Milliman JD and Syvitski JPM (1992) Geomorphic/tectonic control of sediment discharge to the ocean: the importance of small mountainous rivers. *J Geol* 100: 525–544.

Milliman JD, Ren M-E, Qin Y-S and Saito Y (1987) Man's influence on the erosion and transport of sediment by Asian rivers: the Yellow River (Huanghe) example. *J Geol* 95: 751–762.

Milliman JD, Farnworth KL and Albertin CS (1999) Flux and fate of fluvial sediments leaving large islands in the East Indies. *Journal of Sea Research* 41: 97–107.

Thomas MF and Thorp MB (1995) Geomorphic response to rapid climatic and hydrologic change during the late Pleistocene and early Holocene in the humid and sub-humid tropics. *Quarterly Science Review* 14: 193–207.

Walling DE (1995) Suspended sediment yields in a changing envirionment. In: Gurnell A and Petts G (eds) *Changing River Channels*, pp. 149–176. Chichester: John Wiley & Sons.

ROCKY SHORES

G. M. Branch, University of Cape Town, Cape Town, Republic of South Africa

doi:10.1006/rwos.2001.0086

Introduction

Intertidal rocky shores have been described as 'superb natural laboratories' and a 'cauldron of scientific ferment' because a rich array of concepts has arisen from their study. Because intertidal shores form a narrow band fringing the coast, the gradient between marine and terrestrial conditions is sharp, with abrupt changes in physical conditions. This intensifies patterns of distribution and abundance, making them readily observable. Most of the organisms are easily visible, occur at high densities, and are relatively small and sessile or sedentary. Because of these features, experimental tests of concepts have become a feature of rocky-shore studies, and the critical approach encouraged by scientists such as Tony Underwood has fostered rigor in marine research as a whole.

Rocky shores are a strong contrast with sandy beaches. On sandy shores, the substrate is shifting and unstable. Organisms can burrow to escape physical stresses and predation, but experience continual turnover of the substrate by waves. Most of the fauna relies on imported food because macroalgae cannot attach in the shifting sands, and primary production is low. Physical conditions are relatively uniform because waves shape the substrate. On rocky shores, by contrast, the physical substrate is by definition hard and stable. Escape by burrowing may not be impossible, but is limited to a small suite of creatures capable of drilling into rock. Macroalgae are prominent and *in situ* primary production is high. Rocks alter the impacts of wave action, leading to small-scale variability in physical conditions.

Research on rocky shores began with a phase describing patterns of distribution and abundance. Later work attempted to explain these patterns – initially focusing on physical factors before shifting to biological interactions. Integration of these focuses is relatively recent, and has concentrated on three issues: the relative roles of larval recruitment versus adult survival; the impact of productivity; and the effects of stress or disturbance on the structure and function of rocky shores.

Zonation

The most obvious pattern on rocky shores is an up-shore change in plant and animal life. This often creates distinctive bands of organisms. The species making up these bands vary, but the high-shore zone is frequently dominated by littorinid gastropods, the upper midshore prevalently occupied by barnacles, and the lower section by a mix of limpets, barnacles, and seaweeds. The low-shore zone commonly supports mussel beds or mats of algae. Such patterns of zonation were of central interest to Jack Lewis in Britain, and to Stephenson, who pioneered descriptive research on zonation, first in South Africa and then worldwide.

In general, physical stresses ameliorate progressively down the shore. In parallel, biomass and species richness increase downshore. Three factors powerfully influence zonation: the initial settlement of larvae and spores; the effects of physical factors on the survival or movement of subsequent stages; and biotic interactions between species.

Settlement of Larvae or Spores

Many rocky-shore species have adults that are sessile, including barnacles, zoanthids, tubicolous polychaete worms, ascidians, and macroalgae. Many others, such as starfish, anemones, mussels, and territorial limpets, are extremely sedentary, moving less than a few meters as adults. For such species, settlement of the dispersive stages in their life cycles sets initial limits to their zonation (often further restricted by later physical stresses or biological interactions).

Some larvae selectively settle where adults are already present. Barnacles are a classic example. This gregarious behavior, which concentrates individuals in particular zones, has several possible advantages. The presence of adults must indicate a habitat suitable for survival. Furthermore, individuals of sessile species that practice internal fertilization (e.g., barnacles) are obliged to live in close proximity. Even species that broadcast their eggs and sperm will enhance fertilization if they are closely spaced, because sperm becomes diluted away from the point of release. Finally, adults may themselves shelter new recruits. As examples, larvae of the sabellariid reef-worm *Gunnarea capensis* that settle on adult colonies suffer less desiccation, and sporelings of kelps that settle among the holdfasts of adults experience less intense grazing than those that are isolated.

Cues used by larvae to select settlement sites are diverse. Barnacle larvae differ in their preferences for light intensity, water movement, substrate texture, and water depth. All of these responses influence the type of habitat or zone in which the larvae will settle. Most barnacle larvae are attracted to species-specific chemicals in the exoskeletons of their own adults, which persists on the substratum even after adults are eliminated. (Incidentally, this behavior is not just of academic interest: gregarious settlement of barnacles on the hulls of ships costs billions of dollars each year due to increased fuel costs caused by the additional drag of 'fouling' organisms.)

Cues influencing larval settlement can also be negative. Rick Grosberg elegantly demonstrated that the larvae of a wide range of sessile species that are vulnerable to overgrowth avoid settling in the presence of *Botryllus*, a compound ascidian known to be an aggressive competitor for space.

A different aspect of 'supply-side ecology' is the rate at which dispersive larvae or spores settle. The relative importance of recruit supply versus subsequent survival is a topic of intense research. In situations of low recruitment, rate of supply critically influences population and community dynamics. At high levels of recruitment, however, supply rates become less important than subsequent biological interactions such as competition.

Control of Zonation by Physical Factors

Early research on the causes of zonation focused strongly on physical factors such as desiccation, temperature, and salinity, all of which increase in severity upshore. Measurements showed a correlation between the zonation of species and their tolerance of extremes of these factors. In some cases – particularly for sessile species living at the top of the shore – physical conditions become so severe that they kill sections of the population, thus imposing an upper zonation limit by mortality.

For those species blessed with mobility, zonation is more often set by behavior than death, and most individuals live within the 'zone of comfort' that they can tolerate. One example illustrates the point. The trochid gastropod *Oxystele variegata* increases in size from the low- to the high-shore. This gradient is maintained by active migration, and animals transplanted to the 'wrong' zone re-establish themselves in their original zones within 24 hours. The underlying causes of this size gradient seem to be twofold: desiccation is too high in the upper shore for small individuals to survive there; and predation on adults is greatest in the lower shore.

Adaptations to minimize the effects of physical stresses are varied. Physiological adaptation and tolerance are one avenue of escape. Avoidance by concealment in microhabitats is another. Morphological adaptations are a third route. For instance, desiccation and heat stress can be reduced by large size (reducing the ratio of surface area to size), and by differences in shape, color, and texture (**Figure 1A**).

Physical factors can clearly limit the upper zonation of species. It is often difficult, however, to imagine them setting lower limits. For this, we turn to biological interactions.

Biological Interactions

Interactions between species – particularly competition and predation – only began to influence the thinking of intertidal rocky-shore ecologists in the mid 1950s. Extremely influential was Connell's work, exploring whether the zonation of barnacles in Scotland is influenced by competition. He noted that a high-shore species, *Chthamalus stellatus*, seldom penetrates down into the midshore, where another species, *Semibalanus balanoides*, prevails. Was competition from *Semibalanus* excluding *Chthamalus* from the midshore? In field experiments in which *Semibalanus* was eliminated, *Chthamalus* not only occupied the midshore, but survived and grew there better than in its normal high-shore zone. *Chthamalus* is more tolerant of physical stresses than *Semibalanus*, and can therefore survive in the high-shore, where it has a 'spatial refuge' beyond the limits of *Semibalanus*. In the midshore, however, *Semibalanus* thrives and competitively

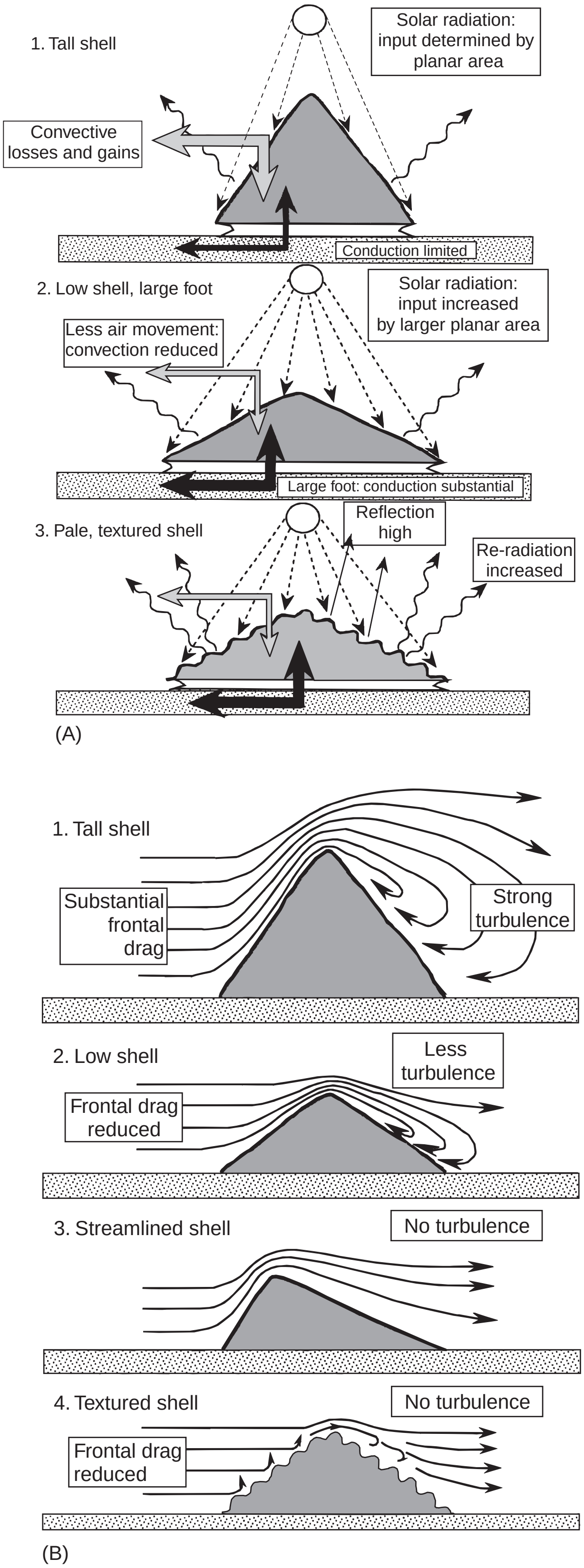

Figure 1 (A) Effects of shell shape, color, and texture on heat uptake and loss. (B) Influence of shell proportions and texture on hydrodynamic drag.

excludes *Chthamalus* by undercutting or overgrowing it.

Other forms of competition have since been discovered. For instance, territorial limpets defend patches of algae by aggressively pushing against other grazers. In areas where they occur densely, they profoundly influence the zonation of other species and the nature of their associated communities.

The role of predators came to the fore following the work of Bob Paine who showed that experimental removal of the starfish *Pisaster ochraceus* from open-coast shores in Washington State led to encroachment of the low-shore by mussels, which are usually restricted to the midshore. Thus, predation sets lower limits to the zonation of the mussels. More importantly, it was shown that the downshore advance of mussel beds reduced the number of space-occupying species there. In other words, predation normally prevents the competitively superior mussels from ousting subordinate species, thus maintaining a higher diversity of species. This concept – the ‘predation hypothesis’ – has since been broadened to include all forms of biological or physical disturbance. If disturbance is too great, few species survive and diversity is low. On the other hand, if it is absent or has little effect, a few species may competitively monopolize the system, reducing diversity. At intermediate levels of disturbance, diversity is highest – the ‘intermediate disturbance hypothesis’. (Incidentally, the idea is not new. Darwin gives an accurate description of this effect in sheep-grazed meadows.)

Paine’s work led to the idea of ‘keystone predators’: those that have a strong effect on community structure and function. Unfortunately the term has been debased by general application to any species that an author feels is somehow ‘important’. Consequently, not all scientists are enamoured of the concept. More recently, it has been redefined to mean those species whose effects are disproportionately large relative to their abundance. This more usefully allows recognition of species that can be regarded as ‘strong interactors’, and which powerfully influence community dynamics.

Many researchers have shown that grazers (particularly limpets) profoundly influence algal zonation, excluding them from much of the shore by eliminating sporelings before they develop. Hawkins and Hartnoll suggested that interactions between grazers and algae depend on the upshore gradient in physical stress, and argued that low on the shore, algae are likely to be sufficiently productive to escape grazing and proliferate, forming large, adult growths that are relatively immune to grazing. In the mid- to high-shore, grazers become dominant

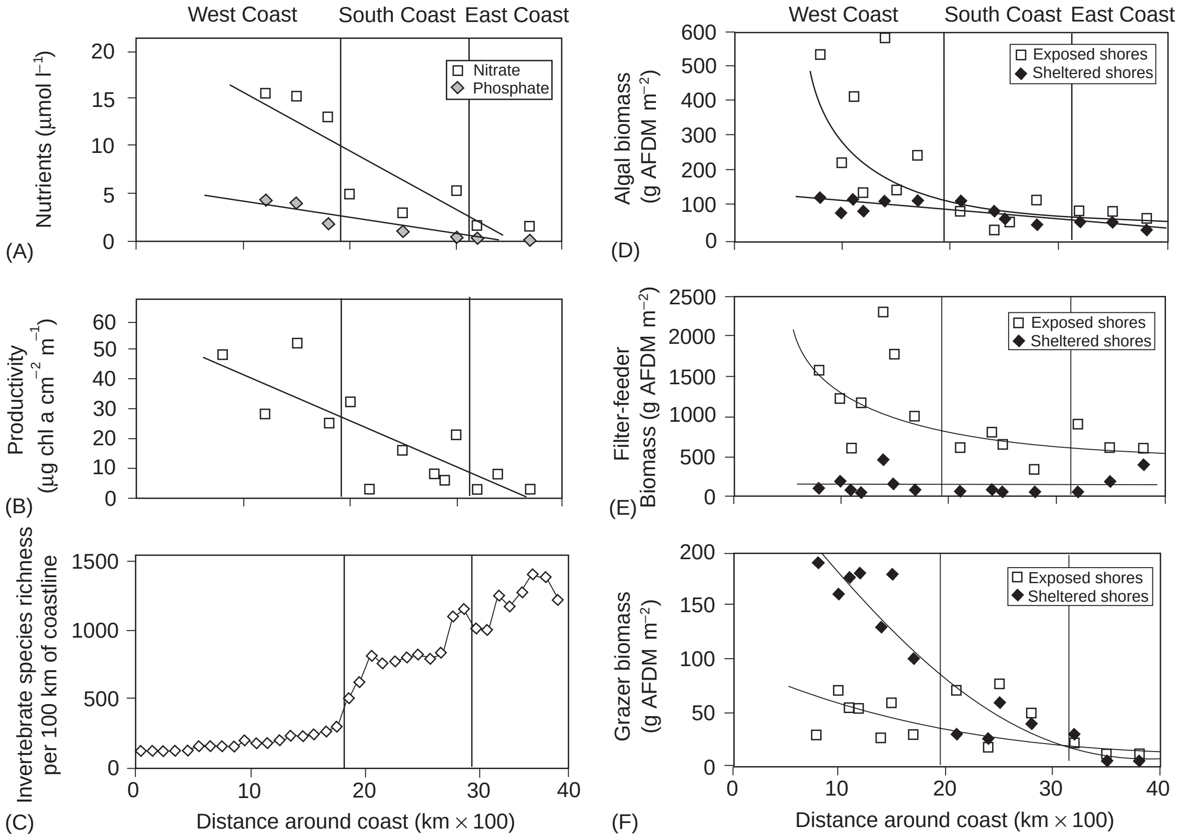

Figure 2 Moving west to east around the coastline of southern Africa (from northern Namibia to southern Mozambique), (A) nutrient input and (B) intertidal primary productivity decrease, (C) invertebrate species richness rises, and there are declines in the biomasses (ash-free dry mass) of (D) algae, (E) filter-feeders, and (F) grazers. Note that biomass is strongly influenced by wave action, either positively (algae and filter-feeders) or negatively (grazers). AFDM.

and algae seldom develop beyond the sporeling stage. A more subtle reverse effect, that of algae-limiting grazers, has also been described. Low on the shore where productivity is high, algae form dense mats. This not only deprives grazers of a firm substrate for attachment, but also of their primary food source, namely microalgae. Grazers experimentally transplanted into low-shore algal beds starve in the midst of apparent plentitude.

The influences of grazers and predators extend beyond their direct impacts on prey. A bird consuming limpets has positive effects on algae that are grazed by the limpets. Such indirect effects occupy ecologists because their consequences are often difficult to predict. For example, experimental removal of a large, grazing chiton, *Katharina tunicata*, from the shores of Washington State might logically have been expected to improve the lot of intertidal limpets, on the grounds that elimination of a competitor must be good for the remaining grazers. In fact, elimination of the chiton led to starvation of the limpets because macroalgae proliferated, excluding microalgae on which the limpets depend. Indirectly, *Katharina* facilitates microalgae, thus benefiting limpets.

The mix of physical and biological controls affecting zonation was investigated by Bruce Menge in 1976 by using cages to exclude predators from plots in the high-, mid-, and low-shore. In the high-shore, only barnacles became established, irrespective of whether predators were present or absent. In the midshore, mussels became dominant and outcompeted barnacles, again independently of the presence or absence of predators. Competition ruled. In the low-shore, however, mussels only dominated where cages excluded the predators. Elsewhere, predators eliminated mussels, thus allowing barnacles to persist. These results elucidated the interplay between physical stress and biological control and were instrumental in formalizing ‘environmental stress models’. These suggest that predation will only be important (exerting a ‘top-down’ control on community structure) when physical conditions are mild. As stress rises, first predation, and then competition, diminish in importance.

Wave Action

It has been shown that wave action is probably the most important factor affecting distribution patterns along the shore. In a negative sense, waves physically remove organisms, damage them by throwing up logs and boulders, reduce their foraging excursions, and increase the amount of energy devoted to clinging on. One manifestation is a reduction of grazer biomass (**Figure 2F**). Adaptations can, however, counter these adverse effects. Tenacity can be increased by cementing the shell to the rock face (e.g., oysters), developing temporary attachments (e.g., the byssus threads of mussels), or employing adhesion (e.g., the feet of limpets and chitons). Shape can be modified to reduce drag, turbulence, and lift (**Figure 1B**). Each organism is, however, a compromise between conflicting stresses. For instance, desiccation is reduced if a limpet has a small aperture; but this implies a smaller foot and thus less ability to cling to the rocks.

Wave action also brings benefits. It enhances nutrient supply, reduces predation and grazing, and increases food supply for filter-feeders. The biomass on South African rocky shores has been shown to rise steeply as wave action increases, mostly due to increases in filter-feeders (**Figure 2E**). Possible explanations include enhanced larval supply and reduced predation, but measurements of food abundance and turnover showed that wave action vitally enhances particulate food.

Wave action varies over short distances. Headlands and bays influence the magnitude of waves at a scale of kilometers, but even a single large boulder will alter wave impacts at a scale of centimeters to meters. As a result, community structure can be extremely patchy on rocky shores.

Productivity

'Nutrient/productivity models' (NPMs) attempt to explain community structure in terms of nutrient input and, thus, productivity. This 'bottom-up' approach concerns how the influences of primary production filter up to higher levels. Nutrient/productivity models were developed with terrestrial systems in mind, but their application to rocky shores has been enlightening. Terrestrial systems depend largely on the productivity of plants, which is usually limited by availability of nutrients and water. On rocky shores, neither constraint is necessarily relevant. The shore is washed by the rise and fall of the tide, which also imports particulate material that fuels filter-feeders independently of the productivity on the shore itself. Even so, local productivity does influence rocky-shore community structure. In one theory, the lower the productivity, the fewer the steps that can be supported in the trophic web. If production is very low, plant life cannot sustain grazers. As productivity rises, grazers may be supported, and begin to control the standing stocks of plants. Further increases may lead to three trophic levels, with predators controlling grazers, which thus lose their capacity to regulate plants.

Nowhere else in the world is the coastline better configured to test ideas about NPMs than in South Africa. The cold, nutrient-rich, upwelled Benguela Current bathes the west coast. The east coast receives fast-moving, warm, nutrient-poor waters from the southward-flowing Agulhas Current. Between the two, the Agulhas swings away from the south coast, creating conditions that are intermediate. From west to east, the coast has a strong gradient of nutrients and productivity (**Figure 2A**, **B**). As productivity drops, so do the average biomasses of algae, filter-feeders, and grazers (**Figure 2D–F**), and the total biomass. On the other hand, species richness rises (**Figure 2C**). At a more local scale, guano input on islands achieves the same effects (**Figure 3**).

Productivity also has more subtle effects on the functioning of rocky shores. For instance, the frequency of territoriality in limpets is inversely correlated with productivity. It seems that the need to defend patches of food diminishes as the ratio of productivity:consumption rises. Indirectly, this has profound effects on community dynamics, because these territorial algal species reduce species richness and biomass but greatly increase local productivity.

Increased productivity is, however, not an unmixed blessing. The upwelling that fuels coastal productivity also results in a net offshore movement of water. This may export the recruits of species with dispersive stages. The scarcity of barnacles on the west coast of South Africa may be one consequence. In California it has been shown that barnacle settlement is inversely related to an index of upwelling. Furthermore, nutrient input can lead to heavy blooms of phytoplankton (often called red or brown tides), that subsequently decay, causing anoxia or even development of hydrogen sulfide. Either eventuality is lethal, and mass mortalities ensue. Records of thousands of tons of rock lobsters spectacularly stranding themselves on the shore in a futile attempt to escape anoxic waters testify to the ecological and economic consequences.

Energy Flow

Flows of energy (or of any material such as carbon or nitrogen) through an ecosystem can be used to quantify rates of turnover and passages between elements of the food web. Developing a complete energy-flow model for a rocky shore is a formidable task. For at least the major species, energy uptake must be measured directly, or estimated by summing the requirements for growth and reproduction and the losses associated with respiration, excretion, and secretion. Critics of ecosystem energy-flow models emphasize the huge investment of research time needed to complete the task, and argue that rocky shores differ so much from place to place that a model describing one shore will often be inapplicable elsewhere.

Nevertheless, energy-flow models of rocky shores have revealed features difficult to grasp by other approaches, as the following examples reveal. First, measurements show that most macroalgal productivity is not consumed by grazers, but adds to a detrital pool that fuels filter-feeders. On sheltered shores, production exceeds demands, and they are net exporters of material. On wave-beaten shores, however, the needs of filter-feeders far exceed intertidal production, and these shores depend on a subsidy of materials from the subtidal zone or from offshore. Tides, waves and currents play a vital role in turning over this supply of particulate materials. Intertidal standing stocks of particulate matter are in the order of $0.25\,\mathrm{g\,C\,m^{-3}}$, far below the annual requirements of filter-feeders (about $500\,\mathrm{g\,C\,m^{-2}\,y^{-1}}$). But if a hypothetical flow of $20\,\mathrm{m^3}$ passes over each square meter of shore per day, it will supply $1825\,\mathrm{g\,C\,m^{-2}\,y^{-1}}$. This stresses the need for small-scale hydrographic research to predict flows that are meaningful at the level of individual filter-feeders.

Second, some elements of the ecosystem have consistently been overlooked because of their small contribution to biomass. An obvious case is the almost invisible 'skin' of microbiota (sporelings, diatoms, bacteria, and fungi) coating rocks. On most shores, their share of the biomass is an apparently insignificant 0.1%. However, in terms of productivity, they contribute 12%, and most grazers depend on this food source.

Finally, there has always been a tacit assumption that sedentary intertidal grazers must depend on *in situ* algal productivity. However, on the west coast of South Africa, grazers reach extraordinarily high biomasses (up to 1000 g wet flesh $\mathrm{m^{-2}}$). Modeling shows that their needs greatly exceed *in situ* primary production. Instead, they survive by trapping drift and attached kelp. This subtidal material effectively subsidizes the intertidal system. Thus sustained, dense beds of limpets dominate sections of the shore, eliminating virtually all macroalgae and most other grazers. Both 'bottom-up' and 'top-down' processes are at play.

Energy-flow models are seldom absolute measures of how a system operates. Changes in time and space preclude this. Rather, their power lies in identifying bottlenecks, limitations, and overlooked processes, which can then be investigated by complementary approaches.

Integration of Approaches

Ecology as a whole, and that addressing rocky shores in particular, has suffered from polarized viewpoints. Classic examples are arguments over competition versus predation, or the merits of 'top-down' versus 'bottom-up' approaches. In reality, all of these are valid. What is needed is an integration that identifies the circumstances under which one or other model has greatest predictive power. A single example demonstrates the multiplicity of factors operating on intertidal rocky shores (**Figure 3**).

Islands off the west coast of South Africa support dense colonies of seabirds. These have two important effects on the dynamics of rocky shores. First, their guano fuels primary production. Second, oystercatchers that aggregate on the islands prey on limpets. Indirect effects complicate this picture. Reduction of limpets adds to the capacity of seaweeds to escape grazing, leading to luxurious algal mats. These sustain small invertebrates, in turn a source of food for waders. The limpets benefit indirectly from the guano because their growth rates and maximum sizes are increased by the high algal productivity. This allows some to reach a size where they are immune to predation by oystercatchers, and also increases their individual reproductive output. But this 'interaction web' embraces less obvious connections. Dense bird colonies only exist on the islands for two reasons: absence of predators, and food in the form of abundant fish, sustained ultimately by upwelling. Comparison with adjacent mainland rocky shores reveals a contrast: roosting and nesting birds are scarce or absent, oystercatchers are much less numerous, limpets are abundant but small, and algal beds are absent.

This case emphasizes the complexity of driving forces and the difficulty of making predictions about their consequences. Top-down and bottom-up effects, direct and indirect impacts, productivity, grazing, predation, competition, and physical stresses all play their role.

Human Impacts

In one sense intertidal rocky-shore communities are vulnerable to human effects because they are

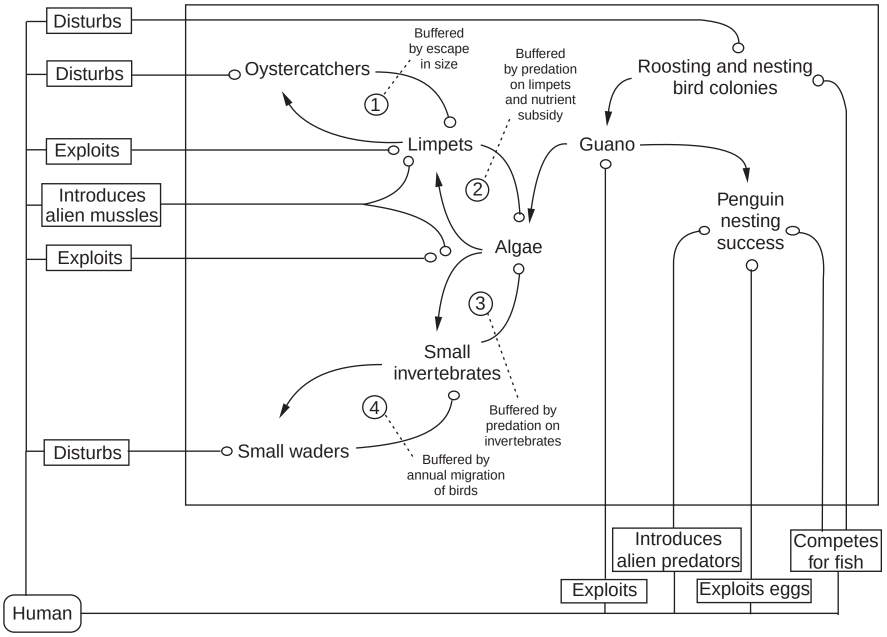

Figure 3 Interactions between organisms on nearshore islands on the west coast of South Africa. Natural interactions, and the processes buffering them (numbered 1–4), are shown inside the box; human impacts influencing them lie outside the box. Lines terminating in arrows and circles indicate positive and negative effects, respectively.

accessible and many of the species have no refuge. In another sense, they are relatively resilient to change. One reason is that humans seldom change the structure and physical factors influencing rocky shores. Tidal excursions and wave action, the two most important determinants of rocky-shore community structure, are seldom altered. The physical rock itself is also rarely modified by human actions. These circumstances are an important contrast with systems such as mangroves, estuaries, and coral reefs, where the structure is determined by the biota. Remove or damage mangrove forests, salt marshes, or corals, and the fundamental nature of these systems is changed and slow to recover. Estuaries are especially vulnerable because their two most important physical attributes – input of riverine water and tidal exchange – can be revolutionized by human actions. Even after massive abuse such as oil pollution, rocky shores recover relatively quickly once the agent of change is brought under control; and there is good evidence that the kinds of communities appearing after recovery resemble those originally present.

Humans impact rocky-shore communities in many ways, including trampling, harvesting, pollution, introduction of alien species and by altering global climate. Harvesting is of specific interest because it has taught much about the functioning of rocky shores.

Almost without exception, harvesting reduces mean size, density, and total reproductive output of the target species, although compensatory increases of growth rate and reproductive capacity of surviving individuals are not unusual. Of greater interest, however, are the consequences for community structure and dynamics. Clear demonstrations of this come from Chile, where intense artisanal harvesting occurs on rocky shores. In particular, a lucrative trade has developed for giant keyhole limpets, *Fissurella* spp., and for a predatory muricid gastropod, *Concholepas concholepas*, colloquially known as 'loco.' Decimated along most of the coast, the natural roles of these species are only evident inside marine protected areas. There, locos consume a small mussel, *Perumytilus purpuratus*, which otherwise outcompetes barnacles. Macroalgae and barnacles compete for space, but only on a seasonal basis. Keyhole limpets control macroalgae and outcompete smaller acmaeid limpets. *Perumytilus* acts as a settlement site for conspecifics and for recruits of keyhole limpets and locos. With a combination of predation, grazing, competition and facilitation, and both direct and indirect effects, the consequences of harvesting locos or keyhole limpets would have been impossible to resolve without the existence of marine protected areas. Even then, careful manipulative experiments inside and outside these areas were required to disentangle these interacting effects.

A second issue of general interest is whether human impacts are qualitatively different from those of other species. The short answer is 'yes', and is best illustrated by a return to an earlier example – interactions between species on rocky shores of islands on the west coast of South Africa (**Figure 3**). In its undisturbed state, each of the key interactions in this ecosystem is buffered in some way. Limpets are consumed by oystercatchers, but some escape by growing too large to be eaten, aided by the high primary production. Limpets and other invertebrates graze on algae, but their effects are muted by predation on them and by the enhancement of algal growth by guano. Waders eat small seaweed-associated invertebrates, but emigrate in winter.

For several reasons, human impacts are not constrained in these subtle ways. First, human populations do not depend on rocky shores in any manner limiting their own numbers. They can harvest these resources to extinction with impunity. Second, modern human effects are too recent a phenomenon for the impacted species to have evolved defenses. Thirdly, humans are supreme generalists. Simultaneously, they can act as predators, competitors, amensal disturbers of the environment, and 'commensal' introducers of alien species. Fourthly, money, not returns of energy, determines profitability. Fifthly, long-range transport means that local needs no longer limit supply and demand. Sixthly, technology denies resources any refuge.

Thus, humans supersede the ecological and evolutionary rules under which natural systems operate; and only human-imposed rules and constraints can replace them in meeting our self-proclaimed goals of sustainable use and maintenance of biodiversity.

See also

Beaches, Physical Processes Affecting. Coastal Circulation Models. Coastal Trapped Waves. Eutrophication. Exotic Species, Introduction of. Internal Tides. Intertidal Fishes. Macrobenthos. Seabird Conservation. Seabirds and Fisheries Interactions. Tides. Upwelling Ecosystems. Waves on Beaches.

Further Reading

Branch GM and Griffiths CL (1988) The Benguela ecosystem Part V. The coastal zone. *Oceanography and Marine Biology Annual Review* 26: 395–486.

Castilla JC (1999) Coastal marine communities: trends and perspectives from human-exclusion experiments. *Trends in Ecology and Evolution* 14: 280–283.

Connell JH (1975) Some mechanisms producing structure in natural communities: a model and evidence from field experiments. In: Cody ML and Diamond JM (eds) *Ecology and Evolution of Communities*, pp. 460–490. Cambridge, MA: Belknap Press.

Denny MW (1988) *Biology and the Mechanics of the Wave-swept Environment*. Princeton, NJ: Princeton University Press.

Hawkins SJ and Hartnoll RG (1983) Grazing of intertidal algae by marine invertebrates. *Oceanography and Marine Biology Annual Review* 21: 195–282.

Menge BA and Branch GM (2001) Rocky intertidal communities. In: Bertness MD, Gaines SL and Hay ME (eds) *Marine Community Ecology*. Sunderland: Sinauer Associates.

Moore PG and Seed R (eds) (1985) *The Ecology of Rocky Coasts*. London: Hodder and Stoughton.

Newell RC (1979) *Biology of Intertidal Animals*. Faversham, Kent: Marine Ecological Surveys.

Paine RT (1994) *Marine Rocky Shores and Community Ecology: An Experimentalist's Perspective*. Oldendorf: Ecology Institute.

Siegfried WR (ed.) (1994) *Rocky Shores: Exploitation in Chile and South Africa*. Berlin: Springer-Verlag.

Underwood AJ (1997) *Experiments in Ecology: their Logical Design and Interpretation Using Analysis of Variance*. Cambridge: Cambridge University Press.

ROSSBY WAVES

P. D. Killworth, Southampton Oceanography Centre, Southampton, UK

doi:10.1006/rwos.2001.0120

Introduction: What Are Rossby Waves?

Among the many wave motions that occur in the ocean, Rossby (or planetary) waves play one of the most important roles. They are largely responsible for determining the ocean's response to atmospheric and other climate changes; their energy dominates the ocean's energy spectrum at long timescales; they are responsible for setting up and maintaining the intense oceanic western boundary currents, and can be generated by those currents; they affect ocean color and biological interactions near the surface; and they moderate the ocean's behavior to decadal features such as El Niño and the North Atlantic Oscillation. The waves have a strong westward