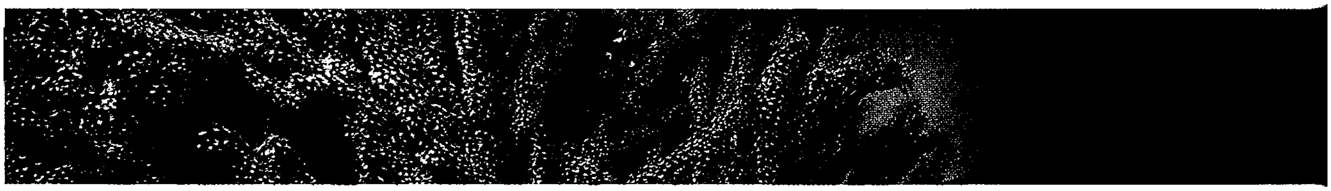


Chapter 5

Rocky and Sandy Shores

CHAPTER SUMMARY

Human settlements abound on coastlines, a pattern of habitation that persists to the present day. Early marine biologists found the shore attractive for their science for similar reasons and the shore habitat is highly accessible. The biodiversity of the shore is exceptionally high compared to land, with all major taxonomic groups represented. Ecological research on shores has underpinned much of present-day marine ecology and has strongly influenced mainstream ecology. In addition, shores are of increasing concern to governmental policy-makers because of their recognized provision of goods and services for humans, such as coastal defence, recreation and fisheries products. Shorelines around the world are experiencing major impacts caused by human population pressure and there is a necessity to defend our economic and social investment in coastal development from the effects of accelerated sea-level rise. Understanding how shores function ecologically is therefore important not simply for intellectual reasons, but for practical purposes if their full value is to be maintained.

5.1 Introduction

● Shores are studied because they are accessible, taxonomically relatively simple and provide ecological goods and services to society (Preface).

The habitat created by the land meeting the sea is the most accessible part of the marine environment for humans. To explore deeper and further out to sea requires rafts, canoes or larger vessels and involves increased risks, while the shore itself, including adjacent shallow waters, offers rich resources that can be collected without great effort. It is therefore no surprise that early human settlements abound on coastlines, a pattern of habitation that persists to the present day.

Early marine biologists found the shore attractive for their science for similar reasons. The shore habitat is highly accessible (rubber boots or bare feet are the only equipment required). The biodiversity of the shore is exceptionally high compared to land, with all major taxonomic groups represented (even insects, if you look hard enough), and the fauna and flora are easily collected for study or manipulated experimentally. As a result, it is not surprising that ecological research on shores has underpinned much of marine ecology and has been the laboratory of preference for many mainstream ecologists.

In addition, shores are of increasing concern to governmental policymakers because of their recognized provision of **goods and services** for humans, such as coastal defence, recreation, and fisheries products (Duarte 2000), and the current threats to these services (Brown & McLachlan 2002; Kennish 2002; Thompson et al. 2002). Shorelines around the world are experiencing major impacts caused by human population pressure and there is a necessity to defend our economic and social investment in coastal development from the effects of accelerated sea-level rise by spending many millions of dollars on coastal defence projects. Understanding how shores function ecologically is therefore important not simply for intellectual reasons, but for practical purposes if their economic value, as well as their aesthetic and cultural values are to be maintained.

- Shorelines around the world are experiencing increasing pressure from human developments.

5.2 What is the Shore?

Defining the shore is not as straightforward as it might seem. The early domination of shore ecology by north-west European and North American scientists who worked in macro-tidal areas has resulted in a very restricted perspective of a shore: the area between high and low water marks. As a result, shore ecology became synonymous with

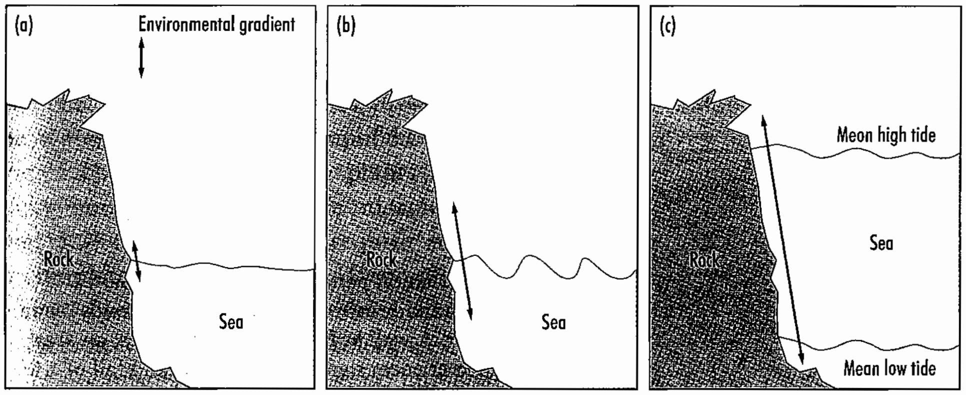


Fig. 5.1 The wet-dry gradient (a) that characterizes the shore is set up by the interface between water and air. Waves will extend this gradient up and down the shore (b), and tides (where present) further amplify the gradient (c). The effect of the tide is thus to greatly expand an existing gradient, tides do not create the gradient *per se*.

intertidal ecology. This was unfortunate for several reasons. First, many shores around the world do not experience significant tides and in such areas changes in air pressure will cover and uncover the shore to a far greater extent than tidal action (Fig. 5.1). Second, the distribution and abundance of shore biota were inevitably understood in the context of tidal rise and fall, yet tides *per se* cannot be responsible for these patterns (Figs 5.1 and 5.2). Third, the emphasis on tides as a controlling factor promoted the view that physical variables limited the distribution and abundance of shore organisms and thereby distracted attention away from the importance of biological processes. Fourth, the functional influence and extent of the shore may extend far into the terrestrial hinterland and down beyond the surf zone hundreds of metres offshore (Brown & McLachlan 1990). The influence of the shore extends even further if a larger scale perspective is taken to include the supply of

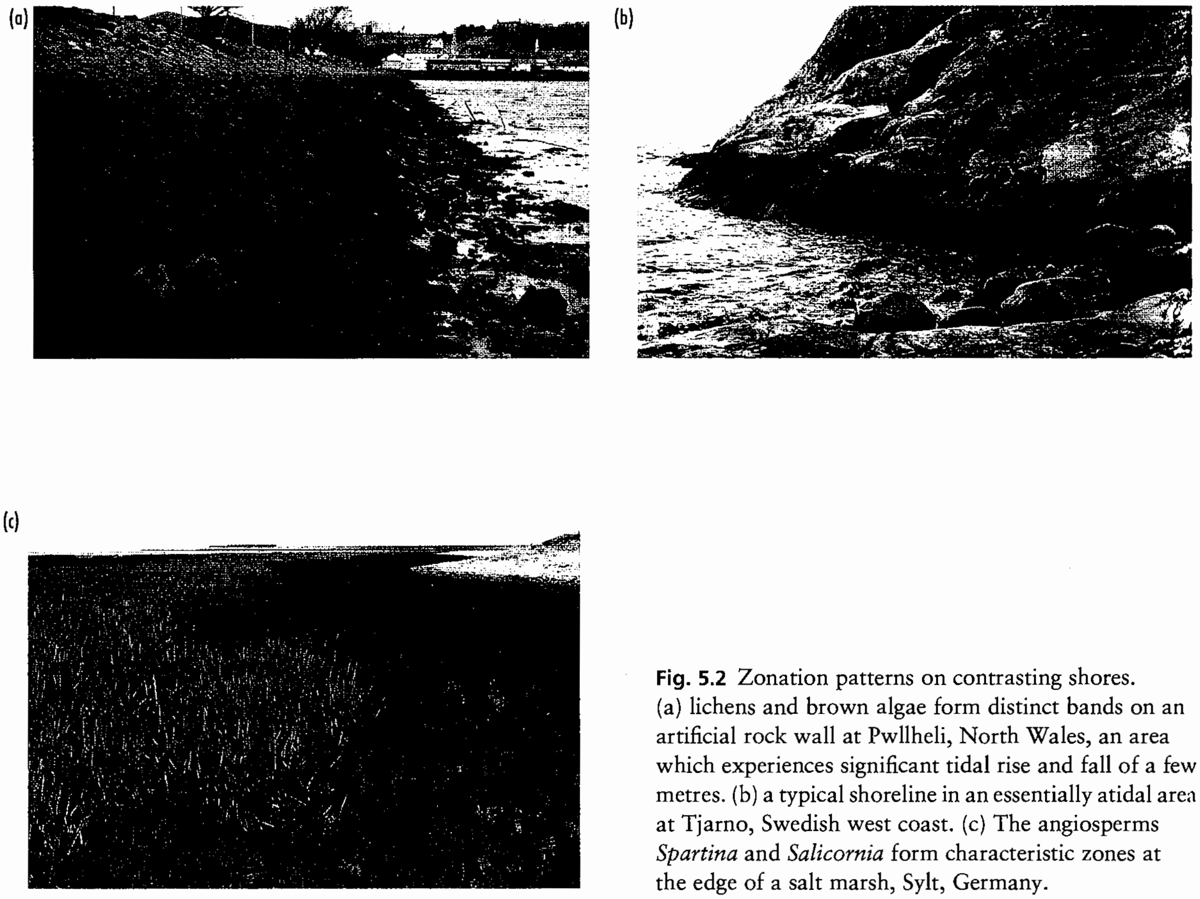


Fig. 5.2 Zonation patterns on contrasting shores. (a) lichens and brown algae form distinct bands on an artificial rock wall at Pwllheli, North Wales, an area which experiences significant tidal rise and fall of a few metres. (b) a typical shoreline in an essentially atidal area at Tjarno, Swedish west coast. (c) The angiosperms *Spartina* and *Salicornia* form characteristic zones at the edge of a salt marsh, Sylt, Germany.

larval stages from offshore water masses, the origins and end points of migratory taxa such as turtles and shorebirds, and the material linkages between shorelines of different types. Thus, as for other marine systems, defining 'the shore' is quite an arbitrary exercise and understanding patterns and processes within an area like the intertidal zone requires acknowledgement of a much larger scale system within which that limited area of habitat is set.

- Not all shores experience significant tides, yet they support a typical 'intertidal' fauna and flora.
- The functional extent of the shore extends well above and well below normally recognized limits.

In this chapter, the focus is very much on rocky and sandy shores. Other kinds of shore habitats (mangrove, estuary, tropical reef) are dealt with elsewhere in this book, but given the broader network in which rocky and sandy shores operate, reference to these other systems draws attention to the important ecological linkages that exist between them.

5.3 Environmental Gradients and the Shore

The shore is characterized by several environmental gradients (termed ecoclines elsewhere; Whittaker 1974). These gradients interact and intersect in quite complex ways to generate specific environmental conditions for shore organisms. All other things being equal, specific and predictable biological assemblages will be found at the intersections of these gradients according to their physical, competitive and physiological ability to occupy particular sections of the gradients, a phenomenon known as zonation (Figs 5.2 and 5.3).

- Different species have different physiological and competitive tolerances and hence occupy different sections of environmental gradients.

There are four main gradients on shores: wetness/dryness; exposure to wave action; substratum particle size; salinity.

5.3.1 Wetness/dryness

The wetness/dryness gradient is set up at the tension between water and air. The environment becomes progressively drier with distance from the water surface and is amplified (not created) by waves and tides (Fig. 5.1). Almost all of the plants and invertebrates encountered on rocky and sandy shores are marine aquatic in phylogenetic origin (Fig. 5.3) and the majority require access to the marine environment to complete their life history. Generally, species have different requirements (tolerances) and are able to live further or nearer to the water surface according to these tolerances. It does not follow that high shore organisms cannot withstand immersion in seawater: many appear to be restricted to high shore levels because of biological pressures (e.g. predation or competition) from species living at lower shore levels (5.4.1 and Chapter 1).

- Most shore species are marine in origin and need regular access to the sea.

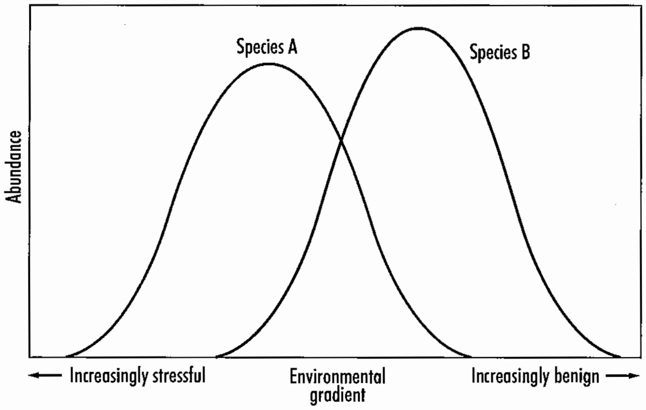


Fig. 5.3 Zonation of two species along a generalized environmental gradient running from stressful to benign conditions (with respect to the organisms). The two species A and B occupy different sections of the gradient according to their ability to tolerate physiological stress (left-hand tail of the distribution) or biotic interactions (right-hand tail of the distribution – see also 5.4). Note that for terrestrial taxa, such as saltmarsh plants, the sea is a stressful environment, while for marine taxa, it is the land that is unfavourable.

5.3.2 Exposure to wave action

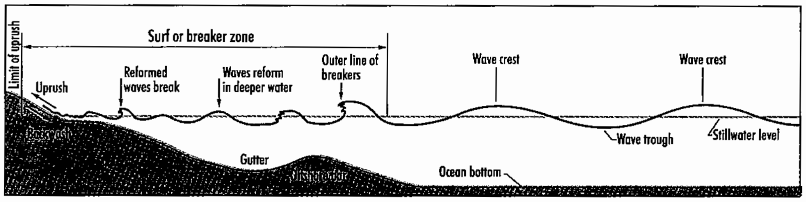
● Wave action is a major determinant of community structure and composition, as well as individual shape, form, and behaviour.

A feature of all coastlines is that they experience wave action to varying degrees (Box 5.1). Waves are generated by the frictional drag of wind on the sea surface and the longer the distance over which the wind blows (termed **fetch**), the higher the waves. Waves may also arrive on the shore in the form of swells; these are the ghosts of large wind generated waves produced by storms far offshore. The forces expended when waves arrive at the shore will depend on how much energy is extracted by the immediate offshore substratum and any associated biological structures, such as kelp forests, reefs, or sandbanks. Thus, shallow sloping offshore areas will tend to dissipate the energy in the waves arriving at the shore, while steeper cliffs will experience a much greater physical impact of wave action. Because waves are wind generated, physically sheltered localities such as fjords, narrow estuaries and shores facing away from prevailing wind directions will have less wave action on average. Wave action, of course, will vary daily and seasonally. Many of the anatomical and behavioural attributes of shore organisms reflect attempts to minimize the risk of dislodgement by wave action and this allows different species to occupy different sections of the wave action gradient.

Shore ecologists use the terms '**wave action**' and '**exposure**' synonymously, and the latter should not be confused with exposure to air when shores are exposed by receding tides, more properly termed '**emersion**'. In addition, the concept of exposure to wave action is difficult to apply

Box 5.1 Wave formation

Waves are generated by friction from winds at the air/water interface. The length of fetch (the distance over which air moves unimpeded by a land mass), wind speed, direction and duration and the depth of water all affect the **period** and **height** of waves. Waves can continue to be propagated even without the influence of wind, this is known as **swell**, which decays gradually over time in the absence of wind. Coasts that are exposed to the ocean typically have swell with a long period. Given the right seabed conditions, these coasts produce some of the best waves sought by surfers. Although the surface features of waves are clear to see, **internal waves** occur beneath the surface, which decay towards the seabed. These internal waves rarely persist beyond a depth of 50 m. However, as waves pass into shallower areas the internal waves will create physical disturbance on the seabed, which will increase with decreasing water depth. This produces a gradient of wave disturbance on the sea floor that decreases with distance offshore and with depth.



sensibly to sandy beaches and mudflats, because of the complex interactions between particle size, beach slope, and wave energy. Sediment shore ecologists thus prefer to describe a beach as having a particular morphodynamic state that occupies a point along a reflective–dissipative spectrum, rather than a wave exposure gradient (see 5.3.5).

- Morphodynamic state is preferred to the term 'wave exposure' for describing sandy beaches and mudflats.

5.3.3 Particle size

Shores can be ordered along a particle size gradient ranging from extremely large particles, such as a cliff or boulder beach, to those made up of very fine particles only a few microns in diameter (Fig. 5.4). Large particles provide a stable surface for attachment, and epifauna and flora dominate such shores. In contrast, finer particle sands are often too unstable to permit surface attachment and the fauna lives within the beach (the infauna and meiofauna (Box 5.2)), unless wave action is sufficiently low. Shores of intermediate particle size are very inhospitable for marine life because they are too unstable for surface dwellers and are comprised of particles that are too large for an infaunal life style (Fig. 5.4). Thus, different species are capable of living in different sections of the particle size gradient and many of them are specialized to cope with the unique conditions presented.

- The sizes of the particles that make up the shore have a huge effect on the kinds of organisms that can survive there.

Box 5.2 Macrofauna and meiofauna

In addition to the commonly encountered larger **infauna** of beaches and mudflats, such as clams, shrimps, and polychaete worms, a rich variety of tiny organisms live on and between the individual particles, including nematodes, harpacticoid copepods, gastrotrichs, archaic groups of polychaetes, kinorhynchs, and flatworms. These are grouped together as the **meiofauna**. Because of their small size (typically less than a millimetre) these taxa are not familiar to most marine biologists, let alone the non-expert. They occur in very large numbers, hundreds per $100\,\text{cm}^2$ of beach, and because of their small individual body size (only a few μg), they have high respiration rates per unit mass. This means that their productivity can be almost as high, and in many cases higher, than that of the macrofauna in the beach. Meiofaunal taxa also occur on rocky shores (Hicks 1985, Gibbons & Griffiths 1986) in association with the microhabitats provided by larger species, but they have been less well studied than those in sediments. Notwithstanding their small size and their taxonomic and identification challenges, meiofauna are an extremely rewarding group to work with, since so little is certain about their ecology and functional importance in marine intertidal systems.

The physical refuge provided for infaunal taxa by fine particle shores brings additional challenges. Coarse (sandy) and fine (muddy) particle beaches will present very different physical and microbiological environments, mainly due to their differences in surface area available for microbial activity and their capacity to retain water at low tide (Fig. 5.5).

5.3.4 Salinity

This gradient has been largely dealt with in Chapter 4 and only a summary is provided here for completeness. The salinity gradient is generated by the meeting of fresh water and seawater and the habitat where this occurs most obviously is the estuary. Here, river water with a very low concentration of ionic salts meets marine water with very high levels of such ions. The degree of physical mixing between seawater and fresh water can range from very little, with the less dense fresh water flowing over the top of the marine water, to complete mixing, where turbulence by large waves can result in similar salinities at the water surface and the seabed. The exact nature of the mixing and hence structure of the vertical and longitudinal salinity gradient will be variable for any one estuary, depending on the relative volumes of fresh and sea water, wind-driven physical turbulence that results in mixing of fresh and sea water and spring–neap tidal patterns. The distribution of the fauna and flora along this gradient will thus represent a response to the average conditions present. The majority of species found in estuaries are marine in origin, with few freshwater taxa penetrating far downstream.

● Interactions between fresh and sea water drive sediment distributions in estuaries.

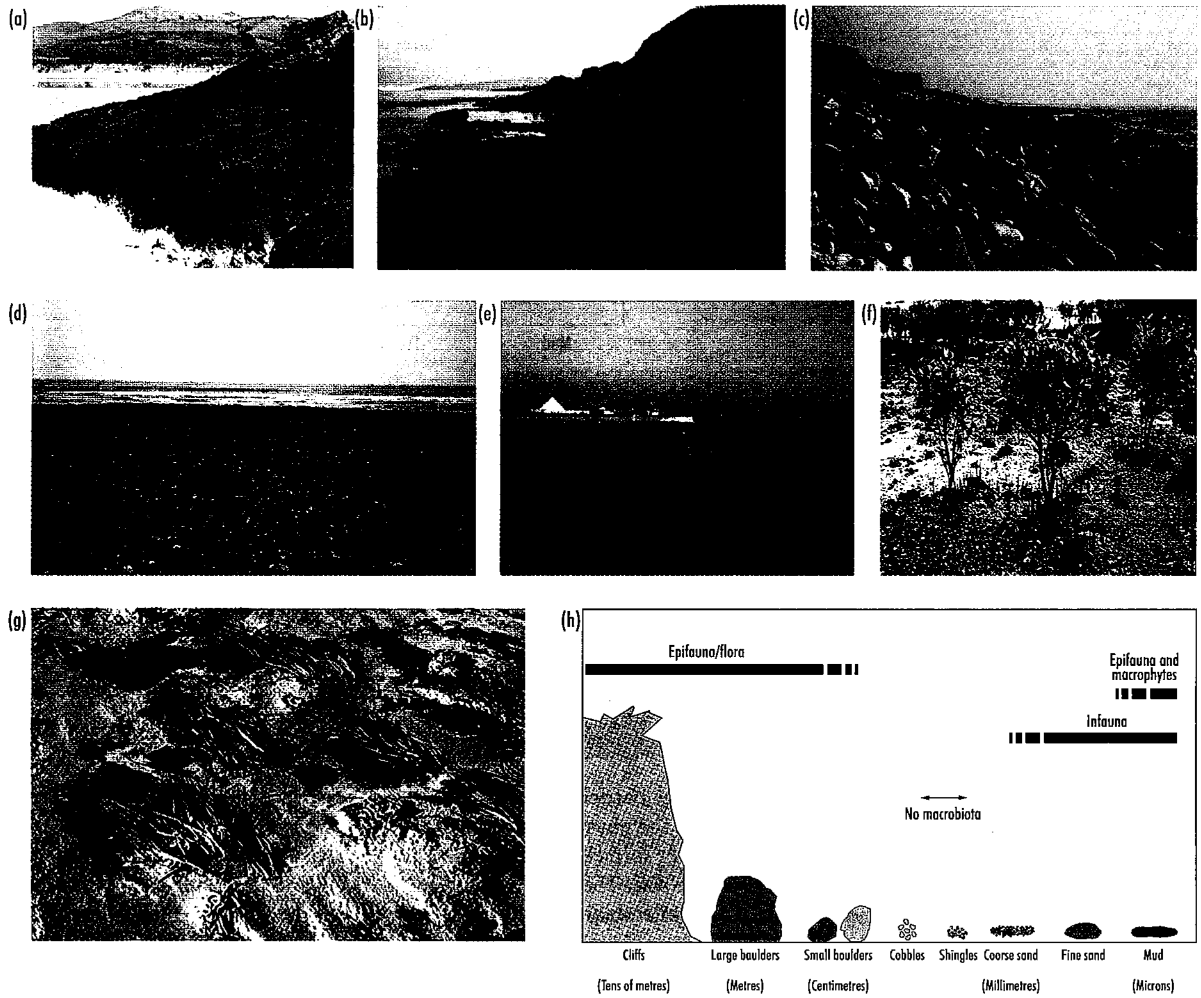


Fig. 5.4 The environmental gradient of particle size, ranging from large rocks and cliffs to mud composed of grains only a few microns in diameter. (a) exposed cliff (Otago Peninsula, New Zealand), (b) sheltered cliff (Little Loch Broom, Scotland), (c) boulder shore (Isle of Wight, England), (d) shingle beach (Norfolk, England), (e) sandy beach (Clacton, England), (f) mangrove (Manakau, New Zealand), (g) seagrass bed (Moray Firth, Scotland), (h) Shore organisms can only live on the sides of the larger particles (epifauna and flora), and between the particles (infauna) on sandy beaches and mudflats (except in extremely sheltered habitats where some epifauna and flora reappear). Intermediate-sized particles that make up shingle and cobble beaches present a hostile environment for both types of organism, because they are too large to retain water and too mobile for surface attachment.

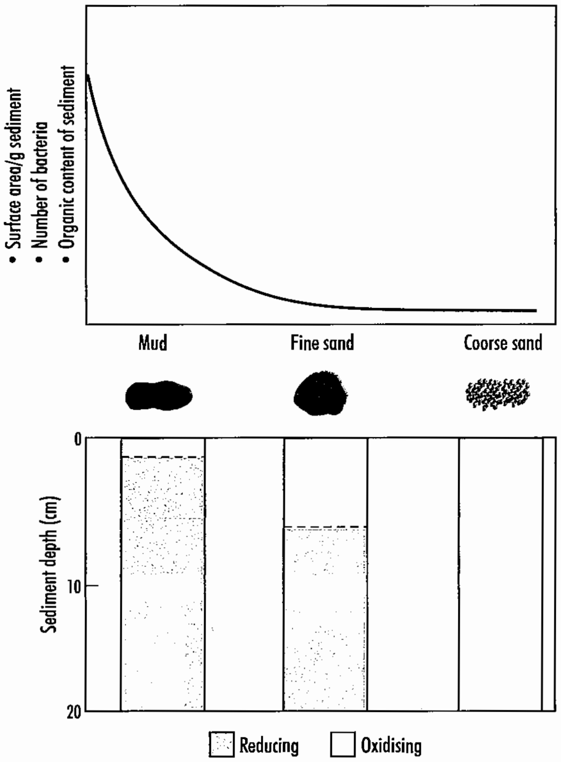


Fig. 5.5 The average particle size that makes up sandy beaches and mudflats has a profound effect of the physico-chemical conditions experienced by the infauna. Muds have a much greater surface area available for microbial activity by virtue of their small individual particle size. They also retain water better than sands and are usually waterlogged. The microbial activity reduces compounds such as iron and sulphate in the sediment creating anoxic conditions the extent of which is reflected in the depth at which the sediment changes colour from orangey-brown (oxidized iron particles) to dark brown or black (reduced iron sulphide).

5.3.5 Interactions between gradients and zonation patterns

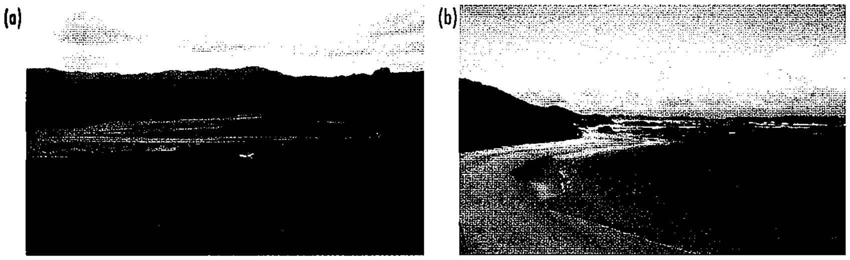
All the above gradients interact to generate particular conditions for life on shores. For instance, increasing wave action will amplify the wetness–dryness gradient, and thereby **uplift** biological zones with increasing wave exposure. Wave action and water movement will sort particles according to their mobility and in the process drive the overall beach environment towards a more reflective or a more dissipative morphodynamic state (Table 5.1). The interactions between salinity and particle size are complex and dealt with in Chapter 4.

● Many different gradients interact to produce conditions suitable for particular species and communities.

The types of fauna and flora recorded at any location on a shore can be understood as the biological responses to the product of these interacting gradients, allowing for biogeography (Chapter 1). The overall

Table 5.1 General features of beaches at the extreme ends of the morphodynamic spectrum. Intermediate morphodynamic states have intermediate features. After Raffaelli and Hawkins (1996). Dissipative (a) and reflective (b) beaches on the Coromandal coast, New Zealand.

	Dissipative beaches	Reflective beaches
Sediments	Fine	Coarse
Waves	Large	Small
Slope	Shallow	Steep
Tidal range	High	Small
Wave period	Long	Short
Swash conditions	Benign	Harsh
Fauna	Rich	Impoverished



patterns of distribution and abundance are revealed as **zonation** patterns, which are most obvious on exposed macro-tidal rocky shores, and least obvious in sheltered sandy flats. Not surprisingly, we understand much better the processes maintaining rocky shore zonation than is the case for other shore habitats.

One of the most important features of rocky shore zonation patterns is the similarity that occurs worldwide. These were described most elegantly by Stephenson and Stephenson (1949, 1972), in a period when marine ecology was developmental and more descriptive. Similar, but not identical, types of fauna and flora occupy similar positions on shore gradients, independent of biogeographical region (Fig. 5.6). The significance of these **universal features of zonation** is that they imply similar and strong underlying structuring processes that operate on all rocky shores: only a limited range of body forms and phylogenies can cope with life on shores. Also, these consistencies in the major zoning species worldwide have permitted the invention of a spatial referencing framework for the unambiguous location (within a shore) of where particular studies were undertaken (Fig. 5.6). Thus, the term midlittoral (or **eulittoral**) would conjure the same mental image of a shore habitat for all rocky shore ecologists.

● Remarkably similar general patterns of zonation recur throughout the world.

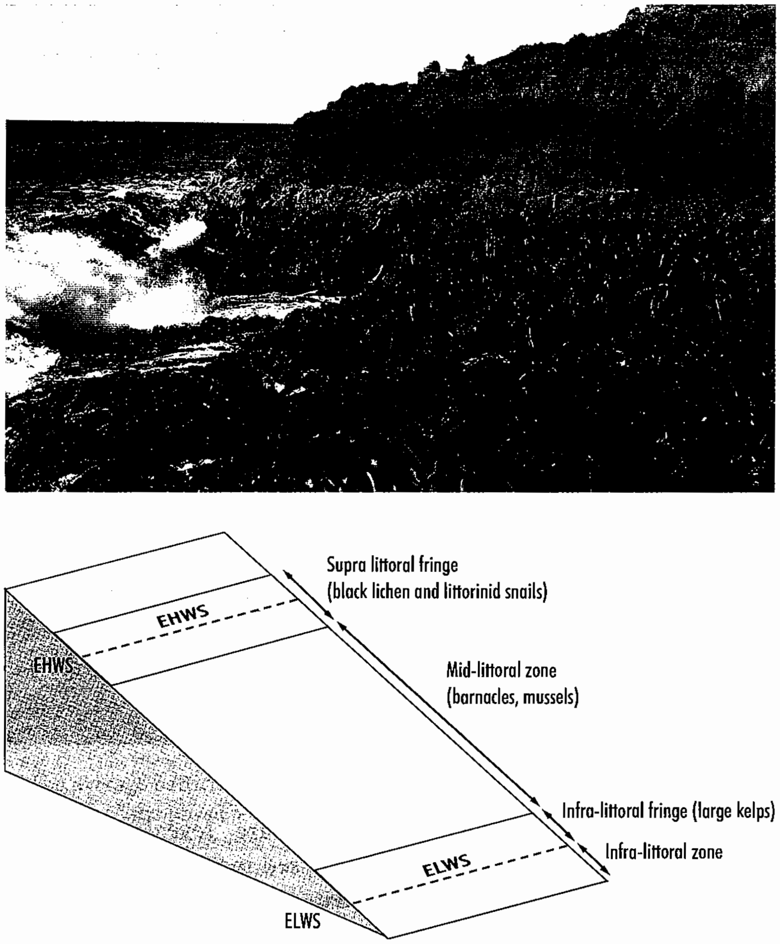


Fig. 5.6 The universal zonation scheme proposed by Stephenson and Stephenson (1972). The main zones are where biota occur worldwide, with slight modifications according to biogeography, and is well illustrated by this rocky shore on the Otago Peninsula, New Zealand.

Similar schemes have been proposed for sandy shores (Fig. 5.7), and there is some evidence of universal zonation patterns for crustaceans (Dahl 1952). However, most general sandy shore zonation schemes are a reflection more of the physical environment of the beach, than its biology (Salvat 1964).

5.4 Causes of Zonation

Given the striking zonation patterns seen on rocky shores, and to a lesser extent on sandy shores and mudflats, it is not surprising that a major preoccupation of shore ecologists has been discovering the **determinants of zonation**. Earlier workers naturally assumed that the tides must be in some way responsible, given the intimate association between the so-called intertidal area and the twice-daily rise and fall of the tides.

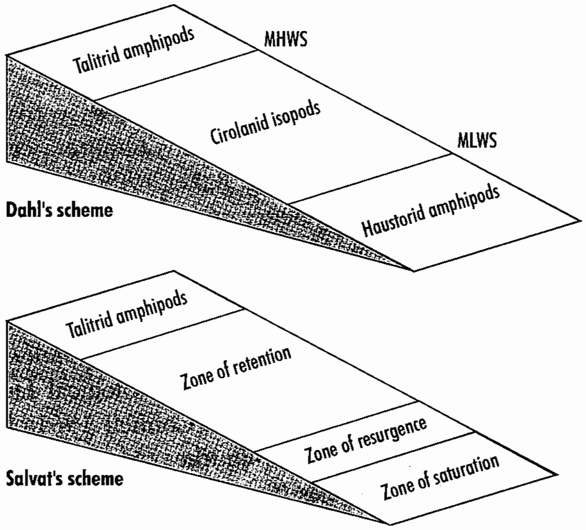


Fig. 5.7 'Universal' zonation schemes for sandy beaches provided by Dahl (1952) based on the occurrence of crustacean groups, and Salvat (1964) based largely on the degree to which water is retained by the sediment at low tide, producing visibly different zones on the shore.

Various schemes and theories were advanced, exemplified by the **critical tidal level** arguments put forward by Colman (1933), and later developed by Doty (1946) and others. It was argued that as one moved down the shore, there were certain regions where only small differences in shore level were characterized by large changes in the period of immersion, when averaged over a year. In other words, the immersion–emersion gradient was particularly steep at these points and thus critical for any species that decided to settle in these regions. Upper and lower distributional limits of several species seemed to coincide precisely with these critical levels. While plausible, indeed compelling, Underwood's (1978) re-examination of this theory revealed the basic science as thoroughly flawed, species distributional limits occurred haphazardly along the shore rather than in groups, and re-plotting of the tidal data did not support the idea of critical levels. Nevertheless, the concept lingers on in several marine ecology textbooks, perhaps because of a reluctance to take the tides out of intertidal ecology.

- Zonation patterns on shores cannot be explained by tidal rise and fall.

Given that the majority of species encountered on rocky and sandy shores are marine and aquatic in origin, we should not be surprised that the **upper zonal limits** of a large number of species have been shown to be associated with **physiological tolerance** to factors such as desiccation and thermal stress. In general, species found higher on the shore are more able to tolerate dryness and thermal stress, than lower shore species. However, it is noteworthy that many of these experiments have been focused on adult individuals. It is often the environmental conditions experienced by the **recruit** (larval) stages that more importantly determine the adult distributions, especially for sessile taxa such as barnacles and mussels. The juveniles of many marine snails recruit to

● Upper distributional limits of species are generally (but not always) set by their tolerance to physical factors.

lower shore levels, and later migrate to higher levels as they become larger and their physiology alters such that they can cope with different environmental conditions.

The determinants of lower zonal limits are not easy to attribute to physical factors. Why should aquatic organisms require a certain period of drying? Several pioneering studies (e.g. Baker 1909) demonstrated that high intertidal species actually grew better under a lower shore tidal regime and Stephenson and Stephenson (1949) suggested that competition and/or predation might be responsible for some zonation patterns. However, it was Connell's classic experiments on the determinants of zonation patterns in the barnacles *Chthamalus montagui* and *Semibalanus balanoides* that provided the most rigorous argument for biological factors setting lower distributional limits of shore species (Connell 1961a,b). The persuasiveness of these experiments lies in the controlled manipulation (removal in this case) of one species (*Semibalanus balanoides*) occupying the zone immediately below another potentially competitive species (*Chthamalus montagui*). Connell was able to show that in the absence of competition for space, a limiting resource on his rocky shore, the higher shore species could survive at lower shore levels than those at which it was normally found. This manipulative approach to understanding the determinants of zonation patterns has been emulated repeatedly by many workers. As a result, it is now something of a paradigm in rocky shore ecology that lower distributional limits of species occur as a result of biological factors, while physical factors set upper limits on distribution. However, there are exceptions, especially amongst the macroalgae (Hawkins & Hartnoll 1983). Thus, grazers may prevent the upshore extension of foliose seaweeds on some Australian shores (Underwood & Jernakoff 1981), red and brown seaweeds grows further upshore in the absence of limpets on the Isle on Man (Hawkins & Hartnoll 1985) and the green seaweed *Codium* may be partly limited by grazing from above (Ojeda & Santilices 1984). Notwithstanding these exceptions, an intriguing question posed by this paradigm is whether it is applicable to zonation along other kinds of gradients, particularly the wetness-dryness gradient on sandy shores, but also to salinity, exposure, and particle size gradients in other habitats.

● Competition and predation have been shown to be important determinants of lower distributional limits of species on many rocky shores.

There has been very little exploration of this question for the last three environmental gradients, but some work has been done on zonation patterns on sandy shores. One of the issues for sandy shore (and mudflat) ecologists is that the description of zonation patterns in these habitats requires the destruction of the medium in which the organisms live: quantitative sampling involves digging out volumes of sediment and separating the fauna, usually by sieving or elutriation. Nevertheless, this approach reveals zonation patterns that are usually not visible at the sediment surface (Fig. 5.8).

● Zonation patterns, as well as their causes, are much harder to detect on sandy beaches and mudflats.

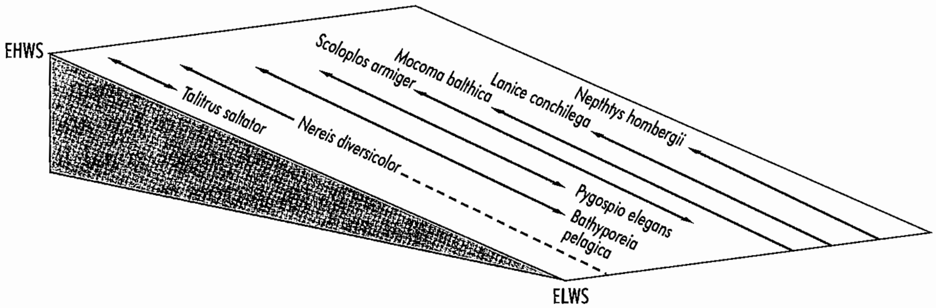


Fig. 5.8 Zonation on a sandy beach, Newburgh, Scotland. Only the most abundant species are represented for the sake of clarity. Data from Raffaelli et al. (1991).

Marine ecologists have sought to understand the role of individual species within sediment communities by systematically removing particular species and studying the consequences. Carrying out such species removal experiments in sandy beaches or mudflats is fraught with interpretational problems if the habitat has to be disrupted to such a severe extent. Just think how difficult it would be to remove 10 individuals of one species from a patch of sandy beach that contains 100 individuals comprising 20 species. A second problem arises in that, unlike the sessile fauna of rocky shores, the infauna is mobile and can easily move back into areas cleared in manipulative experiments. In other words, it is difficult to maintain the integrity of the experimental design of species removal experiments. Third, the beach fauna lives in a three-dimensional environment and displays zonation vertically as well as horizontally, and some species redistribute themselves at each high tide. Experiments aimed at removing potential competitors therefore have an additional layer of complexity. Fourth, it is not clear whether space is a limiting resource for which competition occurs in sandy beaches and mudflats, in the same way that it does on rocky shores. Certainly, the intensive interference competition, where individuals overgrow or crush one another, that is seen between space-occupying species on rocky shores is virtually absent in sediment assemblages, probably because individuals tend to be mobile (as opposed to the many attached biota found on rocky shores) and can simply move away from one another.

● Space is not such a severe constraint on sandy shores as the fauna are mobile and can relocate to avoid competition.

Despite these issues, several investigations have demonstrated the importance of physical factors in setting upper distributional limits, such as Petersen and Black's (1987, 1988) transplant experiments of the bivalves (*Circe* and *Placamen*) to higher shore levels where they grew more slowly and suffered higher mortality due to physical factors. The importance of biological factors in setting distributional limits is illustrated by Posey's (1986) study of a Californian beach. Here, the burrowing activities of the ghost shrimp *Callianassa* excluded a tube dwelling worm *Phoronopsis* from higher shore levels, while the lower distributional limits of the shrimp were probably set by predation by a fish, the sculpin *Leptocottus*. Such manipulative studies are few and far between and, as in the case of Posey's study, both upper zonal limits may be set by biological interactions. Clearly, the factors responsible for zonation in a three-dimensional habitat such as a sandy beach are not as clear as for two-dimensional rocky shores.

5.5 The Organization of Shore Communities

In common with all other biological assemblages, shore communities are organized by a combination of top-down (consumer-driven) and bottom-up (resource-driven) processes. Because many of the classic studies on top-down processes in food webs were first performed on rocky shores, there has been a tendency to generalize these results across all shores and even across all types of ecosystem. Notwithstanding the fact that some of these earlier studies would be unlikely to pass the present-day peer-review process (Box 5.3), they have made a major contribution to mainstream ecological theory. Before we discuss the relative importance of different processes in the dynamics of shore assemblages, it is worth rehearsing the features of shores that make them so amenable to studying these kinds of questions.

● Shore communities are organized by many different kinds of processes, such as predation and energy supply.

Box 5.3 Manipulative field experiments

The most convincing manipulative field experiments are those where the treatment and control plots are highly replicated to provide the necessary statistical power to detect an effect of manipulation. Such powerful designs will convince the most critical reviewer or editor. It is therefore somewhat ironic that the two rocky shore experiments which ecologists are completely persuaded by are fatally flawed in this respect. The first is Lodge's (1948) removal of the limpet *Patella* from a wide strip running down a shore on the Isle of Man and the subsequent bloom of algae in the manipulated area. The second is Paine's (1974) set of experiments on *Pisaster* on the Washington coast, where removal of the starfish saw a massive increase in mussels and a collapse in community structure (Fig 5.9). Neither study used a properly replicated experimental design, and there were essentially no controls (Raffaelli & Moller 2000). Yet the scientific community is persuaded by these experiments that *Patella* and *Pisaster* are keystone species. Why? Because (a) the effects were so dramatic, and (b) the resultant changes in abundance and distribution of algae and mussels were completely outside the 'norm' for similar rocky shore communities. However, Lodge and Paine were lucky to get away with it, the effects of predator removals are often much more subtle and a proper experimental design is advised to all would-be manipulators!

For further discussion, see Raffaelli and Moller (2000).

5.5.1 The role of field experiments

Of all the arguments that can be used to convince scientists that a particular viewpoint is correct, the experimental falsification of hypotheses has proven the most persuasive (i.e. the rejection of the null hypothesis). **Field experiments** have to be properly designed and analysed so that there is no ambiguity in their outcome (Underwood 1981, 1997; Hurlbert 1984). An important aspect of their design is that the experimental plots (areas within which the manipulation occurs) need to be replicated many times and dispersed appropriately over the study area (Chapter 14). This is often very difficult to achieve for many types of taxa and ecosystem (Raffaelli & Moller 2000), but not for shores. The small body size, high densities, and small-scale nature of spatial patterns of shore species means that many relatively small plots can be located within a small spatial extent. The three-dimensional variation within shore sediments is usually compressed into a layer no more than 20 cm deep. In addition, processes of interest tend to operate over relatively short ecological time scales (weeks to years), allowing them to be investigated within the traditional 3- to 5-year research grant period. Finally, of course, shores are highly accessible and enable sampling to occur with high precision; you can be sure that you collected your samples from within the experimental plot you intended to sample. These features mean that it is much easier to investigate certain types of processes on shores compared to other habitats, such as forests or the deep sea.

● Experimental demonstrations of interactions are only persuasive if executed correctly and unambiguously.

However, while shores are highly amenable to the experimental manipulative approach, not all questions can be satisfactorily addressed in this way, especially those questions concerned with processes that operate over large spatial and long temporal scales (Raffaelli & Moller 2000). Seductive as they are, field experiments are not the answer to every problem, although they are a powerful investigative tool.

Despite the experimental design issues that surround some of the earlier field experiments (Box 5.3), there is no doubt that top-down processes are of prime importance on some kinds of shore. Experiments involving the removal of suspected key consumers, such as predatory starfish, or whelks, and herbivorous sea urchins or limpets, have often revealed strong competitive interactions between species whose populations are regulated by the available spatial resource. Often a competitive dominant emerges in the absence of the consumer, with a resulting loss of inferior competitors and a lower overall community biodiversity (Fig. 5.9). While such experiments are dramatically effective in demonstrating the importance of top-down control by what have become termed **keystone predators**, their outcomes need to be placed in context (Pace et al. 1999).

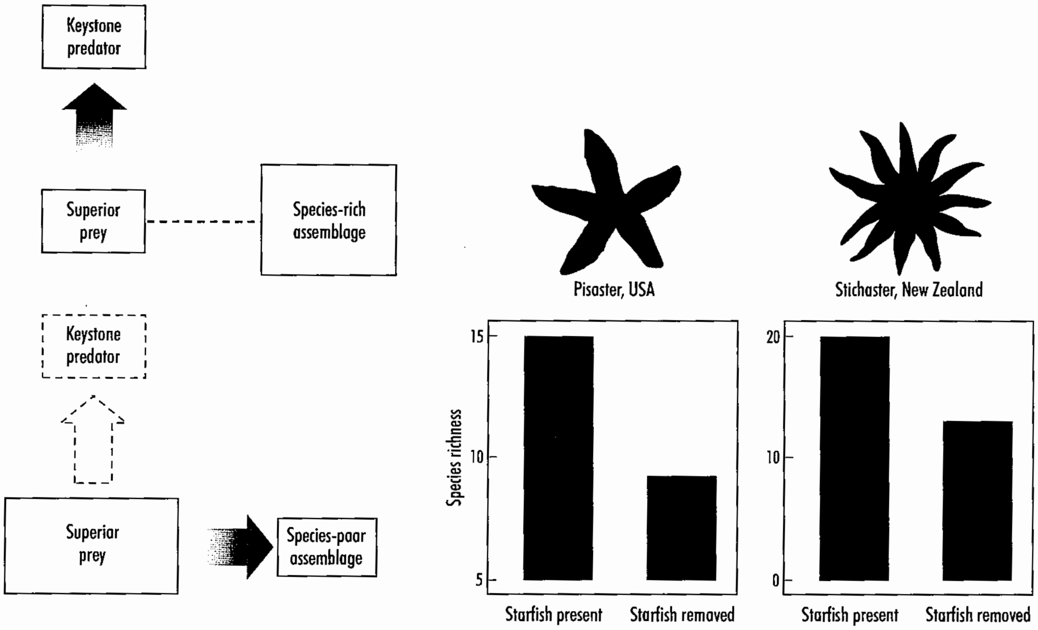


Fig. 5.9 The role of keystone predators in maintaining species richness. Left top: a strong controlling interaction between a competitively superior prey and its predator permits the coexistence of an associated module of other species. Left bottom: breaking the link releases the superior prey, which monopolizes the resources on which the module species depend. After Paine (1980). On the right are examples of how species richness is reduced in the absence of keystone starfish in the U.S. and New Zealand. After Raffaelli and Hawkins (1996).

5.5.2 Keystone predator or prey?

The keystone status of starfish, such as *Pisaster* (Fig. 5.9), or limpets, such as *Patella*, is not due to any inherent attributes of these species. Their status depends entirely on the response of their resource prey to reduced consumption, and in that sense the actual identity of the consumer is irrelevant. In other words, the factors that drive the competitive dynamics of the prey should be the focus of investigation. For instance, while *Pisaster* has been shown to be a keystone predator on exposed coastlines along the north-western USA, on other shores this is not the case. Similarly, the whelk *Morula* has an organizing role on some shores in New South Wales, but by no means all (Fairweather & Underwood 1991).

● A keystone species may simply be another brick in the wall in different circumstances.

One factor that determines whether a 'keystone effect' will be seen in the relatively simple communities of temperate systems (see below) is the recruitment dynamics of the dominant prey. This realization has led to the development of an extremely important, but at the same time incredibly challenging, area of shore ecology known as supply-side ecology (Gaines & Roughgarden 1985; Gaines et al. 1985; Lewin 1986). The significance of this area is best demonstrated by considering the dynamics of species with offshore early life history stages, such as barnacles, mussels, and algae. Recruitment of these taxa usually occurs every year, but it is the strength of a particular year's cohort of recruits that will determine the outcome of competition and hence community organization on the shore. Heavy recruitment by the dominant competitor will, in the absence of a consumer, lead to the exclusion of inferior competitors. However, if recruitment of the dominant competitor is poor, other species will not decline in the absence of the so-called keystone predator. These processes are also critical determinants of the likelihood of the successful colonization of species that have been introduced into new ecosystems through human activities.

- Recruitment processes operating far out at sea may profoundly affect the outcome of interactions on the shore.

The central question for understanding the dynamics of these communities is therefore 'what determines recruitment strength?' The answer rests in the ocean climate determinants of the offshore currents that carry the larvae or spores to the shore. If there are plenty of larvae in the currents and if these sweep the shore at the right time, then recruitment will be strong. In this respect it is unfortunate that there has been an emphasis on the keystone nature of the consumer, because the dynamics of these shores may in fact be driven by events hundreds of kilometres offshore. If this larger-scale perspective is taken, it could be argued that bottom-up, not top-down processes organize the shore.

Finally, in shore communities with a more complex set of predators, such as those found on many tropical shores (Menge & Lubchenco 1981; Menge et al. 1986) and in temperate estuaries and mudflats (Reise 1985; Raffaelli & Hall 1992), the removal of any one predator does not usually lead to the kinds of cascading effects documented for some temperate rocky shores, since the remaining species simply mop up any released prey resource. This effect is known as diffuse predation (Hixon 1991). Keystone predators are not therefore a characteristic of such shores.

5.5.3 Primary and secondary space

Top-down effects on shores are most obvious between consumers and those prey species that are **primary space limited**. That is, they compete aggressively for the rock surface. Such taxa include truly sessile groups, such as algae, barnacles, oysters, and sponges, as well as semi-sessile taxa, such as mussels. Interactions between these taxa are typically of the interference type, including overgrowth, crushing, smothering, and chemical warfare (algal and sponge allelochemicals). Taxa that are not sessile can move away from such interference competition, which explains why competitive exclusion, and hence keystone effects, are harder to demonstrate in the mobile species found in sandy shores and mudflats, as well as for rocky shore gastropods and amphipods. Indeed,

- The structure created by beds of primary-space occupiers, such as mussels, permits a high local biodiversity of associated secondary-space occupiers on rocky shores.

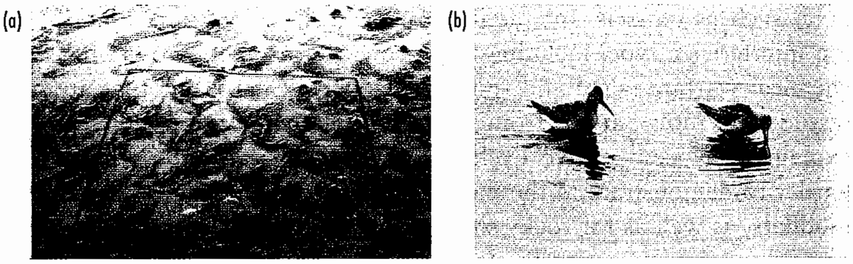
by keeping mussel densities low, *Pisaster* is partly responsible for maintaining a high diversity of primary space occupiers, but reduces biodiversity overall by reducing the habitat available for those secondary-space occupiers living in the highly complex mussel matrix, a system of extremely high biodiversity on rocky shores (Suchanek 1992).

5.5.4 Bottom-up processes

Despite a great deal of effort, much of it involving manipulative field experiments, it has been hard to demonstrate consistently an important role for top-down processes for sandy beach and mudflat communities (Raffaelli & Hawkins 1996). These systems often support a much larger range of consumers, including shorebirds, crustaceans, and fish, which occur in large numbers and have high energy demands (Table 5.2; Chapter 4). One might therefore expect top-down control in such systems, but this has been difficult to demonstrate experimentally. There are a number of factors that might be involved: low natural predator densities, poor experimental design, prey movement in and out of cages, inappropriately sized cages, insufficient time duration for the experiment, and, finally, a real absence of top-down control. There is no doubt that many experiments that have attempted to discern the importance of

Table 5.2 Examples of high consumption rates by shorebirds feeding on (a) macrophyte standing crop, and (b) invertebrate production. Data from Thayer et al. (1984) and Baird et al. (1985), respectively. Inset photographs: (a) seagrass bed Moray Firth, Scotland; (b) wading birds that are typical invertebrate feeders.

Prey	% consumed
(a) Macrophytes	
Zostera	30–75
Ruppia	20
Potamogeton	13
(b) Invertebrates	
Ythan estuary	36
Tees estuary	44
Langebaan lagoon	20



predation in these systems suffer from experimental design problems (Raffaelli & Moller 2000). Experiments in these habitats are typically short-term (weeks to months) and may be too short to reveal anything but the initial, transient dynamics, which may or may not be the same as the longer term behaviour of the system. This is important given that the effects of competitive interactions, for example for food resources, among prey species are likely to be subtle and long-term.

- The outcome of competitive interactions between mobile species may be much less dramatic than for sessile taxa.

Notwithstanding the above criticisms of manipulative field experiments in sediment systems, it would seem that bottom-up processes dominate, with predators limited by their prey, rather than vice versa. Many prey individuals remain inaccessible to predators, living out of reach for much of the time within the sediment and only a proportion of the prey standing stock (as opposed to production) may be predated. The dominance of bottom-up processes is perhaps not surprising given that sandy shores and mudflats tend to be net importers of organic matter from elsewhere, for example, upstream and along the coast in the case of estuaries, and from kelp beds in the case of many exposed sandy beaches.

- Most prey individuals in mudflats and beaches are unavailable to predators like shorebirds and fish, and their numbers are driven by the supply of organic matter and other food resources.

5.5.5 Disturbance and bioturbation

A feature of sediment systems, whether intertidal, sublittoral or deep-sea, is physical disturbance to the sediment fabric and alteration of the physico-chemical environment by the organisms themselves or external events such as storms and ice-scour. Species living within the sediment move through it, ingest and egest particles and draw oxygen-rich water down from the surface to depth (Rhoads 1974). This local-scale biological disturbance (bioturbation) can change the environment for other species, for instance by loosening and destabilizing the sediment fabric and making it more vulnerable to erosion by water movement. Alternatively, species that pump oxygenated water through burrows create a more favourable environment for other species (Fig. 5.10; Chapter 7).

In addition to changing the local environment for associated species, bioturbation will also alter the flux of nutrients between the sediment and the overlying water and in this respect the biodiversity of intertidal flats may have an overall impact on ecosystem functioning (Box 5.4). Many epibenthic predators, including flatfish, crabs, and shorebirds, disturb the sediment surface intensely during their feeding activities (Hall et al. 1993). While the resultant pits and surface features created tend to fill in with fine material and perhaps detritus, on most beaches the local effects are quickly erased by bedload transport (Fig. 5.10).

In summary, the picture that emerges from evaluations of top-down and bottom-up processes on shores is that a mixture of both is always present to differing degrees and this mixture will vary with the relative strength of consumer and resource recruitment, as well as the influence of wider-scale processes, such as ocean currents and catchment run-off.

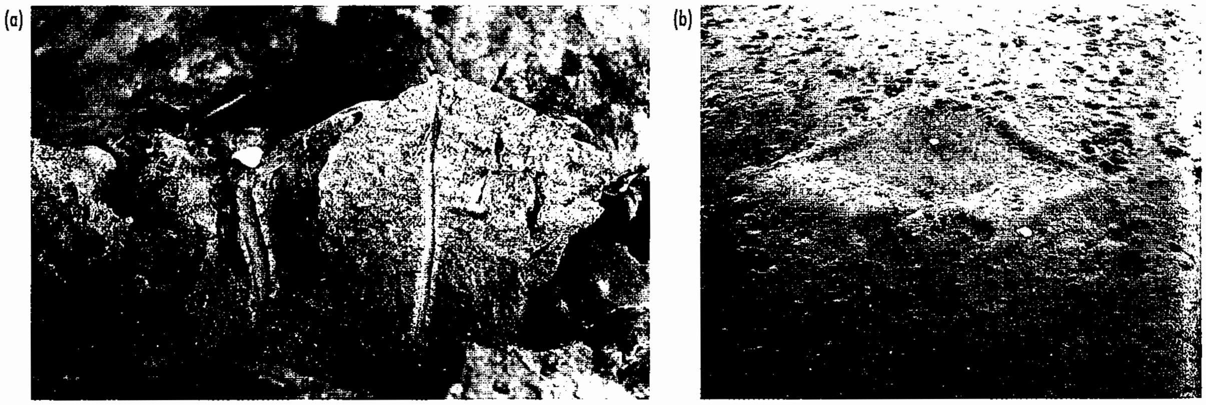


Fig. 5.10. (a) effect of bioturbation by burrowing ghost shrimp *Callianassa*, (Manakau, New Zealand), which piles up a large growing mound (seen here in section) by ejecting processed sediment through the top of its burrow entrance (Tamaki & Flach 2000). Note the oxygenated burrow walls caused by the animal pumping water from the surface (shown as light brown sediment lining burrow). (b) a depression or pit made by an eagle ray feeding at the sediment surface on small bivalves (Manakau, New Zealand). Such pits form significant structures on intertidal flats (Thrush et al. 1993).

The latter is a particularly important concept in the emerging field of coastal zone management in which the interactions between land and the adjacent marine areas are of fundamental importance.

5.6 The Shore Network

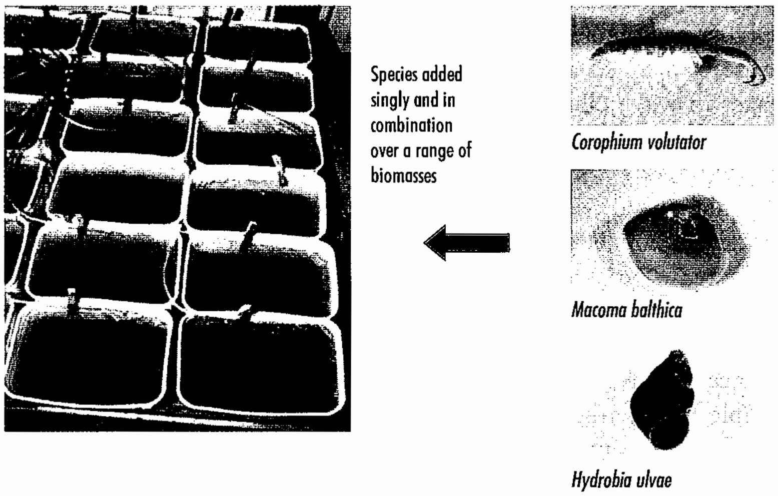
The previous section has stressed both the openness and connectivity of shores. Ecologists are usually required to delimit spatially (and temporally) their study areas in order to make sense of the complexity present, but the linear continuity of the coastline and its openness to the ocean necessitates a broader perspective if one is to truly understand how shores work. While conceptualizing a particular shore as a part of a larger network is relatively straightforward, quantifying those linkages will be a daunting task and one which is best suited to modelling as opposed to empirical approaches. However, there are a number of general features that can be described empirically.

- Shores are highly open systems, receiving and exchanging resources and propagules with each other and with offshore systems.

Coastal water movements have an incredibly significant impact upon the change and pattern in shore organisms, and are responsible for the transport of inorganic nutrients, organic material, sediment and its associated infauna, larvae, and spores within the water column, as well as smaller fish and crustacean consumers. Often, major shifts in community structure and composition on the shore can only be satisfactorily explained by considering near coast hydrodynamics. The irony is that

Box 5.4 Bioturbation in shore habitats

The bioturbatory activities of many infaunal species of beaches and mudflats affect the nutrient flux directly by changing the sediment physico-chemical environment, and indirectly through secondary impacts on the microbial community responsible for many chemical transformations (e.g. sulphate reducing bacteria). Experiments have been conducted to explore the significance of bioturbation for the release of nutrients from sediments, and in particular whether the presence of different species affect the flux (Raffaelli et al. 2003). It appears that a few species, such as the polychaete *Nereis (Hediste) diversicolor*, are extremely important, while others, such as the mud snail (*Hydrobia ulvae*), are less important in this respect. Furthermore, the importance of *Nereis* varies with near-bed flow, probably due to changes in the behaviour of the species in still and flowing conditions (Raffaelli et al. 2003). Finally, the more functional types (active burrowers, sediment reworkers, and oxygenators) present within the sediment, the greater the release of nutrients from the sediment. These experiments imply that the diversity of infauna present in sediments is important for maximizing this particular ecosystem process, but that functional group diversity is more important that species richness per se.



A mesocosm experiment that manipulated assemblage composition to investigate the ecosystem role of biota that perform different functional roles.

many shore ecologists are not trained in this area and that mainstream ecologists seeking to use the shore as a convenient laboratory for testing theory may not be aware of the importance of water movement. Our understanding of such physical processes is further hampered by the paucity of data routinely collected. Clearly, this is an aspect of shore ecology in need of urgent support and development.

● Often, major shifts in community structure and composition on the shore can only be satisfactorily explained by considering near coast hydrodynamics.

In addition to the physical transport of living and non-living material on- and offshore, and between different shore types, larger organisms can make purposeful migrations. These include larger fish, reptiles, birds, and mammals, which undertake such journeys for breeding, feeding, or to find a refuge from bad weather or predators. Their use of the shore can be considerable, especially for warm-bloodied taxa with high energy demands, such as shorebirds and marine mammals (Table 5.2), although, as argued in 5.5.5, cascading effects on the community are rarely detectable.

5.7 The Future of Rocky and Sandy Shores

- Accelerated Sea-level Rise, due to climate change, will have large-scale impacts on sandy beaches and mudflats over the next 50–100 years.

The future of rocky and sandy shores depends on the temporal perspective taken. A series of key analyses looking at impacts and threats to 2025 (Brown & McLachlan 2002; Kennish 2002; Thompson et al. 2002) have identified a continued increase in many of the anthropogenic impacts that shores experience today, mainly because of projected increases in coastal populations worldwide. Looking further ahead to 2080, accelerated sea-level rise (ASLR) will undoubtedly impinge upon low lying sedimentary shores and estuaries, but also on rocky shores because of changes in currents and hence transport patterns, as well as changes in wave climate (Chapter 14).

Beaches are dynamic physical entities, maintained by processes operating above and below the beach as commonly defined (Brown & McLachlan 1990), so that changes in sediment supply and wave climate are likely to impact greatly on beach dynamics. For sandy shores, ASLR may increase erosion, create a steeper beach profile and increase turbidity (Goss-Custard et al. 1990). With less organic matter retained in the beach there will be a lower biomass of infauna. These problems will be exacerbated if beaches are protected by hard engineering, as the available beach area will be progressively sandwiched between a rising sea level and an immovable structure, the so-called coastal squeeze. The net result of sea-level rise for many soft shores will therefore be a smaller, less productive beach, although other scenarios are possible depending on sedimentation patterns and the relative rise of the sea and land (Beukema 2002, Goss-Custard et al. 1990).

- Sea-level rise not only reduces intertidal area, but profoundly alters sediment distributions.

It is likely that rocky shores, at least those below high cliffs, will not be subject to coastal squeeze, since the biology can migrate upwards over time without impediment. However, both rocky and sandy shores in some regions could experience a more severe wave climate, due to an increase in storminess with climate change (IPCC 2001). Of most concern, perhaps, is the suspected relationship between sea level and the return time of storm surges, catastrophic flooding events which can remove entire beaches and mudflats. For instance, one estimate suggests that an increase in sea level of 0.5 m, well within the range predicted by

2080, can alter the return time of a 1.5 m storm surge from 1 in every 100 years to 1 in 10 years or less (IPCC 2001). How shore communities, both soft and hard, would respond to catastrophic disturbances at a frequency that approximates the lifespan of much of the shore biota is hard to predict. However, longer-lived species would have difficulty adapting to such conditions due to their lower fecundity and infrequent recruitment.

● The frequency of catastrophic wave action is likely to increase dramatically with rises in sea level.

● CHAPTER SUMMARY

- Rocky and sandy shores are the most accessible parts of the marine environment and contain representatives of almost all the major classes of animals and plants.
- Rocky and sandy shores occur at either end of an environmental gradient of habitat particle size that ranges from very large (cliffs and boulders) to very small (individual sand grains). Species occupy sections of this gradient and the wetness/dryness (shore level) and wave action gradients and reveal zonation patterns that are most obvious across the shore level gradient.
- The distribution and abundance of these species are determined by their tolerances to physical factors, such as water movement and desiccation, and to biological factors, such as competition, bioturbation and predation.
- Rocky and sandy shores provide excellent laboratories for exploring mainstream ecological concepts. Much of the pioneering research using controlled experimental manipulations has been carried out on the seashore.
- Different kinds of shore are net exporters or importers of energy, especially detrital material. Understanding ecological functioning requires shores to be viewed as connected networks.
- Sandy and muddy shores are particularly vulnerable to climate change induced sea-level rise, because they are often prevented from transgressing inland.

● FURTHER READING

Little and Kitching (2001) is an excellent concise book that deals with rocky shores, while Raffaelli and Hawkins (1996) consider in depth the development of intertidal ecology. Raffaelli and Moller (2000) critically evaluate the use and misuse of experimental approaches in ecology. Reise (1985) is a detailed consideration of the ecology of tidal flats.

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