



## EIGHTEEN

### Intertidal

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#### Introduction

Intertidal ecosystems exist at the interface between land and ocean, occupying the thin strip of shoreline that is regularly covered and uncovered by tides. At the highest of tides these ecosystems are covered or regularly splashed by water, and on the lowest of tides they are fully uncovered and exposed to air. Because intertidal organisms endure regular periods of immersion and EMERSION, they essentially live both underwater and on land and are adapted to a large range of conditions. Since most intertidal organisms are primarily marine in evolutionary origin, they benefit greatly from immersion in seawater during high tide, which moderates temperature, delivers food and nutrients, and facilitates reproduction by mixing gametes and transporting larvae. During low-tide periods, when organisms are uncovered, they can experience large changes in temperature, ultraviolet and solar radiation, desiccation, and even salinity from freshwater inputs or evaporation. Intertidal ecosystems also occur where wave forces and impacts are greatest. The high hydrodynamic forces imposed by intense wave action can crush, break, and dislodge intertidal organisms. Given the severity and challenges of this environment, the intertidal ecosystems of rocky shores in California are home to

a surprising, incredibly high diversity of species. As John Steinbeck famously noted in *The Log from the Sea of Cortez*, “The exposed rocks had looked rich with life under the lowering tide, but they were more than that: they were ferocious with life. . . . Mussels, sculpins, kelps, and urchins; anemones and sea stars of all sizes and colors; barnacles, worms, limpets, and abalone; algae that look like corals; others that look like tar—the diversity of rocky shores rivals that of tropical rainforests.”

Intertidal habitats can have either soft-bottom or hard-bottom substrates. Soft-sediment habitats include sandy beaches and intertidal wetlands such as mudflats and salt marshes. Soft-bottom habitats are generally protected from large waves but tend to have more variable salinity levels. They also offer a third habitable dimension—depth; many soft-sediment inhabitants are adapted for burrowing. Hard-bottom intertidal habitat can consist of either human-made (e.g., jetties, pilings, and seawalls) or natural rock surfaces. Natural rocky shores are found along exposed headlands as well as in more wave-protected habitats. They range from consolidated rocky benches to cobble beaches. Many of the organisms found on rocky shores are SESSILE and live attached to

the rock, although a wealth of mobile predators and grazers of these sessile organisms inhabit the shore as well. Because other chapters in this book examine sandy beaches and wetlands, this chapter focuses on the intertidal ecosystems of rocky shores.

Rocky intertidal habitats provide a range of ecosystem services such as shoreline stabilization and protection of upland areas from the wave erosion and the impacts of storm surges and sea level rise. They provide haul-out areas for seals and support the diets of foraging birds as well as other diverse organisms vital to the base of the food web (UNEP 2006, Arkema et al. 2013). Rocky intertidal ecosystems also support valuable recreational and commercial fisheries for invertebrates such as mussels and limpets and for edible seaweeds. They provide for subsistence, ceremonial, sport, and commercial gathering and hunting of a diversity of intertidal organisms. Finally, rocky shores are greatly valued for their aesthetic qualities and offer easily accessible coastal areas for recreation, education, and research. In an attempt to quantify these values, Hall et al. (2002) estimated a mean of \$7 per family per visit that users would be willing to pay to prevent reductions in the status of southern California's rocky intertidal zone.

Rocky intertidal shores occur along the entire length of the California coastline. In some regions, long stretches of rocky habitat dominate the shoreline, while in others (southern California, in particular) small rocky outcroppings are separated by long expanses of sandy beaches. Approximately 800 miles of rocky habitat occur along the California coast, comprising about 35% of the entire shoreline of California's outer coast. Rocky shores support an array of intertidal species living on rock faces, crevices, undersides, and tide pools. Some coastal areas, particularly rocky headlands and exposed outer coasts, experience tremendous wave action; here only the most tenacious organisms survive. Sheltered embayments and coastal areas protected by offshore rocks, reefs, or islands receive considerably less wave shock and support a variety of more delicate forms. The ability to withstand desiccation and overheating while exposed to air by low tides is an important factor in determining where marine organisms occur in the intertidal. Organisms living in tide pools of many rocky shores avoid some of the problems associated with desiccation but must still contend with elevated temperatures and rapidly changing salinities and oxygen levels.

### Significance and History of Rocky Intertidal Research

We cannot begin a discussion about California's rocky intertidal ecosystems without reference to Ed Ricketts. Ricketts was a scientist and careful observer of nature who opened a biological supply company in Pacific Grove, California, in 1923. He collected and observed organisms and became one of the first marine biologists to describe them in an ecological context. His classic book *Between Pacific Tides*, coauthored with Jack Calvin and J. Hedgpeth and published in 1939, is widely regarded as the authoritative text on intertidal ecology. It continues to be revised and expanded and remains as an important point of reference for marine biologists. Ricketts

Photo on previous page: A diverse community of intertidal algae and animals from the wave-swept shores of Monterey Bay. Photo: Luke P. Miller.

elegantly described the seashore as “probably the most prolific zone in the world, a belt so thickly populated that often not only is every square inch of the area utilized by some plant or animal, but the competition for attachment sites is so keen that animals settle upon each other—plants grow upon animals, and animals upon plants” (quoted in Tamm 2004:86).

Until the early part of the twentieth century, much of marine biology and ecology was descriptive and followed in the traditions of early plant ecologists (Benson 2002). Ricketts was one of the key marine scientists of the 1930s to pioneer the modern approach to community ecology of rocky shores. Community ecologists investigate patterns, processes, and mechanisms that describe or explain the composition and dynamics of populations interacting and persisting in a particular habitat. Huge advances in intertidal community ecology in the 1930s and 1940s were facilitated by marine laboratories, primarily on the California coast. The Hopkins Marine Station (Stanford University), the Kerckhoff Laboratory (Caltech), and the Scripps Institution of Oceanography (UC San Diego) operated year-round with full-time research staffs by 1930. George MacGintie, the founder of the Kerckhoff laboratory, known for his studies of Elkhorn Slough (MacGintie 1935), argued strongly for more long-term field studies. Willis G. Hewatt of Hopkins Marine Station adopted MacGintie's recommendation for long-term study but also incorporated field experiments to investigate community dynamics (Hewatt 1937). Their work catalyzed a new approach to the study of the dynamics of intertidal communities. From these humble beginnings, scientists studying rocky intertidal ecosystems have steadily continued to expand the science of ecology, developing new theories and insights about community and ecosystem dynamics both in the intertidal and more broadly.

## The California Coast

### Coastal Geology and Topography

California is one of the most biologically and geologically diverse regions in North America. The current geological configuration of the California shoreline arises from tectonic activity over millions of years (Hayes and Michel 2010). The majority of California's coast, from the southern border with Baja north to Mendocino, sits on the Pacific plate. Many of the rock formations that make up this coastline (those of the FRANCISCAN COMPLEX) were accreted onto the edge of the North American plate starting about 150 million to 130 million years ago as the Farallon plate and later the Pacific plate were subducted beneath the North American plate. Between 10 million and 30 million years ago, the Pacific plate stopped subducting and instead began to travel northwest relative to the North American plate. This shift gave rise to the San Andreas fault, which turns offshore near Mendocino toward the north. Both the accreted marine sediments of the Franciscan complex and granite formations originally from the southern Sierra Nevada mountains have been carried to their current locations by the northwest movement of the Pacific plate (Harden 2004).

In places where sedimentary rock (e.g., sandstone, mudstone, or shale) makes up the shore, erosion often forms broad, intertidal benches (Figure 18.1). By contrast, erosion-resistant igneous and metamorphic rocks (e.g., granite, basalt, schists) are typically cut into steep, topographically complex



FIGURE 18.1 Examples of an easily eroded sedimentary intertidal bench (above) and an erosion-resistant granite shoreline with high topographic relief (below). Photos: Jayson Smith (above), Luke P. Miller (below).

shapes (Griggs and Trenhaile 1997). The resulting interspersed pattern of erosion-prone and erosion-resistant rocks determines the overall pattern of alternating headlands and beaches along the southern and central California coasts. North of Mendocino, the shoreline is a product of recent **SUBDUCTION**, volcanic activity, and other **OROGENIC** processes. The vertical location of wave-induced erosion depends on sea level, which has fluctuated through geological time in conjunction with the coming and going of ice ages. Currently, sea level is 120 meters higher than at the peak of the last ice age, and it is rising at a rate of at least 22 to 44 centimeters per century as Earth warms (Harden 2004).

The large-scale pattern of California coastal topography is modified by small-scale geological processes: folding, terrestrial erosion, and local uplift or subsidence. The most obvious results of some of these processes are the **MARINE TERRACES** found along much of the coast. Marine terraces are formed by (1) the erosive activity of waves, which sculpts wide benches in the intertidal zone, followed by (2) sea level declines dur-

ing glacial maxima, and (3) subsequent tectonic uplift of the shoreline out of reach of the waves when sea level rises again during glacial minima. Several periods of sea level change and continued tectonic uplift have created multiple, stepped marine terraces throughout San Diego, Orange, Los Angeles, San Luis Obispo, Santa Cruz, San Mateo, Mendocino, Humboldt, and Del Norte Counties. These areas are often flanked by present-day rocky intertidal benches (Griggs et al 2005).

### Biogeographic Patterns

**BIOGEOGRAPHIC** patterns of California's rocky intertidal communities have strong spatial structure and correlate closely with both geography and sea surface temperature patterns (Blanchette et al. 2008, 2009). Temperature is a useful proxy for tracking the movement of oceanic water masses. Temperature can also directly affect critical biological functions including growth, survival, and reproduction. Biogeographic

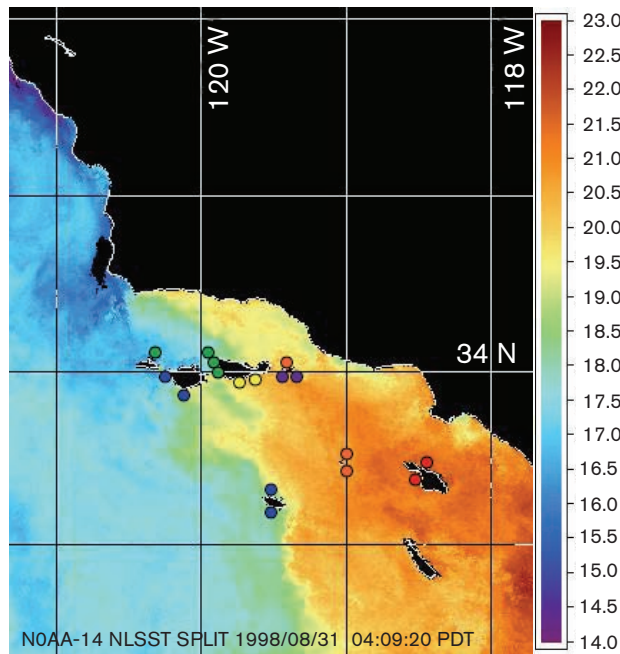


FIGURE 18.2 Biogeographic patterns of rocky intertidal community structure at the California Channel Islands. Sites with dots of the same color are most similar to one another in their species composition. Community similarity is strongly influenced by sea surface temperature. Source: Blanchette et al. 2009.

patterns of community similarity along the west coast of North America largely involve shifts in relative abundances of taxa rather than wholesale changes in species assemblages among regions. Many of the most abundant species characterizing particular biogeographic regions are not absent from any region, but differ consistently and substantially in abundance among regions. However, several exceptions to these general grouping patterns occur, suggesting that while similar processes shape species distributions and abundances across taxa and life histories, important local features such as topography, geology, and wave exposure, as well as species interactions, can also be important drivers of rocky intertidal community composition (Blanchette et al. 2008).

All major California rocky intertidal biogeographic regions are delimited by coastal features associated with transitions in oceanographic conditions, and/or changes in geomorphology and substrate type (such as long stretches of sandy beaches or changes in coastline orientation) (Blanchette et al. 2008). Point Conception is one of the most notable transition regions on the California coastline and the most important biogeographic and oceanographic discontinuities on the west coast of North America (Figure 18.2; Valentine 1966, Doyle 1985, Burton 1998). Two major water masses meet here—the southward-flowing California current and the westward-flowing southern California countercurrent (Hickey 1993). The northern region experiences consistent, strong, coastal upwelling that brings cold, nutrient-rich waters to the surface, resulting in both cold coastal sea surface temperatures and high nutrient concentrations. The Santa Barbara Channel, immediately southeast of Point Conception, experiences weak seasonal upwelling, which tends to occur in the winter months (Blanchette et al. 2002, Winant et al. 2003). The California Channel Islands, located just offshore from Point Conception, lie within this highly diverse oceanographic region.

They experience variable mixing between the cold waters of the California current and the warm, nearshore waters of the southern California countercurrent (Huyer 1983, Hickey et al. 2003). As on the mainland, temperature strongly determines the composition of Channel Island intertidal communities (Figure 18.3).

## The Physical Environment

The effects of the exceptionally severe intertidal environment on population and community dynamics appear at many different scales, from regional-scale variation in the timing and amplitude of tidal fluctuations to local topographic effects on exposure of individuals to stressful hydrodynamic forces and temperatures. The alternating exposure of intertidal organisms to aerial and marine conditions is controlled largely by the cycle of the tides. As the moon orbits Earth, and Earth orbits the sun, gravity and celestial motion interact with the ocean to create the a periodic fluctuation in sea level—the tides—that determines how often and for how long shoreline organisms are exposed to terrestrial conditions. The temporal and spatial variation of the tides underlies all other aspects of the intertidal physical environment.

Two high tides and two low tides occur in the course of each tidal day (24 hours, 50 minutes). On the coast of California the two high tides have different heights, as do the low tides—a pattern know as mixed semidiurnal tides (Figure 18.4). The inequality of high tides and low tides means that organisms low in the intertidal zone (below the higher low tide) are emersed only once a day. Similarly, organisms high in the intertidal zone (above the lower high tide) are immersed only once a day. In contrast, organisms in the middle of the zone make the transition from air to water and back twice a day. These patterns of immersion and emersion strongly influence the stress to which the physiology of intertidal plants and animals must adapt.

The amplitude of the tides (the difference between higher high tide and lower low tide) is typically 1–3 meters but varies with the moon's phase and the seasons. Tidal amplitude is greatest when the moon is new or full (spring tides) and least at the first-quarter and third-quarter moons (neap tides). The disparity of the tides (the difference between higher and lower high tides and between higher and lower low tides) is typically greatest near the summer and winter solstices and least near the spring and fall equinoxes. Spring tides are most notable because they emerse organisms lower on the shore than other tides do in the remainder of the tidal cycle.

A variety of secondary factors modulates these general patterns. Because the moon's orbit is elliptical, the distance between Earth and the moon varies. The moon's gravitational effect on the ocean therefore fluctuates by almost 40% over the 27.3 days of its orbital period. When the moon's closest approach to Earth coincides with new or full moon, tidal amplitude increases, exposing plants and animals that otherwise would not be emersed. The reverse occurs when the moon is farthest from Earth. Similarly, tidal amplitudes increase when Earth is nearest the sun (early January) and diminished when Earth is farthest away (early July). The angle between the plane of the moon's orbit and Earth's equatorial plane varies with a period of 18.6 years, which can also affect the amplitude and disparity of the tides (Denny and Paine 1998).



FIGURE 18.3 Rocky intertidal community buried by sand in July. Photo: Carol Blanchette.

Because the tidal day is slightly longer than the solar day (24 hours), the timing of the tides shifts. For example, lower low tide tomorrow is (on average) 50 minutes later than it was today, although the precise timing is affected by the amplitude fluctuations discussed earlier. The timing of tides on the California coast also varies with latitude—the farther north, the later the tide. An 8:00 low tide in San Diego does not reach Point Reyes until 9:30 and Humboldt Bay until 10:15. Summertime spring low tides in California typically occur in the morning, so this latitudinal shift in the time of the tide means that the farther north a site, the more time it is exposed to potentially stressful midday terrestrial conditions. Both the timing and amplitude of tides can be affected by seafloor topography. Tides inside the San Francisco Bay have much lower amplitude and occur nearly an hour later than tides just outside, for instance. For an accurate prediction of the tides at any particular location, it is best to consult the site-specific predictions provided by the National Oceanographic and Atmospheric Administration (<http://www.tideandcurrents.noaa.gov/>). Even then, one can expect some deviation of actual tides from those predicted—as much as 10–20 centimeters—due to weather-driven changes in barometric pressure. For more detailed explanation of the tides, consult Brown et al. (1999) or Cartwright (1999).

#### THE CONTRAST BETWEEN TERRESTRIAL AND AQUATIC ENVIRONMENTS

The physical differences between seawater and air have profound effects on individual physiology and community structure (Denny 1994). Many of these effects are tied to temperature and therefore to the specific heat capacities of these two media. Specific heat capacity is the amount of heat energy required to raise the temperature of 1 kilogram of a substance 1°C. Water has an unusually high specific heat capacity, more than four times that of air. As a result, water temperature varies much less than air temperature. In Monterey, for instance, annual maximum sea surface temperature is 16°C, only 6°C

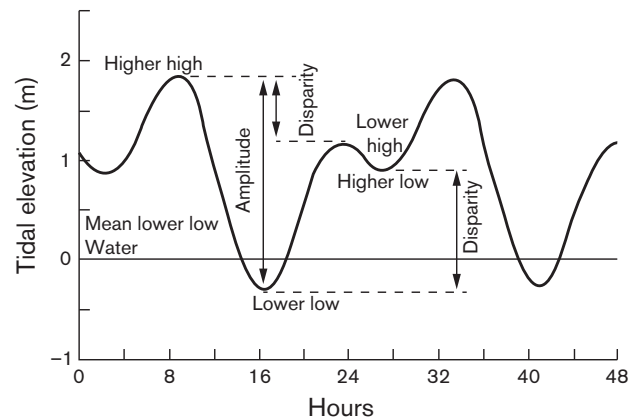


FIGURE 18.4 Example of mixed semidiurnal tides, in which there are two high tides and two low tides differing in amplitude every lunar day. Source: Denny 1988.

warmer than the annual minimum. By contrast, the low specific heat of air allows for rapid changes in temperature; air temperature can vary by more than 20°C in a single day.

Air and water temperature variations contribute to variation in the body temperatures of intertidal organisms. During submersion at high tide, the water's high thermal conductivity ensures that the temperature of an organism is the same as the water around it. Thus submerged body temperature can vary by at most a few degrees Celsius in a day as the sun heats surface waters or upwelling delivers cold subsurface water. During aerial exposure at low tide, body temperatures of intertidal organisms are affected by air temperature but also by the multiple, interacting environmental factors (e.g., solar heating, conduction of heat to or from the rock, evaporative cooling). As a result, on sunny days, the body temperature of intertidal organisms can be considerably warmer (10–15°C) than the surrounding air and can vary over very fine spatial scales; animals on south-facing sides of rocks can be many degrees hotter than nearby animals on shaded surfaces

(Helmuth and Hofmann 2001, Denny et al. 2011). Emerged body temperature can also be colder than the surrounding air, especially at night, as organisms lose heat by infrared radiation to the sky.

The temperature of an organism's body affects most physiological processes, such as metabolic rate (Jansen et al. 2007) and efficiency of enzyme functioning (Somero 2011). Increases in metabolic demand, and thus oxygen demand, in turn can lead to oxygen deficiency at the cellular level (Pörtner and Farrell 2008). While the relative importance of intertidal body temperatures in water and in air remains unclear, and varies between species, both can have significant effects on rates of mortality, growth, and reproduction (Blanchette et al. 2007, Somero 2011). Experiments show that these impacts can be due to both rare but extreme events (Harley and Paine 2009, Denny et al. 2009) and chronic exposure to suboptimal temperatures (Petes et al. 2008, Sará et al. 2011 and 2012). For example, Harley (2008) reported mortality of mussels and limpets in March and April 2004 in Bodega Bay, California, following exposures to a series of sunny, warm days when low tide exposed animals to the air during the mid-day.

Evaporative cooling allows organisms to avoid (or at least postpone) high temperature stress. Each gram of water evaporated removes 2,500 joules of heat energy from the organism. Excessive water loss can be lethal, however. Thus a trade-off exists between desiccation and thermal stress. Many mobile organisms seek refuge from potentially desiccating conditions underneath algal canopies or in crevices and tide pools. Some intertidal animals (e.g., littorine snails [*Littorina* spp.]) retreat into their shells at low tide, sealing in water and relying instead on their ability to cope with subsequent high temperatures. Lacking shells or waxy cuticles, seaweeds readily lose water, allowing them to stay cool for a time. Seaweeds have also evolved physiological mechanisms to cope with the resulting desiccation.

In addition to temperature and desiccation stress, intertidal organisms must contend with broad variation in salinity, sand burial, and other conditions. Variability in salinity is typically low during high-tide submersion but can increase dramatically at low tide during rain events or from exposure to freshwater runoff from streams or storm drains. Movement of sand along the coast can bury intertidal organisms in seasons of limited wave scouring, typically in summer (see Figure 18.3). Sand movement and tolerance of sandy conditions is especially important for rocky intertidal communities in southern California, where rocky benches are typically interspersed with long stretches of sandy beach.

## WAVE EXPOSURE

As winds blow, they transfer energy to the ocean surface, producing waves (Denny 1988). In the area directly affected by wind, waves—known as *seas*—are steep and disorganized, with periods of 4 to 6 seconds. But waves can travel great distances; as they move away from the winds that generated them, their character gradually changes. Waves that arrive from a distant storm—known as *swell*—oscillate with periods of 8 to 20 seconds. On a typical day the waves impinging on a shore are a complex combination of seas and swell. The interaction of intertidal organisms with ocean waves—their *wave exposure*—is mediated by the slope of the seafloor. As waves progress from deep to shallow water, accompanying water motion changes from a nearly circular orbit confined to

the upper portion of the water column to a shoreward-seaward oscillation extending all the way to the seafloor. An increase in velocity accompanies this shift in flow pattern. In deep water a wave with a period of 10 seconds and a trough-to-crest height of 1 meter causes a maximum water velocity of 0.3 meter per second. When the same wave has *shoaled* to a depth of 2 meters, velocity increases tenfold. As waves shoal even further—to a depth approximately equal to their height—they break. Breaking sets the maximum velocity waves can produce before reaching shore. Velocity at the crest of a breaking wave is approximately 4.4 times the square root of wave height, more than 4 meters per second for a 1 meter high wave and more than 6 meters per second for a 2 meter high wave.

Whether these high velocities are imposed on *BENTHIC* organisms depends in large part on the slope of the seafloor. If the slope is gradual, waves break seaward of the intertidal zone and lose energy (and velocity) to *VISCOUS* turbulent processes as they move up the shore. In this case the intertidal community is relatively protected. By contrast, if the shore slopes steeply, waves break directly on the intertidal zone, where crest velocity can be amplified by the water's interaction with the rock's small-scale topography. When this occurs, velocities of 10 meters per second are common, and storm waves can cause speeds in excess of 30 meters per second (approximately 67 miles per hour). Where shoreline topography is complex, water velocity can vary substantially over short distances. While the seaward faces of rocks might see extremely high water velocities, the leeward sides of the same rocks can be relatively sheltered, allowing a different suite of animals and plants to survive. The exposure of a site also depends on the direction from which waves arrive. Waves that approach on a path perpendicular to shore lose the least energy before reaching the intertidal zone and therefore have the greatest impact. Those approaching on a path more parallel to shore have a smaller effect.

Wave-induced water velocities have both detrimental and beneficial effects. Hydrodynamic forces (drag and lift) are proportional to the square of velocity (Vogel 1994), and—given the extreme velocities associated with waves—can pose challenges for intertidal organisms. Many organisms found on wave-swept shores, such as limpets (e.g., *Lottia* spp.) and chitons (e.g., *Leptochiton* spp.), have evolved unique, low-profile shapes to reduce the forces imposed on them by waves and to reduce their likelihood of becoming dislodged by wave action. Wave-induced disturbance (when organisms are torn from the rock by wave action) has important ecological consequences for the diversity and function of rocky shore communities. For example, the California mussel *Mytilus californianus* is the competitive dominant for space on exposed shores in California, but forces imposed by breaking waves can rip them from the rock. Although this disturbance harms mussels, the dislodged animals are food for sea anemones, and the open space they leave behind makes room for fugitive species such as the sea palm, *Postelsia palmaeformis* (Dayton 1973, Paine 1988, Blanchette 1996). Hydrodynamic forces can also constrain movement by predators and herbivores, which is bad for the consumers but good for their prey. The same forces that cause disturbance also splash water high on the shore, transporting food to barnacles (Cirripedia) and keeping both plants and animals moist and cool. The dynamics of intertidal communities vary in predictable fashion along gradients of wave exposure at least in part in response to wave-induced water motion. These patterns are discussed later in the chapter in the context of intertidal ecology.

## Organisms of California's Rocky Intertidal Ecosystems

The narrow ribbon of California's marine coast hosts an extraordinary diversity of flora and fauna. Terrestrial life resistant to saltwater encroaches from inland; subtidal species able to survive limited air exposure or dynamic tide pool conditions extend up the shore; and other organisms thrive solely within the rocky intertidal ecosystem. No exact enumeration of California shore species exists, even if tiny organisms are not considered. At least 669 species of intertidal and subtidal seaweeds are known in California (Abbott and Hollenberg 1976), while over 3,700 rocky and sandy coast invertebrates have been identified from central California to Oregon (Carlton 2007). A major intertidal survey throughout southern California found 213 seaweed species (Murray and Littler 1989) and 349 invertebrate species (Seapy and Littler 1993); however, a contemporary, intensive inventory within mussel beds "conservatively" discovered 141 algae and 610 invertebrate species (Kanter 1980). Adding to coastal diversity are tide pool and migratory intertidal fishes along with visiting shorebirds and a few mammals.

Rocky intertidal organisms belong to a broad range of evolutionary (phylogenetic) groups that include seaweeds and flowering plants (Chromista and Plantae); sponges (Porifera); hydroids and sea anemones (Cnidaria); flatworms (Platyhelminthes); peanut worms (Sipuncula); segmented worms (Annelida); barnacles, isopods, amphipods, shrimps, crabs, and insects (Arthropoda); octopus, chitons, snails, sea slugs, and bivalves (Mollusca); sea urchins, sea stars, brittle stars, and sea cucumbers (Echinodermata); and tunicates, fishes, birds, and mammals (Chordata). An ecologically useful way to characterize intertidal life forms is by how they acquire energy to sustain life. Common groupings include primary producers (that acquire energy from sunlight), suspension feeders (that filter or trap drifting microbiota and detritus), grazers (that consume seaweeds), and carnivores (that capture animals). Species within and among these trophic groupings interact in intricate food webs. From a resource management perspective, another set of groupings includes those harvested or impacted by humans, those designated for special protection, and those introduced from faraway shores.

### Primary Producers

Photosynthetic seaweeds provide a productive nutritional base for intertidal food webs, compete for limited shore space, and often create structural habitat for other organisms. California's diverse sun-lovers range from tiny blue-green bacteria (cyanobacteria) through commonly categorized green (Chlorophyta), brown (Heterokonta), and red (Rhodophyta) seaweeds, to true flowering surfgrass (Tracheophyta). Reds are the most species-rich, followed by browns, greens, and the two species of surfgrass. Seaweed structural forms adapted to intertidal lifestyles include wave-resistant films or crusts; leathery, desiccation-resistant rockweeds; filamentous turfs with high surface area for nutrient and light uptake; stony coralline algae; and larger, bushy growths and fleshy blades that rise above the substrate when submerged.

Dominant primary producers on California shores often create intricate structural habitats, hosting rich floral and faunal assemblages that shelter within or attach as epiphytes. Key dominant producer types include erect corallines (e.g.,

*Corallina*) and soft turfs (e.g., *Endocladia*, *Gelidium*), tough rockweeds (e.g., *Silvetia*, *Fucus*), fleshy blades (e.g., *Ulva*, *Chondracanthus*, *Mazaella*), branching bushes (e.g., *Stephanocystis*, *Sargassum*), large bladed or bladdered kelps (e.g., *Laminaria*, *Eisenia*, *Egregia*), and meadowy surfgrass (*Phyllospadix*) (Figure 18.5).

### Suspension Feeders

As adults, many rocky intertidal invertebrates are sessile, an adaptation to hold space and minimize wave dislodgement. Their food arrives primarily as phytoplankton, zooplankton, or detritus particles suspended in rushing seawater. Some species use active mechanisms for straining this tiny food during submerged periods; these include sweeping sieve-like legs (e.g., barnacles) and pumping water through comb-like filters (e.g., sponges, bivalves, tunicates). Others feed more passively by extending sticky or filtering appendages for longer periods of time. Tube snails (e.g., *Serpulorbis*) employ mucous nets; sea anemones (Anthozoa) have stinging tentacles; crevice-dwelling sea cucumbers (e.g., *Cucumaria*) and peanut worms (e.g., *Themiste*) have sticky, branched tentacles; and plume worms (e.g., *Spirobranchus*) and colonial moss animals (Bryozoa) extend feathery filters.

Suspension feeders such as acorn (e.g., *Chthamalus*, *Balanus*) and stalked (e.g., *Pollicipes*) barnacles, and anemones (e.g., *Anthopleura*), can dominate intertidal reefs through sheer numbers. Other filter feeders are important habitat-forming bioengineers; these include sand-castle worms (e.g., *Phragmatopoma*) that fill in crevices with sandy tube colonies, mussels (e.g., *Mytilus*) that form dense thickened beds with interstitial microhabitats, and pholad bivalves (e.g., *Penitella*) that bore holes in sedimentary reefs. These holes then host numerous small organisms.

### Grazers

California's intertidal seaweed consumers (herbivores) can be relatively sedentary if they trap drift seaweeds (e.g., abalone, sea urchins) or graze algal films within a small area (e.g., many limpets and chitons); however, others, such as top snails, sea hares, and shore crabs, forage more widely. Herbivorous mollusks have file-like radulas, urchins use beak-like jaws, and shore crabs employ claws to scrape seaweed films or larger plants. Grazers such as periwinkles (e.g., *Littorina*), limpets (e.g., *Lottia*), turban snails (e.g., *Chlorostoma*), chitons (e.g., *Nuttalina*), shore crabs (e.g., *Pachygrapsus*), and sea urchins (e.g., *Strongylocentrotus*) can occur in great numbers where conditions are suitable. Hermit crabs (e.g., *Pagurus*) may be abundant in tide pools, scavenging plant and animal materials. Owl limpets (*Lottia gigantea*) can dominate upper intertidal rocks, where they maintain grazing territories by removing most other organisms.

### Carnivores

Diverse predators are ecologically important in upper levels of intertidal food webs. Some like crabs and octopus are active crevice or tide pool residents, while other mobile predators are migratory—lobsters and fishes moving inshore to forage at higher tides and seabirds arriving to hunt at lower tides. Some



FIGURE 18.5 A broad meadow of surfgrass (*Phyllospadix torreyi*) covers the low shore. Photo: Carol Blanchette.

carnivores are slow-moving (e.g., predatory snails, sea slugs, and sea stars). Sedentary sea anemones snare creatures that wander or drift onto them. Intertidal adaptations for capture of prey include drilling (e.g., snails like *Ceratosoma* and *Acanthinucella*), poisoning (e.g., *Octopus* and the cone snail *Conus*), rasping or piercing (e.g., nudibranchs), prying or engulfing (e.g., sea stars, such as *Pisaster* spp.), stabbing or hammering (e.g., black oystercatchers, *Haematopus bachmani*), and picking at or swallowing whole (e.g., most fishes and shorebirds).

The ochre sea star (*Pisaster ochraceus*) is well known as a keystone predator that can greatly affect ecological conditions in communities of its mussel prey. Ochre sea star populations have declined due to disease outbreaks associated with warm water conditions in the 1970s and the recent El Niño periods of 1982–1983 and 1997–1998 (Eckert et al. 2000). A massive sea star wasting disease epidemic that has not been associated with warm water, and has affected all species of sea stars, began in summer 2013 and has extended as far north as Alaska (Stockstad 2014). Shorebirds commonly can be seen foraging at low tide on intertidal reefs; more elusive terrestrial mammals (including rats, cats, raccoons, and foxes) may hunt for shore crabs and other invertebrates at night.

### Species of Special Concern

Surfgrass (*Phyllospadix*) and sea palms (*Postelsia palmaeformis*), recognized as important but susceptible habitat-forming plants, are specifically protected from disturbance and sport harvest (although sea palms are not protected from commercial harvest in California). The black abalone (*Haliotis cracherodii*), once abundant and extensively gathered for food, suffered such catastrophic declines, particularly in southern California, during the 1980s (due to overfishing and withering syndrome disease) that it was listed as a federally endangered species in 2009. Species introduced to California marine waters by hitchhiking on ships or other means present ecological threats to native species. Most introduced species are known from sheltered bays and harbors, with relatively few

discovered on the open coast. Maloney et al. (2006) found 16 non-native species in representative outer-coast intertidal reefs (667 species were native and 59 others were of unknown origin). The most widespread invaders were two seaweeds: a large brown bladderweed (*Sargassum muticum*) and a small red turf (*Caulacanthus ustulatus*).

### Benthic-pelagic Coupling

Rocky intertidal ecosystems are inextricably linked to the oceanic environment through the delivery of food, nutrients, and propagules (both larval invertebrates and algal spores). The oceanographic processes driving the delivery of these constituents span large spatial scales and thereby connect distant communities (see Chapter 6, “Oceanography”). Rocky intertidal organisms may also alter the amounts and kinds of materials in the waters that pass over, among, and through them, and transform the PELAGIC (offshore) waters arriving to benthic (bottom-dwelling) organisms further upshore or along the shoreline. The exchange of essential materials between the two ecosystems is referred to as benthic-pelagic coupling (Figure 18.6). The nature and degree of coupling can strongly influence the rate and extent of recovery from natural or anthropogenic disturbances, productivity, and the relative abundances and diversity of species that make up rocky intertidal communities (Menge et al. 2003, Blanchette et al. 2008).

Sessile animals and plants that live attached to the rocks rely on ocean currents to deliver food and nutrients. Much of the food of suspension-feeding invertebrates such as mussels and barnacles consists of phytoplankton, single-celled photosynthetic organisms (e.g., diatoms and dinoflagellates) common to coastal waters. Microscopic zooplankton, including meroplankton (larval forms of nonplanktonic adults) and mixotrophic plankton (plankton that depend on a variety of carbon sources), that feed on smaller planktonic forms (including phytoplankton) are also ingested by sessile, suspension-feeding invertebrates. Some suspension feeders feed



on even smaller planktonic forms, such as the bacteria, ciliates, and flagellates that form the microbial food webs of pelagic waters. In addition to the living components of their diets, many of these animals consume small detrital particles derived from the breakdown and decay of seaweeds and other marine plants (collectively referred to as macrophytes) from nearby algal beds, kelp forests, and seagrass meadows.

Macrophytes of rocky shores all depend on the flow of water over their THALLI or leaves to deliver nitrogen, phosphorus, and other nutrients for use in essential metabolic pathways (such as photosynthesis, protein synthesis, respiration, Adenosine Triphosphate (ATP) synthesis, DNA replication, RNA transcription) supporting growth and reproduction. Nitrogen and phosphorus in seawater can be present in several inorganic and organic forms, but the inorganic forms nitrate ( $\text{NO}_3^-$ ), ammonium ( $\text{NH}_4^+$ ), and (ortho-) phosphates ( $\text{HPO}_4^{2-}$  and  $\text{PO}_4^{3-}$ ) are most readily available to macrophytes. Although both phosphorus and nitrogen can limit macrophyte growth, nitrogen is generally more limiting along California's coast. The most important source of new nutrients (as opposed to nutrients remineralized and recycled through microbial food webs) for macrophyte growth is from the process of coastal upwelling.

### Coastal Upwelling

Although upwelling regions are only about 1% of the ocean's surface, they are the source of approximately 50% of the sea-food humans harvest from the oceans each year. The high primary productivity of phytoplankton in these regions propagates upward to support a diverse and productive ocean food web. Both intertidal macrophytes and suspension-feeding invertebrates can benefit from the nutrient-rich waters delivered by coastal upwelling (see Chapter 6, "Oceanography"). Upwelled waters fuel the growth of macrophytes, phytoplankton, and, indirectly, the rest of the planktonic food web that supports suspension-feeding invertebrates. Since both macrophytes and phytoplankton can strip nutrients from the water column, this productive boost fuels competitive interactions between these two groups. The dense blooms of phytoplankton that can form in response to upwelled nutrients reduce light reaching benthic-dwelling macrophytes by preemptively intercepting it for their own use (Kavanaugh et al. 2009). Clearer, colder, nutrient-rich waters conducive to lush growth of macrophytes tends to prevail near and just to the south of coastal upwelling centers (which often coincide with headlands) (Broitman and Kinlan 2006).

As newly upwelled waters move away from where they were shoaled, they bring along an initial inoculum of phytoplankton that will eventually proliferate and grow in the sunlit surface waters, but this occurs over a period of several days. Thus older, warmer, phytoplankton-rich waters tend to occur further downstream and/or offshore of upwelling centers. Depending on the prevailing trajectory of newly upwelled waters and the strength and duration of upwelling favorable winds, the locations of "downstream" or "aged" waters with abundant phytoplankton can vary. Local topography and bathymetry, including offshore banks and canyons, help create relatively predictable nearshore circulation patterns (Woodson et al. 2012). This results in a mosaic of shoreline habitats with qualitative and quantitative differences in the degree of benthic-pelagic coupling with respect to inorganic nutrients for macrophytes and organic nutrition for invertebrates (Blanchette et al. 2009, Krenz et al. 2011, Watson et

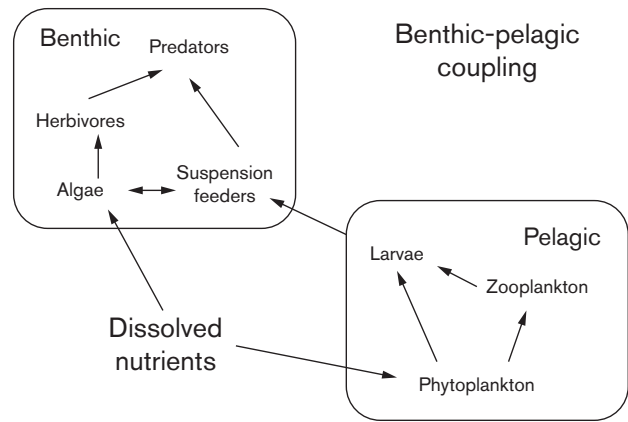


FIGURE 18.6 Conceptual diagram of coupling between the benthic marine intertidal ecosystem and the pelagic marine ecosystem. Dissolved nutrients fuel the growth of phytoplankton as well as macroalgae. Larvae from the pelagic environment settle in the benthic intertidal environment. Source: Carol Blanchette.

al. 2011). Locations closer to upwelling centers are more conducive to lush growth of macrophytes, while those receiving more aged waters that deliver a rich suspension of planktonic foods, or occurring just downshore from upwelling centers that receive detrital macrophytes and drift-algae, will tend to favor the growth of invertebrates that feed on suspensions of organic particulates and larger drift-algae (Broitman and Kinlan 2006, Lester et al. 2007).

### Complex Life Histories

Many, but not all, intertidal animals have complex life histories that include indirect development and dispersal of pelagic larval forms. Some invertebrates such as mussels have a plankton-feeding (planktotrophic) larval stage coupled with a suspension-feeding adult stage and thus experience strong, direct benthic-pelagic coupling throughout their life cycles. Invertebrates such as urchins (Echinoderms in the class Echinozoidea) without suspension-feeding as adults are still influenced by their larval transit through the pelagic realm and may experience indirect coupling with the pelagic environment later in life through the availability of drift seaweed. Invertebrates such as predatory whelks (e.g., *Kelletia kelletii*) with direct developing, crawl-away larvae (no pelagic phase) can still be influenced by benthic-pelagic coupling because their prey have pelagic larvae (Wieters et al. 2011). Not all rocky intertidal invertebrates are strongly influenced by benthic-pelagic coupling. Chitons (molluscs in the class Polyplacophora), for example, have short-lived, nonfeeding (lecithotrophic) larvae and as adults depend primarily on in situ algal resources.

The influence of the pelagic phase of life on intertidal invertebrate populations varies strongly and depends in part on larval characteristics. Larval stages may be short-lived or long-lived. They may need to encounter and capture their own planktonic food or be accompanied by a maternally sourced, lipid-rich nutritional package instead, or sometimes a combination of the two (Denny and Gaines 2007). In feeding larvae, such as the VELIGERS of mussels (bivalve molluscs), planktonic food availability can affect juvenile survivorship and growth on the shore (Phillips 2002). Thus timing of lar-



FIGURE 18.7 Examples of distinct bands of organisms (zonation) in the rocky intertidal. Photo: Jayson Smith.

val release to match the availability of phytoplankton is probably an important influence on survivorship of feeding larval forms (Phillips 2004). Planktonic larvae are also subject to predation while in the pelagic zone. Fishes can markedly reduce the survivorship of a well-fed cohort of larval barnacles previously destined to arrive on the rocky shores just beyond a kelp forest (Gaines and Roughgarden 1987). Despite their microscopic size, dispersing larvae are not always at the mercy of the currents; larvae can effect changes in their horizontal position within the water column and thus move themselves into onshore- or offshore-flowing waters. In the end, most larvae do not make it back to shore. The realized dispersal, metamorphosis, and settlement of invertebrates to the intertidal zone depends on a highly favorable convergence of the timing of release and duration of the larval stage, larval behavioral tactics, the nearshore circulation dynamics that generate currents, waves, fronts, and eddies, and conditions on the shore that permit or prevent survival of settling larvae.

### Intertidal Ecology

Rocky intertidal ecosystems have long served as a proving ground for developing and testing ecological theory. Their alternating exposure to marine and terrestrial conditions creates steep environmental gradients that help to explain the striking patterns of distribution and abundance seen on most rocky shores. Several features combine to make rocky shores ideal outdoor laboratories, including variable physical conditions over short distances and the presence of small organisms that are mostly sessile or sedentary, often reach high densities, have short generation times, and are readily experimentally manipulated.

### Patterns on the Shore

Zonation is the characteristic pattern of distribution and abundance observable as successive bands of organisms as one moves from the low shore to the high shore (Figure 18.7). Zonation is perhaps the best-known pattern in rocky intertidal communities. It occurs universally in rocky intertidal

regions (Lewis 1964, Stephenson and Stephenson 1972) even where tidal range is only a few tens of centimeters. A typical rocky shore can be divided into a spray zone or splash zone above the mean high-tide line and covered by water only during storms and an intertidal zone that lies between the high and low tidal extremes (Figure 18.8). Along most shores, the intertidal zone can be clearly separated into high, middle, and low intertidal subzones with characteristic assemblages and patterns of zonation. Along the California coast, barnacles (*Chthamalus* and *Balanus*) characterize the high zone, rockweeds (*Silvetia*, *Fucus*) the upper-mid zone, mussels (*Mytilus*) the lower-mid zone, and an assemblage of macrophytes, typically red algae, kelps, and surfgrass, the low zone.

Gradients in wave exposure provide an important backdrop against which community structure varies horizontally in space (Lewis 1964). Even over short distances, patterns of distribution and species composition can shift dramatically from wave-exposed headlands to nearby wave-sheltered coves while still displaying sharp vertical zonation (e.g., Dayton 1971, Menge 1976). Exposure to sun as well as waves can also influence species composition, with entirely different assemblages occurring on north-facing and south-facing rocky surfaces. At smaller scales within zones, organisms can also be patchily distributed. Patchiness can be generated by wave-borne disturbance, which removes clumps of organisms from the rocks. The gaps formed in mussel beds are a classic example of patchiness (Dayton 1971, Paine and Levin 1981). Disturbance due to wave action can, in some cases, determine the structure of the entire intertidal community. This can happen through a process of ecological succession, when species replace one another through time following a disturbance. A classic experiment examining the effects of disturbance and succession on community structure took place in an intertidal boulder field on the southern California coast (Sousa 1979). The frequency with which boulders are overturned, and therefore disturb the communities of organisms living on them, depends on a combination of wave action strength and the sizes of the boulders themselves. Sousa (1979) found the greatest diversity of organisms on medium-sized boulders that were overturned occasionally, providing an intermediate level of disturbance. Boulders that were overturned constantly could only support ephemeral assemblages, and those rarely overturned were dominated by competitively superior species. Sousa's study and others in rocky intertidal ecosystem have supported the general hypothesis that a moderate level of disturbance is important to the maintenance of diversity in these ecosystems.

### Community Dynamics

For many years marine ecologists assumed that the structure of rocky intertidal communities was under largely physical control (e.g., Lewis 1964). Explanations for species distributions, for example, were sought through study of species' tolerances of waves, thermal stress, and desiccation. Many thought that species could not live in particular zones because they could not tolerate the physical conditions there. We now know that while physical factors are important, they are only part of the story. In 1961, Joe Connell published two papers that elegantly and convincingly demonstrated that the lower limits of two zone-forming barnacles were set by species interactions. At Millport, Scotland, he found that interspecific competition for space determined the lower limit of

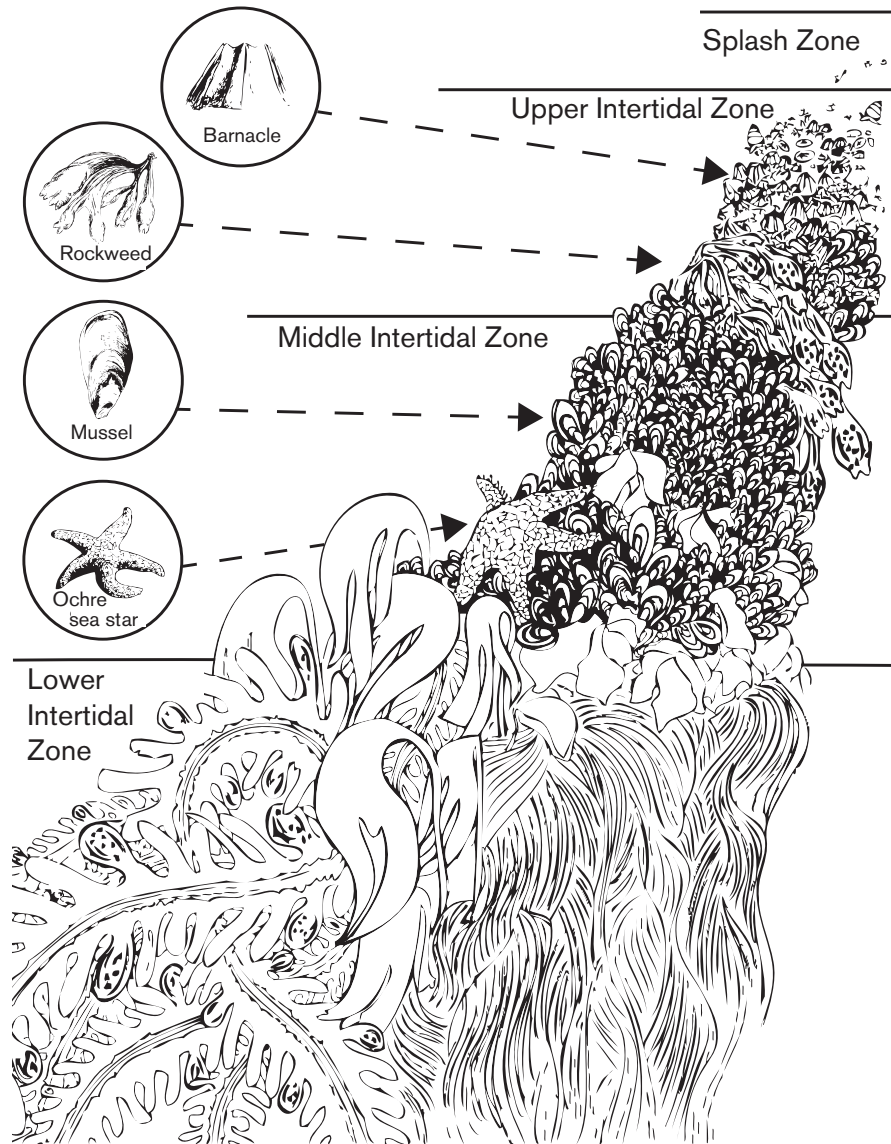


FIGURE 18.8 Conceptual diagram of zonation depicting the intertidal zones. Source: Illustration by Aeon Brady.

the upper-shore barnacle, and that both intraspecific competition and predation by whelks determined the lower limit of the lower-shore barnacle (Connell 1961a, Connell 1961b).

While biotic drivers set the lower limits for both species, physical factors set the upper limits. Although upper-shore barnacles were outcompeted by lower-shore barnacles, the inability of lower-shore barnacles to persist in the high zone due to desiccation stress provided refuge for upper-intertidal barnacles to exist, as they were more tolerant to long periods of emersion. Five years later, Paine (1966) published the early results of a study on the Washington coast clearly demonstrating that predation by a sea star (*Pisaster ochraceus*) maintained the lower limits of midshore mussel beds (Figure 18.9). Because the upper limit of sea stars typically reaches only the lower intertidal zone, mussels can persist in the middle intertidal zone because of release of predation. Due largely to these two influential studies, attention shifted dramatically in the 1960s toward the view that community patterns can be controlled by biotic factors as well. Both studies provided evidence for the ecological paradigm in rocky intertidal habitats

that the lower limits of species are set by biotic interactions while the upper limits are driven by physical factors.

Paine's work not only demonstrated that predation could determine the lower distributional limit of a competitively dominant intertidal organism but also made important conceptual advances. His study was one of the earliest experimental demonstrations of the predation hypothesis, which states that predation can control the diversity of species in a community (Paine 1966). By selectively feeding on a dominant competitor, thereby preventing competitive exclusion, predators can facilitate the coexistence of many species of both dominant and subordinate competitors. In this case, sea star (*Pisaster*) predation mediated the abundance of the competitive dominant mussel (*Mytilus*), allowing for a myriad of competitively inferior species, such as barnacles and seaweeds, to persist. Paine's study established the concept of "keystone species"—species that have disproportionately large effects on their communities relative to their abundances (Paine 1969, Power et al. 1996). Finally, Paine's study was one of the first clear demonstrations of indirect effects.



FIGURE 18.9 The keystone predator, sea star (*Pisaster ochraceus*), feeding on its prey, the California mussel (*Mytilus californianus*). Photo: Jayson Smith.

Indirect effects are the effects of one species on a second, mediated through a third. In the *Mytilus-Pisaster* example, *Pisaster* has large, positive indirect effects on many subordinate competitors of *Mytilus*. The existence of indirect effects was first noted through the unexpected or surprising outcomes of experiments investigating species interactions (e.g., Paine 1966 and 1974, Dayton 1971). The broader significance of indirect effects was underappreciated, however, until theorists (e.g., Holt 1977, Bender et al. 1984) helped spur research to explicitly quantify their impact on community structure (see, e.g., Dungan 1986, Schmitt 1987, Wootton 1994).

### Recruitment Dynamics

In rocky shore ecosystems two aspects of larval biology powerfully influence population dynamics and community structure. The first is the behavior of larvae in selecting settlement sites; the second relates to the quantities of larvae that recruit to the shore. A considerable body of work has shown that barnacle larvae have very specific requirements when they settle. The position of larvae in the water column (Grosberg 1982), the texture of the rock face (Crisp and Barnes 1954), the presence of conspecifics (gregarious settlement) (Knight-Jones 1955, Minchinton and Scheibling 1993), and chemical cues from coexisting species (Raimondi 1988) are among many factors that influence recruitment success.

The effect of a variable supply of new individuals on benthic populations has also long been of interest in marine ecology (see reviews by Underwood and Denley 1984, Young 1987 and 1990, Grosberg and Levitan 1992) and has been dubbed “supply-side ecology” (Lewin 1986). However, ecologists have only recently focused explicitly on the relative degree to which community structure is affected by settlement (the act of colonization and metamorphosis by propagules; Connell 1985) and recruitment (survival of settlers for some longer but usually arbitrary period of time Connell 1985) versus postrecruitment factors, such as predation and competition. Most early research on the influence of recruitment dealt with bar-

nacle populations and the impact of variable recruitment or settlement densities on adult density (e.g., Gaines and Roughgarden 1985, Connell 1985, Raimondi 1990). In central California, for instance, abundances of adult *Balanus glandula* in the high zone vary from nearly complete coverage of the available rock surface at wave-exposed sites to low cover on more wave-sheltered sites (Gaines and Roughgarden 1985). Rates of recruitment were up to twenty times higher at wave-exposed sites compared to wave-sheltered sites. These and other studies also strongly suggest that when recruitment is low, patterns of abundance and community structure may be more strongly influenced by the supply rate of new individuals than by agents of postrecruitment mortality. For example, the negative relationship between an index of upwelling intensity and the recruitment of barnacle larvae (Roughgarden et al. 1988) is a strong indicator that offshore transport dictates barnacle densities via negative effects on recruitment.

### Community Regulation

Whether and when biological communities are regulated by consumers (top-down) or primary productivity (bottom-up) remains a fundamental question in all of ecology (Oksanen et al. 1981, Fretwell 1987, Polis et al. 2000, Schmitz et al. 2000, White 2001). Some recent research in marine ecosystems has provided evidence for both top-down and bottom-up controls on communities (Burkepile and Hay 2006). A unique aspect of rocky shores is the occupation of primary space by two distinctly different groups of competing organisms: algae and filter-feeding invertebrates. Marine ecologists have spent considerable effort to understand the factors that contribute to the community pattern resulting from differences in the relative proportion of these two groups. One major mechanistic hypothesis linking nearshore oceanography to community pattern relates to the spatial and temporal variability in coastal upwelling. Latitudinal variation in upwelling intensity has been suggested as an important factor in the recruitment of benthic invertebrates along the U.S. West Coast.

The upwelling/relaxation model asserts that planktonic larvae are swept offshore by Ekman transport, where they accumulate along coastal fronts and are occasionally returned to shore when upwelling-favorable winds relax (Roughgarden et al. 1988, Shanks et al. 2000). Consistently strong upwelling along much of the California coast has been proposed to limit invertebrate recruitment (Gaines et al. 1985, Gaines and Roughgarden 1985, Roughgarden et al. 1988, Strub and James 1995), resulting in communities dominated by macrophytes in areas of strong upwelling. Regions of strong coastal upwelling may also influence community structure through positive direct effects on macroalgae, which compete for space with mussels and barnacles (Schiel 2004, Blanchette et al. 2006). Coastal upwelling delivers cold, nutrient-rich water to shore, and locations of strong upwelling are characterized by high nutrient concentrations, which have been shown to have positive effects on the abundance (Bustamante et al. 1995, Broitman et al. 2001) and growth rates (Blanchette et al. 2002, Nielsen and Navarrete 2004) of benthic macroalgae. Strong coastal upwelling is predicted to favor macroalgal dominated communities through both direct positive effects of nutrients on algae and indirect effects of reduced competition with recruitment-limited invertebrates for space. However, the relative importance of these two mechanisms is still not well understood.

## Human Impacts

With approximately 68% of Californians living near the shoreline in 2008 (Wilson and Fischetti 2010), coastal ecosystems experience multiple threats from human activities. High urbanization can affect coastal ecosystems through air and water pollution, land development, habitat destruction, commercial and recreational harvest, recreational use, and introduction of non-native species, among other human-induced environmental changes. Rocky intertidal ecosystems are especially under threat because they lie at the land-ocean interface and thus receive direct runoff of terrestrial pollutants, coincide with settling locations for oceanic oil spills, and can be easily accessed during low tides for exploitation. Over the past several decades, many changes in species abundances have been observed in the rocky intertidal, including large declines in black abalone populations in southern and central California (Miller and Lawrenz-Miller 1993, Richards and Davis 1993, Altstatt et al. 1996); shifts in southern California macroalgal community structure from large fleshy species to more disturbance tolerant, turf-forming seaweeds (Widdowson 1971, Thom and Widdowson 1978, Goodson 2004, Gerard 2005); declines in mussels in southern California (Smith, Ambrose, and Fong 2006) and mussel bed-associated macroinvertebrate diversity statewide (Smith, Fong, and Ambrose 2006); regional extinction of the dorid nudibranch (*Felimare californiensis*) (Goddard et al. 2013); shifts in species range limits (Sagarin et al. 2007, Zacherl et al. 2003), and increases in non-native species (Cohen and Carlton 1995, Murray et al. 2005).

## Water Pollution

Water pollution includes manufactured chemicals such as DDT, elevated levels of naturally occurring chemicals such as heavy metals and nutrients, altered natural temperature

regimes, and modified biota such as the introduction of non-native species. Water pollution in the rocky intertidal can be linked to terrestrial runoff, storm drain flow, aerial deposition, sewage effluent, wastewater discharges, and oil spills, and can involve chronic or pulse disturbances from either point or nonpoint sources. The impacts of water pollution on rocky intertidal species' health and normal ecosystem functioning are highly variable but are relatively understudied (Crowe et al. 2000, Thompson et al. 2002).

Although chronic input of oil washed into storm drains far exceeds oil spills (Foster et al. 1988, Suchanek 1993), the low rate of input as well as quick dilution has made it difficult to measure direct effects of the former. Pulse disturbances of large quantities of oil have received more attention. The combined impacts of oil coating, direct lethal toxicity, sublethal impacts on health, and clean-up efforts using chemical dispersants and physical removal can harm many rocky intertidal populations. Mass mortality of macroalgae and benthic invertebrates can result from chemical toxicity and smothering by oil, while high-pressure, hot-water clean-up efforts can have equally devastating, if not worse, effects including lengthened recovery time (Paine et al. 1996, Peterson et al. 2003). Sublethal impacts include physiological, carcinogenic, and cytogenic effects, resulting in population-level and community changes (Suchanek 1993, Peterson et al. 2003).

The largest oil spill in California and the third largest in the United States occurred near Santa Barbara in 1969, dumping about 4 million gallons of crude oil (Clarke and Hemphill 2002). Notable short-term impacts included marked losses of rocky intertidal barnacles and macrophytes (Foster et al. 1971, Straughan 1973); understanding of the spill's long-term effects, however, remains poor. Also near Santa Barbara, the 1997 Torch/Platform Irene Oil pipeline rupture spilled 6,846 gallons of petroleum, oiling approximately 17 miles of coastline. In 2007 the container ship *Cosco Busan* struck a San Francisco bridge, spilling 53,569 gallons of fuel, which oiled 200 miles of wave-protected and wave-exposed coastline. In 2009 the tank vessel *T/V Dubai Star* spilled 400 gallons of oil, reaching 10 miles of San Francisco Bay shoreline. Oil from these more recent spills coated portions of the rocky intertidal zone and its inhabitants, but their impacts were complex to measure, complicated by natural temporal variation and a lack of baseline information (Torch/Platform Irene Trustee Council 2007, Raimondi et al. 2009 and 2011). Some generalized effects of the spills included declines in barnacles, mussels, and rockweeds and increases in opportunistic algae.

In addition to oil, surface runoff from urban and agricultural sources discharges high amounts of fresh water, nutrients, heavy metals, pesticides, and other substances into California coastal waters (Schiff et al. 2000). Influxes of nutrients can cause declines in PERENNIAL seaweeds and increases in opportunistic seaweeds that use the nutrients to grow and bloom. For example, the addition of nutrients, in this case sewage-based, on San Clemente Island led to a decrease in slowly growing brown algae and seagrasses and an increase in opportunistic green algae and cyanobacteria (Littler and Murray 1975). Little work has examined the field effects of even single heavy metals on rocky intertidal ecosystems (Crowe et al. 2000), let alone of synergistic effects of multiple contaminants. Effects of sublethal levels of heavy metals and other contaminants can include opportunistic algal blooms (Castilla 1996) and impacts on larval development of benthic invertebrates (Fichet et al. 1998).

## Recreational Human Visitation and Exploitation

Rocky intertidal habitats during low tide provide a glimpse of the natural marine world without the need for specialized underwater equipment and training. In heavily urbanized areas of California, visitation to some rocky intertidal locations can reach fifty thousand to seventy-five thousand visitors per year (Ambrose and Smith 2005, Ware 2009, Laguna Ocean Foundation 2012). People visit these habitats for recreation, education, and subsistence harvesting and engage in activities such as collecting, rock turning, handling, and trampling. Through both experimental manipulations and observational comparisons of high- and low-use locations, some detrimental impacts of these activities have been documented. These effects include locally depleted floral and faunal populations, reduced biodiversity, shifts in the size and age structure of populations, and altered ecological processes (e.g., Castilla and Bustamante 1989, Duran and Castilla 1989, Brown and Taylor 1999, Espinosa et al. 2009).

Harvesting of rocky intertidal organisms is relatively common in California and extends back thousands of years (Braje et al. 2007). People engage in legal harvesting as well as illegal poaching of protected species. Commercial harvesting of intertidal seaweeds is a growing cottage industry, especially in northern California (Thompson et al. 2010). Subsistence and ceremonial harvesting of intertidal mussels, seaweeds, and other intertidal organisms remains an important practice for the members of California's many Native American tribes. Organisms are harvested for food, fish bait, and souvenirs, with mussels, octopuses (*Octopus*), abalone (*Haliotis*), limpets (*Lottia*), urchins (*Strongylocentrotus*), snails (e.g., *Chlorostoma*), crabs (*Pachygrapsus*), seaweeds (e.g., *Postelsia*), and sea stars (*Pisaster*) often targeted.

Local declines in the abundances of many of these species have been attributed to overharvesting. For example, mussels (Smith et al. 2008), large conspicuous invertebrates such as keyhole limpets and sea hares (Ambrose and Smith 2005), and various echinoderms and gastropods (Addressi 1994) occur in lower abundances at heavily visited sites. Recreational harvest of red abalone virtually eliminates it from the intertidal zone, although it can be found intertidally in locations well protected from both legal harvest and poaching (Rogers-Bennett et al. 2013). Overharvesting can shift the size structures of intertidal populations (e.g., owl limpets) toward smaller and younger individuals, as humans tend to be size-selective predators (Fenberg and Roy 2008, Kido and Murray 2003, Ambrose and Smith 2005, Sagarin et al. 2007).

## Management

Along the California coast, especially adjacent to heavily urbanized centers, a clear need exists to manage and protect rocky intertidal ecosystems. Conservation of rocky shores currently focuses on designations such as areas of special biological significance (ASBS) and/or marine protected areas (MPAs). The ASBS designation focuses on water quality, with thirty-four locations (32% of the California coast) managed by the State Water Resources Control Board. Within ASBS boundaries, state policy prevents discharge of any wastes in order to maintain natural water quality (SWRCB 2005). MPAs focus on the protection of marine organisms. As a result of the California Marine Life Protection Act passed in 1999, a network of 124 MPAs and 15 special closures (covering 16% of

coastal waters) are now under the jurisdiction of the California Department of Fish and Wildlife. Within reserves, marine life is protected through limitations or bans on harvesting. MPAs in northern California also explicitly protect tribal rights to ceremonial and subsistence harvest of intertidal organisms. MPAs are very effective in protecting subtidal marine life (Halpern 2003), but their effectiveness in protecting rocky intertidal habitats needs to improve. Collecting in rocky intertidal MPAs continues to occur despite regulations (Murray 1997, Murray et al. 1999, Ambrose and Smith 2005). In addition, management is solely focused on collecting while other impacts are not clearly addressed (Smith et al. 2008).

While current management practices are strong and successful, improved conservation requires adaptive management and supplemental strategies. Publicly owned treatment works (POTWs) are well regulated, but storm water runoff management is still in its early stages, as is understanding of the singular and synergistic effects of pollutants. Continued and expanded long-term monitoring of rocky intertidal resources, such as that conducted by the Multi-Agency Rocky Intertidal Network (MARINE), provides vital baseline information to document impacts from oil spills and other anthropogenic disturbances. Increased support is needed for local organizations that help fill some management gaps. Groups such as numerous regional Baykeepers organizations, the Orange County MPA Council, Heal the Bay, and others provided essential local oversight, monitoring and research, and educational and outreach services. Restoration of rocky intertidal habitats is still nascent but could aid species recovery, as shown through the successful reestablishment of rockweeds (Whitaker et al. 2010) and surfgrass (Bull et al. 2004) following localized extirpation. Finally, conservation efforts of the future can be expanded by promoting public understanding of the economic and other values of rocky intertidal shores (e.g., Hall et al. 2002).

## Climate Change

Global climate change is the backdrop against which all ecological and socioeconomic interactions now occur. The rocky intertidal zone has long served as a model system for examining the effects of the physical environment on the physiology and ecology of organisms, and as such has emerged as a natural laboratory for exploring the effects of environmental change (Connell 1972, Paine 1994). Impacts of climate change on patterns of distribution, abundance, and the provision of ecosystem services have been reported worldwide (Helmuth, Broitman et al. 2006), with numerous examples in California (e.g., Barry et al. 1995, Zacherl et al. 2003, Smith et al. 2006, Hilbish et al. 2010). While the exploration of the complex and often nonlinear effects of environmental change on intertidal ecosystems remains an active and growing area of research, several key themes—as well as knowledge gaps—have emerged in the search to understand and potentially forecast likely impacts (Howard et al. 2013).

## Future Scenarios

Coastal habitats face myriad threats from global change, including increases in temperature, increased rates of coastal erosion, sea level rise, decreases in ocean pH, and altered circulation patterns (Howard et al. 2013). Globally, ocean acidity has increased by 30% (from an average pH value of 8.2 to 8.1) over

the past century (Feely et al. 2004) with a further decline of 0.3 to 0.4 pH units expected by 2100 (Orr et al. 2005). The average temperature of the upper layers of the ocean has increased 0.2°C since 1955 (Bindhoff et al. 2007) and is expected to increase by 0.4°C to 1.1°C in the next few decades. Projections of future climate, which depend significantly on greenhouse gas emissions, suggest an increase in mean air temperature of 2°C to 5°C by 2100 in California, with the greatest amount of change occurring in summer (Cayan et al. 2009).

Notably, these global averages mask much higher levels of variability in environmental change (Hoegh-Guldberg and Bruno 2010), and coastal environments are likely being altered more quickly than offshore waters. Measurements of pH in Monterey Bay show a decrease about 8.1 to 8.05 from 1993 to 2009, although this is one of the few longer-term measurements from the region (Monterey Bay Aquarium Research Institute 2010 Annual Report. 2011). Hofmann et al. (2011) describe the results of a one-month time series of continuous pH measurement at seven sites along the coast of California and report high variability from site to site, with fluctuations of 1 pH unit (i.e., an order of magnitude variability) at sites such as Elkhorn Slough and levels at some sites approaching those predicted for the open ocean in 2100. California's coastal upwelling waters are typically very acidic, with pH values as low as 7.5 (Feeley et al. 2008, Gruber et al. 2012). Models predict a continuing decline in pH in these waters over time (Hauri et al. 2009) (Figure 18.10). Recent work has shown a mosaic of pH along the California coast, with persistent spatial variation in the cumulative frequency of exposure to relatively corrosive (pH <7.7) conditions (Hofmann et al. 2014).

Nearshore water temperatures vary considerably from northern to southern California. Water temperatures in northern California are fairly homogeneous across latitude (31.5–40.5°N) with a mean temperature of 13.5°C and a mean annual range of 3.4°C (Payne et al. 2011). South of Point Conception in the Southern California Bight, waters are considerably warmer (17.8°C) and more variable (annual range of 5.6°C) (Payne et al. 2011). Geographic patterns of intertidal (aerial) temperature are even more complex, exhibiting a mosaic pattern in which extremes in temperature do not necessarily increase with decreasing latitude (Helmuth, Mieszowska et al. 2006).

In general, the impacts of climate and related change in the intertidal can be categorized as direct physiological effects—the influence of environmental change on the survival, growth, reproduction, and physiological performance of individual organisms—and indirect effects, the cascading influence of altered behavior and physiological performance on species interactions, including predation, competition, and facilitation (Harley et al. 2006, Blanchette et al. 2008). Direct effects are better understood. Sanford (2002) showed that increased water temperatures enhanced feeding rates by the keystone sea star on mussel prey in central California. In contrast, increased sea star temperatures in air reduced feeding by 40% at the same site (Pincebourde et al. 2008). Competitive ability between barnacles in experiments depends on their relative physiological tolerances to thermal stress (Wethey 1984), and field collections in San Francisco Bay showed that small-scale distributions of native and invasive species of mussels were linked to aerial body temperature (Schneider and Helmuth 2007). Although understanding of emergent impacts on species assemblages remains incomplete, shifts in species phenology and ranges, increases in rates of species invasions and disease spread, and changes in

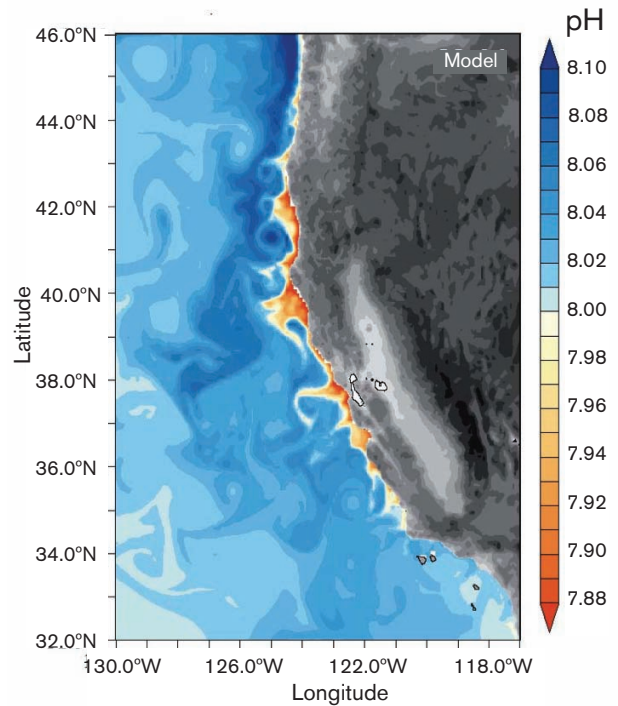


FIGURE 18.10 Model simulated snapshot of surface pH for the month of August. Low-pH waters in nearshore areas are the result of seasonal upwelling in summer, while the elevated pH in offshore waters reflects the photosynthetic removal of CO<sub>2</sub> from the water as it is transported offshore. Source: Hauri et al. 2009.

the abundance of ecologically and economic important species have been reported worldwide, including on the coast of California (Harley et al. 2006, Howard et al. 2013).

### Interactions between Stressors

Climate change is often “the trigger that fires the bullet,” delivering the coup de grace on organisms already impacted by other stressors such as overharvesting and eutrophication (Harley and Rogers-Bennett 2004, Crain et al. 2008, Firth and Williams 2009). As such, the impacts of environmental stressors are best considered in the context of other climatic and nonclimatic drivers of physiology and ecology. Crain et al. (2008) conducted a meta-analysis of marine studies that examined multiple stressors and found that cumulative effects were more or less evenly divided among additive (sum of individual stressors), synergistic (overall impact more than the sum of the individual stressors), and antagonistic (impact less than the sum of the individual effects) types. Overharvesting, for example, predisposes populations of fish to collapse when exposed to stressors such as pollution and climate change (Hsieh et al. 2008, Sumaila et al. 2011). Taken in sum, these studies signal a need to understand the processes by which climate change impacts intertidal organisms, at scales ranging from subcellular to ecosystem (Helmuth 2009).

### Summary

Intertidal ecosystems exist at the interface between land and ocean and occupy a narrow band of the coast that is above

water at low tide and under water at high tide. Organisms occupying intertidal areas have evolved unique adaptations to withstand the wide variation in physical conditions (temperature, salinity, desiccation) characteristic of these environments. Although intertidal habitats can have either soft (sand, mud) or hard (rocky) bottom substrates, we have focused this chapter on rocky intertidal ecosystems, which occur along the entire California coast. Rocky intertidal ecosystems of the Pacific coast support a high diversity of invertebrate and algal species and have served as a model ecosystem for experimental marine ecology.

The organisms inhabiting rocky intertidal ecosystems tend to occur in characteristic bands or zones determined in part by time of submergence (underwater) and emergence (above water). Along the coast of California the high intertidal zone, which is inundated only during high tides, has species including rockweed, acorn barnacles, turban snails, and lined shore crabs. The middle intertidal zone, exposed to the air at least once a day, is home to creatures such as sea lettuce, aggregating anemones, chitons, gooseneck barnacles, mussels, and ochre stars. The low intertidal zone, exposed only during very low tides, is inhabited by kelps, coralline algae, surfgrass, giant green anemones, purple sea urchins, and bat stars. Ecological processes, such as competition, predation, and recruitment, play an important role in determining the species composition of intertidal assemblages. Many invertebrate and algal species that occupy the shoreline as adults have early life history stages such as spores and larvae that may spend days to months drifting in the ocean before settlement on the shore. These early life history stages are one important connection between the benthic (rocky bottom) habitat of the intertidal and the pelagic (open ocean) realm. Intertidal organisms also depend on water movement for delivery of food and nutrients as well as reproduction and dispersal.

People use intertidal ecosystems for food and recreation; however, these ecosystems are also sensitive to anthropogenic impacts from water pollution, oil spills, harvesting, and trampling. Following the California Marine Life Protection Act (1999) a statewide network of marine protected areas has been established along the California coast, and many of these reserves include significant portions of rocky intertidal habitat. Climate change likely poses the most serious threat to intertidal ecosystems, where many species are already living close to their physiological tolerance limits. Increases in temperature, coastal erosion rates, and sea level rise; decreases in ocean pH; and altered circulation patterns resulting from changing climate conditions all could significantly impact intertidal ecosystems in the coming decades.

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## Glossary

- BENTHIC** This refers generally to organisms that live in close relationship with the substrate bottom and many that are permanently attached to the bottom.
- BIOGEOGRAPHIC** Refers to the distribution of organisms in the context of geographical space.
- COMPETITIVE EXCLUSION** The proposition that states that two species competing for the same resources cannot coexist if other ecological factors are constant. When one species has even the slightest advantage or edge over another, then the one with the advantage will dominate in the long term.
- CONSPECIFIC** Members of the same species.
- EMERSION** Refers to the time that organisms spend out of or uncovered by water.
- FRANCISCAN COMPLEX** An assemblage of sandstone, shale, chert, and mildly metamorphosed basalts derived from ocean floor material accreted onto the California coast by subduction. These rocks comprise large portions of the California coast and Coast Range mountains.
- MARINE TERRACE** Broad, flat expanses of coastal land originally created by erosion of waves when the land was at sea level. Multiple sea level changes and tectonic uplift later raise the flat terraces above sea level, leaving characteristic stepped hills.
- OROGENIC** Any geological process that leads to the formation of mountains. Often caused by the pressures of colliding and subducting tectonic plates or volcanic activity.
- PELAGIC** This refers to organisms that are not associated with the bottom and occur in the water column or in the open sea.
- PERENNIAL** These are plants and seaweeds that live for more than two years and is generally a term used to differentiate from annuals, which complete their life cycle in one year.
- SESSILE** This refers to organisms that are directly attached to the bottom or substrate.
- SHOAL** This term refers to when water becomes more shallow.
- SUBDUCTION** The geologic process by which the edge of an oceanic tectonic plate is forced beneath another plate. Subduction can create coastal mountains due to pressure lifting land behind the subduction zone.
- THALLI** These are the undifferentiated vegetative tissues of macroalgae, and generally refer to the entire individual seaweed organisms in the case of macroalgae.
- VELIGER** The planktonic larva of many kinds of gastropod and bivalve molluscs.
- VISCOUS** Refers to the properties of fluid that resist deformation to stress. Viscous fluids are generally thought of as being more “thick” (e.g., honey).

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