CHAPTER 16

The Tidelands

Rocky Shores, Soft-Substratum Shores, Marshes, Mangroves, Estuaries, and Oyster Reefs

Coastal benthic habitats are among the most productive marine environments. They receive a high nutrient supply, which is influenced both by terrestrial nutrient sources and by strong coastal phytoplankton production. The richness of these habitats also makes them feeding and nursery grounds for migratory species, particularly fishes, crustaceans, and birds. The elevated nutrient supply and the visitations by predators often lead to cycles of population increase of prey species, followed by population crashes because of predation. The great abundance of organisms also leads to rapid depletion of resources and strong interspecific competition. Because tidelands are so accessible to ecologists, we know most about marine ecological processes from these habitats.

Rocky Shores and Exposed Beaches

Vertical Zonation and the Protected, Wave-Swept Coast Gradient

- **Vertical zonation, the occurrence of dominant species in distinct horizontal bands, is a nearly universal feature of the intertidal zone, but many localities do not "obey" the rules.**

The **intertidal zone** is the shoreward fringe of the seabed between the highest and lowest extent of the tides. An important feature of the rocky shore intertidal zone and, to a lesser degree, the soft-sediment shore, is **vertical zonation**, the occurrence of dominant species in distinct horizontal bands (**Figure 16.1**). For example, a general pattern of zones is found throughout temperate and boreal rocky shores (**Figure 16.2**). From highest to lowest, the zones are (a) a black lichen zone, (b) a periwinkle (littorine gastropod) zone with sparse barnacles, (c) a barnacle-dominated zone either overlapping with a mussel-dominated zone or with mussels below, and (d) a zone dominated variously, but usually by seaweeds. On North American rocky shores, mussels of the genus *Mytilus* dominate below the barnacle zone. Vertical zonation occurs on sand- and mudflats, but it is rarely as distinct as on rocky surfaces.

While overall patterns of zonation exist, on a gross scale, it is equally noticeable how often there is *not* a predictable pattern of dominance at different levels of the tide zone. Most commonly, one sees **patches** dominated by different species at the same tidal levels or patches unoccupied by organisms.

- **Different assemblages occur in protected and wave-swept waters in the same area.**

Figure 16.2 shows an expansion of the vertical extent of organisms in wave-swept areas and differences in the types of organisms that occur in wave-exposed sites relative to protected waters. In some cases, wave-exposed sites have species that do not occur in protected waters. On the Pacific coast of North America, the large California sea mussel *Mytilus californianus* is found in exposed wave-swept coasts, but protected bays have a smaller species of mussel. In other cases, it is more a matter of relative dominance. In protected temperate waters of northern Europe and New England, seaweeds dominate rock surfaces, whereas barnacles and mussels dominate more wave-exposed open coasts (**Figure 16.2**).

FIG. 16.1 Zonation on a rocky shore in British Columbia. Seaweed zone below and mussel zone (dark blue color) above. (Photograph by Jeffrey Levinton)

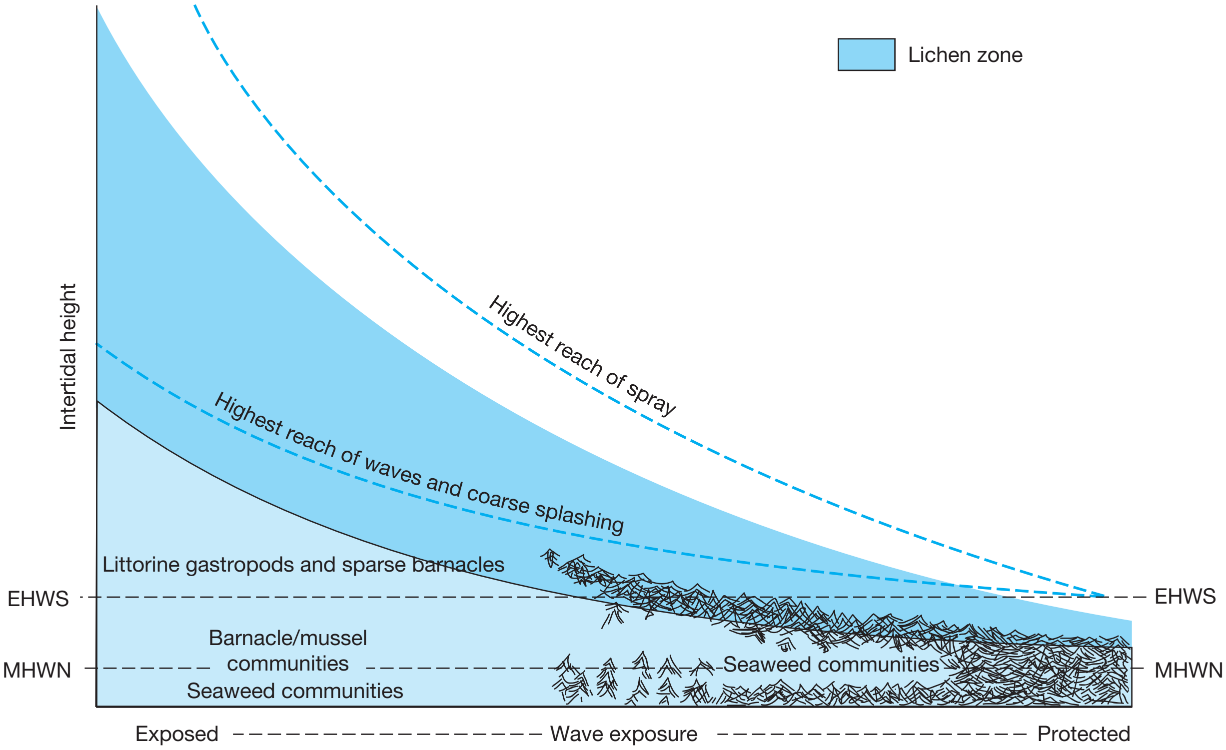

FIG. 16.2 The effect of wave exposure in broadening biotic zones of the rocky intertidal zone of the British Isles: EHWS, extreme high water spring tide; MHWN, mean high water neap tide. In quiet-water habitats, represented on the right of the diagram, the mid-intertidal zone is dominated by seaweeds, but with more wave exposure, barnacles and mussels come to dominate. The upper intertidal is dominated by herbivorous snails in all cases with a band of lichens toward the top. In strongly wave-swept habitats (left), the vertical zones are expanded. (After Lewis, 1964)

Factors Affecting Rocky Intertidal Organisms

- **The intertidal zone is alternately a marine and a terrestrial habitat. At the time of low tide, heat stress, desiccation, and shortage of oxygen increase, and opportunities for feeding and respiring decrease.**

With increasing tidal height, more of the shore is exposed to air for a greater proportion of the day. The highest part of the intertidal zone is essentially a terrestrial environment, but organisms living at the low-tide level are less affected by aerial exposure. At low tide, intertidal sandy sediments may be quite dry, but finer-grained sediment retains water and many organisms can maintain activity within burrows and even at the sediment surface.

At the time of low tide, marine organisms face both heat and desiccation stress. On a hot day, invertebrates rapidly heat up, although they possess several adaptations to counteract thermal stress. If body fluids become warm past a critical temperature, physiological function and even the stability of proteins may diminish. In the worst case, intertidal organisms can literally dry up. In summer, this happens commonly to fragile species, such as thin green seaweeds. Organisms such as barnacles and mussels survive drier and more exposed areas because their shells can enclose water at low tide and seal the soft parts from desiccation. Organisms lacking external skeletons do not usually occur on open rocks exposed to the sun but are more common in moist cracks or in tidal pools (**Figure 16.3**).

Heat and desiccation stress vary on quite small spatial scales. As might be expected, sessile animals on sun-exposed and flat rocks will gain far more heat than those in a moist crack or in the shade. The timing of low tide during the day also can have profound effects on the heat inputs experienced by sessile intertidal organisms (Helmuth, 1999). In the outer, exposed coast of Washington, for example, spring low tides in summer come in the morning, when air temperatures are often only 15°C. In contrast, summer spring low tide in Puget Sound comes at midday, when air temperatures can surpass 25°C. Small-scale spatial differences in microhabitat and timing of low tides may, therefore, have far greater effects than overall annual variation and even broad-scale latitudinal variation, at least on the west coast of North America, where climatic latitudinal gradients are slight. On the east coast of North America, the latitudinal gradient is probably the main factor in heat stress differences between localities over long latitudinal-geographic distances.

Body size and **body shape** both influence the degree of heat and water loss. As body size increases, the surface area, relative to body volume, decreases, and this aids in reducing water loss because proportionally more of the body is not exposed to surface evaporation. However, the decrease in surface area relative to body volume that often comes with increasing size is a *disadvantage* with regard to heat loss. Small animals, with their higher relative surface area, tend to lose heat faster. The combination of these two factors must strike a balance. An intertidal animal cannot be too small or else it will dry up in the sun. If it grows too large, however, it may not be able to dissipate heat fast enough through its body surface. Shape has an important effect. Long and thin organisms will dry up much more easily than spherical ones. This is one reason that a sea anemone contracts into a small equidimensional cylinder during low tide. The change in shape reduces surface area and water loss.

Intertidal invertebrates can avoid overheating by **evaporative cooling**, combined with **circulation of body fluids**. As a result of such processes, intertidal snails are usually cooler than inanimate objects of the same shape, size, and color. Higher-intertidal animals are better adapted to desiccation than lower-intertidal species. Movement of the cirri (feeding appendages) in intertidal acorn barnacles increases with increasing temperature but declines near an upper thermal limit (**Figure 16.4**). Upper-intertidal barnacles tolerate high temperatures better than do barnacle species found in the lower intertidal. Species living in the high-intertidal zone in the tropics tend to maintain coordinated ciliary motion at higher temperatures than do species living in the low-intertidal zone or subtidal zone.

Genetically based variation in shell color is related to reflection of sunlight. Along the east coast of the United States, for example, the mussel *Mytilus edulis* has light and dark shell color forms (see Figure 4.23), which are genetically determined. On the east coast of North America, the light-colored form is found more frequently toward the south (**Figure 16.5**). Dark mussels gain heat more rapidly and are superior in environments where cold air temperatures are common, whereas light mussels reflect heat in the sun and are superior in the south, where high-temperature stress is a problem.

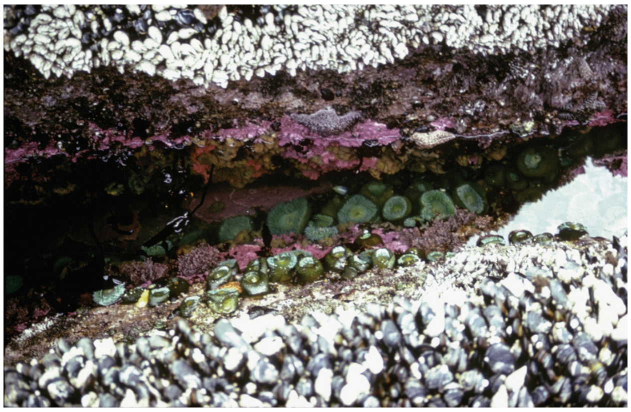

FIG. 16.3 A tidal pool on an exposed shore in Washington State. Note the presence outside the pool of desiccation-resistant barnacles and mussels, and more sensitive anemones, hydrocorals, and sea stars within. (Photograph by Jeffrey Levinton)

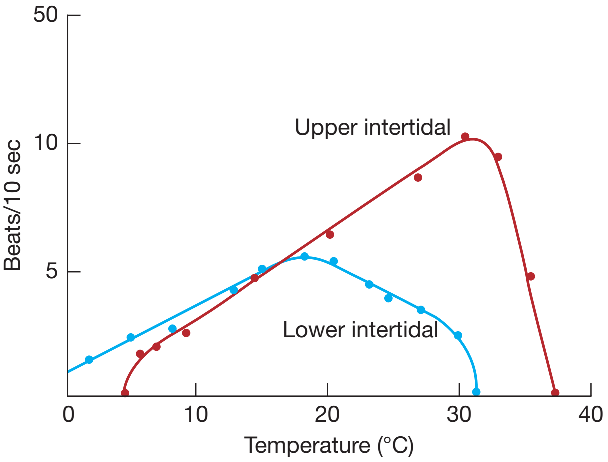

FIG. 16.4 Beating frequency of cirri (feeding appendages) in relation to increasing temperature in an upper-intertidal (red curve) and lower-intertidal (blue curve) barnacle species. (After Southward, 1964)

Species living in the high part of the shore retain cellular function at higher temperatures than those living in lower shore levels (**Figure 16.6**). In Chapter 5, we discussed the use of **heat-shock proteins** to maintain protein function under high temperature stress. Lower-intertidal animals and very shallow subtidal animals acclimate to reduced conditions of heat stress and tend to produce more heat shock proteins when exposed to temperature stress, as compared to higher-intertidal animals (Tomanek and Sanford, 2003). Species of snails living higher in the intertidal are superior in producing heat-shock proteins at higher temperatures than species living in the lower intertidal (Tomanek, 2002). We would expect that summer-acclimated individuals would be more tolerant to temperature stress, which can be seen in induction of heat-shock proteins. Buckley and colleagues (2001) studied the heat-shock protein Hsp70, which is induced under high temperature stress. For the west coast mussel *Mytilus trossulus*, mussels collected in February had a threshold activation of Hsp70 at 23°C, whereas mussels collected in August had a threshold temperature of 28°C.

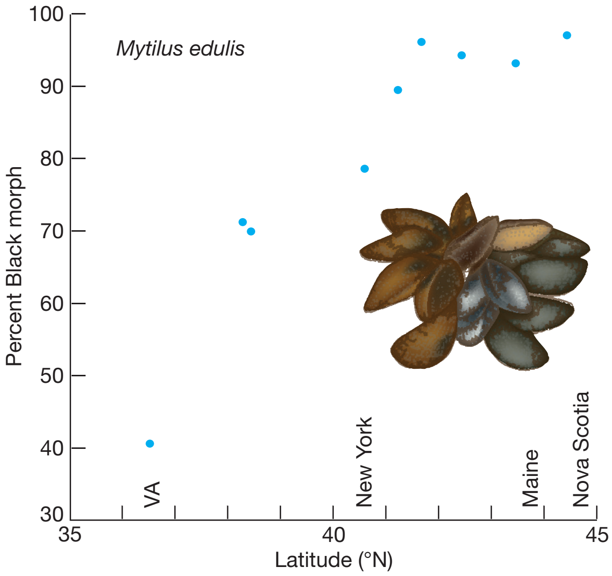

FIG. 16.5 Latitudinal variation in black and brown shell color forms of the blue mussel *Mytilus edulis*. The brown morph reflects solar radiation more efficiently and is favored in lower latitudes. (Data from Innes and Haley, 1977, and Mitton, 1977)

Climate change is altering the geography of temperature stress of intertidal communities.

Global climate change patterns include increases of sea-surface temperature, which is having strong effects on rocky-shore communities. A few decades ago, planktonic larvae of the blue mussel *Mytilus edulis* settled in the region and even south of Cape Hatteras, North Carolina. But the southern range end of this species is moving steadily northward as air and water temperatures have increased (Jones et al., 2009). Mussels transplanted to areas in North Carolina where mussels once thrived now experience catastrophic mortality. Community species membership is also changing as climate warms. In rocky shores of Monterey Bay, California,

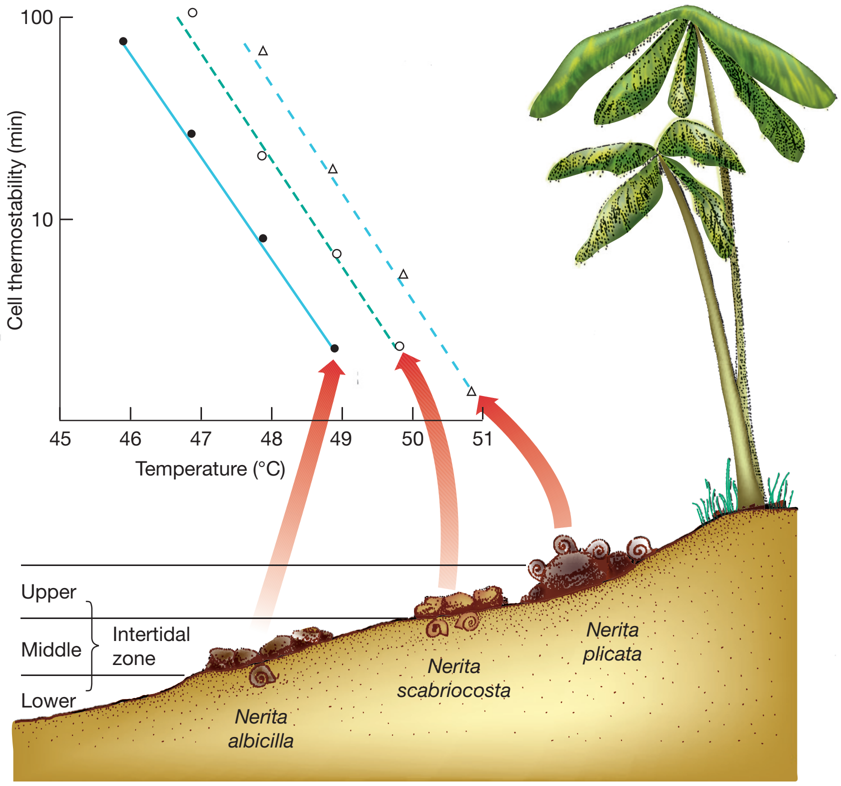

FIG. 16.6 Survival of ciliated epithelial cells in three species of the intertidal gastropod genus *Nerita* and the relation of temperature tolerance to position on shore. (After Ushakov, 1968)