of the earth, but both oxygen and carbon dioxide content have changed dramatically through time. Oxygen concentration is thought to have been only about 15% throughout the early Phanerozoic but, starting in the mid-Devonian (~380 million years ago), exhibited a substantial rise associated with terrestrialization by plants, reaching values potentially as high as 35% by the end of the Carboniferous (~290 million years ago) in what is known as the late Paleozoic oxygen pulse (Fig. 2). This increase in oxygen content, coupled with constant nitrogen content, also yielded a more dense atmosphere at any given elevation. Viscosity of the atmosphere, by contrast, would have remained fairly constant. Overall, heightened oxygen levels would have increased the amounts of this gas available to terrestrial plants and animals via diffusion from the atmosphere, although increased atmospheric density would partly mitigate this effect via a reduced diffusion coefficient. Because the amount of oxygen dissolved in seawater is an approximately linear function of that in the surrounding air under equilibrium conditions, elevated atmospheric oxygen would also have increased availability of this gas to plants and animals in water.

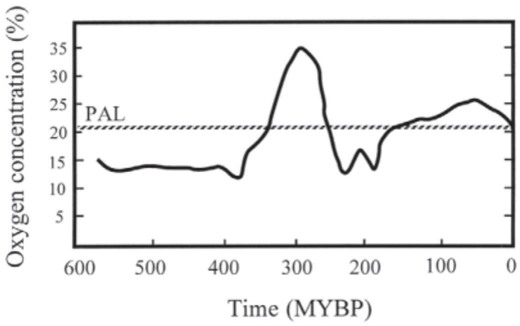

FIGURE 2 Variation in oxygen content of the atmosphere through Phanerozoic time, relative to the present atmospheric level (PAL). MYBP = million years before present.

Following the end-Carboniferous peak in atmospheric oxygen, levels declined as a result of complicated, interacting geological and biological causes, and by the end-Permian (~250 million years ago) atmospheric oxygen reached levels as low as 15% (see Fig. 2). Thereafter, oxygen concentration rose slowly to reach a secondary peak of 25–30% by the end of the Cretaceous (~65 million years ago) and then declined to present-day values of about 21%. At sea level, therefore, the density of air has fluctuated considerably both upward and downward at different stages of the Phanerozoic.

The picture for carbon dioxide, by contrast, is one of approximately continuous drawdown in the Phanerozoic from highs of about 0.5% to the present-day level of 0.03%. Such changes in the availability of carbon dioxide, the raw material of photosynthesis, have had important consequences for the physiology of marine algae and other plants, as evidenced by paleontological analyses of stomatal density and other proxies of photosynthetic activity.

The concept that air has varied historically in oxygen content is, in scientific terms, one that is fairly recent, and the full implications for organismal physiology and biophysics are only now being realized. The effects of variable air density on heat exchange, together with variable oxygenation of tidepools, are the most likely to have been relevant to intertidal organisms.

SEE ALSO THE FOLLOWING ARTICLES

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ALGAE, OVERVIEW

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Marine algae are photosynthetic organisms that fuel the base of the food chain in marine ecosystems and provide habitat for a huge diversity of intertidal and subtidal organisms. They include the microscopic phytoplankton that drift in the pelagic zone and form thin films on rocks, as well as the large seaweeds and kelp forests that line many rocky shores. Algae are an evolutionarily, ecologically, and functionally diverse group of organisms that play critical roles in the structure and functioning of rocky-shore ecosystems.

ALGAL DIVERSITY

Intertidal algae encompass an extraordinarily diverse array of photosynthetic organisms, found growing on rocky shores, that are not true plants, technically speaking (Fig. 1). They include the macroscopic and multicellular seaweeds as well as the microscopic single-celled phytoplankton (although the Latin word *algae* literally means "seaweed," and these will be the focus of this chapter). The algae are an evolutionary hodgepodge (not a monophyletic group) that includes all eukaryotic, photosynthetic organisms that lack leaves, roots, flowers, and other organ structures that define true plants and the prokaryotic cyanobacteria. With the single exception of the surfgrasses (found only along the west coast of North America, where they thrive and compete with seaweeds for space on the shore), true plants are not found growing on rocky shores. The phyletic (or deep) diversity of algae that live along wave-swept shores (and of all photosynthetic organisms in the ocean) is far greater than that found among all the photosynthetic organisms that inhabit land. This is the same pattern found when contrasting animal diversity on land and in the sea, and it reflects life's early origin and diversification in the ocean. The genetic differences among the various taxa grouped together as the algae are far greater than the genetic differences among the admittedly more species-rich group of true plants found on land. It is the combination of deep evolutionary diversity, a crowded coexistence on rocky shores, and a disturbance-prone environment that makes the study of tidepool algae especially fascinating.

FIGURE 1 Diverse assemblage of algae uncovered on a rocky shoreline during an extreme low tide. Photograph courtesy of Jacqueline L. Sones.

ALGAL ORIGINS

All photosynthetic organisms, including seaweeds, are ultimately derived from early anaerobic, photosynthesizing bacteria (prokaryotes) that appeared on Earth approximately 3.8 billion years ago. Oxygen-producing, photosynthetic organisms (very similar to the cyanobacteria found living on Earth today) appeared in the ocean about 100–200 million years later and completely transformed Earth's atmosphere by filling it with oxygen (an event often referred to as the oxygen revolution), and as a result had a pervasive influence on the evolution of all life forms on Earth. By about 1.7 billion years ago, multicellular photosynthetic organisms had evolved and can be found in the fossil record. The algae evolved into about 12 phyla (or divisions) of uni- and multicellular photosynthetic organisms, with all but one being eukaryotic. Several of the major lineages of algae arose as the result of endosymbiotic events whereby a single eukaryotic cell engulfed and co-opted either a cyanobacterium or a eukaryotic alga that ultimately became the plastid (a subcellular structure or organelle) used to effect photosynthesis. Evidence of these historic endosymbiotic events can be found in analyses of genetic relationships, subcellular structures, photosynthetic pigments, and biochemistry of the algae. The seaweeds that we find on rocky shores today belong to three phyla or lineages of algae: the Rhodophyta, the Chlorophyta and the Heterokonta.

REDS, GREENS, AND BROWNS

Seaweeds are commonly described as coming from one of three color groups: reds, greens, and browns. These colorful names (taxonomically Rhodophyta, Chlorophyta, and Heterokonta, respectively) reflect their evolutionary relationships and the characteristic suite of pigments each group uses to collect and dissipate light energy. However, these colorful groupings can often be misleading to the novice trying to identify seaweeds on the shore; some "red" seaweeds can look brown or even black and some can look green, for example. The various colors that we see among the seaweeds result from the specific complement of pigments they possess and the relative abundances of each that are characteristic for a species. The relative abundance of the different pigments can also vary substantially within a species, or even an individual alga, in response to environmental conditions.

All the seaweeds (as well as land plants and cyanobacteria) have chlorophyll *a,* the primary pigment responsible for photosynthesis. There are two other common chlorophyll molecules: chlorophyll *b,* found in land plants and the green algae, and chlorophyll *c,* found in the brown algae. In addition to the chlorophylls, all algae have accessory pigments called carotenoids that can either transfer light energy to chlorophyll *a*, to enter the photosynthetic pathway, or direct it away from chlorophyll *a* when excess light is absorbed, protecting the molecules of the photosystem and dissipating the excess energy as heat. Fucoxanthin, for example, is the caratenoid that imparts a brown color to the kelps and other brown algae. The red algae (and cyanobacteria) also have another group of accessory pigments called phycobilins that give them their distinctive reddish hue. The relative abundance and presence or absence of these accessory pigments in combination with the chlorophylls determines the characteristic colors of the seaweeds we see on the shore.

FIGURE 2 Pink coralline algae surrounding the herbivorous chiton *Katharina tunicata*. There are both crustose and upright forms of coralline algae, as well as fleshy red algal crusts. Also visible are the grooved fronds of two young sporlings of the sea palm, *Postelsia palmaeformis*, blades of the red alga *Mazzaella flaccida,* and the branched red alga *Microcladia borealis.* Photograph by the author.

STORING ENERGY AND CELLULAR WALLS

In addition to the differences we see in the pigments among the three major lineages of seaweeds, there are characteristic differences in the biological molecules these organisms use to store the products of photosynthesis and for structural support. Seaweeds (and sea- and surfgrasses) produce a variety of polysaccharides that form part of the matrix of their cell walls (unlike freshwater algae and land plants). Some are gel-forming compounds that confer both structural support and elasticity—clearly a useful characteristic for algae living on wave-swept rocky shores. The red algae store starch as granules within the cell's cytoplasm in a unique form called floridean starch. They form their cell walls from cellulose and a matrix of polysaccharide compounds, including the agars that are used in biotechnology applications (e.g., gel electrophoresis and culturing bacteria) and the highly sulfated carrageenans used as food thickeners. Some red seaweeds also impregnate their cell walls with calcium carbonate; these typically appear pinkish-red in color, are tougher than their noncalcified relatives, and are collectively called the corallines (Fig. 2). Green and brown seaweeds also use cellulose to construct their cell walls, and a few species incorporate calcium carbonate. Most brown seaweeds produce alginates as part of their cell wall matrix; alginates are extracted for use in textile production, to make medical dressings, and as food stabilizers and thickeners. For energy reserves brown seaweeds use lipid droplets or soluble carbohydrates called laminarans within the cytoplasm, rather than the starches red and green seaweeds use. The green seaweeds are further distinguished by storing starch within their plastids, a characteristic they share with land plants.

SEAWEED ARCHITECTURE, GROWTH, AND FUNCTIONAL FORMS

Seaweeds have an amazing diversity of forms given their anatomical simplicity. In contrast to true plants, they lack true tissues and organs, and have very few specialized cell types, typically just vegetative and reproductive cells, although there are some interesting exceptions. Specialized transport cells called trumpet hyphae or sieve elements (which are analogous to the sieve elements found in the vascular system of true plants and are shaped like a trumpet) are found in some kelps (members of the brown order Laminariales), including the giant kelp-forest-forming seaweeds *Macrocystis* and *Nereocystis*.

While many people are familiar with the spectacular beauty of kelp forests, uninitiated visitors to the seashore may simply view seaweeds as a slippery and sometimes smelly nuisance, especially when tangled masses have been washed ashore as wrack and begin to decompose after being dislodged by storms or as a result of an unusual bloom (this latter phenomenon often occurs as a result of nutrient pollution and may be especially problematic in systems where herbivores have also been overexploited by humans). Many delicate and intricately branched forms become plastered to the rocks during emersion at low tide, forming an amorphous and relatively unappealing-looking mat. However, seashore enthusiasts often come to appreciate the architectural and anatomical diversity of seaweeds after observing them more closely, perhaps with the aid of a magnifying glass or a microscope, or by observing seaweeds suspended in the water of a tidal pool.

The thallus (or "body") of an alga can be as simple as a chain of single cells arranged in a linear filament, or one or two layers of cells arranged in a sheetlike blade, where all the cells are essentially identical. More complex forms can have several layers of cells, differentiated into an outer cortex of highly pigmented cells and an inner medulla of larger, nonpigmented cells. In addition to sheetlike forms there are branched, tubular, and lobed forms, as well as saclike forms that can hold water (Figs. 3, 4). Most forms attach to the rock at a single point by a holdfast, which can be a simple disclike structure or a rootlike structure made up of haptera (Fig. 5). Some are entirely attached to the rock with encrusting thalli several cell layers thick; these can be soft and fleshy, or hard and calcareous, and either smooth or rugose in form (see Fig. 2). Filaments can also form intricately branched thalli with exquisite branching patterns (Fig. 6). Some branched forms are not just simple filaments but have intricate banding patterns caused by additional layers of outer (cortical) cells organized around nodes, or the cells can be arranged to look like stacked wagon wheels in a form described as polysiphonous, or they may be thicker and differentiated into an outer cortex and an inner medulla, several layers of cells thick. Some sheetlike seaweeds grow from the fusion of many chainlike filaments, while some large, thickly branched seaweeds are formed from a few multinucleated siphons (essentially one to a few giant cells wrapped, folded, and intertwined together) (Fig. 7). Seaweeds grow in different ways; some, such as the sea lettuce *(Ulva)*, grow by dividing cells found throughout the thallus, while some have cells that divide only at the

FIGURE 3 Diversity of functional forms of red, green, and brown algae. Photograph by the author.

FIGURE 4 A bed of the saccate red alga *Hallosaccion glandiforme*. Photograph courtesy of Sarah Ann Thompson.

FIGURE 5 The sea palm, *Postelsia palmaeformis*, shares major anatomical features with other seaweeds including a holdfast at its base composed of haptera that attaches it firmly to the rock (or, in this case, a mussel), a tall, stalklike stipe, and a pom-pom-like crown of fronds. Photograph courtesy of Sarah Ann Thompson.

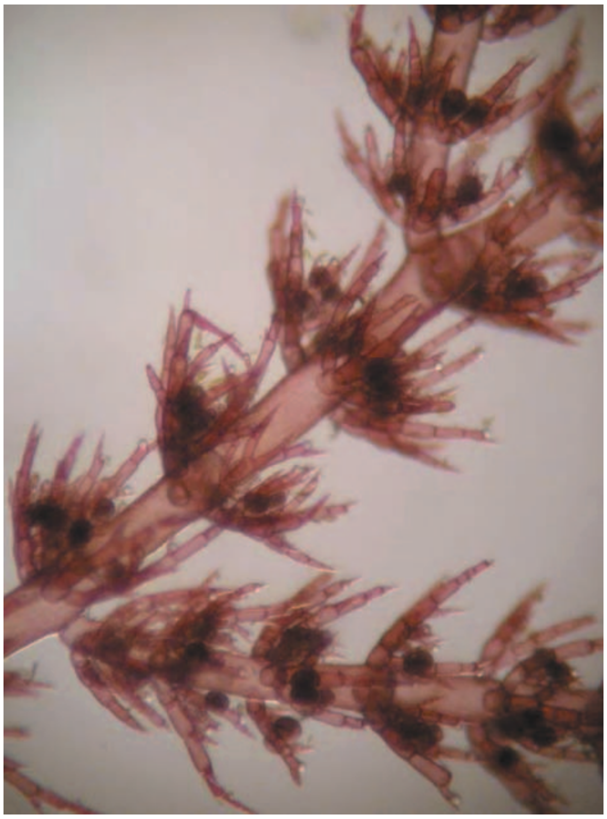

FIGURE 6 The red alga *Platythamnion villosum* is a delicately branched filament made up of chains of single cells. This specimen is a tetrasporophyte, one of the diploid, free-living phases of the typical red algal life history. The dark circular structures attached to the branchlets are the tetraspores (groups of four haploid spores that are produced by meiosis), which will eventually be liberated and give rise to male and female gametophytes of identical morphology in this species. Small, clear gland cells are also visible at the ends of some of the branchlets. Photograph by the author.

FIGURE 7 The green alga *Codium fragile,* which is composed of just a few large multinucleated cells. Photograph courtesy of Sarah Ann Thompson.

edges of the blades (the apices of the joined filaments in some red seaweeds). Many of the large kelps have regions of actively dividing cells between the stemlike stipe and the blade (see Fig. 5), while the bladderwracks (members of the brown-order Fucales) (Fig. 8) have a single cell that divides at the tip of each branch.

FIGURE 8 The bladderwrack, *Fucus garderii* (broader blades), and another member of the order Fucales, *Pelvetiopsis limitata* (thinner) growing in distinct intertidal zones. Photograph by the author.

Large seaweeds such as the bladderwracks and kelps often bear one or more gas-filled bladders called pneumatocysts (Fig. 9), or, like the Southern Hemisphere species *Durvillaea antarctica* (Fig. 10), grow with many sponge-like pockets (similar to the closed-celled neoprene used to make wet suits and mouse pads) that provide added buoyancy to keep the alga suspended at the water's surface, where light for photosynthesis is abundant (Fig. 11). Those without such buoyancy aids often have stiffer, yet very flexible, stipes, such as those of *Postelsia palmaeformis* (an alga resembling a miniature palm tree that could have been drawn by Dr. Seuss; see Fig. 5) and *Lessonia nigrescens* (an alga resembling an intertidal bush), that help keep their photosynthesizing fronds suspended and intact while being battered by waves (Fig. 12).

Although there is stunning diversity in seaweed forms, there are many recurrent themes in their architecture that are the result of convergent solutions to similar environmental challenges and phylogentic (evolutionary) constraints. Seaweeds growing on rocky shores must acquire light and nutrients to grow while also staying attached to the rock, often in the face of the enormous forces of lift, drag, and acceleration imposed upon them by breaking waves. They simultaneously must overcome competitors

FIGURE 9 Balloon-like pnuematocysts along the sides of the strap-like stipe of the brown alga *Egregia menziesii*. Photograph courtesy of Sarah Ann Thompson.

FIGURE 10 The brown alga *Durvillaea antarctica* floating at the surface of the water, where light is plentiful. Photograph by the author.

FIGURE 11 Pnuematocysts keep the alga *Egregia menziesii* floating at the water's surface. The stiif stipe of *Pterygophora* keeps it elevated in the water. In the lower left, *Cystoseira* uses chains of smaller floats to keep its fronds aloft. Photograph by the author.

for limited resources (primarily space, light, and nutrients), and they must escape from being eaten by hungry herbivores. Scientists often aggregate seaweeds with similar architecture or body forms into groups that reflect functional forms (e.g., blades, tubes, filaments, or crusts) rather than evolutionary relationships, especially when studying seaweed physiology or susceptibility to herbivores.

FIGURE 12 The large, shrublike brown alga *Lessonia nigrescens* growing on rocks covered with pink, encrusting coralline algae. Photograph by the author.

LIFE CYCLES

Describing the "typical" life cycle for seaweeds is no easy task. Reproduction of new individuals can occur via sexual or asexual reproduction. Asexual reproduction can occur in some seaweeds by fragmentation, whereby a portion of an intact seaweed breaks off and grows into a fully functional mature seaweed from the fragment, or by parthenogenesis, whereby reproductive cells that are not successfully fertilized germinate and grow nonetheless.

Many species have a life cycle that alternates between a diploid phase (with paired chromosomes) and a haploid phase (with half the number of unpaired chromosomes, the complement of chromosomes typically found in sperm and egg cells). These two phases, with different numbers of chromosomes, may both look exactly the same (isomorphic), or they may be very different (e.g., a crustose and a branched form, or a tall, bush-like form and a microscopic filament), in which case the species is called heteromorphic. The haploid phases (gametophytes) exist as separate male and female individuals, producing male and female reproductive cells (gametes). The male and female gametes generally unite and grow into the diploid form (sporophyte), although sometimes—and this is surprisingly common among the algae—they can grow into another free-living haploid form again if fertilization does not occur. It is in the diploid form that meiosis occurs (a form of cell division in which the resulting cells have only half the number of chromosomes). These cells may be flagellated (zoospores) and swim around in the water before settling down and attaching to the substratum. Zoospores, however, are only found among the brown and green seaweeds.

In contrast, the red seaweeds have no flagellated or motile cells during any part of their life cycle, a distinctive product of their unique evolutionary history. They also alternate between phases with different numbers of chromosomes, but instead of just two phases they typically alternate among three phases. Two are diploid: the tetrasporophyte, which produces tetraspores via meiosis (see Fig. 6) and the carposporophyte. One is haploid: the male and female gametophytes. Interestingly, one of the diploid phases, the carposporophyte, is considered a parasite of the female gametophyte, because it is not free-living and instead grows inside the female gametophyte subsequent to fertilization of an egg, essentially cloning many spores from the single fertilized egg that eventually are released, settle, and grow up to be free-living tetrasporophytes (whose spores germinate into the gametophytes). This extra phase is thought to be an evolutionary solution to the problem of limited fertilization success among the red algae because they lack flagellated sperm cells. Presumably the nonswimming male gametes (spermatia) have a harder time getting themselves over to a receptive egg. The carposporophyte provides a means to increase the number of individuals produced from a single fertilization event, theoretically compensating for the lowered frequency of successful fertilization among the red algae. An interesting consequence of this unique life history strategy is that the high frequency of parasitic red algal species (though these are generally colorless) is thought to have been evolutionarily facilitated by the presence of this third "parasitic" phase.

Some brown seaweeds have a more familiar life cycle, one very similar to that found in animals. The mature diploid sporophytes simply produce eggs and sperm by meiosis, these are released to the environment, and the flagellated sperm fertilizes the egg cell, completing the cycle by growing into the sporophyte again. There is no free-living gametophyte phase. Among many species of brown algae, egg cells have been found to produce sexual pheromones that induce flagellated sperm cells to swim toward the egg cells and swarm around them until one has succeeded in fusing with the egg.

Seaweeds can be annuals, completing their entire life cycle every year, or perennials, persisting and holding onto precious real estate on the shore for several years at a time. Reproduction is often stimulated by predictable environmental cues such as changes in day length and temperature as the seasons change.

COPING WITH THE ENVIRONMENT AND OTHER ORGANISMS: PATTERNS ON THE SEASHORE

One of the most ubiquitous patterns found along rocky shorelines worldwide is the zonation of organisms, including seaweeds, into characteristic bands from low on the shore to high on the shore (Fig. 13). These zones are created by the interplay of stresses created by the regular pattern of advancing and retreating tides each day and the physiological tolerances of each species, in concert with the biological interactions among the different species of seaweeds and other organisms. Species can engage in positive or negative interactions with each other: some species can facilitate the success of seaweeds (a positive interaction), while others compete with them for space on

FIGURE 13 Intertidal zonation of seaweeds, surfgrasses, and sessile invertebrates along wave-swept rocky shores. Photograph by the author.

the shore or graze them off the rocks (negative interactions). The outcome of these interactions, such as who wins the battle for space, may be altered by such factors as how hot or dry the environment is, how often it is disturbed by waves, or by how many herbivores or even predators are found in a place.

Tides, Waves, and Environmental Gradients

Seaweeds living low on the shore do not dry out as often as seaweeds high on the shore do, because the former spend a greater proportion of each day covered by water. As a result they may grow faster and do better in the face of competition from another species trying to encroach on the same patch of rock, or they may be better able to outgrow the limpets or snails that are slowly nibbling away at their fronds. Because seaweeds low on the shore spend more time in the water, they also have more time to acquire essential nutrients from the water, such as nitrogen and phosphorus. They are also subjected to fewer extremes of temperature than seaweeds higher on the shore, which may be exposed to air for many hours, and quite possibly to the heat of the noonday sun or the bitterest cold at midnight.

Sunlight can be a mixed blessing for seaweeds. Too little sun, and seaweeds cannot photosynthesize enough to grow and reproduce, limiting how deep in the water they can live, but too much light can outstrip a seaweed's capacity to use or dissipate all the light energy it captures with its pigments. Excess light energy that is not used or dissipated causes damage to subcellular structures and molecules involved in photosynthesis, ultimately limiting how high on the shore a seaweed can live. Algae can avoid absorbing too much light by altering the complement or amount of pigments they produce, or by physically rearranging the pigment-containing organelles within their cells so that they are not completely facing the sun. A seaweed's architecture or functional form can also influence the proportion of incident sunlight absorbed. Thin blades expose virtually all their cells to light, while species composed of many cell layers expose only a fraction of their cells to full sunlight, because much of it is captured by the first few layers of cells. Branched forms allow some light to penetrate to branches at lower levels rather than being completely intercepted at the surface.

When more light is absorbed than can be used in photosynthesis, free radicals are often produced, which can damage molecules involved in photosynthesis and other essential cellular functions. Seaweeds have intricate biochemical mechanisms to scavenge these free radicals and deactivate them, protecting themselves from the damaging effects that may ensue to some degree, but these biochemical mechanisms can be compromised by other environmental stresses, including limited nitrogen, desiccation, and extremes in temperature—all of which tend to be exacerbated in concert with increasing exposure to sunlight higher on the shore. When these stresses, alone or in combination, pass a critical threshold, the seaweed will ultimately succumb and die, leaving behind its withered, bleached, and ghostly-looking thallus for a time before it is inevitably washed off the rock. Before that critical life-or-death threshold is passed, growth and reproduction may be reduced as the seaweed devotes energy to repairing stress-related damage, compromising its ability to compete successfully with space-hogging, sunlight-stealing neighbors or to outgrow munching herbivores.

Crashing waves can be both destructive and necessary for seaweeds. Some rely on waves to rip other organisms off the rock (such as the mussel beds that dominate space on many shores), creating a bare space they can colonize before becoming encroached upon again by a superior competitor. Seaweeds such as the annual sea palm (*P. palmaeformis;* see Fig. 5) use the predictable disturbance of winter storms to great effect. Their microscopic, filamentous reproductive phases (gametophytes) germinate from spores that settle onto the rock below the mussel bed and derive shelter there from heat and desiccation. But then, in a marvelous twist of fate, of all the juvenile sporophytes conceived beneath the mussel bed, the ones most likely to survive and reproduce are the ones that settle where winter storms will eventually rip the cover of the mussel bed away, allowing light to reach the growing sporophyte and creating space for them to occupy as they grow.

Waves can also rip and tatter seaweeds whose mechanical properties or growth form are ill-suited to the incredible forces of drag, lift, and acceleration imposed by the larger, breaking waves that impinge on more wave-exposed portions of the shore. Thus seaweeds whose forms are less robust to the full force of breaking waves are found on wave-protected shores or coves, whereas others that have evolved more hydrodynamic forms, or have material properties that allow them to both sustain their iron grip on the rock and simultaneously be flexible and elastic in the face of crashing waves, occupy the most wave-exposed outer rocks and headlands.

Seaweeds living in the more wave-exposed locations do not have it all bad, however. They can live higher on the shore because the sea spray and splash from the crashing waves keep things moist. Also, for some seaweeds the motion of waves tossing their fronds around can help to maximize the amount of sunlight they can absorb and use, thereby increasing their photosynthetic rate. They also benefit from the plentiful supply of nutrients delivered by the high water flow in these locations. Seaweeds in very quiet coves or areas of the shore where water flow is much lower may suffer from nutrient limitation. Morphological features can overcome some of these problems of living in low-flow habitats. Bumps or projections help create turbulent mixing of water near the nutrient-absorbing surfaces of the seaweed. Additional surface area for absorbing nutrients can also be provided in the form of specialized hairs or projections.

Sand, cobbles, and boulders are all moved around by waves and ocean currents. Sand in fast-flowing water can scour delicate algae and vulnerable young forms from the rock. It can also periodically bury rocks where seaweeds grow in the course of the seasonal movement of sand on and off of beaches every year. Seaweeds that can tolerate the scouring and anoxic conditions that develop on these sand-influenced rocky shores are the only ones that persist here (these are often referred to as psammophilic, or sand-loving, species). Cobbles can be set to churn and tumble in tidal pools, eliminating all but the toughest calcified crusts. Boulder fields with rocks of different sizes are interesting habitats; larger, heavier boulders are moved from time to time by waves, but less frequently than smaller boulders and cobbles. Interestingly, these different frequencies of disturbance for boulders of different sizes result in a mosaic of higher algal diversity than if the boulders were never moved by waves at all or if they were all moved around with equal frequency. This results from the combined effect of disturbance and the predictable sequence of colonization by seaweeds as a community develops on a patch of bare rock (this process is called ecological succession). A similar phenomenon occurs on rocky benches, where different-sized patches of mussel beds are removed periodically by large waves or by mussel predators (typically sea stars), opening up new space for colonization by seaweeds and other organisms. A high-diversity community forms along the shore from the mosaic of patches of different ages and sizes.

Interacting with Other Seashore Denizens

A space of one's own is often the hardest thing to acquire on a rocky shore. Imagine being an algal spore, trying to find a suitable place to get attached to and grow up in. There are many animals already living attached to the rocks, including some, such as mussels and barnacles, that filter water to capture particles just your size and flavor for food; a spore must escape these filter feeders before it can even settle down out of the water. Some seaweeds pull off this escape act by growing atop mussels that might otherwise consume them (Fig. 14). A few have even devised ways to survive transiting through the digestive tract of molluscs or other grazers, and in some cases they germinate more readily after doing so. Apparently the spores benefit from the close association with the nutritious waste products that now surround them. Eventually, though, to survive a spore must settle down in a place that is not too hot, dry, and sunny. A nice, moist nook or cranny in a rock, in between the crowds of barnacles, or among the stipes or holdfasts of more mature seaweeds might do, but only if these neighbors do not overgrow the young sporeling or emit some kind of toxic chemical to deter it from encroaching on their space. Once settled, the germinating spore and tiny juvenile that emerges has to be lucky enough to keep from being scraped off the rock by the rough, rasping tongues of snails, chitons, and limpets or the gnawing jaws of sea urchins or fishes. Once established, the young alga must maintain its space on the shore by avoiding or outgrowing consumers and continuing to outcompete its competitors.

FIGURE 14 *Endocladia muricata,* a red alga, growing atop suspension-feeding mussels. Photograph by the author.

Some seaweeds unwittingly facilitate the recruitment of their best competitors; their very form condemns them to the fate of encouraging an ecological succession that spells their ultimate doom. For example, juvenile mussels prefer to settle onto finely branched, turf-forming algae and ultimately overgrow them. The seeds of surfgrasses have specialized projections that allow them to catch on finely branched red algal turfs or coralline algae, and they too ultimately overgrow the seaweeds that snagged them from the water. Sometimes, though, seaweeds win the battle; for example, the holdfast of a fast-growing kelp can grow right over smaller barnacles, mussels, and other seaweeds. Later, the shady, moist environment below the canopy formed by larger species, such as kelps or bladderwracks, can also become the perfect habitat for understory species that could not survive in that location otherwise. Encrusting forms frequently conquer space by overgrowing other organisms; along zones of intense competition between different encrusting species (including seaweeds, sponges, and other colonial invertebrates), one can typically discern who is currently winning the battle by seeing who is growing on top of whom. On wave-exposed rocky shores, the predictable sequence of algal succession starts with so-called ephemeral or early successional species, including colonial diatoms and anatomically simple seaweeds that grow as thin sheets, tubes, and filaments. These seaweeds tend to reproduce often; thus their reproductive propagules are readily available to colonize newly opened spaces on the shore. These species tend to be highly palatable to a wide range of consumers, including snails, limpets, chitons, fish, and crustaceans, as well as being weak competitors for space. These characteristics predispose them to being ephemeral in nature. Eventually more complex algal forms or sessile invertebrates, more resistant to being eaten or outcompeted for resources, come to dominate the shore.

Strategies to Avoid Consumption

Seaweeds use a wide array of strategies to escape from being eaten by snails, limpets, chitons, sea urchins, fish, crustaceans, and other rocky shore grazers. Some of these strategies may be simply the result of evolutionary luck, while others have evolved in response to strong selective pressure. Calcification in algae, for example, is unlikely to have evolved in direct response to consumer pressure, because it appears to be a by-product of photosynthesis, but it can confer a distinct advantage to seaweeds facing the rasping bites of snails or other consumers by making the alga both tougher and less nutritious. Coralline algal "barrens" are often all that are left behind after grazers ravage a tidepool or a kelp bed. Anatomically simple forms such as filaments and thin blades tend to be most vulnerable to consumers. Crusts, blades with toughened outer cuticles, and more leathery forms are typically less favored because of their inherent toughness.

Chemical defenses are the weapon of choice for some seaweeds to deter would-be consumers, enabling surprisingly delicate and otherwise potentially very palatable species to survive even in the midst of their would-be consumers. There are several classes of chemicals, usually produced as secondary metabolites, that have antiherbivore properties, including terpenoids, phlorotannins, DMS (dimethyl sulfide), and even sulfuric acid. Brown seaweeds in the genus *Desmerestia* avoid being eaten by sea urchins by virtue of the sulfuric acid they contain; the five-part calcium carbonate jaw that urchins use to mow down kelp beds is readily dissolved by these acid "brooms." Toxic chemicals may be produced constitutively (present all the time), although in some the chemicals may need to be activated: nonactive forms are stored and are activated only via a chemical reaction that occurs when cells are damaged. Some delicate and seemingly palatable species of green and red algae in the genera *Ulva, Enteromorpha,* and *Polysiphonia* produce DMS as an activated defense and are actively avoided by urchins. Other seaweeds produce their defensive compounds only in response to stimuli related to grazing damage; this is called an inducible defense. The advantage is that the alga need to expend energy to produce the noxious chemical only after being subjected to a real and imminent threat. The bladderwrack *Fucus garderi* is known to respond in this way when grazed upon by small snails. Other organisms often take advantage of the "free" noxious chemicals found in seaweeds to defend themselves from predators. For example, decorator crabs found along the Gulf and Southern Atlantic coasts of North America preferentially dress themselves in the noxious seaweed *Dictoyota mensualis* to avoid being eaten by omnivorous fish.

Having two distinct anatomical forms within a life cycle is another way that seaweeds obtain refuge from their consumers. For example, the brown algae *Petalonia fascia* and *Scytosiphon lomentaria* alternate between a crustose form and a more delicate form consisting of a thin blade or tubular upright. In the presence of grazers the crustrose phase persists while the upright phase is absent or scarce. Since grazers of these species tend to be most abundant and active in the summer months, the upright phase of the algal life history was thought to be responding to seasonal cues and would never appear in the summer. However, removing grazers during the summer months induces the uprights to appear and thrive. The crusts are much more resistant to grazing but grow more slowly than the upright forms that are preferred by most grazers. Being a shape-shifter may confer a distinct evolutionary advantage on an alga, especially when one shape is more likely to survive a regularly occurring onslaught of hungry herbivores.

Biodiversity

The diversity of seaweeds found along rocky shores is tremendous. However, the distribution of seaweed diversity among the various rocky shorelines of the world's oceans is not uniform, nor is it entirely random either. Diversity patterns emerge at different spatial scales and have different underlying causes. Seaweed diversity tends to be greatest lower on the shore and in more wave-exposed locations. Physical disturbances by waves tend to increase diversity by removing competitively dominant species and making room for subordinate species to gain a foothold, albeit a temporary one. Lower on the shore the abundance of herbivores may have similar effects, especially if they prefer to eat species that would otherwise dominate the shoreline. The interplay of physical and biological factors along environmental gradients of tidal emersion and wave exposure along a stretch of seashore are complex, but this interplay plays a major role in determining the number and kinds of seaweeds encountered in tidepools.

Less well understood is the cause of the variation seen in the numbers of seaweed species found in tropical vs. temperate vs. polar shorelines. In terrestrial ecosystems and for many marine species, a greater number of species can be found in the tropics than at higher latitudes. Puzzlingly, seaweeds are a major exception to this pattern. Along the Atlantic coasts of Europe and North America, seaweed diversity increases as expected as one travels from the poles to the tropics, but along the Pacific coasts of North and South America seaweed diversity declines in tropical latitudes. Understanding why seaweeds exhibit these seemingly anomalous latitudinal diversity patterns along some shorelines may help us to understand the underlying causes of large-scale diversity patterns in nature more generally.

CONSERVATION

Seaweeds, despite their "weedy" name, are not invulnerable to human impacts. We collect algae from wild populations to extract their specialized biological molecules to use in a variety of industrial processes, from making textiles to thickening milkshakes to herbal remedies. Many coastal cultures have culinary traditions that include seaweeds, and modern interest in seaweeds as a healthy and tasty part of our human diet is increasing. Asian cultures use seaweed regularly in a wide range of dishes, including the increasingly ubiquitous miso soup, sushi, and seaweed salad that we see on restaurant menus. We wrap our seafood and rice in nori (made from the red algae in the genus *Porphyra*) to create sushi rolls. In Chile, the honeycombed *Durvilleae antarctica* is collected on the coast and brought inland to be sold in city markets and made into an *ensalada de ulte*. A few species are cultivated for harvesting, including *Porphyra, Gelidium, Gracilaria, Laminaria,* and *Undaria,* but a large proportion of what we use is collected from wild populations. Careful planning is needed to maintain sustainable levels of exploitation of these natural populations as interest in seaweed products increases.

Seaweeds can create problems as invasive species when they are inadvertently introduced by people to locations outside their natural range. Perhaps the most infamous example is the case of the green alga *Caulerpa taxifolia* in the Mediterranean. Where it was introduced, it carpeted vast expanses of sea floor, excluded native seaweeds, and reduced the availability of suitable habitat and forage for native animals. Recent introductions have occurred in other locations, including a harbor in San Diego County, California, most likely via the aquarium trade, as this alga and its close relatives are commonly used in saltwater aquaria. *Sargassum muticum,* a brown alga native to northwestern Pacific shores, can now be found along the shores of the northeastern Pacific, the Atlantic, and the Baltic Sea. It probably arrived to these shores as packaging used in transporting oysters for aquaculture. The kelp *Undaria pinnatifida,* a native of Asia, where it is extensively cultivated for food and sold as *wakame,* is another species that is now invasive in Europe, New Zealand, Argentina, and California. A subspecies of the green alga *Codium fragile,* native to Asia, is possibly the most invasive alga known. It was transported outside its range, most likely via the aquaculture trade or on the hulls or in the ballast water of ships. This species is now found along the shores of Africa, Australia, Europe, and North and South America and has become an economic problem, because it fouls shellfish beds, especially in the northwest Atlantic. Eradication of invasive species is generally fraught with enormous and often insurmountable challenges and costs; preventing inadvertent introductions through education and regulation is clearly the best hope to prevent future invasions.

Development and nutrient pollution can strongly alter the abundance and distribution of seaweeds. For example, in the Baltic, eutrophication has promoted the growth of phytoplankton and other smaller, more ephemeral seaweeds. Because these smaller photosynthetic organisms live suspended in the water (phytoplankton) or often grow as epiphytes (on top of other organisms), they can intercept the light before it reaches the larger seaweeds growing on the rocks below. The result is that depth distribution and abundance of *Fucus,* an important habitat-forming species in the Baltic, is now sharply reduced.

Global changes that impact the ocean environment such as global warming have the potential to impact seaweed communities as well. Ocean productivity is linked to atmospheric phenomena such as El Niños; these and other climatic fluctuations influence the amount of nutrients that are brought up from the ocean's depth and fuel the growth of all photosynthetic marine organisms. Changes in the abundance of phytoplankton or nutrients in the ocean water that overlay seaweed-covered shores are likely to significantly alter the ecological character of these shorelines.

The slippery and slimy seaweeds that can sometimes make walking along the shore at low tide a challenging affair are a fascinating yet often overlooked component of healthy, functioning marine ecosystems. We know that many species depend upon seaweeds for food and habitat. We know their moist cover provides a desirable refuge for many intertidal inhabitants during low tide. Despite the enormous productivity and diversity of seaweeds, we still know surprisingly little about the contribution that seaweeds make to coastal ecosystem production and functioning. The enormous diversity in form, life history, ecology, and evolutionary history of seaweeds make them both challenging and very rewarding to study.

SEE ALSO THE FOLLOWING ARTICLES

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ALGAE, CALCIFIED

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Calcified algae are a unique subset of marine seaweeds that incorporate calcium carbonate—essentially, limestone—into their thalli. As a group, they are quite diverse, because calcification has evolved independently in the three major divisions of macroalgae: Rhodophyta, Chlorophyta, and Ochrophyta (red, green, and brown algae, respectively). Today, calcified algae dominate biotic communities in many subtidal, intertidal, and tidepool environments worldwide. They build reefs, contribute to sediments, and are home to numerous plants and animals. In sum, their unique attributes enable them to play key ecological and geological roles in marine ecosystems.

THE DIVERSITY AND IMPORTANCE OF CALCIFIED ALGAE

Among the different groups of calcified algae, the mode and extent of calcification varies widely. For example, the brown alga *Padina* develops a thin white calcified coating, whereas the green alga *Acetabularia* and the red alga *Liagora* incorporate low concentrations of calcium carbonate directly into their flexible thalli. Other, more rigid but still flexible, calcified algae include the red alga *Galaxaura* and the green algae *Udotea* and *Penicillus*. The most heavily calcified algae include the green alga *Halimeda* and the so-called "coralline" red algae, which impregnate every cell wall with calcium carbonate and can even resemble stony corals.

These heavily calcified algae are most abundant and, arguably, most important. They exist in two fundamentally different forms. One has calcified segments separated by flexible joints called genicula. These "articulated" calcified algae include the green alga *Halimeda* (Fig. 1A) and red algal genera such as *Amphiroa, Corallina, Calliarthron*, and *Bossiella* (Fig. 1B). The other growth form lacks genicula and typically grows as an encrusting pink patch on hard substrata (Figs. 1C–E) but can also be found unattached in sediment habitats (Fig. 1F). Algae with this nongeniculate morphology, or "crustose" coralline red algae, include common genera such as *Lithothamnion, Clathromorphum, Lithophyllum,* and *Phymatolithon*. These two heavily calcified growth forms are ubiquitous, growing throughout the euphotic zone from the Arctic to the Antarctic, from temperate regions to the tropics. Most calcified algae grow on hard substrata, but some live on other plants or anchor in shallow marine sediments.

Among calcified algae, crustose coralline red algae and the articulated green *Halimeda* stand out as ecologically and geologically important. *Halimeda* is abundant in coral reef environments and, by some estimates, generates most of the total calcium carbonate there. Accumulated *Halimeda* segments produce the sand on most of the world's coral reefs, lagoons, and beaches. Crustose coralline red algae are perhaps the most abundant organism (plant or animal) to occupy hard substrata within the world's