributed according to grades of sediment rather than tidal levels; some animals correlated with numbers of associated sediment bacteria. Additionally, penetrability of the substratum at various intertidal levels is important to macrofauna in terms of movement within the sand and re-entry after vertical migrations into the water column (Fincham, 1971). Deposit feeders are often found in the areas of finest sediment where organic content is great, whereas suspension feeders opt for coarser conditions where high degrees of water filtration facilitate their lifestyle. Thus, differences in the intensity of water force at tidal levels may create a "zonation" of feeding types (Peterson, 1991).

Habitat disturbance by the burrowing and feeding activities of adjacent organisms (bioturbation) may also create a level of disruption sufficient to influence zonation (Peterson, 1991). For example, dense aggregations of burrowing Myctirid or Scopimeran crabs (soldier crabs and sand "bubblers") may prevent colonisation of other animals at that area of the shore. In stable tidal flat environments, the burrowing activities of ghost shrimps (yabbies) have been shown to actively exclude tube-dwelling polychaetes owing to the potential burial of these worms by the surrounding biological sediment action (Brenchley, 1981; Peterson, 1991).

However, although bioturbators may limit the distribution of more sedentary species, their burrowing activities may actually enhance the three-dimensional environment for more commensal species. Bivalves, small crabs and errant polychaete species may utilise or share the burrows, thus creating a characteristic zonation pattern at that level of the shore (Peterson, 1991).

10.1.5 Recruitment processes

Recruitment variabilities may be a major contributor to abundance on a beach type (morphodynamic state) where a given species is able to survive. Although little is really known of beach macrofaunal recruitment processes (Defoe, 1996), variations in the settlement of larvae with tidal elevation are likely. Passive larvae are most able to settle in areas of calm water and are thus most likely to enter the sand environment where sheer stress of water movement on the sediment bed is less - usually the lower shore. Beach species may thus be separated inter-tidally based upon the active/passive settlement mechanisms of their larvae and the degree of larval sorting by water movement.

Whatever the process, positions of juvenile macrofauna on a beach does not present the irreversible commitment imposed on sessile rocky shore species. Lack of competition for space is also less likely to present limits on settlement distribution for beach species. Additionally, beach macrofauna (juveniles or adults) have the option of re-entering the water column for transport and re-location to more favourable benthic conditions during environmental extremes (Peterson, 1991).

In the case of crustaceans, many species have evolved larval brooding mechanisms so that positioning of juvenile settlement is influenced by the location of the parent (Defoe, 1996). These larvae, however, also have the potential to move to more suitable areas via active or passive behaviours. Thus larval recruitment processes of beach macrofauna have little influence on the ultimate positioning of species on the inter-tidal shore.

10.2 Sandy beach zonation schemes

The above factors suggest that inter-tidal zonation of beach species is much subdued in comparison to that of other intertidal environments. Nevertheless, some attempts have been made to formulate a ubiquitous sandy beach zonation scheme to match that of rocky shores.

10.2.1 The zonation scheme of Dahl (1952)

Eric Dahl (1952) proposed three standard zones for the beach fauna (Fig. 10.1). These assemblages were defined according to the distribution of intertidal beach crustaceans and resemble the tri-partate scheme accepted for rocky shores. According to Dahl's scheme, the intertidal beach consists of:

a) The sub-terrestrial fringe. This term refers to the upper beach which is only wetted by seawater at the highest of tides. The zone is characterised according to latitude with talitrid amphipods ("sand-hoppers") dominating the area in temperate regions, changing to Ocypodid ("ghost") crabs in more tropical climates. It seems likely that these animals fill a similar ecological niche and have much in common ecologically. They possibly replace each other between tropical and temperate regions due to the different effects (stresses) of atmospheric weather on the upper shore (Eltringham, 1971)

b) The mid-littoral zone. This area encompasses most of the intertidal beach and is flooded with every incoming tide. Swash action is a dominant force here (Brown and McLachlan, 1990). The area is characteristically inhabited by Cirolanid isopods (a cosmopolitan beach animal group) which are most active when covered by the tide. They do not dig deeply and this possibly limits them to sand which never completely dries.

c) The sub-littoral fringe. This area exists seaward of the effluent line and is usually moist and thixotropic. The number of ecological niches increases and, as a result, a greater number of species inhabit the area. In terms of crustacea, this zone is characterised by Hippid crabs (sand or "mole" crabs) in the tropics, and by Haustoriid and other amphipods in more temperate regions. Both these animals are nocturnal and can live at levels of the shore where waves are breaking. They are also morphologically similar which suggests a degree of convergent evolution (Eltringham, 1971).

This scheme has been accepted (with local modifications) for exposed beaches around the world (eg. McLachlan et al., 1981; McLachlan, 1985; Jaramillo, 1987; Jaramillo et al., 1993 Jaramillo, 1994).

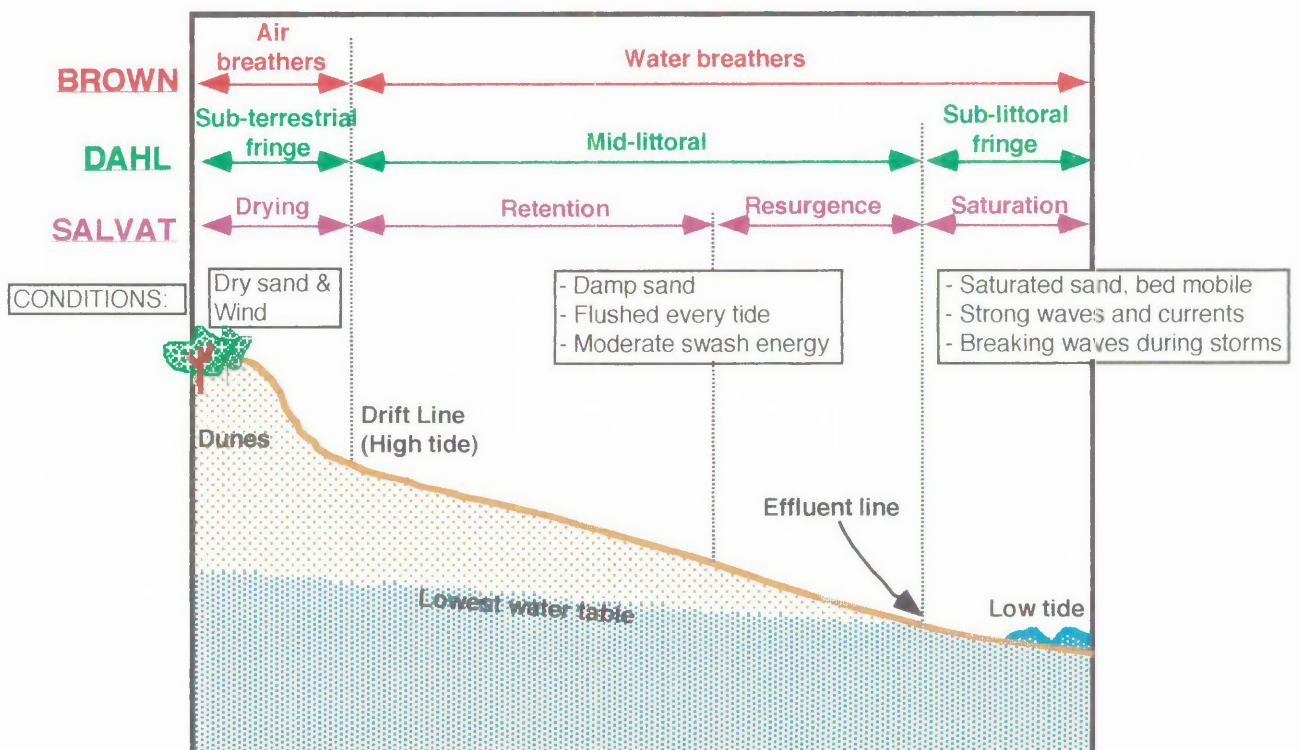


Figure 10.1: Comparison of sandy beach zonation schemes

[After McLachlan, 1983a; Nybakken, 1994]

10.2.2 The zonation scheme of Salvat (1964)

Salvat (1964) envisaged the intertidal beach to be stratified according to moisture gradients. On beaches with medium-fine sand, he quantified four zones differing in interstitial hydrodynamic characteristics (Fig. 10.1):

a) Zone of dry sand. This area is distinguished from the rest of the beach by erratic tidal emersion and includes the sediment above the level of neap high tides. During the long periods of exposure this sand may lose much of its capillary water and vary greatly in interstitial temperature.

b) Zone of retention. This area is reached by waters of all tides, the sediment usually lacking very fine particles and loosely packed. Consequently, large amounts of seawater may filter through the pores, allowing a slight accumulation of organic material. During emersion this area is likely to lose gravitational water, however much is retained in the capillary network of the sand. Thermal variations with tide may be important on the surface.

c) Zone of resurgence. This area experiences intense interstitial water circulation at both rising and falling tide. At low tide, the gravitational water from the zone above will drain through this region. This resurgence continues as long as the interstitial water level remains above that of the tide - sometimes forming rivulets of water on the beach face. The sediment here is more compact than the level above owing to accumulations of fine particles and organics. It thus has reduced interstitial porosity.

d) Zone of saturation. The sediment here lies below the low tide effluent line and is continually wet. There is little interstitial water circulation owing to fine particles and organic matter clogging the narrow interstices. Porosity and permeability are low.

This scheme of zonation has also been widely accepted (eg. Withers, 1977; Bally, 1983a,b; Wendt and McLachlan, 1985; Borzone et al., 1996). However, many authors have found that their data could fit that of either (or both) Dahl and Salvat - often combining the ideas to describe beach macrofaunal distributions in both physical and biological terms. The schemes of Dahl and Salvat are easily converged with:

- i) the **Sub-terrestrial fringe** and **Zone of dry sand** forming a unit,
- ii) the **Sub-terrestrial fringe** and **Zone of saturation** forming a unit, and

iii) Salvat's **Zones of resurgence** and **retention** corresponding to the **mid-littoral** area of Dahl (eg. McLachlan, 1983a; Defoe et al., 1992; Braziero and Defoe, 1996; Jaramillo et al., 1996)(Fig. 10.1).

Pollock and Hummon (1971) also investigated interstitial characteristics of a sandy beach; extending the scheme of Salvat (1964) on the upper shore. They divided Salvat's **Zone of dry sand** to include a **Zone of drying**. The distinction was made by the level of spring high tides; the **Zone of drying** is irregularly reached by high spring tide waters, whereas the **Zone of dry sand** almost never receives an input of tidal seawater. Pollock and Hummon (1971) also concluded that "so well do Salvat's definitions of surface zones on fine grained beaches apply to depth zones in a larger grain beach that changes in the terminology used are not required".

10.2.3 The scheme of Brown

The schemes of Dahl (1952) and Salvat (1964) have been widely employed to describe beach macrofaunal distribution. However the success of the schemes in biological terms has varied greatly with sharp faunal boundaries never conclusively demonstrated (Wendt and McLachlan, 1985). This prompted Alec Brown (in McLachlan, 1983; Brown and McLachlan, 1990) to hypothesise that only two universal zones of macrofauna occur on sandy shores: a high-shore zone of **air-breathing** fauna and a lower shore assemblage of **water-breathers**. These zones are more or less divided by the high tide drift line (Fig. 10.1). Some authors, however, believe that this scheme is an oversimplification of a more structured and complex faunal community (Borzzone et al., 1996).

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Each of the above classifications hold much value in attempting to distinguish patterns of distribution of beach macrofauna. Because macrofaunal communities seem so structured by physical factors across all beaches, it is likely that within beach distributions operate the same way. It is thus logical that the physical and biological "levels" somewhat correspond in all the above schemes. The contention between them is essentially over the existence of faunal boundaries in the lower shore. However, in reality, these zones (and supporting data) only apply to low tide distributions as detected at the time of research. This is a time of physiological stress for most beach macrofauna. Beach organisms may shift across the beach with the changing position of

the tide in order to maintain position in an optimal hydrodynamic environment. Thus, depending on the capabilities of the fauna present, these “zonations” may not persist over a complete tidal cycle or longer temporal span. Nevertheless, although there is much disagreement as to the exact nature of faunal boundaries, it is widely accepted that sandy beach organisms are unevenly distributed across the entire tidal gradient. An extensive review has been published by McLachlan and Jaramillo (1995).