

end of this season. Fincham (1971) pinpointed an overall decrease in sand-dwelling amphipods during winter as due to mortality and not off-shore migration. Similarly, Rudnick *et al.* (1985) demonstrated a summer peak in species diversity coupled with a winter decline.

Likewise, seasonally prominent oceanic fronts may cause steep surface water temperature gradients and have been tied to discontinuities in macrofaunal community composition (Larsen and Doggett, 1990). In equatorial regions, unstable conditions associated with monsoon months cause cyclic changes in beach ecology due to environmental stress at a certain time each year (Dwivedi *et al.*, 1973; Nair, 1978).

On a temperate beach of high wave energy, Leber (1982) found decapod crustaceans and molluscs were most numerous in the warmer months, while haustoriid amphipods became dominant for a short time in winter. In this case, seasonal temperatures appeared to command animal movement and numbers. Seasonal changes in intertidal distribution of beach species have also been recorded in colder areas (Eltringham, 1971; Souza and Gianuca, 1995; Jaramillo *et al.*, 1996) (see also Part C).

1.2.4 The role and importance of beach macrofauna in the ecosystem

Large plants cannot live in the shifting substrate of sandy beaches and little light is available among the sand grains to support microscopic flora here. Most food chains associated with intertidal sandy beaches thus begin with primary production conveyed by the sea and surf-zone (McLachlan, 1983b; Jones and Short, 1995). Through consumption of primary resources and sequentially becoming victims to higher predators, beach macrofauna can occupy key positions in these food chains.

The biological beach consists of trophic systems involving diatoms, water column microbes, interstitial organisms, macrofauna and mega-fauna (such as fish and birds). Macrofauna and meiofauna have individual food webs with virtually no overlap in energy exchange - the interstitial system usually being considered the most important in terms of nutrient recycling. As part of a *microbial loop*, bacteria may either take up nitrogen in competition with phytoplankton or excrete it, depending on the carbon:nitrogen ratio in the sediment¹⁵ (McLachlan *et al.*, 1981; McLachlan and Bate, 1984; Brown and McLachlan, 1990). However, the presence and importance of these various components differ with beach type (Fig. 1.5).

¹⁵ At C:N ratios above a certain level (approximately 15) microbes will compete with phytoplankton for inorganic nitrogen. Below this level they will regenerate it.

Dissipative beaches have well developed surf-zones with cellular circulation patterns which can retain diatoms (a rich source of primary production) and other organic materials (Fig. 1.5). This type of system is thus not dependant on inputs from beyond the surf-zone and may be considered semi-closed. Conversely, reflective beaches are heavily reliant on outside organic inputs as there is no legitimate surf-zone. Thus, these are truly open systems (McLachlan, 1980b; McLachlan and Romer, 1990). As a consequence of differing nutrient deposition over time, the importance of macrofauna to beach ecosystems is not constant. Variations of this type are especially prominent on transitional intermediate beaches.

Turnover estimates of a sandy beach on the west coast of South Africa indicate that bacteria may explain around 87% of annual production, with 10% by meiofauna and 3% by macrofauna (Koop and Griffiths, 1982). Although their contribution in terms of overall beach production is poor, beach macrofaunal organisms are important in that they may also interact with sub-tidal faunal assemblages, the food chain ending in fishes and carnivorous invertebrates. Shore-living birds may also form major predators of beach macrofauna, though there is little other production exchange with terrestrial systems.

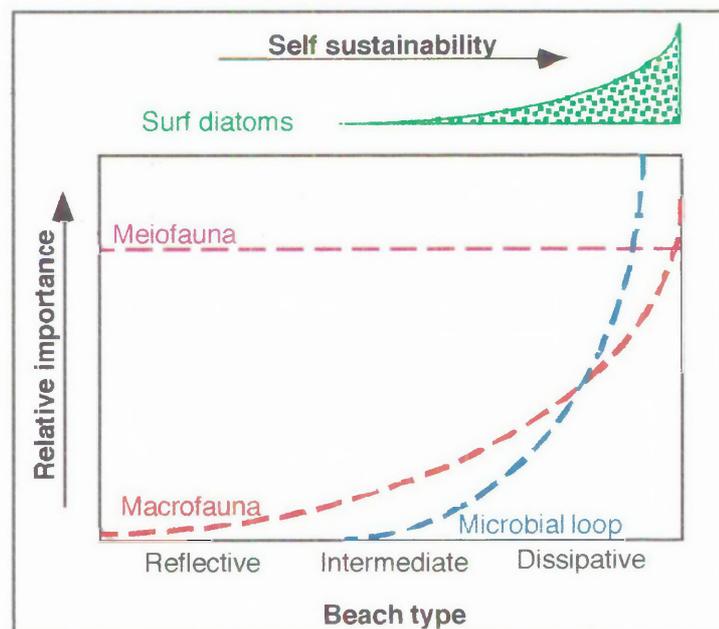


Figure 1.5: Conceptual model of the relative importance of the three sandy beach food chains across the spectrum of beach types.

[after Brown and McLachlan, 1990]

1.3 History of research on sandy beach communities

1.3.1 Early studies

With the exception of some knowledge of particular beach animals as human and fish food sources, little was scientifically known of beach faunal communities until the early 1900's. Indeed, one of the earliest papers to sketch the ecology of beaches examined shores in Sydney (Australia) (Hedley, 1915). Hedley chose the subject because it had been "hitherto but little cultivated". In attempting to list some of the common animals, he realised that "sand-surf organisms do not strictly belong to any particular class, yet all might qualify for each"; concluding that "no marine community leads so strenuous a life as does the sand beach fauna". Hedley hoped his address would "serve as an invitation to the pursuit of the study" and, slowly, the insight of many of his statements were verified in the literature.

Substantial beach community studies could be considered to have begun with the work of Adolf Remane on German coasts and in Naples in the 1920's and 1930's (Swedmark, 1964). Other studies were also attempted in the United Kingdom (Newman, 1935). However, the first complete study to enumerate all beach macrofaunal taxa was undertaken later in the United States of America (Pearse *et al.*, 1942). It took three years to accomplish. Following this, distribution of beach macrofaunal animals was also demonstrated to vary with season (Brady, 1943) and population studies were established.

The first ubiquitous intertidal zonation scheme for beach fauna was proposed by Dahl in 1952. The scheme was based on the distributions of beach crustaceans and is similar to that for rocky shores (Dahl, 1952). Other faunal studies also continued during this decade (Colsman and Seagrove, 1955; Gauld and Buchanan, 1956) with the science of sandy beach ecology advanced enough to receive its first review in 1957 (Hedgpeth, 1957). Hedgpeth attempted to link hydrodynamic processes (as mostly understood by engineers) with biological and ecological information from the available papers.

Additional localised community studies ensued in the 1960s, describing some of the dynamic relationships of sandy beach fauna (Scott, 1960; McIntyre, 1968). Relationships of macrofauna to exposure and disturbance were examined in the latter half of the decade (Morgans, 1967) along with the first investigations into the production ecology of sandy beaches - including intertidal flats (McNae and Kalk, 1962; Brown, 1964; Pamatmat, 1968; Steele and Baird, 1968; McIntyre, 1970). Salvat (1964) also proposed an alternative beach faunal zonation scheme based on physical factors of the beach habitat.

In the 1970s research widened geographically and Eltringham (1971) published the first volume on life in sand and mud. Journal publications included several “community structure and production” articles¹⁶ with additional attention toward the effects of exposure (Dexter, 1972; Eleftheriou and Nicholson, 1975) and seasonal variation (Ansel *et al.* 1972; Holland and Polgar, 1976; Dexter, 1979). Relationships between sand grain size and macrofaunal composition were also included in these papers, although it was discerned that sediment characteristics alone were not sufficient to characterise beach faunal communities (Eleftheriou and Nicholson, 1975).

Consequent to the above, interest expanded in beach animal communities as related to their total physical environment (Howard and Dorjes, 1972; Gray, 1974). Following this, studies were initiated on the effect of contamination and organic enrichment on intertidal beach communities (Pearson and Rosenberg, 1978; Read *et al.*, 1978). It was still accepted, however, that little absolute information was available on the environmental factors governing community structure and function in these habitats (Holland and Dean, 1977).

During the 1980s macrofauna was shown to be ecologically distinct from beach meiofauna/microfauna (Koop and Griffiths, 1982; Leber, 1982; Warwick, 1984). Research was also developing in the spatial and temporal variations of sandy beaches, particularly in southern Africa¹⁷. Zonation studies were likewise a major focus (see Part C). In fact, in 1983 beach researchers converged for the first time when the *First International Symposium on Sandy Beaches* was held in Port Elizabeth (South Africa) (McLachlan and Erasmus, 1983). Here world-wide research on sandy shores was officially consolidated and discussed, ultimately favouring a future systems approach to beach ecology (McLachlan and Bate, 1983). At this time, Dexter (1983, and following in 1984, 1985) provided primary scientific accounts of macrofaunal community structure in a physical variety of Australian sandy beaches. Sandy beach faunal research continued to expand in the 1990's (see next section).

Physical aspects of beaches have long been studied (Bruce, 1928). However, although three-dimensional models of sandy beach physical structure and variability had been

¹⁶For example: Trevallion *et al.* (1970), Ansell and Trevallion (1972), Dwivedi *et al.* (1973), Philip (1974), Kay and Knights (1975), Achuthankutty (1976), Dexter, 1976, Eleftheriou and McIntyre (1976), Holland and Dean (1977), McLachlan (1977), Withers (1977), Boesch (1978), Nair (1978), Jones (1979), McLachlan *et al.* (1979).

¹⁷ Examples: Dexter (1981), Shelton and Robertson (1981), Leber (1982), Bratstrom and Johanssen (1983), Gianuca (1983), Knott *et al.* (1983), Straughan (1983), Narayanan and Sivadas (1986). African examples: Dye *et al.* (1981), McLachlan *et al.* (1981), Wooldridge *et al.* (1981), McLachlan (1983), Ansari *et al.* (1984), McLachlan *et al.* (1984), McLachlan (1985), Tarr and Bally (1985).

undertaken (Sonu, 1973), reflective and dissipative beach extremes were not described until Guza and Inman (1975) studied wave formation of beach cusps¹⁸. Clifton (1976) followed this research with a four-part conceptual model of wave-formed sedimentary structures. Many other authors pursued these ideas and documented flow controls on sediment structures and associated formations (Short, 1983). In 1980, McLachlan proposed a rating system for beaches in reference to exposure which is still used today (McLachlan, 1980a). He also recognised the potential for exposed sandy beaches to act as semi-closed ecosystems (McLachlan, 1980b) (refer section 1.1.2c).

In 1983, Wright and Short presented the six beach morphodynamic states now modelled corresponding to the dimensionless fall velocity, Ω (Wright and Short, 1983; Short and Wright, 1983). This opened the way for beach ecologists to begin to relate and predict macrofaunal communities according to a comprehensive index (i.e. numerical values corresponding to combined physical beach processes).

1.3.2. Macrofauna and morphodynamics

At the turn of the decade, McLachlan (1988,1990) united the effects of swash climate and beach morphodynamic state and proposed that macrofaunal diversity, abundance and biomass could be arithmetically related to this setting. Morphodynamic factors were also related to zonation (see chapter 10). At this stage, Ω provided the best correlations with diversity and abundance, followed by beach slope (McLachlan, 1990). Biomass appeared more closely related to effects of surf-zone resources (such as wave height). The results testified that dissipative beaches harbour a more diverse and abundant faunal community when compared to their reflective counterparts (Fig. 1.6). The close fit of diversity/abundance data to Ω provided the first suggestion that variations in physical factors are a vital organisational force behind the structure of beach macrofaunal populations and communities.

Because breaking waves take place away from the intertidal area, the increase in macrofauna towards dissipative conditions was thought to be related to the effects of swash climate on the beach face (McLachlan, 1990; McArdle and McLachlan, 1992) (refer section 1.1.4). Swash climate is fundamentally controlled by beach slope and wave height - beach slope more relevant towards the reflective limit, wave height towards dissipative, and both consequential in intermediate beaches (McArdle and McLachlan, 1992).

¹⁸ A **cusp** is produced by beach accretion and appears as a regular undulation in the high tide swash area.

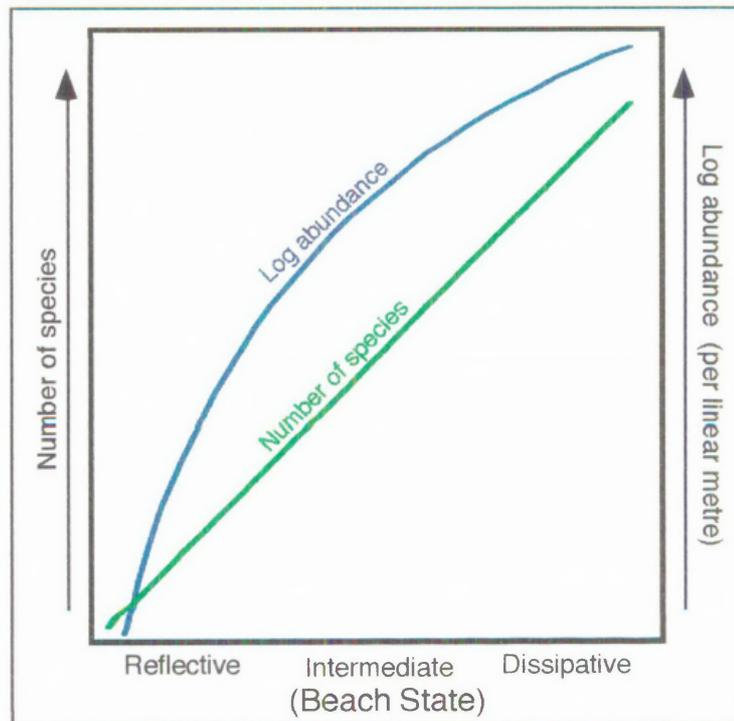


Figure 1.6: The relationship between beach morphodynamics and macrobenthic species number and abundance.

[After McLachlan, 1988;1990]

Macrofaunal community expansion with increasing Ω has held over a wide range of geographical and climatic conditions (Jaramillo and Gonzalez, 1991; Defoe *et al.*, 1992; Jaramillo and McLachlan, 1993; Jaramillo, 1994; Borzone *et al.*, 1996) with differences between regions often attributed to latitudinal or zoogeographic effects (such as changes in atmospheric and ocean climate)(Dexter, 1992). However, improvements in the understanding of beach indexing and correlations with macrofauna soon emphasized the importance of tidal range in the description. The BSI was devised accordingly (refer section 1.1.5).

The plotting of macrofaunal curves against the BSI showed an improved fit for each of species number, abundance and biomass for a wide geographic variety of beaches (including a medley of tidal ranges). It was thus proposed that the importance of physical limitations on beach fauna prevailed over zoogeographical considerations - and additional useable data was called for (McLachlan *et al.*, 1993). Further, the term *swash exclusion hypothesis* was coined to express the idea that the increasingly harsh swash associated with reflective beach conditions precludes many animals from living in these environments.

In 1994, beach researchers again gathered at “*Sandy Beaches '94 - an International Symposium on Sandy Beaches*”, Valdivia, Chile. Here the prevailing ideas on beach ecology were again consolidated and elucidated. The present study primarily stems from the questions posed by McLachlan *et al.* (1993) with extra considerations inspired during “Sandy Beaches '94”.

1.3.3 The status of ecological beach research in Australia

The first ecological surveys of Australian beaches since Dexter (1985) emerged in 1995-1996. Local researchers investigated temporal and spatial variability as well as the effects of mesh and sample size in estimating beach macrofaunal communities (e.g. Haynes and Quinn, 1995; Hacking, 1996; James and Fairweather, 1996).

Using a small Australian spectrum of wave- to tide-dominated beaches, McLachlan *et al.* (1996) further investigated links between the swash exclusion hypothesis, tides and geography. The results of this work added to the “community curves” shown in Figure 1.6. It appeared that species number, abundance and biomass continue to increase as beaches move from dissipative to ultradissipative and tidal sandflat systems. However, because samples only represented a small number of beaches with a marked difference in latitude between micro- and macro-tidal sites, it was impossible to ascribe this effect completely to beach morphology¹⁹. The solution requires a comparison of beach types of similar morphodynamic range from different latitudes (McLachlan *et al.*, 1996). This was a major consideration of the present study.

1.4 Marine biogeography of eastern Australia: status and present relevance to beaches

1.4.1 What is biogeography?

Biogeography is the observation of a particular distribution pattern found for groups of species; the concept implying a considerable degree of similarity among distribution boundaries of organisms. Biogeographical analysis is based on hierarchical classifications of animals and potentially reflects their evolutionary history (Poore, 1994). Although there is an absence of obvious limiting boundaries to the spread of

¹⁹ The most widely recognised pattern in species richness is the increase that occurs from the poles to the tropics over a variety of habitats and biotic groups (Begon *et al.*, 1990). The macrotidal ultradissipative beaches in McLachlan *et al.* (1996) were located in the tropics and so the increase in the macrofaunal communities might not have been solely due to beach state.

of animal life in the sea, every seashore animal has its own geographical limits. Following section 1.3.3, one of the aims of this thesis is to compare ranges of beaches in different marine biogeographical provinces of eastern Australia.

A marine province is a "coastal region characterised by a relatively distinct and homogeneous flora and fauna. Only a small percentage of species are common to adjacent provinces and water temperatures usually differ by more than 5°C." (Womersley, 1981). Intertidal organisms have been extensively used as provincial indicators in Australia because the taxonomic information available for these is the most extensive (Knox, 1963). Latitudinal distribution patterns of these marine organisms along the eastern Australian coastline primarily depict the fact that the region extends over three of the world's marine climatic realms: tropical, warm temperate and cool temperate waters (Briggs, 1974). These are positioned in Figure 1.7.

Across this range of eastern Australian coastline, practically all other environmental factors may also vary greatly: climate, water temperature, currents, turbidity, wind pattern, rainfall, salinities, tidal regimes, water qualities, incidence of light, bathymetry, island types and substrata, wave actions, biological actions, global histories and geological movements.

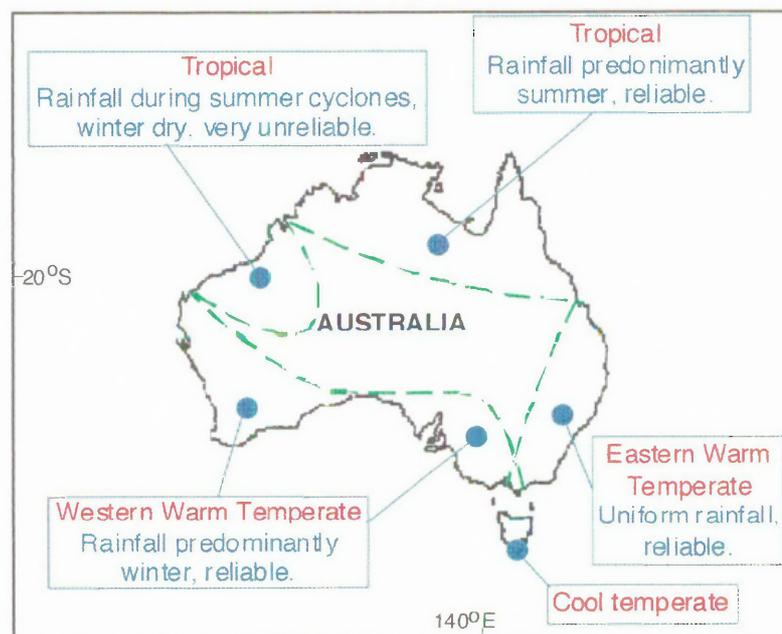


Figure 1.7: Australian coastal climatic regions
[After George, 1969 in Poore, 1994; Bennett, 1992]

1.4.2. Current marine provinces of eastern Australia

There are differing views as to the location of the boundaries of Australia's marine provinces as a result of studies of different taxa. Poore (1994) supplies a biogeographic interpretation based on the view of Knox (1963) (Fig. 1.8). These eastern Australian provinces include:

- a) **Solanderian** - Torres strait to about 25°S,
- b) **Great Barrier Reef** - the entire Great Barrier Reef area,
- c) **Peronian** - south of 25°S, including New South Wales and some of the eastern Victorian coastline,
- d) **Maugean** - the southern Victorian Coastline and all of Tasmania,
- e) **Flindersian** - south Western and South Australia.

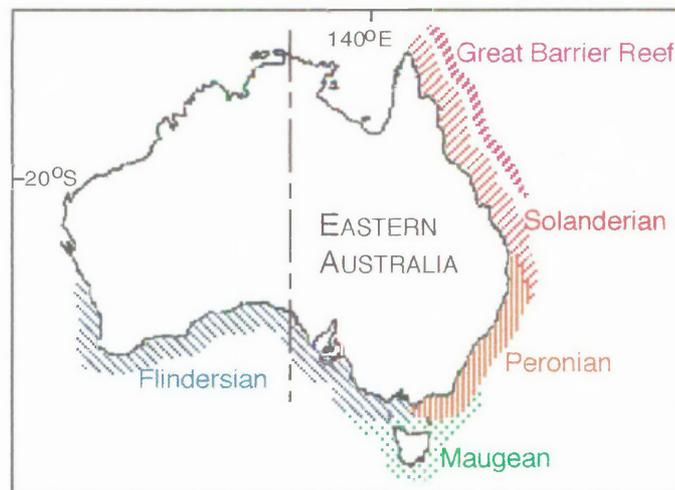


Figure 1.8: Eastern Australian marine biogeographic provinces according to Knox (1963). [After Poore, 1994]

However, Wilson and Allen (1987; in Poore, 1994) dispute these marine provinces, preferring to adopt a simplified model first described by Wilson and Gillette (1971) (Fig. 1.9). This approach, while not recognising the Maugean region or the Great Barrier Reef province, uses a transition zone between tropical and warm-temperate regions as a means of dealing with doubt surrounding the positions to boundaries of provinces.

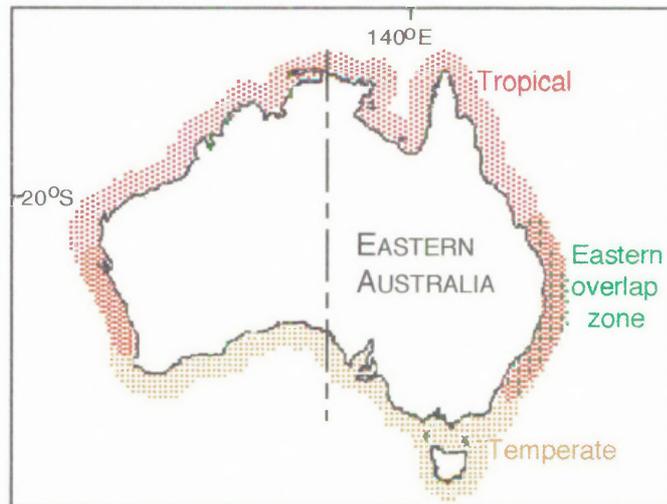


Figure 1.9: Eastern Australian marine biogeographic provinces according to Wilson and Gillette (1971). [After Poore, 1994]

This debate points towards the need for more information on the distributions and relationships of Australian marine species. Given that there are, as yet, no standardised boundaries for Australian marine provinces, the beaches proposed for this study are located away from the current biogeographical borders. "Tropical" beaches are located centrally in the Solanderian/Tropical areas (refer figures 1.8 and 1.9) near the cities of Mackay and Yeppoon, Queensland. "Warm temperate" beaches are located within the Eastern Overlap Zone/Peronian provinces, around Coffs Harbour and Cabarita, N.S.W. Beaches from southern Australia are located within the Flindersian/Temperate region near Goolwa and Robe, South Australia (Fig. 1.10). Although this southern area has been termed "western warm temperate" by Bennett (1992), the beaches here will be termed "cool temperate" throughout this study to avoid confusion (see also Chapter 3.2)

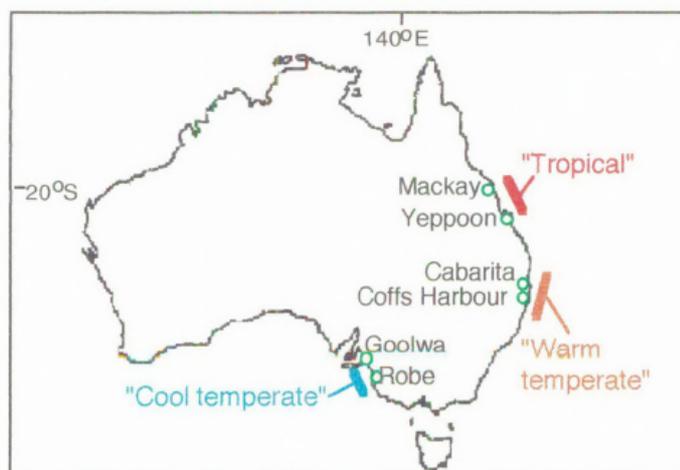


Figure 1.10: Study site "regions" for the present research

1.5 Objectives and scope of this study

This project follows the work of McLachlan *et al.* (1993) and McLachlan *et al.* (1996). The general hypothesis states:

Hypothesis: The macrofaunal communities of Australian sandy beaches are related to and similarly controlled by the physical characteristics (ie. morphodynamic states) of the beaches, independent of the biogeographical province in which the beaches are found.

This incorporates four specific aims:

1. To investigate trends in species number, organism abundance and biomass across a morphodynamic series of sandy beaches. → **PART B**
2. To compare beach state/fauna relationships between the different biogeographic regions found along the eastern Australian coastline. → **PART B**
3. To investigate the macrofaunal communities of ultra-dissipative/tidal flat beaches and compare the results with those for other beach types. → **PART B**
4. To investigate how the physical beach-face processes associated with each of the beach types influence the intertidal distribution of the species of macrofauna present (within and between provinces). → **PART C**

The overall scope of the study is to:

- a) provide the first broad range ecological and descriptive account of the intertidal macrofauna of exposed sandy beaches in eastern Australia,
- b) explore patterns in beach faunal community parameters across different geographic regions and beach states and investigate differences in community structure and intertidal distribution in relation to abiotic factors, and
- c) compare trends found in Australian beach macrofauna with similar data from around the world in order to contribute to a global synthesis of patterns in intertidal communities on sandy beaches.