
## *Rocky Interetidal Zonation*

The first paragraph in our discussion of tides (found in the section: Coastal Processes) introduces us very briefly to tide pools and biological zonation and shows this picture of curious adults and children at low tide marveling at the animals and seaweeds clinging to the steep faces of massive rocks. What is immediately obvious to these explorers, and almost anyone observing our rocky coast at low tide, is that these creatures are not evenly distributed. They are segregated into horizontal bands or "zones" across the vertical rock surface, beginning high up with small barnacles and a few snails and limpets, progressing downward through the dichotomously branched seaweed *Pelvetiopsis* and the Nori seaweed *Porphyra*, into a band of thatched barnacles, mussels, and gooseneck barnacles, downward still to a zone that includes ocher stars and some large-bladed seaweeds such as *Hedophyllum*, and finally to the colorful anemones, encrusting sponges, sea urchins, jelly-like colonies of tunicates, other large-bladed seaweeds like *Laminaria* and *Lessoniopsis*, among many other both stationary and crawling organisms.

These zones are biological phenomena that appear to be related to the rise and fall of the sea, and in attempts to verbally label these stratifications as they relate to tides, they have been given various names by various authors. Historically, these names have differed for different parts of the world, depending on the type and range of tides, size of waves, and other factors such as drying, sunlight, and rain. For anyone really interested, Maxwell Doty (1957) extensively reviewed zone classifications that were used up to the time of his writing. For our own Pacific coast, some authors have used what is called the "universal scheme" a general pattern for tides around the world set forth in 1949 by T. A. and Anne Stevenson, long-time and world-wide researchers of intertidal dynamics, who divided the intertidal area – the littoral zone - into three subzones: the supralittoral zone, the midlittoral zone, and the infra(=sub)littoral zone, the midlittoral zone covering most of the area. Between the zones they described fringe areas, the supralittoral fringe and the infralittoral fringe, which demark, respectively, the highest of the high tides and the lowest of the low tides. This scheme is complicated. Other authors describe four zones: zones 1, 2, 3, and 4 or, more descriptively in Gloria Snively's book "Exploring the Seashore in British Columbia, Washington and Oregon (1978)": the spray zone, the high tide zone, the middle tide zone, and the low tide zone. For simplicity, if we really need tags for this biological stratigraphy, I prefer this latter framework. The physical factors that define these zones are:

**Spray zone**: The highest reaches of the shore where waves splash only during the strongest winter storms at high tides. Otherwise this zone is terrestrial and, except for rain or snow, dry. It is an area influenced mostly by heat, light, wind, and fresh water.

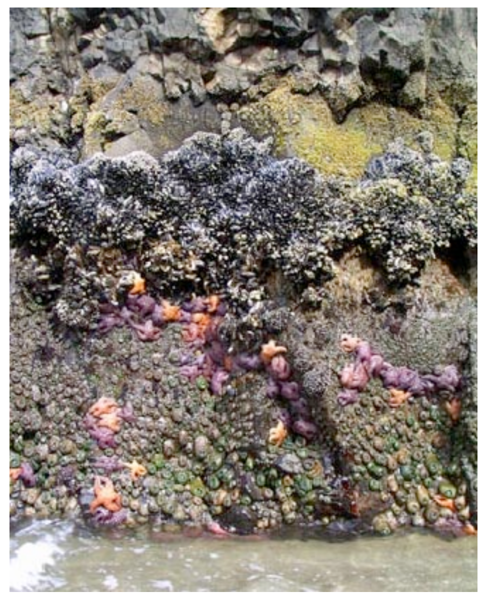
**High tide zone**: The shoreline just below the spray zone, covered with seawater only during high tides. It also is influenced by temperature, light, wind, and, in addition, water cover and salt content.

**Middle tide zone**: The part of the seashore covered by the semidiurnal tides twice a day (see the article on tides). Two times a day seaweeds and animals are covered and uncovered by seawater, allowing periodic exposure to air.

**Low tide zone**: Organisms are almost always covered with seawater and exposed to air only at the lowest of tides. This zone is more stable because the temperature and salinity of the water are fairly constant, much more than the variable physical conditions of air.

**What causes zonation?** At first glance, the natural and obvious assumption is tides. But the actual reasons are much more complex and, historically, have been the subject of controversy. The Stevensons' rejected tides as a direct cause, saying that zonation results from the air-water interface and various gradients, such as light penetration, below the surface and other factors, such as spray, above the surface. Their premise was that zonation was caused by influences related to tides, but not the tides themselves. Doty and others, on the other hand, attributed zonation more directly to tides, emphasizing that of all the environmental factors such as temperature, wind, rain, and waves that may be important to zonation, only tides vary uniformly with the biological zones. More recently, Benson (2002) has discussed other historical perspectives on studies of zonation, and more up to date summaries of the causes of these biological stratifications are presented in books such as, Pacific Seashores (1977), Seashore Life of the Northern Pacific Coast (1983), and Between Pacific Tides, 5th edition (1985).

The zones listed above are only convenient labels that give us verbal handles on very complicated biological circumstances that know no distinct boundaries and vary with time and geography. It is recognized that tides do play a part, but there are a multitude contributing influences. The shore zone between the tides – the littoral zone – is an ecotone, a transition from sea to land, and like other ecotones, such as the abrupt change from forest to grassland, there are edge effects where certain species spend most or all of their time in this transitional habitat. Along this edge, the tides and the other environmental forces that play on the intertidal zone have created innumerable ecological niches, a term that includes not only the physical space in which an organism lives, but how it lives in relation to other organisms and all the vagaries of its physical environment. A niche is how an organism functions in a community. Species compete for these niches – no two species can occupy the same niche at the same time, at least not for very long – but because there are so many niches in the rocky intertidal habitat, there are often a lot of species that live between its upper and lower reaches. We will take a look at the some of the governing factors that result in this diversity, and how some organisms have adapted to their individual littoral environments.


Zone banding seen at low tide.

**Desiccation** is the main limiter in the spray and high tide zones, where organisms are wetted only occasionally by splashes from waves or during the highest of tides. Let's look at how some organisms adapt. Highest up on the rocks in our area you will find the snail *Littorina* and the limpet *Lottia digitallis*. These animals are mobile and move to the upper spray zone,
often to cracks and crevasses because these features offer protection and support algae, their food. *Littorina* can seal the entrance to its shell to prevent water loss by closing its door-like operculum. *Lottia digitallis* uses its muscular foot to firmly clamp its shell to the rock, sealing the edges against moisture loss. These animals may also be able to withstand a more desiccation than their counterparts living lower in the intertidal zone. Just below these snails you will find the common acorn barnacle *Balanus glandula*, and the small acorn barnacle *Chthamalus dalli*. Once a wave throws a larva of these barnacles (the cypris larva) high onto rock and it finds a suitable site to settle, it cements itself to the surface where it remains for life. A barnacle cannot move from place to place like the snails and limpets in search of water, food and shelter. On hot days, it is heated by the


Limpets

sun. To avoid drying out, it has two pairs of 'hatches', the terga and the scuta, that close and seal the entrance to its cone-shaped 'shell'. These two species of barnacles can remain sealed for days to weeks, retaining their moisture, and yet are still able to respire oxygen from air. They open only to feed when splashed by a wave or submerged during the highest tides. Feeding is a rare opportunity for these barnacles, so when they are wetted, they begin to feed immediately.

Acorn barnacles

Algae, on the other hand, living in the spray and high tide zones can dry out yet survive. Consider three algae that live on our upper rocky shore, *Porphyra* sp. (probably *lanceolata*), the monofilament green alga *Urospora peniciliformis,* and *Endocladia muricata*. All of these will lose considerable amounts of water when exposed to the air and sun. The thin blades of *Porphyra* can dry enough to become stiff and brittle and will crumble in your hand. One *Porphyra* species in Florida was found to lose up to 95% of its water and survive up to twenty hours. Some algae (like *Porphyra)* may go into a sort of suspended animation by reducing photosynthesis and respiration, and then on reemergence resume these activities. *Urospora* can survive more than twenty days of air exposure. There is evidence that organisms that can withstand drying do so by replacing water with sugars to prevent the destruction of cell membranes.

*Porphyra* sp.

*Urospora peniciliformis*

*Endocladia*, in contrast, can photosynthesize better in air than in water. Another alga that can live high up on the rocks, one that avoids desiccation by becoming adapted to runoff from freshwater seeps, is the bright green alga *Ulva (=Enteromorpha) intestinalis*. You can see this seaweed on the cliffside along Tunnel Beach.

*Endocladia muricata*

*Ulva (=Enteromorpha) intestinalis*

**Temperature**, **wind** and **humidity** are three environmental variables that contribute to desiccation, and all can change rapidly. Winter freezing is generally not a problem along our rocky shore, but humidity and summer heat modified by wind and seasonal fog, can have their effects. Wind and fog may moderate the effects of solar heat, wind by evaporative cooling, fog by blocking direct sunlight and by reducing evaporation from body tissues.

Temperature and desiccation are thought to be the limiting factors for the upper distribution of the mussel *Mytilus californianus*. The internal body temperature of these sessile bivalves may reach more than 30ºC on a sunny day, producing stress. There are a multitude of physiological and behavioral adaptations to deal with stress which allow animals and algae to reach an optimum tolerance for heat that does not exceed the cost of living in their particular niches. For example, on hot days the body temperatures of many animals in the high intertidal, including mussels, can rise to the point of heat shock, a condition that often produces so-called heat-shock proteins (stress proteins). These proteins, induced not only by heat but other stresses as well, may offer protection against stress by reducing the aggregation of damaged proteins and by restoring those that are mildly damaged.


*Pachygrapsus crassipes*

Animals that crawl or walk can avoid heat stress by moving to areas shaded by other organisms or into rocky crevices. The picture to the right shows the lined shore crab *Pachygrapsus crassipes*, which, in our area, lives high in the intertidal, tucked into a narrow rocky crevice where it is not only sheltered from sunlight but also from predators such as shorebirds. The small sea cucumber, *Cucumaria pseudocurata*, can be found sheltered deep in mussel beds where it is shaded, the air remains more humid, and it is protected from predation.

**Tide pools** can have their own particular set of problems. These pools of seawater, left in rocky depressions after the tide recedes, can heat in the sun, evaporate and become more saline, or be diluted freshwater when it rains
or snows. Such conditions can present animals and algae with any number of stresses, especially if the pools are small, wide and shallow, or located high in the intertidal zone where flushing by tides and waves is less frequent. Pools that are shallow with a large surface will heat more quickly than those that are deep and narrow. Tide pools with lots of algae will have, because of photosynthesis, high levels of dissolved oxygen during the day, and because of respiration, little dissolved oxygen during the night, forcing mobile animals to move to the surface. Also, photosynthesis will use dissolved carbon dioxide, raising the pH during the day, and, conversely, respiration will give off carbon dioxide, lowering the pH at night. Yet, many tide-pool residents have adapted to wide-changing environmental variables. They are often eurythermal, that is they can withstand wide temperature variations. Some may be euryhaline, able tolerate changes in salinity. Mobile animals may move out of tide pools.


*Ulva* and *Porphyra*

**Light** is especially important for seaweeds. This is why you see seaweeds growing on tops of rocks in the intertidal zone and seldom underneath. Green algae and the rockgrass, *Phyllospadix* sp., use chlorophyll to make food and require the red and blue parts of the light spectrum. Red light is absorbed very rapidly by seawater, so these “plants” tend to live in shallow water. However, other algae, both browns and reds, may also live high in the intertidal. They are also photosynthetic, using chlorophyll to make food, but they also have accessory pigments (which is why these algae are brown or red) that absorb wavelengths near the center of the spectrum, such as green light. These pigments are able to pass this energy to chlorophyll to augment photosynthesis.

What about animals? How do they respond to light? The larvae of many invertebrates have pigmented light sensitive organs called eyespots that influence or govern their behavior in the presence of light. For example, the colorful, calcareous tubeworm *Serpula vermicularis* (a North Atlantic species that is a close relative of and once thought to be the same as our own *S. columbiana*) prefers shadowed intertidal habitats and is common on the undersides of rocks. Beyond the tides, in deeper water where light is absorbed or scattered by suspended particles, phytoplankton, dissolved organic matter, and turbulence, these worms need not be so sheltered from light. It has been found that the worm’s early trochophore larva, which has no eyespot, is briefly photopositive or photoneutral, but then after a few days develops an eyespot and becomes photonegative and eventually settles in low-light areas. This kind of switching from photopositive to photonegative is not rare. Yet, many other animals have pelagic larvae that are photopositive through most of their existence, and this is common of many intertidal animals. These kinds of phototactic responses can determine the vertical distributions of intertidal animals.

As an aside, adult serpulid (and sabellid) worms have eyespots on their plume-like gills, their radioles, which are displayed while feeding and breathing. They use these photoreceptors to sense any light changes that may signify danger and, at the first sign, will rapidly retract into their protective tubes.

**Competition** becomes a limiting factor as we move lower in the intertidal zone. We find that organisms compete for space, for food, for light, for shelter, for exposure, for a certain amount of wetting as the tidewater moves in and out, for a particular way of life when resources are in limited – in short, for a particular niche. There is competition both between species and within species. Let's consider competition for space and the two barnacles *Balanus* and *Chthamalus*. *Chthamalus* has a slightly higher distribution in the intertidal zone than *Balanus*, but their regions overlap. It has been found that the smaller *Chthamalus* is crowded out by the larger *Balanus*, and the latter usually wins in this competition for space in the area of overlap. You can also see space competition within a species of barnacle such as *Balanus*. When barnacle larvae settle, they do so fairly close to each other, especially where there are choice settling sites such as cracks in a rock. After settling, it is pretty much every barnacle for itself. As they grow, they begin to crowd, and it comes to a point where the only direction for growth is upward. As a result, you will find dense beds of tall, skinny barnacles jamb-packed together instead of the more normal cone shape of individuals that are separated.


Barnacles crowded into cracks in a rock

**Predation** becomes important around the middle tide zone. For example, while looking at a rock face at low tide, you can see what is called the mussel/goose barnacle assemblage. The California mussel, *Mytilus californianus*, and the goose barnacle, *Pollicipes polymerus*, live attached to rocks in a close association. The lower limit of this assemblage is often determined by the ocher star, *Pisaster ochraceus*, which feeds on the mussels, especially the smaller individuals which are easier to open. (The ocher star is not only ocher colored, but it comes in a range of colors from yellow-orange to purple with a variety of browns in between.) This sea star feeds on mussels by wrapping its arms around the two shells, attaching its tube feet to each, and exerting a steady pull. After a time, the adductor muscles holding the shells together, fatigue, and the mussel begins to gape. When the shells separate, even a fraction of a millimeter, *Pisaster* extrudes its stomach out its mouth, inserts it between the shells into the interior of the mussel where digestion of the mussel's tissues begins. *Pisaster* seems reluctant to range high into the mussel/goose barnacle assemblage, probably to avoid desiccation. Mussels higher than this migration limit of the sea star usually grow large, and often become too big for *Pisaster* to open. Incidentally, although *Mytilus californianus* is its favorite food, *Pisaster* does not limit its prey to mussels. It also eats other bivalves, limpets and other snails, and barnacles.


**Top:** Zonation showing mussels in the upper part of the picture, *Pisaster*, a band of sea anemones, a band of sponges, and finally Laminarian sea weeds. **Bottom:** *Pisaster* clasping a mussel.

Also on the rock face, often below *Pisaster*, is the bright green sea anemone *Anthopleura xanthogrammica*, a sessile and therefore opportunistic predator. While *Pisaster* is motile, albeit slow, and can hunt prey, *Anthopleura* is attached to the rock (it can move a little) and is forced to catch whatever happens to pass by in the current. Its tentacles contain stinging cells – nematocysts – with a potent toxin that can stun prey, such as small fish. It will also eat mussels, sea urchins, and crabs. After its catch is paralyzed, it draws the food to its mouth where it is ingested, then digested.

**Herbivores**, those animals that graze on micro and macro algae, are present in all zones. Limpets will eat *Endocladia* in the spray zone; the black chiton, *Katharina tuncata*, feeds on macro brown and red algae in the upper and middle zones; sea urchins eat kelp in the middle, lower, and sub-tidal tide zones. Chitons and gastropods feed with a radula, a tongue-like structure supporting rasp-like teeth. They may scrape the rocks for micro-algae or graze on the thallus of a seaweed. The purple urchin, *Strongylocetrotus purpuratus*, can be found in the middle and lower zones, sometimes residing in shallow holes in the rock that they have carved with their spines (more on this in another section). The red urchin, *Strongylocetrotus franciscanus*, occurs in the lower zone and subtidally. Both are ravenous algae eaters but depend mostly on drift kelp, kelp that has broken loose from its substrate and drifts with the current. The urchins are able to catch these seaweeds with their tube feet as they pass by. However, if food is scarce, they may rove and forage for attached kelp.


*Katherina tunicata*


Red and purple urchins

**Microhabitats** can come in a number of forms. Crevasses, underneath boulders, beneath the canopy of overlying macroalgae are a few. Microhabitats can offer protection from drying, predation, light, and heat. They provide homes for both attached organisms such as sponges, anemones, mussels, bryozoans, and tunicates and mobile species like starfish, snails, nudibranchs, chitons, and urchins

**Waves** bring water for moisture and food in the form of nutrients and plankton, but organisms living along the outer rocky coast both depend on and are at the mercy of pounding surf. The relentless beating by waves during winter storms can dislodge organisms. The byssal threads of mussels, which are normally substantial anchors, can give way, allowing the animals to be ripped from the rocks and die in the surf. They may also be smashed into oblivion by drift logs carried onto the rocks by breakers. Some organisms have adapted well to rough water. Seaweeds such as *Laminaria setchellii* (pictured above) and the strap seaweed, *Lessoniopsis littorallis*, have tough but flexible stipes (stems) that give with the waves. The stipeless sea cabbage, *Hedophylum sessile*, has a highly branched holdfast to secure it to the rock surface. Most notable is the sea palm, *Postelsia palmaeformis*, which resembles a miniature palm tree and grows only on the seaward side of the most exposed rocks where wave shock is extreme. This rugged seaweed has a hollow but tough and giving stipe and a highly branched holdfast that cements the alga to the rocky substrate. Other adapted algae are the calcareous, encrusting corallines that, with no protruding parts, may be essentially immune to wave shock.


*Lessoniopsis littorallis*

The rocky outer coast with its rich diversity of niches and colorful organisms is a draw for visitors, whether or not they know much about the living things they are looking at or why they reside there. It is the hope of the people at WEBS that articles such as the one you have just read will enrich the experience of those who come to see the shoreline between the Capes.

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