A

ABALONES

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Abalones are marine snails that play only a minor role in the functioning of marine communities yet are culturally and commercially important and are iconic species of kelp-dominated habitats. They were once tremendously abundant along the shores of much of the temperate zone, with large aggregations piled two or more layers deep along large stretches of rocky sea floor (Fig. 1). Abalones were prized for their meat and shells by indigenous communities worldwide, particularly along the coasts of California, Japan, and New Zealand. Their shells are well represented in middens, such as on the Channel Islands off southern California, that date as far back as 10,500 years ago. The tough shells, lined with iridescent mother of pearl, were used as ornaments and to fashion practical implements such as bowls, buttons, and fish hooks. In New Zealand Maori culture, abalone shell is extensively incorporated into carvings and ornaments. These historical uses have translated into high demand in modern times to such an extent that most abalone populations are greatly depleted from their historical abundances, with some species even considered to be in danger of extinction. There are now management practices in place worldwide to sustain and extend populations, based on knowledge about their biology and ecology.

DISTRIBUTION AND BIOLOGY

Abalone is the generic name that refers to the group of single-shelled molluscs of the class Gastropoda, family Haliotidae, and the single genus *Haliotis*. There are many

FIGURE 1 Once-abundant coastal populations of most abalone species are now severely depleted, and dense aggregations are usually confined to small patches in remote places. Shown here, New Zealand abalone (*Haliotis iris,* locally called "paua") of about 16 cm in shell length at a remote offshore island in a 5-m depth of water. Photograph by Reyn Naylor, National Institute of Water & Atmospheric Research Ltd, New Zealand.

regional names for *Haliotis* species, including paua from New Zealand, perlemoen in South Africa, and ormers in Europe. There is no consensus on the number of species of abalone, but estimates range from 70 to around 130. There are many subspecies, and some co-occurring species form hybrids with gradations of characteristics. The taxonomy of many of these variants is unresolved.

Abalones occur from the warm waters of tropical coral reefs through to the cool temperate zone. Their major abundances are along coastlines where kelp beds occur, particularly New Zealand, Australia, South Africa, Korea, Japan, China, the west coast of North America, and the Atlantic coast from Senegal to Spain, France, and the British Isles. An anomalous occurrence is the commercially fished species *H. mariae,* which is restricted to two areas of the tropical waters of Oman where cool, nutrient-rich, upwelled water sustains a kelp forest. *Haliotis* is an ancient

genus, 60 to 100 million years old. One current view, based on DNA analyses of species worldwide, is that it originated in the ancient land mass of the Southern Hemisphere and speciated as the continents drifted into their present positions. There is disparity in sizes of tropical and cold-water species. Tropical species rarely exceed 50 mm in length; large-bodied species occur only in cold-water areas dominated by kelp and other macroalgae, which provide energy-rich food. Many of the commercially important species reach large sizes. For example, *H. iris* from New Zealand, *H. ruber* from Australia, *H. discus hannai* from Japan, and *H. midae* from South Africa can reach lengths of around 180 mm, and the giant of them all, *H. rufescens* of California, can grow to more than 300 mm. Different species of abalone occur from the intertidal zone to depths of hundreds of meters. However, their major distribution is in near-shore waters generally less than 30 m in depth. Their sleek hydrodynamic shells make abalones well suited for survival in turbulent waters.

Abalones have a relatively simple biology. A muscular foot, which comprises most of the weight of the animal, holds them tenaciously to rock surfaces by means of a contact mucilage and powerful contractions. The foot can raise the shell several centimeters above the substratum, which allows the abalone to trap drift algae as it tumbles along the sea floor. As in other gastropods, food is rasped by a radula, a double-rowed band of spiked chitinous material inside the mouth. Respiration occurs through the gills, which sit just below a series of holes that radiate in an arc along the top of the shell. These holes are also avenues for expelling waste products and releasing gametes during reproduction.

Growth occurs by adding to the shell margin to accommodate the expanding body size. The shell itself is a marvel of composite construction. It is secreted by epithelial cells of the mantle, a thin tissue that lines the inner surface of the shell, and is composed of layers of two crystalline forms of calcium carbonate embedded in a protein called conchiolin. These are laid down in a lattice construction that makes the shell very tough to crack or shatter. The outer layers are mainly calcite and the inner layer is nacreous aragonite, which can thicken throughout the life of the animal, enabling not only growth but also repairs to cracks and eroded areas of shell. This nacre gives the inner shell its characteristic luster. Species with beautiful iridescent coloring, such as *H. iris* with its swirling blends of green, blue, purple, and pink, are used to grow mabé or blister pearls, which are fashioned into jewelry.

Growth rates are influenced by a wide range of environmental conditions, especially temperature, food availability, and water circulation. In good conditions, larger species may increase an average of 25 to 30 mm in length annually for 5 or 6 years. However, in more quiescent areas, where algal drift is not plentiful and sediments may accumulate on the sea floor, growth can be only a few millimeters per year. Linear growth, however, may be deceptive because abalones have a geometric increase in body size with linear growth of the shell. A California red abalone *(H. rufescens)* of 200-mm shell length, for example, may weigh five to ten times more than one of 100 mm. Large individuals of many species can be 30 or more years old, although these are now rare.

Reproduction in abalones tends to be highly seasonal and related to water temperature, although there is considerable variation among species. For example, three species of California abalone have different spawning periods. White abalone, *H. sorenseni,* are highly synchronized in an annual spawning event that occurs during a few weeks of winter. Green abalone, *H. fulgens,* spawn through summer and early autumn, and pink abalone, *H. corrugata,* are the least synchronized and have spawning episodes throughout the year. These differences may relate to aggregation behavior and the likelihood of encountering other abalone, which is essential for reproductive success.

Abalones are dioecious, and populations generally have an equal proportion of males and females. Gonads usually form when animals are 2 to 3 years old. The sexes are readily determined by pushing the foot aside and looking at the color of the gonad, which surrounds the liver in a horn-shaped structure between the foot and the shell. Abalones are broadcast spawners, and reproduction begins with a few individuals releasing eggs and sperm directly into the water through the respiratory holes. This triggers others to move closer and release their gametes. In large gatherings, there can be a cloud of sperm wafting in the water current above the abalones, which enhances the chances of successful fertilization. Small females may release only a few thousand eggs, but the largest individuals may release 7 to 10 million eggs. Because these large abalone have traditionally been targeted in fisheries, there has been a tremendous loss of reproductive potential in abalone species worldwide.

ECOLOGY AND FISHERIES

There are four major bottlenecks in the life cycle of abalone: fertilization, larval development, the settlement process, and movement from juvenile to adult habitats. Each of these has critical features essential for continued survival. Once fertilization occurs, eggs of about 0.2 mm in diameter begin a perilous journey, but they do have resources

FIGURE 2 (A) One-week-old red abalone *(Haliotis rufescens)*, about 1 mm long, on a thin crust of calcareous red algae; chemicals produced by such algae help trigger settlement of late-stage larvae from the plankton. (B) Juvenile red abalone, about 1 cm long, cryptically colored against a background of encrusting red and filamentous algae, note tentacles protruding from the head region. Photographs by Jessie Alstatt, Science Director, Santa Barbara Channelkeeper.

in the yolk that will sustain them for the larval period. The developing larvae do not feed, but they can absorb nutrients from the water. They go through a series of stages, forming the necessary structures for life on the sea floor. Later veliger stages have a foot, larval shell, and feeding apparatus. These larvae drift in coastal currents but have the ability to swim up and down in the water column using the cilia of their velum. After 1 to 2 weeks, depending on the seawater temperature, larvae are ready to settle. The consensus is that most larvae do not travel more than a few kilometers from spawning sites because of their quick development time and ability to stay in the near-shore zone.

Finding a suitable settlement site is no easy matter. Larvae sink to the sea floor and begin testing surfaces by touching them, hovering over them, and moving along to another place. Many species of abalone preferentially settle on thin encrusting red algae, which contain a chemical trigger that induces settlement (Fig. 2). Once this occurs,

the larva drops its velum and begins life as a juvenile, initially feeding on algal films and diatoms. Many species of abalone migrate to the undersides of large rocks in 1 to 10 meters' depth, where they will live and grow for up to 3 years. They are very vulnerable to a wide range of predators at this stage, including the numerous predacious reef fish, such as the large sheephead wrasse *Semicossyphus pulcher,* that patrol kelp forests, and the lobsters, crabs, and carnivorous whelks that share their secretive boulder habitats. As they grow, abalones feed mostly on drift seaweed that becomes trapped in cracks and crevices.

When abalones reach around 70 mm in length, they begin to emerge from their juvenile habitats to spend their adult period on more open areas of reef. Here they lead a mostly sedentary life, feeding passively on drift seaweed. As they get beyond about 120 mm, abalones worldwide have few natural predators. A major exception is along the west coast of North America, where sea otters *(Enhydra lutris)* occur. Otters have a high energy demand, consuming up to one-fourth of their body weight in food daily, and their favorite food is abalone, which they remove by repeatedly smashing the shell with a rock. Where otters are abundant, species such as the California red abalone, *H. rufescens,* tend to recede into cracks and crevices at least an otter's arm length deep.

PROBLEMS AND SOLUTIONS

No story about abalone is complete without mention of the history of extraction. Put simply, abalones have been overfished worldwide. The California fishery (Fig. 3) shows a pattern common elsewhere. A species is heavily exploited, then the fishery moves on to other species
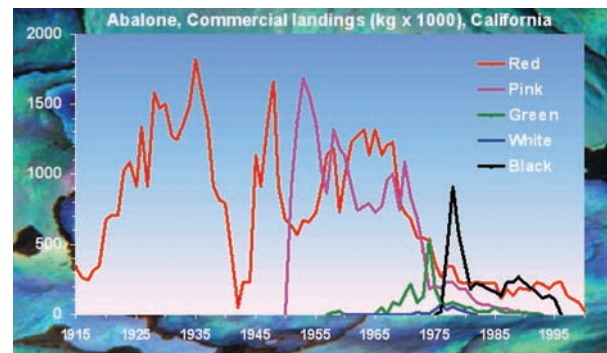
FIGURE 3 Commercial landings of California abalone over the twentieth century, showing serial depletion of five species. White abalone *(Haliotis sorenseni)* are now so rare they are listed as an endangered species. Background shows the iridescent nacre on the inside of an abalone shell. Graphic by Kim Seaward, Marine Ecology Research Group, Christchurch, New Zealand. Data derived from California Department of Fish and Game reports.

sequentially. Abalones have been fished commercially since at least 1850 in California. Initially this involved intertidal populations of green and black abalone *(H. fulgens and H. cracherodii)*, but then was extended to subtidal populations of these and other species, especially the red abalone *H. rufescens*. More than a million pounds of several abalone species were extracted annually from the early 1900s, with peaks of more than five million pounds in the 1950s and 1960s. Catches declined to less than a million pounds again by the early 1980s. Finally, in 1997 commercial and sport fishing for abalone was stopped in southern California. It is still allowed north of San Francisco but only by free diving. These sorts of stock depletions and catch restrictions apply to most abalone fisheries now.

Why does it take so long for restrictions to come in? Part of the reason is that fisheries for sedentary species such as abalone tend to be serially depleted. Catch rates tend to stay high until populations are near collapse because people become very efficient at minimizing the effort involved in spotting and catching abalone. Other reasons are the magnitude and variety of modern pressures that interact to affect populations, such as market demand, commercial harvest, increasing sport harvest, illegal fishing, expanding sea otter populations, habitat degradation (especially from pollution and sedimentation of juvenile habitats), disease, variable recruitment, illegal fishing, and often weak management and enforcement. These interactive effects have positive feedbacks on populations. Although there are minimum size limits in commercial fisheries, usually set at around 120 to 130 mm when animals have had several years to reproduce, these alone have not saved populations. Furthermore, the removal of the largest individuals takes away most of the egg production of a population. Thinning of aggregations to isolated individuals reduces the chances of fertilization. Degradation of settling and juvenile habitats results in diminished recruitment. As seawater warms, there may also be a higher incidence of disease. The incidence and spread of "withering foot syndrome," caused by a bacterium that is lethal in temperatures over 18 °C, has severely depleted populations of the black abalone *H. cracherodii* throughout southern California.

Strong management of depleted stocks worldwide, an expanding aquaculture of abalone (particularly in Asia), and reseeding of depleted coastal areas may lead to rejuvenation of natural populations while filling market demand. Strict TACs (total allowable catches) and regional catch restrictions have greatly helped in the sustainability of some fisheries, such as in New Zealand and Australia, whereas closures and marine protected areas are seen as avenues to recovery in severely depleted areas. An optimistic projection would see abalones returned to at least being common again in coastal waters. For the present, however, it is clear that much of the adaptability of populations and buffering from climate and other environmental vagaries is compromised for many of the world's abalone.

SEE ALSO THE FOLLOWING ARTICLES

Adhesion / Food Uses, Ancestral / Management and Regulation / Snails / Symbolic and Cultural Uses

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ADHESION

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To survive on intertidal rocks, organisms generally must have a way of holding their positions. Because they are often specialized to live on the limited substrate and unique conditions of the intertidal zone, being swept away would be tantamount to death. Thus, many of the best-known biological adhesives are produced by intertidal animals. These adhesives can be solids or gels, and they form strong attachments to irregular surfaces despite the presence of water.

MARINE ADHESIVE MECHANISMS

There are a wide variety of organisms that attach strongly to intertidal surfaces (Fig. 1). Animals such as barnacles permanently cement themselves to hard surfaces. Mussels

FIGURE 1 A wide variety of organisms adhere strongly to rocks in the intertidal environment. Barnacles attach with a solid cement under their base (A). Mussels use byssal threads that adhere to the surface via small plaques (B). Sea urchins secrete an adhesive material underneath their tube feet (C). Limpets can secrete an adhesive gel underneath their foot or use suction (D). Photographs by K. Kamino (A), J.H. Waite (B), Romana Santos (C), and L. Miller (D).

are also well known for using a permanent, solid adhesive. This adhesive is macroscopically more complex in that it involves hardened plaques that attach to the surface and connect to the organism through tough threads. This structure is called the byssus. Many other organisms use glues that are less solid. A large number of molluscs use glues that are gels. These gels consist of networks of large polymers that trap water. The tube feet of echinoderms also use gels for attachment. The stiffness of these gels can vary considerably, with some being remarkably firm and elastic. Finally, many algae can attach to rocks using tough holdfasts.

Whether the adhesives are solid cements or relatively soft, wet, gel-based structures, they face similar issues. They must be able to adhere to wet, irregular surfaces, and they must maintain their integrity despite the presence of water.

BASIC PRINCIPLES OF GLUING

Two primary processes that govern the effectiveness of a glue are adhesion and cohesion. Adhesion is the ability of the glue to stick to a surface. It involves spreading across a surface and bonding to it. Cohesion provides the mechanical strength for the glue to resist deformation. It depends on interactions within the glue, specifically between the molecules that make up the bulk of the glue. Many artificial glues start in liquid form so that they can

spread across a surface easily. Once the glue has bonded adhesively to the surface, the glue then cures; that is, it hardens to provide cohesive strength. Glues can fail at the adhesive interface—for instance, by peeling off a waxy surface. They can also fail cohesively, in which case the glue itself breaks or deforms, leaving a patch of glue still firmly adhering to the surfaces.

Adhesion

Glues often have a relatively low viscosity (resistance to flow) at first, so that they can spread across a surface. The ability of a glue to flow during the initial stages of adhesion is essential. This is because it is extraordinarily difficult for two solid objects to come into full contact, as a result of their surface roughness (Fig. 2A). Even surfaces that look and feel perfectly smooth at the macroscopic level typically have a great deal of microscopic roughness. Nanometer-scale roughness, which is nearly unavoidable, is sufficient to prevent most of the area on the surfaces from coming into direct contact. The surfaces may touch and adhere at some points, but those points cover only a small fraction of the available area. A viscous material, however, can flow to fill all the gaps and indentations. Thus, it can achieve far more intimate contact with the surface (Fig. 2B). Pressure-sensitive adhesives such as tapes and tacky glues also depend on flow to achieve this contact. These adhesives have a high viscosity, but they are still
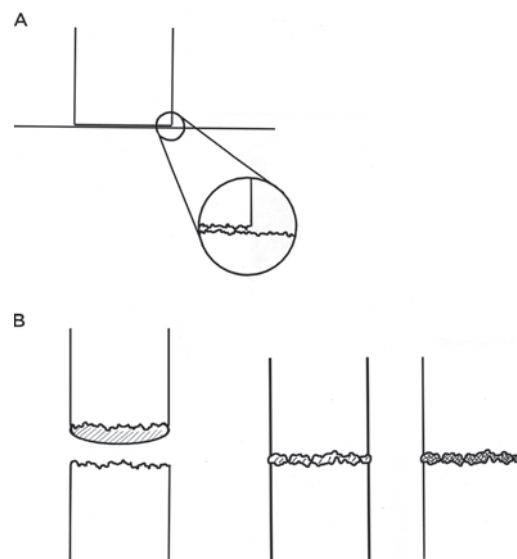

FIGURE 2 Most solids, regardless of how smooth, cannot achieve intimate contact with other solids because of nanoscale surface roughness (A). Adhesives help by flowing to fill the gaps and achieve full contact (B). After wetting the surfaces, adhesives often harden to provide cohesive strength. Illustration by C. Chew.

sufficiently soft and deformable that a reasonable pressure will force them to flow into the gaps and indentations on the surface. Without such pressure, the area of contact is insufficient to provide a strong adhesive force.

Some biological adhesives, such as those from barnacles and mussels, appear to be secreted in a viscous form that hardens over time. Other animals secrete highly viscous gels that may or may not stiffen after secretion. These gels may also be forced into contact with the surface in the same way as a pressure-sensitive adhesive. Underwater, spreading may be assisted by the fact that the surface is already wet. Instead of relying on bulk flow of the material, the polymers can diffuse through water to the wetted surface. Of course, this merely replaces one problem with another, because the adhesive must then displace the water to contact the surface directly.

In addition to being able to flow, a glue must be able to wet the surface. Wetting involves the interactions between a fluid and a surface. If the fluid and the surface are incompatible, wetting will not occur. For example, water cannot interact with Teflon or wax, so it beads up on those surfaces rather than spreading. If a glue does not wet a surface, adhesion will be weak.

Whether or not wetting occurs is determined by the potential energy of the exposed surfaces relative to the interfacial energy between the adhesive and substrate (Fig. 3). The potential energy of an exposed surface results from the fact that it often takes energy to create new surfaces. A high-energy surface results when molecules that had been interacting with similar molecules, as in a bulk solid, are exposed to a medium that they cannot interact with, such as air. Energy is required to create such a surface. A more stable, low-energy surface results when the solid interacts well with the medium, as polar solids do with water.
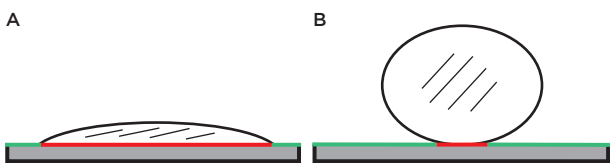
FIGURE 3 The ability of an adhesive to wet a solid depends on the surface energies of the materials involved. If the solid–adhesive interface (red) is stable due to strong interactions, it will have a low energy. If this energy is lower than the energy of the solid in contact with the surrounding water (green), wetting will occur (A). In essence, a stable, low-energy interface replaces the higher-energy surface. If the energy of the solid–adhesive interface is higher than the solid's surface energy in water, wetting will not occur (B). Note that a more detailed analysis would also factor in the energy of the adhesive–liquid interface.

When an organism places an adhesive on a surface, the adhesive will wet or fail to wet the surface, depending on which minimizes the total potential energy of all the surfaces. Thus, wetting occurs when the solid–adhesive interface has a lower energy than the other surfaces exposed to the medium.

Good wetting usually occurs when there is chemical interaction between molecules in the adhesive and the surface. Such chemical bonding can occur in a variety of ways. Hydrophobic regions may come together to minimize contact with water, oppositely charged regions may interact, and more specialized forms of bonding may occur, possibly involving interactions with metals or oxides on the surface. Additionally, most molecules can interact through van der Waals forces, which occur when two molecules come into close proximity and the charge on one causes a corresponding redistribution of charge on the other. This creates locally charged regions that can interact. Van der Waals forces can occur between most surfaces; the key is to make sure the surfaces get into close enough contact over most of their area.

Adhesive interactions are complicated greatly by the presence of water. Even if a glue can spread and bond to a dry surface, it may not work underwater. Unless the water bound to a surface is displaced, the glue will adhere to a thin layer of water rather than directly to the surface. This forms a substantial weak link in the adhesion, because water can flow, causing adhesive failure. The basic problem is that water interacts strongly with polar and charged surfaces. For an adhesive to work well, it must displace this bound water by having an even stronger affinity for the surface. Furthermore, many adhesive interactions involve attraction between charged molecules. Because water is polar, it will also be attracted to charged regions of the glue polymer. Thus, it will cover and effectively mask the binding regions of the adhesive molecule as well as masking the surface to which the glue is trying to adhere. In energetic terms, the surrounding water may make the separate solid and glue surfaces lower in energy and thus more stable than the solid–glue interface (Fig. 3).

In addition to the presence of water, any glue must contend with other impurities. There will always be a layer of organic material fouling surfaces underwater, and this may need to be displaced. Glues may also adhere to dirt and small bits of organic material that are loosely bound to the surface instead of to the firm surface underneath. Given these considerations, the ability of marine organisms to adhere strongly in the intertidal environment is impressive.

While the nature of the chemical bonds allowing this adhesion is often not fully clear, a good deal of work has identified several possibilities. Mussels use a number of small proteins that are rich in the rare amino acid 3,4-dihydroxyphenylalanine (DOPA). This amino acid may form strong interactions through a variety of mechanisms. With its two hydroxyl groups it is strongly polar and readily forms hydrogen bonds to polar surfaces. It can also form complexes with metals such as iron that may be present on the surface. Like mussels, barnacles use a number of relatively small proteins at their adhesive interface, and some appear specialized for adhering to different surfaces. Many adhesive proteins have a notably high percentage of polar regions, particularly hydroxyl groups, and charged regions. These likely assist in displacing water from the surface and binding to polar surfaces such as the rocks of a tidepool.

Cohesion

In addition to adhering to a surface, a glue must have sufficient mechanical strength to resist deformation. The proteins that make up the bulk of the secretion are likely to be fibrous or take on an extended configuration. Typically, these fibers or sheets are linked together to create a highly viscous or solid material. These may be linked into a random network as shown in Fig. 4, or they may be in a highly ordered array. Such linkages may result from
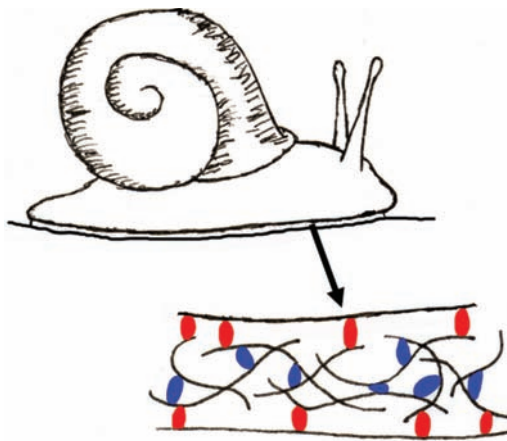
FIGURE 4 The glues of marine invertebrates typically consist of crosslinked networks of proteins. If one were able to view the adhesive gel of a snail at the molecular level, it might appear as shown in the expanded view. Crosslinks between the proteins (blue) provide cohesive strength, and bonding between the proteins and the surfaces (red) provides adhesive strength. In other animal glues, the proteins may be crosslinked into a more orderly array. Illustration by C. Chew.

chemical crosslinks between polymers or from physical tangling between long polymers that are packed into a high concentration. As with adhesion, the presence of water is a serious detriment to good cohesive strength. Water within the glue may mask crosslinking sites just as it does in adhesion. Thus, the crosslinks within the glue must be able to form and avoid degradation despite the presence of water.

The physical network of polymers can take a variety of forms. In the case of mussels, the byssal threads are composed of collagenous fibers with either silk-like or elastin-like regions, thus conferring stiffness or elasticity. These fibers are crosslinked into tough threads. The plaques where the byssal threads meet the substrate include smaller proteins that are rich in the amino acid DOPA, which may be involved in crosslinking. DOPA residues can link together covalently in a process known as quinone tanning. Some algae may depend on a similar type of crosslinking to join polysaccharide chains. Barnacle adhesives are also made of crosslinked proteins, with large (~100 kD) proteins linked by hydrophobic interactions and other possible interactions. Many snails adhere using glues that are gels. Such gels are often based on giant proteins or protein–polysaccharide complexes (>1000 kD). These giant molecules would normally form a loose network by tangling interactions, but they also appear to be crosslinked by other proteins that are present in the glue. In some molluscs, such as limpets, the bulk of the glue consists of proteins that are closer to 100 kD in size, and these also appear crosslinked. The mechanism of crosslinking in these gels is unknown, but it appears to depend on charged molecules. Proteins seem to make up the key constituents of a number of other well-studied algal and echinoderm adhesives. Overall, for many of the biological adhesives that are used in the marine environment, crosslinked proteins seem to be essential for providing cohesive strength.

In addition to cohesive interactions between molecules, there are a wide variety of engineering factors that affect the ability of the glue to resist deformation. Although great stiffness would seem desirable in an adhesive, it doesn't always provide optimum performance. Many glues deform markedly during detachment. This deformation involves breaking crosslinks, rearranging large molecules, and dragging them past each other. This process can dissipate a great deal of energy before dislodgement occurs. This may be one reason why flexible, gel-based glues are so effective. Even relatively stiff glues often have mechanisms for energy dissipation. Failure

is rarely through simple crack formation or uniform flow of a viscous glue.

Finally, it is worth noting that biological adhesives are often complex mixtures of polymers. Some polymers may be involved in adhesion, some in cohesion, and others may perform other tasks. For example, echinoderms such as sea stars appear to use a dual-gland system in which one gland secretes an adhesive material and a neighboring gland secretes a separate, de-adhesive material. The deadhesive appears to cause release of the attachment.

SUCTION ADHESION

A number of marine animals use suction to adhere, most notably octopuses and squid, but also a number of gastropods and possibly a wide variety of other animals as well. Suction in the marine environment is quite different from suction in dry environments. In dry environments, suction cups are filled with air and work by creating a partial vacuum. Underwater, the suction cups are filled with water. The cup exerts an expanding force on the water, but water has cohesive strength and is essentially inexpansible at physiological pressures. Thus, when the suction cup pulls on the water, it reduces the pressure in the trapped water with no detectable expansion.

Suction works well underwater because water adheres well to the underwater surfaces. Furthermore, because the water is trapped underneath the sucker, it cannot flow. The cohesive strength of the bonds between water molecules is quite large. Thus, water resists expansion remarkably well, as long as it adheres to all the surfaces. There are two major causes of failure of suction underwater: (1) failure to maintain a seal, so that the water can flow in, or (2) adhesive failure, in which the water does not fully wet the surface and thus an air pocket in the unwetted area expands rapidly as the pressure in the surrounding water drops. This often results from the presence of microscopic air bubbles trapped on particles. These microscopic air pockets form weak spots in the adhesion of water to the surface. Despite the presence of such weak spots, suction underwater appears to be considerably more effective than suction in air.

SEE ALSO THE FOLLOWING ARTICLES

Barnacles / Bivalves / Locomotion: Intertidal Challenges / Materials, Biological / Materials: Strength

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AIR

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The intertidal zone is characterized by regularly alternating exposure to air and water. Intertidal plants and animals can also be partially submerged for extended periods and thus will be simultaneously exposed to both media. Air differs physically from seawater in diverse and important ways that influence the forces experienced by organisms, their ability to effect gas exchange, and their overall thermal balance with respect to the surrounding environment. Unlike the chemical composition of seawater, the gaseous constituents of the atmosphere have changed dramatically through geological time. Such variation has had important biophysical and physiological consequences for intertidal organisms.

THE PHYSICAL PROPERTIES OF AIR

The physical properties of air derive from its constituent molecules, predominantly nitrogen (~78%) and oxygen (~21%) in today's atmosphere. Additional constituents such as argon (~1%) and carbon dioxide (~0.03%) are much less important from a physical perspective, although levels of the latter molecule have critical consequences for photosynthetic capacity by plants.

For humans, the most obvious difference between water and air is their relative density (the mass per unit volume), with water being some 800 times denser than air. Interestingly, both air and water behave as fluids rather than solids in that they resist the rate of deformation in response to an applied force, rather then resisting deformation per se. Such resistance is a function of the fluid's dynamic viscosity, the value of which for water is approximately 55 times greater than that of air. Also, the dynamic viscosity of air is relatively insensitive to temperature, whereas that of water is strongly (and inversely) thermally dependent. Comparable differences between the two fluid media characterize a number of

physical parameters (Table 1). Of particular importance for heat exchange between organism and environment in the intertidal zone is the heightened thermal conductivity of water. Finally, diffusion of oxygen is dramatically slower in water than in air because of the much higher density of the former medium. Overall, air and water represent two dramatically different physical environments from the perspectives of energy, gas, and momentum exchange between organism and surrounding medium.

TABLE 1

Ratios for Key Physical Parameters of Their Values in Water to Those in Air

Physical Parameter	Ratio of Water to Air
density	800
dynamic viscosity	55
thermal conductivity	23
oxygen diffusivity	0.0001
oxygen concentration	0.0265
carbon dioxide concentration	0.708

NOTE: Values refer to a temperature of 20 °C.

EFFECTS OF INTERMITTENT EXPOSURE TO AIR

If we consider a sea anemone, first suspended within the depths of a tidepool, and then exposed to air as the tide recedes, the physical consequences of these two contrasting environments become clear. The much greater density of water renders the anemone effectively buoyant within water (Fig. 1A), whereas gravity dominates in air and induces retraction of tentacles and a flaccid body posture (Fig. 1B). Given the linear dependences of hydrodynamic forces on fluid density, water currents within the tidepool often exert substantial forces on the sea anemone, whereas wind motions typically exert but minimal aerodynamic drag because of the much lower density of air. Issues of structural support against gravity thus become paramount when intertidal taxa are exposed to air, and attachment mechanisms to substrate together with postural changes become evident, as in the case of the drooping sea anemone. As a further, botanical example, stands of marine algae collapse upon emergence from water, precluding photosynthesis by all but the uppermost fronds.

In water, plants and animals of the intertidal are isothermal (i.e., at the same temperature) relative to the surrounding water because of its high rate of heat conduction.
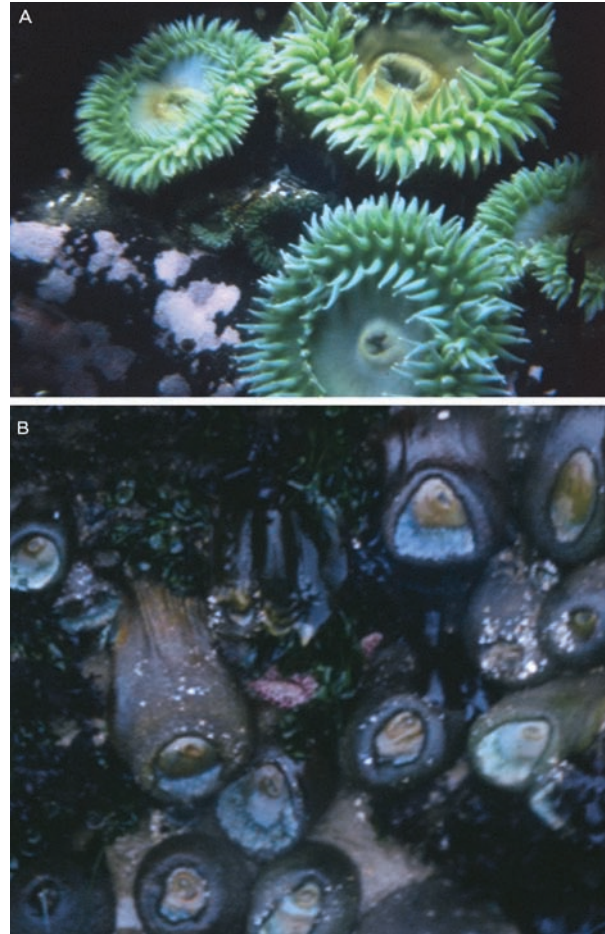

FIGURE 1 Sea anemones submerged within a tidepool (A) and exposed to air (B). Photographs courtesy of Jonathon Stillman.

In air, the situation is more complicated. Direct absorption of solar radiation, now unattenuated by water, increases body temperature. Heat loss, by contrast, is typically much lower in air than in water. Intertidal plants and animals thus typically heat up when exposed to the air as the tide recedes, although convective cooling by the moving wind may partially mitigate this effect, particularly on overcast days. Nonetheless, vaporization of endogenous water reserves is one major strategy used by intertidal taxa to overcome heating when exposed to air, a phenomenon clearly irrelevant when an organism is immersed within a tidepool.

HISTORICAL VARIATION IN ATMOSPHERIC COMPOSITION

One of the most interesting features of the atmosphere has been the variation over geological timescales in its gaseous composition. Nitrogen content of the atmosphere is believed to have been fairly constant since the formation

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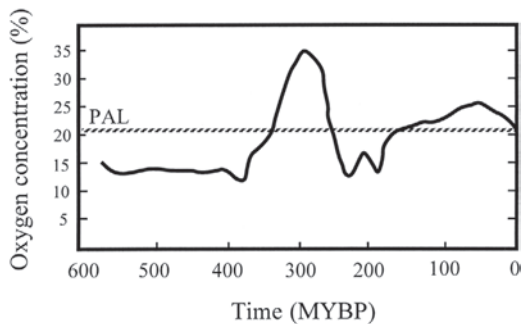
FIGURE 2 Variation in oxygen content of the atmosphere through Phanerozoic time, relative to the present atmospheric level (PAL). MYBP = million years before present.

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

Desiccation Stress / Diffusion / Heat Stress / Seawater

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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

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

shores, and a disturbance-prone environment that makes the study of tidepool algae especially fascinating.

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.

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

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.

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

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 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.

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
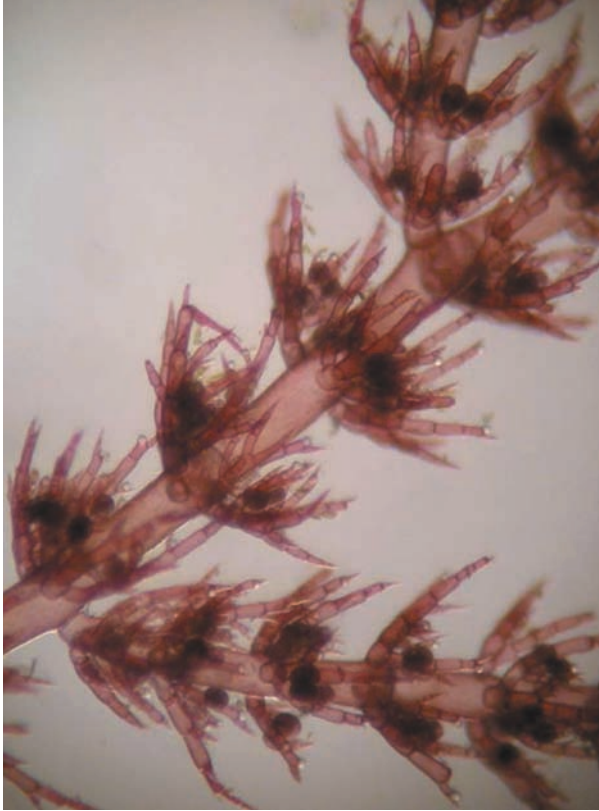
FIGURE 6 The red alga *Platythamnion villosum* is a delicately branched filament made up of chains of single cells. This specimen is a tetrasporophyte, one of the diploid, free-living phases of the typical red algal life history. The dark circular structures attached to the branchlets are the tetraspores (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 spongelike 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

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

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.

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 bladder-wracks, 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 crustose 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

Biodiversity, Significance of / Food Uses, Modern / Introduced Species / Zonation

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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
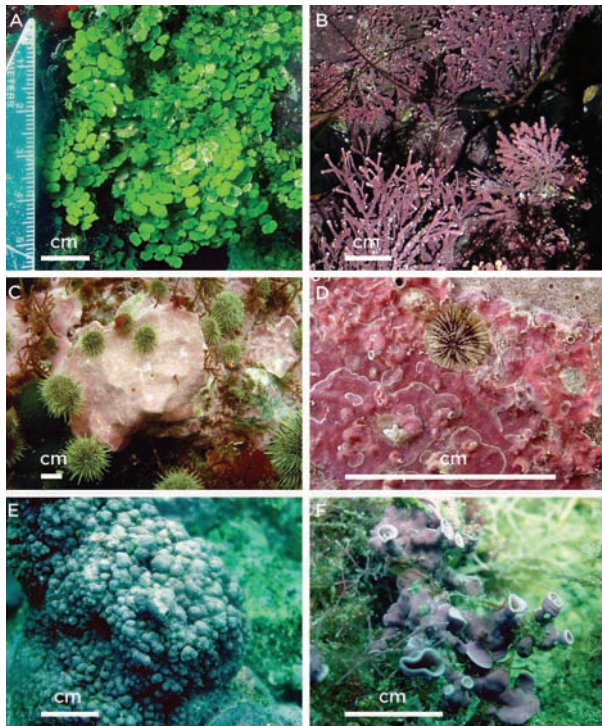
FIGURE 1 Morphological and ecological variety of calcified algae. Bars = 1 cm. (A) Articulated green alga (*Halimeda* from Honduras in the Caribbean) growing on a coral reef. (B) Articulated red algae (*Calliarthron* and *Bossiella* from Monterey Bay, California) growing in low intertidal zone tidepools. (C) A massive crustose coralline (*Clathromorphum* from Alaska's Aleutians islands) that can grow to be a meter thick despite grazing sea urchins. (D) A thin crustose coralline (*Titanoderma* from Bonaire, Netherlands Antilles in the Caribbean) with a newly settled reef-building coral. (E) A slightly branched crustose coralline (*Hydrolithon* from Honduras in the Caribbean). (F) A branched or rolled maerl morphology (*Lithothamnion* from Guatemala in the Caribbean) growing unattached on sediment. All photographs by R. Steneck.

marine photic zone. They are abundant on most rocky subtidal areas, intertidal shores, and tide pools, lending a pink hue to these environments. They have been collected in the Bahamas by a submarine at more than 260 m water depth, making them the deepest attached benthic algae in the world. Growth bands from living corallines in Alaska's Aleutian Islands reveal they can live to be at least 700 years and probably well over 1000 years, making them the longest-lived algae and one of the longest-lived marine organisms known. Vast regions of Japan; the North Pacific, North Atlantic, Tropical Indopacific, Mediterranean, and Caribbean; and Antarctica have 50–100% of shallow hard substrata covered by crustose coralline algae. In tropical wave-exposed areas, encrusting coralline algae create one of the most ecologically important noncoral constructed reefs, called "algal ridges." These specialized reefs have been constructed by coralline algae accumulating over

thousands of years, resulting in a calcium carbonate reef over 10 meters thick. Algal ridges create their own rocky intertidal zone by projecting as much as one to two meters above mean low water.

ORIGINS: PHYLETIC AND MORPHOLOGICAL EVOLUTION

Calcareous red algae have left behind a fossil record that extends back to Precambrian times (over 600 million years ago). Thus, their evolutionary history exceeds that of most extant organisms. During the Paleozoic era (570–245 million years ago), a variety of calcified articulated and crustose taxa evolved and went extinct. About 360 million years ago, calcified crusts with modern anatomical characters, similar to those of present-day coralline red algae, evolved. They formed moundlike reefs during the Carboniferous period, well before dinosaurs first evolved. These early nongeniculate calcareous algae were morphologically simple, resembling a potato chip.

Nongeniculate corallines today exhibit considerable variation in form. Some species encrust hard substrata as a thin or meshlike crust only 20 μm thick (Fig. 1D), whereas other species can grow to nearly a meter in thickness (Fig. 1C). These corallines can grow over hard substrata as entirely adherent or as leafy crusts resembling their ancestral potato-chip-like cousins. Some develop protuberances or nonflexible branches that give the group further morphological variety. Nongeniculate morphologies range from subtle, low-profile bumps (e.g., Fig. 1E) to conspicuous spindly shapes, to an elaborate matrix of interconnected branches forming hemispherical a heads half-meter in diameter. Branches themselves can be simple pinnacles, ornamented with secondary protuberances, bladelike or even rolled leafy forms creating tubular branches (Fig. 1F). However, the biomechanical constraint of being heavily calcified and inflexible prevents branches from extending too far into fast-moving currents, and most are relatively diminutive—well less than 1 cm in height.

Erect fronds of articulated algae overcome the biomechanical limitations of calcification by producing flexible genicula between calcified segments. This jointed architecture evolved convergently among the green algae, such as *Halimeda* (Fig. 1A) and the coralline red algae (Fig. 1B). Furthermore, paleontological, developmental, and phylogenetic analyses suggest that, even among coralline red algae, articulated fronds evolved from crusts at least three separate times in evolutionary history. Such a striking example of convergent evolution suggests that the development of flexible joints is an adaptive solution for

attaining vertical height under the constraints of calcification. Articulated fronds can be diminutive, such as those produced by the coralline *Yamadaea*, which consist of only a couple segments that extend a few millimeters above the basal crust, or rather large, as in the green *Halimeda* (Fig. 1A) or the coralline *Calliarthron* (Fig. 1B) whose fronds can grow more than 20 cm long. Segment morphologies range from cylindrical to flattened to highly ornate, with a single frond often spanning the entire morphological range from base to apex.

Most calcified algae are firmly attached to hard substrata, but some corallines grow unattached as large balls, called rhodoliths, or as smaller branched forms, called maerl, which look like (and are the size of) a child's "jacks." Often these growth forms develop by breaking free from the substratum and growing unattached on the sea floor while rolling periodically from water motion. Rhodoliths can range from golf ball to basketball size, but the majority are baseball sized. The more diminutive maerls produce biogenic sediments resembling calcified tumbleweeds. Both rhodolith and maerl deposits are scattered globally. A so-called "coral" beach on the northwest coast of Scotland is actually composed of maerl fragments of a free-branching coralline alga.

ECOLOGY: DOMINANCE, HABITATS, AND INTERACTIONS

Calcified algae are ubiquitous biogeographically and span the depth gradient from the intertidal zone to the deepest reaches of the benthic euphotic zone. It is their remarkable abundance and absence under certain conditions that tells us much about the ecology of this group.

Although calcified algae can dominate tidepools and shallow subtidal habitats, they are less common or absent from middle to upper intertidal regions because they are susceptible to drying out (desiccation). Unlike noncalcified "fleshy" seaweeds, whose thalli may be as much as 80–90% water, some articulated corallines, such as *Calliarthron,* are less than 30% water and dry out very quickly. Densely branched calcified turfs, such as some *Corallina* species, resist desiccation by retaining water within their fronds during low tide, like paint between the bristles of a paintbrush. As a result, this growth form can live much higher in the intertidal zones than other coralline algae can. The coincidence of low tides and high temperatures can cause emergent corallines to bleach, often killing part, but not necessarily all, of their thalli.

The abundance and ecological success of crustose coralline algae is at first glance enigmatic. As a group, they are among the slowest-growing algae in benthic marine photic zone and are frequently overgrown and outcompeted for space by fleshy algae. Yet they thrive under conditions of frequent and intense physical and biological disturbance. Calcareous algae are the only forms found where sand and small rocks scour the sea floor, and they thrive where herbivory is most intense. Coralline algae often dominate wave-exposed habitats, such as the shallow seaward face of algal ridges, where water velocities dislodge other organisms or prevent them from persisting.

Shallow-water crustose corallines also appear to have a symbiotic dependence on intense and frequent grazing by herbivores, such as limpets, sea urchins, and parrotfish. For example, the long spined sea urchin *Diadema antillarum* was extremely abundant and the dominant herbivore throughout the Caribbean until 1983 and 1984, when it suffered a mass mortality throughout the Caribbean, during which over 90% of the population died. As a result, fleshy algae rapidly increased in abundance, and the entire coralline community declined 80–100% at monitored sites on the coral reefs of St. Croix and Jamaica.

The relationship between scraping herbivores and corallines is a long-standing one. Paleontological studies have found that as sea urchins and grazing parrotfish evolved and became abundant in shallow seas, so too did the crustose corallines diversify and come to dominate many coastal zones. In the western North Atlantic, a particularly tight algal–herbivore association evolved. The species *Clathromorphum circumscriptum* (closely related to the species depicted in Fig. 1C) is commonly associated with the limpet *Tectura testudinalis*. Limpet grazing benefits coralline thalli by removing epiphytes that would otherwise shade or smother the calcified thalli, while the regions where the alga grows (its meristem) and reproduces (its conceptacles) remain safely beneath the heavily grazed thallus surface. This coralline is also a nursery habitat for limpets, and if they are removed, the *Clathromorphum* dies. There are many examples of similarly tight associations. For example, the chiton *Choneplax lata* bores into and eats the tropical coralline *Porolithon pachydermum,* keeping the alga free of epiphytes; the tropical crab *Mithrax sculptus* lives between and is protected by the calcified branches of the crustose coralline *Neogoniolithon strictum* and performs a similar cleaning duty. Thus, many plant–herbivore interactions between crustose corallines and their grazers are more of a positive facilitation than the negative interaction most commonly seen between fleshy algae and their herbivores.

Unlike their crustose counterparts, erect calcified fronds are more often fodder for hungry herbivores,

although their calcium carbonate makes them far less preferable than fleshy seaweeds. Being more susceptible to herbivores, articulated calcified algae use a wider variety of herbivore deterrents. For example, the articulated green alga *Halimeda* fortifies its thallus with chemical herbivore deterrents as it produces new (uncalcified and relatively vulnerable) segments at night, when herbivory is low or absent. By the next day the segments have hardened, and the combination of calcium carbonate and chemical deterrents is sufficient to minimize subsequent herbivore damage. Besides being relatively inedible, the calcium carbonate in algae can deter grazing fish that use acid to digest their algal prey. Thus, even the lightly calcified algae, such as the brown alga *Padina,* may receive some protection from herbivores.

Many organisms have evolved to live in or on calcified algae as an alternative hard substratum. For instance, certain species of bryozoans, hydroids, fleshy seaweeds, and calcified crusts grow directly on articulated coralline fronds in tidepools. Amphipods and polychaetes wrap themselves in calcified articulated fronds, and worms burrow into calcified crusts. Abalone, sea stars, limpets, chitons, and reef corals often recruit to coralline algae. Reef corals, in particular, chemically detect, metamorphose, and settle on (Fig. 1D) or near coralline algae, which presumably indicate favorable coral habitat. Similarly, many corallines grow as epiphytes on sea grasses and other algae and on the shells of snails, mussels, and barnacles. Occasionally the thickness of coralline accumulations far exceeds that of the shell of the organism on which it is growing.

Several species of calcareous green algae including *Halimeda* and less heavily calcified forms of *Udotea* and *Penicillus* are uniquely capable of colonizing sandy substrates in tropical lagoons. These "rhizophytic" algae anchor themselves in the sediment with hairlike cells called rhizoids. Rhizoids can extract nutrients from substrates as do the roots of higher plants. These rhizophytic algae add organic matter and stabilize sediments, thereby facilitating the colonization and succession of sea grasses. Similarly, articulated coralline algae facilitate the succession of California's intertidal seagrass *Phyllospadix* by literally snagging its seeds in their fronds. This allows the angiosperm to take root and come to dominate patches in the intertidal zone.

By incorporating calcium carbonate into their thalli, this phyletically and morphologically diverse group of algae became unique and ecologically important. As a group, calcified algae occupy more biogeographic zones and live in a wider range of habitats than most other algae or other primary producers in the sea. They coexist with deep grazing herbivores, live on many types of substrata, and provide critical habitat for numerous other organisms.

Increasing metabolic costs associated with global climate change may offset the advantages of calcification. Carbon dioxide in our atmosphere combines with water to form carbonic acid, which rains back to Earth. As this greenhouse gas builds up in our atmosphere, the world's oceans are becoming increasingly acidic, which in turn increases the energy required to calcify. Recent increases in disease may indicate that oceans are becoming a more stressful environment for calcified algae.

SEE ALSO THE FOLLOWING ARTICLES

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ALGAL BIOGEOGRAPHY

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Algal or seaweed biogeography is a discipline that addresses two essential questions: What are the patterns of species distributions, and how are these distributions influenced by the history of the earth? The former question addresses species ranges as a function of

contemporary interactions with their environment (ecological), whereas the latter attempts to reconstruct the origin, dispersal, and extinction of species (historical). In recent decades, a third question has become increasingly important: How are biogeographic patterns influenced by human activities?

WHAT IS BIOGEOGRAPHY?

Biogeography is a hypothesis-driven observational science, rather than an experimental science, because its spatial and temporal scales are far too large for experimental manipulation. Sometimes, however, nature provides an experiment in the form of large-scale natural disturbances such as the emergence of new volcanic islands, widespread destruction by a volcanic eruption, or ice ages. Experiments of a different sort are presented when human activities lead to the elimination or introduction of species and the connection or disruption of previously separated or connected populations. Both natural and human-induced disturbances offer unique opportunities for biogeographers to understand the whys, hows, and why nots of species distributions.

Three stimuli have led to the emergence of biogeography as a widely respected science since the 1950s and 1960s. First, biogeography evolved from a descriptive science coupled with traditional taxonomy, to a concept-orientated discipline concerned with developing and testing biogeographic hypotheses using mathematical, statistical, and modeling analyses. Second, new technologies offered biogeographers powerful tools for data collection. For example, computers permit rapid compilation, manipulation, and analysis of enormous quantities of many different data sets, including species distributions and climate, oceanographic, and geological data. Orbiting satellites, surface and submerged buoys and vessels, and ground-based systems automatically collect real-time measurements of the earth's environment. Finally, numerous molecular methods and corresponding analyses have been developed over the past decade that enable biogeographers to develop increasingly accurate spatial and temporal reconstructions of a species' history and migrations. As a result of molecular methodology, a new specialization of biogeography has emerged, termed phylogeography, which tracks, in space and time, "lineages" within a species based on the similarity of various DNA sequences. The molecular methods also have been important for studying those species (seaweeds and many invertebrates) that do not leave a fossil record because of their body structures (e.g., soft) or habitats (e.g., wave-swept rocky substrates).

The third factor contributing to the growth of biogeography as a discipline is that human societies have recognized the critical importance of understanding and managing their impact on the earth. Interest in the late 1960s and early 1970s focused on relatively small-scale problems, but beginning in the 1980s, it became apparent that humans were radically transforming the earth on a regional and global scale. Consequently, there is a critical need for biogeographers to measure and predict these changes as well as to find ways to manage or minimize the effects.

BIOGEOGRAPHIC DATA

The Temperature Contribution

What kinds of data are collected by marine biogeographers, and how are the data analyzed? For seaweeds inhabiting wave-swept rocky intertidal shores, biogeographers compile maps that correlate species presence/absence (preferably biomass or areal cover) with key variables such as air and water temperature and degree of physical isolation. Both air and water temperatures are important factors influencing the distribution of intertidal organisms, because they profoundly affect survivorship, growth, and reproduction.

Long-term temperature data are used to generate surface seawater isotherms (boundaries of the same average water temperature averaged over many years), which are combined with both experimentally determined temperature limitations and distributional maps of the species to identify species ranges. By examining maps for several species, biogeographers can identify areas that are characterized by drastic changes in species composition over a relatively small distance.

The Geological Contribution

The notion that continents moved to their present position from a different configuration in the past was presented to a very skeptical scientific community in 1912 as the theory of continental drift. The theory was not widely accepted until the 1960s, however, when the theory of plate tectonics provided a realistic mechanism for the movements of continents. Briefly, the theory of continental drift states that, about 230 million years ago, the land masses observed today formed a single land mass called Pangaea (Fig. 1A), which, about 225–200 million years ago, split into Laurasia (the modern Northern Hemisphere continents) and Gondwanaland (modern Antarctica, South America, Africa, Australia, and India) (Fig. 1B). Gondwanaland began to separate
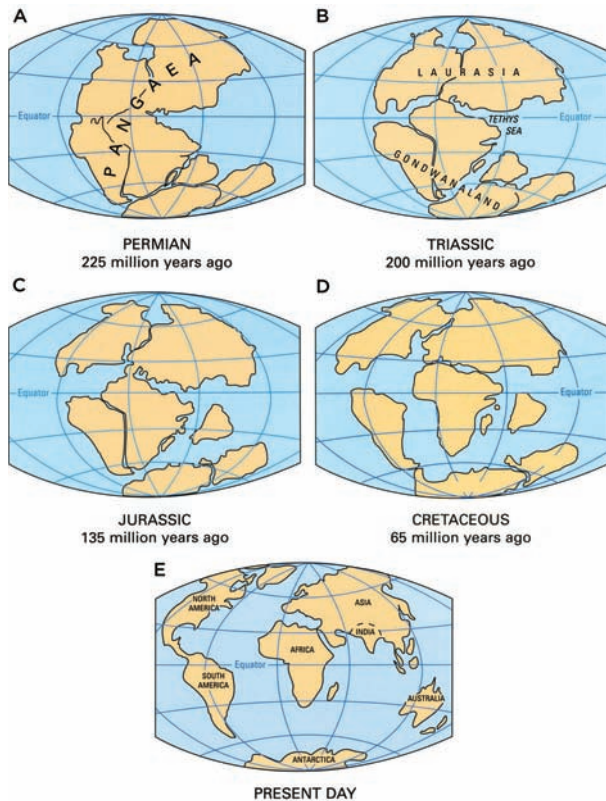
FIGURE 1 Continental drift. (A) The supercontinent Pangaea, which began to fragment approximately 225 million years ago during the Permian Period of geological history. (B–D) Configurations of land masses during subsequent periods; (E) present land masses. Because continental drift is a dynamic process, the configuration of continents will change continuously, albeit in a predictable manner, as subsequent millennia accumulate. Map from Kious and Tilling (1996).

into its component continents about 200 million years ago (Fig. 1C), whereas North America separated from the European/Asian land mass about 100 million years ago (Fig. 1D). The present distribution of land masses (Fig. 1E) was apparent about 10 million years ago, but the process of land mass expansion and contraction is a dynamic process. For example, the Pacific Ocean is becoming smaller each year and will disappear in about 200 million years, whereas the Atlantic Ocean is getting larger.

Vicariance and dispersal are two mechanisms proposed to explain biogeographic patterns. According to the vicariance mechanism, species distributions reflect the splitting of an ancestral population by the development of environmental barriers (physical obstructions or perhaps drastic differences in air or water temperature) that prevented interbreeding between the separated subpopulations. These separated subpopulations evolved into separate species, all of which are closely related because of their common ancestor. The dispersal mechanism maintains that ancestral populations dispersed from a center of origin to found new species and that it is not necessary to invoke physical barriers as a separating mechanism. Although the relative contribution of each mechanism has been heavily debated, both can explain the biogeographic distributions that we now observe.

GENERAL PATTERNS OF SEAWEED DISTRIBUTION

Several general patterns of seaweed distribution are of interest to marine biogeographers. One pattern is that tropical regions exhibit a high degree of similarity in species composition on a worldwide basis. The most accepted explanation is that, for the last 100–150 million years there always has been a warm-water belt encircling the globe, thereby ensuring connection between widespread populations and maintenance of gene flow. The belt has been closed by land bridges only relatively recently: once when the connection between the Mediterranean Sea and Indian Ocean (the ancient Tethys Sea) was closed about 17 million years ago, and again when the connection between North and South America (Isthmus of Panama) was formed 3–4 million years ago.

Another pattern is that cold-water species of the Northern Hemisphere differ fundamentally from those in the Southern Hemisphere, because increased cooling throughout the Tertiary Period (65 to 2 million years ago) and subsequent glaciations of the Quaternary Period (2 million years ago to present) allowed species to evolve in each hemisphere. Although some cold-water species might have moved between the hemispheres during the glacial periods, when the tropical warm-water belt became narrower and cooler, no exchange could occur during the interglacial period, when the tropical region became much broader and warmer. Consequently, the species in each hemisphere evolved separately, leading to the fundamental differences observed today.

A different pattern is that highly related or identical seaweed species occur over vast distances in the Southern Hemisphere. Because the West Wind Drift (a relatively fast west-to-east current) is not blocked by barrier-forming continents in the Southern Ocean, dispersal of marine organisms is unimpeded, thereby promoting a high degree of connectivity (and therefore gene flow) between widely separated populations. For example, in

the ecologically important giant kelp *Macrocystis pyrifera,* sequence analysis of a nuclear gene region has shown that there are far fewer differences between populations in Chile, South Africa, Australia, and New Zealand than there are between populations in the much smaller region from Baja California, Mexico, to Central California, United States.

A final pattern of interest is that species of seaweeds and invertebrates in the North Pacific are vastly different and more diverse than those in the North Atlantic, because the North Pacific is much older than the North Atlantic. Nevertheless, there has been exchange of species between the two areas at various times during the last 3 million years, and the advent of molecular methodology has stimulated recent research on the North Pacific–North Atlantic exchange.

THE NORTH PACIFIC–NORTH ATLANTIC EXCHANGE

The much higher percentage of land mass in the Northern Hemisphere relative to the Southern Hemisphere, coupled with sea level changes associated with the Ice Ages, increases the complexity of oceanic circulation and severely restricts exchange between the North Pacific and North Atlantic (compared to the ease of exchange between the South Pacific and South Atlantic). Five phases over the past 265 million years are central to understanding the North Pacific–North Atlantic exchanges with respect to marine organisms, including intertidal seaweeds. During Phase 1 (some 230–65 million years ago), the Pacific Ocean was wide open to the cold-water Arctic Ocean, whereas the North Atlantic was not formed until about 165 million years ago, when North America and Europe began to drift apart. In Phase 2 (about 65–50 million years ago), the North Pacific was separated from the Arctic Ocean by the Bering Land Bridge, creating a vast cool-water area that undoubtedly facilitated evolution of cool-water species. The isolated and cold-water Arctic Ocean may have served as a refugium for species that later colonized the North Atlantic. During Phase 3 (50–6 million years ago), the North Atlantic was connected to the Arctic Ocean, whereas the North Pacific was still separated by the Bering Land Bridge. Two major cooling events occurred in this phase, one about 40 million years ago and another from 10 to 5 million years ago; the latter leading to global glaciation and worldwide fluctuations in sea level. In Phase 4 (6–3 million years ago) the Bering Strait opened, connecting the North Pacific and North Atlantic via the Arctic Ocean; additionally, the Isthmus

of Panama formed, separating the tropical Pacific and Atlantic Oceans. These two events led to a profound change in the major surface currents of all oceans and a further decline in average sea surface temperatures. Examination of over 100 fossil mollusc species has revealed that before the onset of Pleistocene glaciation (1.6 million to 11,000 years ago), at least eight times more species migrated from the North Pacific to the North Atlantic than vice versa.

QUATERNARY GLACIATIONS AND THE LAST GLACIAL MAXIMUM

For many biogeographers, Phase 5 is the most exciting in terms of the North Pacific–North Atlantic exchange. During this phase (2 million to 18,000 yrs ago), and especially in the last 130,000 years, the Bering Land Bridge repeatedly emerged and submerged as a result of numerous glacial (ice-building, sea level decline) and interglacial (ice reduction, sea level rise) periods, leading to closures and openings of the North Pacific–North Atlantic connection. The advance and retreat of vast ice sheets over much of North America and Northern Europe profoundly shaped the distributions of virtually all marine and terrestrial species currently found in both areas. During cold glacial periods, the diminution of the warm-water tropical belt allowed the dispersal of Arctic and Antarctic species across the equatorial area, which then became isolated during the following interglacial. Additionally, lower sea levels (130 m lower than present) during the last glacial maximum (LGM) (20,000–18,000 years ago) increased the potential for dispersal of intertidal species. As sea levels rose when the ice receded, broad species distributions were fractured, leading to increased isolation of populations and subsequent speciation.

How have the last glacial–interglacial periods influenced the distributions of rocky shore intertidal seaweeds in the Northern Hemisphere? A traditional analysis of the number of seaweed species (ignoring those species introduced by humans) reveals a significant gradient: highest numbers in Northern Europe, intermediate in Iceland, and fewest in the Canadian Maritime Provinces and New England. The gradient also is apparent in invertebrate species and is most easily explained by post-LGM dispersal from Europe. During the LGM the North American ice sheet extended as far south as Long Island, New York. Because no rocky substrates exist south of Long Island, essentially all species associated with rocky substrates in the northwest Atlantic

became extinct. Iceland also was covered by ice, leading to a similar extinction of rocky shore species. However, ice sheets in Northern Europe covered only Scandinavia and Great Britain, leaving uncovered to the south vast areas of rocky shores, which served as glacial refugia. As the ice sheets retreated in Northern Europe from 20,000 to 7000 years ago during the current interglacial period, species from the refugia in Southern Europe colonized first Northern Europe, then Iceland, and finally, the Canadian Maritimes/New England area.

Many species of seaweeds occur both in the North Pacific and North Atlantic Oceans, but in most cases, identity of the species is based on morphological similarity. It is very possible that species common to both oceans may in fact be distinct species despite similar morphologies. With the development of molecular methods, seaweed biogeographers have been able to detect the presence of sibling or cryptic species, as well as to examine colonization and migration pathways in the North Pacific and North Atlantic.

Fucus (Heterokontopyta, Phaeopyceae, Fucales)

Rockweeds are a dominant component of the biomass associated with rocky shores throughout the North Pacific and North Atlantic Oceans and are important facilitator species, because they provide shelter and food for virtually all intertidal invertebrates. The genus *Fucus* is one group of rockweeds that has been extensively studied in the last decade. Molecular work has determined that the Fucaceae, the family containing the genus *Fucus* as well as several other genera, probably evolved and diversified in southern Australia. An ancestral *Fucus* species migrated across the equatorial region to the Northern Pacific from 35 to 7 million years ago during a period of global cooling. After the Bering Strait opened (6–3 million years ago), one or two ancestral *Fucus* species migrated to the North Atlantic via the Arctic Ocean and radiated into a wide range of habitats. Currently, far more species of *Fucus* are present in the North Atlantic, where they are found from the high intertidal to shallow subtidal of rocky open coast regions as well as in calm, brackish-water environments, than in the North Pacific.

During the LGM, the advancing ice and cold water forced most European species of *Fucus* to glacial refugia in the south (including the Mediterranean). As the ice retreated during the early portion of the current interglacial period, populations began a rapid colonization of areas to the north, but at the same time the former

refugial areas became too warm for the cold-water *Fucus* species. Today, *Fucus* species are restricted to only three areas of the former southern refugium: the Canary Islands, the northwestern shores of Morocco (an area of localized upwelling and cool water), and the northern Adriatic Sea. The latter population is a glacial relict, surviving from a formerly Mediterranean-wide distribution. It clearly has been geographically isolated from all other *Fucus* species and populations for some 18,000 years, and just as clearly, it has diverged as a new species during this time. The Canary Island and Moroccan populations also are highly isolated and are likely to be nascent species.

Some areas, previously thought to be devoid of intertidal seaweeds because of ice coverage and low temperature, recently have been revealed to be glacial refugia. For example, several different types of mitochondrial DNA sequences are present in populations of *F. serratus* in the southwestern Ireland and western English Channel areas, implying persistence of populations during the LGM. As the ice receded, individuals from southwestern Ireland possessing one type of mitochondrial DNA rapidly colonized the northern half of Great Britain, the entire western coast of Norway up to the Russian border, and the Kattegat strait between Denmark and Sweden. Thus colonization was due to a single group of highly related colonizers (=colonization sweep) rather than to several groups of unrelated individuals.

Chondrus (Rhodopyta, Gigartinales)

Chondrus is another ecologically and economically important intertidal seaweed genus. Several species are present in the western North Pacific, but only one, *C. crispus,* is found in the North Atlantic, where it often forms large and nearly monospecific stands in the low intertidal zone. Recent molecular analysis has revealed that, like *Fucus,* the genus *Chondrus* evolved in the North Pacific and an ancestral species migrated into the North Atlantic via the Arctic Ocean within the past 5 million years. But unlike *Fucus,* the ancestor did not radiate into numerous species or habitats in the North Atlantic.

Palmaria palmata (Rhodophyta, Palmariales)

Molecular analyses of the red alga *Palmaria palmata,* known as dulse and commonly found on Atlantic rocky shores, also are enhancing our understanding of post-LGM biogeography. Many different types of chloroplast genes are found in *Palmaria* populations in the western English Channel area, but only one occurs in the areas further north. The pattern is essentially identical to that

displayed by *F. serratus,* thereby strengthening considerably the argument for glacial refugia along the southwestern Irish coast and in the western English Channel, followed by a rapid colonization sweep to the north by a single, related group of individuals.

Acrosiphonia arcta (Chlorophyta, Acrosiphoniales)

Molecular methods have traced the biogeographic track of the intertidal green alga *Acrosiphonia arcta:* from Chile, to the eastern North Pacific Ocean from California to Alaska, to Greenland and Iceland, and finally, to northern Europe. Although future molecular analyses may well reveal the presence of several cryptic species within this wide distribution, it is clear that the genus has migrated from the Southern Hemisphere to the Northern Hemisphere and from the North Pacific to the North Atlantic. Again, as for all species of seaweeds, only molecular methods can reveal the history, because fossil records are highly unlikely.

HUMAN INFLUENCES ON BIOGEOGRAPHY

In recent years it has become increasingly clear that humans have profoundly impacted the distributions of marine species through local extinction, inadvertent species introductions, and modifications of species habitats. Shipping and the aquaculture and fishery industries are the primary means by which marine species have been introduced to new areas. Because marine species have been transported from one area to another by maritime activities for millennia, several marine biogeographers believe that the long history of species introductions almost certainly has corrupted our present worldwide views of coastal biogeography.

Although biogeographers can sometimes recognize that a marine species has been introduced within recent times, they often are unable to identify the source of the introduced species. Molecular techniques and analyses, however, have provided clues. For example, the rockweed *F. serratus* was documented as an introduction to Nova Scotia in the late 1800s, and molecular analysis has revealed Northern Ireland as the likely source. Similar molecular methodology combined with historical records has determined that the introduction of *F. serratus* into Iceland originated from the Oslo Fjord region of Norway sometime between ca. 1750 to 1900, whereas its introduction to the Faeroes originated from an Icelandic population between 1982 and 1997.

Another example of a human-mediated introduction is the green seaweed *Codium fragile* ssp. *tomen-* *toides.* Originally a native of the cool waters off northern Japan, it has expanded its range throughout the world, first appearing on the Dutch coast around 1900 (probably associated with oysters imported for aquaculture), then rapidly spreading along European coastlines and the Mediterranean Sea. It was reported in Long Island Sound (United States) in 1957 and expanded north into the Gulf of St. Lawrence by 1996. In the Pacific Ocean it was introduced to San Francisco Bay (United States) and New Zealand in the 1970s, Australia in the mid-1990s, and Chile in 2001. Molecular analysis has revealed at least two separate introductions: the North Atlantic and Chilean populations originated from a set of one to three regions of Japan, whereas the Mediterranean populations stemmed from a different set of one to three regions of Japan.

The field of biogeography currently is experiencing a vigorous period of productivity, largely because of advances in technology and analysis. Consequently, biogeographic studies of seaweeds have increased markedly in the last decade, and the growth is expected to be exponential in the years to come. Regardless of whether or not a species distribution has been influenced by human maritime activities, source-sink relationships can be identified, and pathways of dispersal will be determined. Biogeographers also have the ability to distinguish the presence of cryptic species from species groups with near-identical morphology. Consequently, our present views of biogeographic patterns, global biodiversity, and speciation undoubtedly will expand.

SEE ALSO THE FOLLOWING ARTICLES

Biodiversity, Global Patterns of / Dispersal / Introduced Species

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ALGAL BLOOMS

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When the biomass of a group of phytoplankton increases excessively at a spot in the ocean, the microalgae are said to bloom. Algal blooms are highly colored and can be seen by the naked eye and monitored by satellites. There are many types of algal blooms, differing in how they form, the kinds of phytoplankton they contain, and the effects they have on secondary production.

GENERALITIES

Algal blooms begin with the rapid growth of phytoplankton in response to an ample supply of light for effective photosynthesis and an oversupply of plant nutrients for cell growth and division. Physical processes are very important in establishing these bloom conditions. High algal biomass (Fig. 1) accumulates only if primary production of phytoplankton particulate organic carbon

FIGURE 1 A spring bloom of phytoplankton dominated by diatoms (mostly *Skeletonema costatum*) in Tronheim Fjord, Norway. Photograph courtesy of G. Johnsen.

(POC) is faster than the sum of all the ways phytoplankton POC can be lost from the environment (respiration, excretion, grazing, sinking, advection). Most algal blooms support major increases in secondary production (biomass accumulated at higher trophic levels). As blooms end and phytoplankton die, they release large amounts of dissolved organic carbon (DOC) that support microbial communities and the regeneration of plant nutrients. The high metabolic activity of the microbes consumes oxygen gas from the surrounding water. If the oxygen is not resupplied by water motion, bloom waters approach anoxia (no oxygen) and animals are suffocated. In aging blooms, dead and dying phytoplankton tend to aggregate and sink as large particles (marine snow). Algal blooms export a large amount of particulate organic carbon to benthic communities and can be a significant food source for detritivores. At any time, blooms may be physically swept away by currents as coastal circulation changes.

SPRING DIATOM BLOOMS

The most common and most predictable algal blooms occur in the spring months at temperate latitudes and during spring–summer months at polar latitudes (Fig. 2). They last from weeks to months. These spring blooms are highly productive, accounting for more than 10% of the annual primary production by phytoplankton at some locations. Grazing of phytoplankton appears especially efficient in typical spring blooms compared to blooms associated with upwelling.

The seasonality of spring blooms help explain how they are formed (Fig. 3). As winter and spring winds subside, nutrients are abundant and increased sunlight penetrates and starts warming the upper water column. Warm water is less dense than cold water and thus remains at the surface (thermal stratification), forming an upper mixed layer (UML) in which phytoplankton and nutrients are confined. Increased warming causes shallowing of the mixed layer depth (MLD), bringing the thermocline closer to the surface, and the seasonal increase in sunlight causes deepening of the photic zone. For effective photosynthesis and plant growth, the stable density stratification of water must occur near enough to the surface so that phytoplankton are not mixed out of the photic zone.

To understand and predict the timing of the start of spring blooms, the concept of a critical depth was introduced by Harald Sverdrup in the 1950s. He defined critical depth as the depth above which total phytoplankton photosynthesis in the water column is equal to total

Chlorophyll a Concentration (mg /m^3)
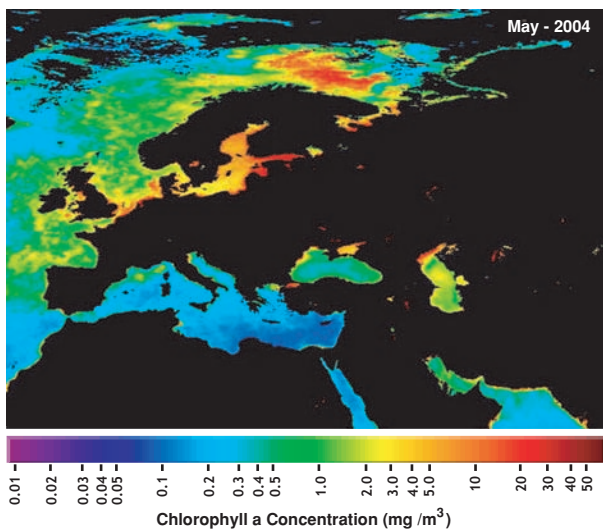
FIGURE 2 Remote image of chlorophyll *a* distribution of the marine waters of northwest Europe, averaged for May 2005. Note the many distinct phytoplankton blooms and their large-scale coverage. Image courtesy of Modis Land Response Team, NASA/GSFC.
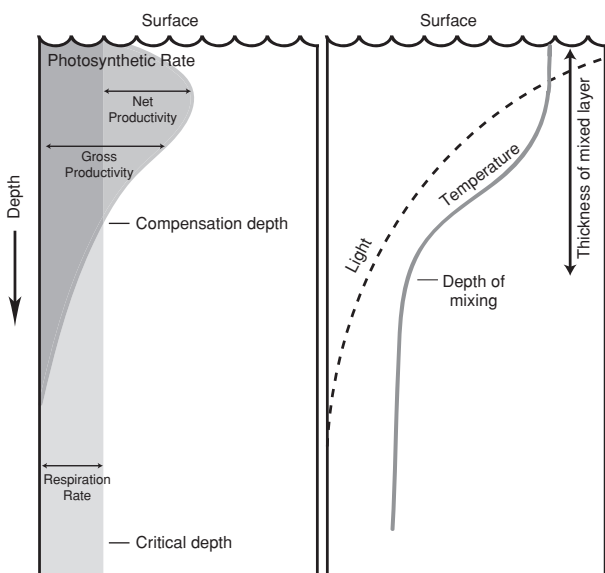
FIGURE 3 (Right) Examples of depth profiles of photosynthesis and respiration rates of phytoplankton and how calculations would be made of gross and net primary productivity. (Left) Examples of depth profiles of light availability and water temperature. See text for discussion of critical depth and upper mixed layer.

phytoplankton respiration in the water column. Subtracting rates of phytoplankton respiration from rates of photosynthesis gives the value of net primary production (NPP) (Fig. 3), a measure of the growth potential of phytoplankton. Net primary productivity occurs only above the critical depth. If the thermocline is deeper than the critical

depth, phytoplankton will be mixed below the critical depth and total algal biomass will not increase in the upper mixed layer. Bloom conditions are met when the MLD becomes shallower (by further warming) or the euphotic zone becomes deeper (by increasing sunlight). Early field observations of spring blooms successfully used the concept of critical depth to explain the differences in timing of spring blooms observed onshore and offshore and at different latitudes.

Today, a modification of Sverdrup's critical depth is used to predict the timing of spring blooms. It is now recognized that when DOC is abundant, some phytoplankton take DOC into the cells and thereby supplement photosynthesis with heterotrophy. Their combined rates determine the growth rate of phytoplankton. Furthermore, the rate of loss of phytoplankton organic carbon by respiration has been expanded to include losses due to the release of dissolved organic carbon from phytoplankton by excretion. Excretion can be significant as phytoplankton transition from exponential to stationary phases of growth. Other loss processes of phytoplankton particulate inorganic carbon include grazing, sinking, and advection out of the area.

Spring blooms have recognizable stages. In the first stage, phytoplankton growth accelerates and phytoplankton particulate inorganic carbon increases. With abundant silicate in the nutrient-rich waters, diatoms grow faster than other phytoplankton groups and come to dominate the microalgae assemblage in the bloom. These diatoms are a high-quality food source for herbivores. Excretion is small, and the little dissolved organic carbon released is highly susceptible to photochemical and microbial degradation. The second stage is characterized by declining nutrient supply and algal growth rates. Grazing is sufficient to lower total phytoplankton particulate inorganic carbon. A smaller fraction of net primary productivity is going into food chains, because excretion increases greatly and the released dissolved organic carbon pools promote carbon cycling in the microbial loop. The third stage is marked by nutrient stress, senescence, sinking, and induction of survival strategies by bloom phytoplankton. Excretion rates are low unless weakened phytoplankton cells are lysed by viruses. Detritivores begin feeding on abundant aggregates of dead and dying cells (marine snow) that sink and settle on benthic communities. Spring blooms can briefly cycle back to earlier stages if short periods of wind mixing disrupt the thermocline and additional plant nutrients are mixed upward. These episodic inputs of new nutrients can stimulate new production and a brief resurgence of rapidly growing diatoms,

thereby prolonging the lifetime of spring blooms from weeks to months.

OTHER TYPES OF PHYSICALLY FORCED ALGAL BLOOMS

Fall turnover occurs when air temperatures begin to cool surface water temperatures. The colder water sinks and disrupts the thermocline. Wind-driven mixing accelerates fall turnover. Nutrients from the depth are mixed upward and cause an algal bloom that promotes secondary production. Due to the loss of the UML and the seasonal decline in sunlight, turnover blooms tend to be smaller in algal biomass and do not last as long as spring blooms.

Wind-driven upwelling along coastlines brings large volumes of cold and nutrient-rich waters from depth to the surface. Large near-surface blooms of diatoms result and are evident when matching satellite images of chlorophyll (Chl) biomass with images of cold surface temperatures. Bathymetric upwelling (or upward mixing) over the continental shelf brings deep waters closer to the surface, but not necessarily all the way. Blooms of diatoms can form at depth, and their presence may be missed by satellite images. The circulation patterns associated with both types of upwelling include transfer of large amounts of phytoplankton particulate inorganic carbon to downstream benthic communities. When upwelling ceases, diatom growth continues until nutrients are depleted and then they sink in large quantities. There are major wind-driven upwelling sites along the coasts of California, Peru, and parts of Africa. The high NPP in these waters supports major fisheries. Bathymetric upwelling occurs where bottom currents or subsurface intrusions of offshore currents upwell in response to interactions with the bottom. Areas of significant bathymetric upwelling associated with high NPP are found along coasts of the southeastern United States, eastern Australia, and the west Antarctic Peninsula. There are many other locations where both types of upwelling have not been studied.

Ice-covered shores can form algal blooms in the thin layer of fresher surface waters that is generated as the sea ice melts in the spring. Ice edge blooms occur before spring blooms in polar fjords and bays. Ice edge blooms can persist between wind-mixing events, as long as there is a melting marginal ice zone (MIZ) associated with the retreating sea ice and sufficient light to promote photosynthesis. The MIZ of the Antarctic and Arctic cover enormous areas of the coastal ocean. The algal biomass is a major food supply in early spring for zooplankton and herbivorous fish and larvae. MIZ phytoplankton biomass settles to the bottom and supports rich benthic communities.

There are many other algal blooms associated with other distinct physical and chemical environments in the ocean. For instance, cryptophyte blooms form in glacial ice melts that cover ice-free environments along the west Antarctic Peninsula in spring and summer. Water circulation generates mesoscale and submesoscale eddies that bring plant nutrients into the photic zone and promote episodic increases in NPP. The outflow of rivers and streams into the ocean promote algal blooms in waters generally heavy in organic and mineral particulate matter. Rain can stimulate miniblooms (often picophytoplankton). The highly adaptable, opportunistic, and diverse nature of marine phytoplankton communities contribute to their success in creating bloom environments.

HARMFUL ALGAL BLOOMS

Harmful algal blooms (HABs) disrupt existing ecosystem balance in many different ways. They may reduce or eliminate sunlight reaching submerged plants, lead to anoxic conditions that suffocate animal and plants, or sink en masse to bury benthic communities. There are HABs that produce chemical toxins that sicken and kill animals, including humans. The frequency of toxic HABs appears to be increasing and may be linked to eutrophication in the coastal zone.

Red tides are blooms of dinoflagellates that are rusty red in coloration. They occur worldwide. Not all red tides are harmful, but there are times when anoxia develops at the end of a nontoxic red tide and results in massive fish kills. Anoxia is associated with red tides occurring in the summer, when they occur in warmer surface water that has been stratified a long time without disruption. Red tides arise at other times of year and may lead to anoxia if stratified waters become eutrophic as a result of runoff from agricultural land and sewage outfalls. These runoff events rarely promote diatom blooms, because there is usually little silicate in polluted waters.

Certain dinoflagellate species produce a group of potent neurotoxins called saxotoxins. They are among the most deadly algal toxins and are the cause of paralytic shellfish poisoning (PSP). Saxotoxins build up harmlessly in grazing herbivores but then are passed up the food chain to poison carnivores, including humans. PSP symptoms include numbness, shaky and unsteady movements, incoherence, and, in extreme cases, respiratory paralysis and death. For this reason, harvesting of local shellfish (e.g., mussels, clams, abalone) is prohibited at times when toxic dinoflagellates are present. Saxotoxins are also volatile and may become airborne in regions of high wave action. If inhaled, they irritate the respiratory systems of mammals, including humans.

Another type of toxin, domoic acid (DA), is produced by several diatom species in the genus *Pseudo-nitzschia.* DA is a neuroexcitory amino acid that causes amnesic shellfish poisoning (ASP) in humans. Symptoms include gastrointestinal disorders (vomiting, diarrhea, abdominal pain) and neurological problems (confusion, memory loss, disorientation, seizure, coma). *Pseudo-nitizschia australis* has been increasingly present in California coastal waters following its first discovery in Monterey Bay in 1991, where it caused massive death of seabirds feeding on anchovies that had consumed this toxic diatom. Abundant *P. australis* appears in upwelled waters along the central California coast, and major blooms have been associated with the spring upwelling season. The toxin builds up in several types of fish and shellfish that, when consumed, can account for the death of thousand of marine animals each year, including seals, sea lions, sea otters, whales, dolphins, and seabirds. The magnitude of present toxigenic effects of DA on marine animals and seabirds alter the ecological balance of marine ecosystems along the coast of California.

Brown tides are not known to produce a toxin, but they are harmful to nearby animals and plants in other ways. Blooms are caused by a very small pelagophyte, *Aureococcus anophagefferens.* Brown tides have been observed annually in some coastal embayments and estuaries of the northeastern United States and along the eastern coastline of the United States since 1985. The toxic pelagophyte prefers lower salinity and shallower waters where nutrient loading of sediments is high. Brown tides do not end in anoxia, because they occur where tidal flushing and constant mixing of shallow waters keep their habitat well aerated. Brown tides, however, inhibit grazing by filter feeders (perhaps because of their small size) and block sunlight from reaching submerged plant communities. Brown tides coincide with hard-clam spawning and have been linked to a reduction in larval recruitment. Brown tides have also been linked to the death of large areas of seagrass.

Cyanobacterial blooms are also widespread in the sea. Examples of toxic coastal blooms of cyanobacteria can be found in the Baltic Sea (Fig. 2) and along parts of the Australian and New Zealand coastlines during summer months. They begin with resting cells of *Nodularia spumigena* or *Aphanizomenon flos-aquae* that have overwintered on the sediment and in the water column, respectively. The cue for *N. spumigena* resting cells to reenter their vegetative state is a drop in water salinity brought on by springtime river runoff and ice melt. *N. spumigena* reform resting cells when coastal waters become saltier in late summer. *N. spumigena* produces the toxin nodularin, which inhibits protein phosphatases, which are important regulatory enzymes. Ingestion of water containing *N. spumigena* kills livestock and dogs. Fish and crabs try to avoid these blooms. Humans are prohibited from eating shellfish during times of blooms. *A. flos-aquae* does not produce nodularin but makes other compounds that affect zooplankton and may be responsible for the death of some fish or crustaceans. Both types of cyanobacteria blooms are associated with decreased grazing of some herbivores and inhibition of some microbial activities.

SEE ALSO THE FOLLOWING ARTICLES

Diseases of Marine Animals / Microbes / Nutrients / Phytoplankton / Temperature Change / Upwelling

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ALGAL COLOR

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The colors of intertidal algae range across the visible spectrum from red to green to black. These colors reflect several things: the pigments for photosynthesis among three evolutionary groups of marine plants, the fundamental organization of their bodies, and their physiological ecology including how plants respond to solar radiation (energy budgets) and stress responses to high light that are characteristic of many tidal settings.

EVOLUTIONARY DIVERSITY

Among the plants that emerge with low tides along coastlines worldwide, there are three major groupings of eukaryotic algae, green algae (Chlorophyta), macroscopic

brown algae (class Phaeophyceae, Ochrophyta), and red algae (Rhodophyta). All of these possess chlorophyll *a* (Chl *a*) as the pigment that initiates the first steps of photosynthesis, yet only a few are green like the Chl *a* molecule. The wide range of colors arise from different light-harvesting pigments that funnel light energy to Chl *a* in the process of photosynthesis (Table 1). These light-harvesting pigments are commonly the basis of photosynthesis under low ambient light levels. Ironically, most tidal algae run photosynthesis as shade plants, as if they were growing in the dark understory of kelp forests. This feature puts most tidal algae at risk in sunny intertidal settings.

TABLE 1

Major Photosynthetic and Photoprotective Pigments for Macroalgae by Evolutionary Division

Algal division and common names	Major pigments
Chlorophyta—green algae	chlorophyll *a, b,* siphonein, siphonoxanthin, β-carotene
Ochrophyta (Phaeophyceae)—brown algae	chlorophyll *a,* chlorophyll c_1, c_2, fucoxanthin, β-carotene
Rhodophyta—red algae	chlorophyll *a,* phycobilins (phycocyanin, phycoerythrin, allophycocyanin), α- and β-carotene

Intertidal and shallow subtidal regions in tropical coasts, for instance, are subjected to high levels of light that may even inhibit photosynthesis, leading to photobleaching and death of tissues. Life in higher tidal elevations increases stresses of UV radiation and leads to excessively high light levels. Tidal algae respond with complex and surprising physiological adjustments in these harsh habitats.

A surprising way in which many tidal algae can change color over the course of a low tide is that they dry out in air. Water loss begins instantly as the surface of a plant comes into contact with dry air, regardless of their evolutionary status. Algal tissues even shrink as water loss extends over long tidal exposures. As they dry, many become black (an optical effect that results from decreases in cell volume as tissue water is lost) and almost brittle. To tell which group you are looking at, make sure the plants are well soaked in seawater!

FUNCTIONAL ANATOMY

Besides an evolutionary grouping, algae can also be grouped by their body plan. For the larger forms, photosynthetic tissues are positioned as the outermost tier of cells interacting with the air and marine environments. Typically for the vast majority of large algae, including the phaeophyte *Sargassum*, tissues are composed of exceptionally small, densely packed pigmented cells (cortex) that grade to colorless larger cells (medulla). This tissue type is called a true parenchyma. A parenchymatous organization is the typical anatomy many other brown algae such as *Chnoospora*, a tropical wave zone alga, and temperate intertidal fucoids, for example, *Fucus* or *Pelvetiopsis*.

Several morphological oddities can be found among tidal algae, such as filaments of green algae such as *Cladophora* that, in aggregate, form turfs of stiff uniseriate filaments. A profoundly different body plan comes with siphonous green algae, for example, *Codium*. Siphonous green algae have a startling simplicity—their entire form is a single cell! Upon microscopic examination, their chloroplasts are clearly olive green. Yet in the field, many of these plants appear to be nearly black. The difference in apparent color (black) and actual pigments (green) arises from the density of chloroplasts being so great that they absorb almost all incoming light.

HOW TO INTERPRET ALGAL COLORS IN LIGHT OF ENERGY BUDGETS AND STRESS BIOLOGY

Most marine algae can be identified by their color—green, brown, or red, especially if you are in cool-water intertidal areas. The colors we see are reflected light that these plants are *not* using for photosynthesis. This may sound counterintuitive until you consider that the colors absorbed by these plants are used up as they are converted to excitation energy for photochemistry—called absorptance. Other colors of light have two major routes—those colors not absorbed can pass through the plant (transmittance) or they can be bounced back out of the plant (reflectance). Reflectance actually varies substantially among the three groups of algae as well as between forms that are calcified and not calcified. A selection of these is shown in Fig. 1 to highlight known differences. Absorptance and transmittance can vary as well.

Because these differences in color among tidal and shallow subtidal algae are so easily seen, early researchers in photosynthesis turned to marine algae to quantify how much light different algae absorb for photosynthesis. Drs. Francis Haxo and Lawrence Blinks, working at Hopkins Marine Station in California, pioneered comparative photosynthesis research with their study of absorbance and action spectra for photosynthesis of a selection of brown, green, and red algae; they were the first to quantify the link between high levels of absorbance and
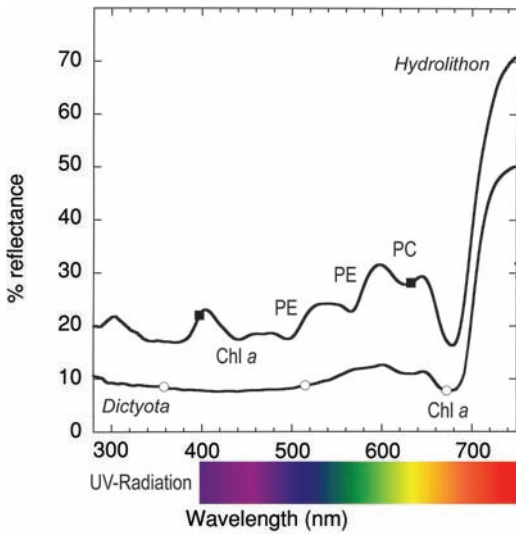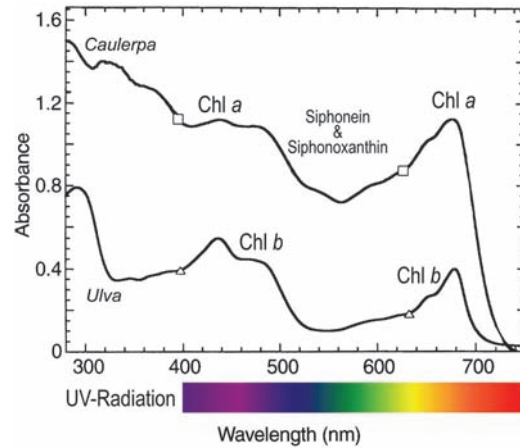
FIGURE 1 *In vivo* reflectance spectra for intertidal and shallow sublittoral species show that algae possess a wide range of reflectance properties. Spectra acquired from *Hydrolithon onkodes,* a coralline alga (■), and *Dictyota acutiloba,* a foliose brown alga (○), show differences in the color and quantity of light reflected from their surfaces. Pigments responsible for reflectance minima indicated by abbreviations. Pigments include chlorophyll *a* (Chl *a*), phycoerythrin (PE), and phycocyanin (PC).

high levels of photosynthesis for algae from kelp forest regions. Recent studies extend this work by examining the overall pattern of light energy as a budget for tidal and shallow reef algae by documenting comparative absorptance, reflectance, and transmittance among algae from high light environments.

Species of tropical tidal algae can absorb from about two-thirds to more than 90% of the light that hits their surfaces. For many algae, reflectance can range from less than 10% to about one-fourth of the light that hits their surfaces (Fig. 1). Transmittance through algal tissues ranges from zero for thick crusts to about one-fourth of the surface light for thin sheets like *Ulva.* Emerging from these studies is a new appreciation of the extent to which plant form regulates pigment densities, photosynthesis, and limits damage from high light. Many of these factors are likely to lead to ecological success.

To illustrate how variable absorbance is across the spectrum, quick inspection of Fig. 2 shows the ability of living *Ulva* to absorb some colors of white light varies from high energy blue photons to lower energy red photons by the action of Chl *a* and *b* (Table 1). This kind of spectrum is called an *in vivo* spectrum because the tissue is alive at the time of the measurement. Two areas of broad absorbance emerge—the blue (400 to 500 nm) and red (600 to 700 nm) regions. Not surprising for this green alga is the low level of absorbance for the central green (500 to 600 nm)

region, because this alga reflects green back to your eye, as was shown by Haxo and Blinks in 1950. This alga is only two cells thick, transmits roughly 27%, and reflects about 7%, with the principal proportion of reflectance in the green spectrum region. Other green algae show differing levels of absorbance across the white light spectrum (e.g., *Caulerpa racemosa;* □, Fig. 2), but they all exhibit the green-window effect—little absorbance in the 500 to 600 nm range.

FIGURE 2 *In vivo* absorbance spectra for intertidal and shallow reef green algae *Caulerpa racemosa* (□) and *Ulva fasciata* (△) show broad absorbances in blue and red colors but substantially less absorbance in green wavelengths by these plants. Pigments responsible for absorbance maxima indicated by abbreviations. Pigments include chlorophyll *a* (Chl *a*), chlorophyll *b* (Chl *b*), siphonein, and siphonoxanthin. (Modified from Beach *et al.* 1997.)
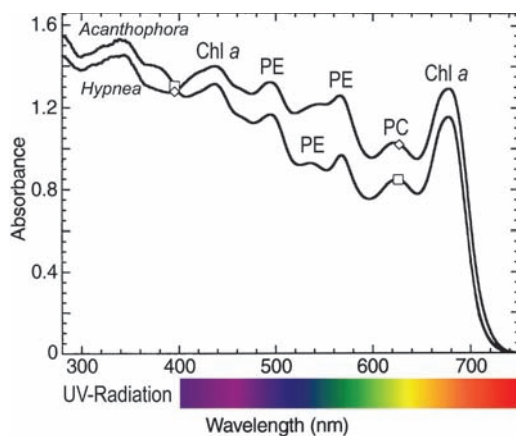
The *in vivo* absorbance spectrum for a brown alga such as *Sargassum* or *Chnoospora* documents some of the differences that you can see by eye (Fig. 3)—the brown color of the plant body tells you that different wavelengths—brown in color—are reflected by brown algae (Fig. 2). These visual changes are the result of increased absorbance of green wavelengths by an unusual pigment, fucoxanthin, that functions in photosynthesis of brown algae.

Absorbance properties of pigments in living organisms are generally additive. As a plant makes more pigments for photosynthesis or photoprotection, the result is to add the absorbance of fucoxanthin on top of the broad blue and narrower red absorbances of the two chlorophyll pigments, Chl *a* and *c*, also found in brown algae (Table 1). Fucoxanthin absorbance adds a new spectral region to the colors absorbed by chlorophylls, extending abilities of brown algae such as *Sargassum* to harvest this abundant color in the ocean as well as coastal environments.
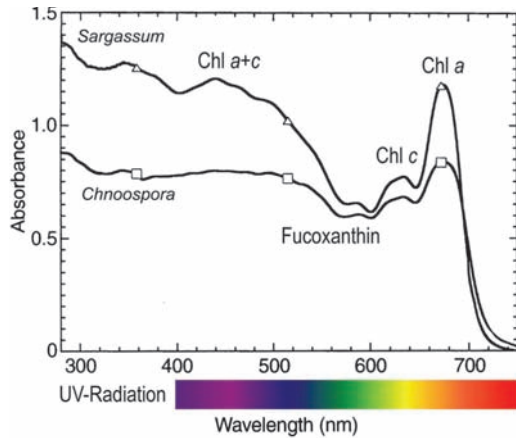
FIGURE 3 *In vivo* absorbance spectra for intertidal and shallow reef brown algae *Chnoospora minima* (□) and *Sargassum polyphyllum* (△) show broad absorbances that include some of the green spectral region. *Sargassum* can dominate tidal benches in tropical settings and absorb significant amounts of light intensity as well as color via its parenchymatous anatomy and pigments. Pigments responsible for absorbance maxima indicated by abbreviations. Pigments include chlorophyll *a* (Chl *a*), chlorophyll *c* (Chl *c*), and fucoxanthin. (Modified from Beach *et al*. 1997.)

In vivo absorbance spectra for red algae such as *Acanthophora, Hypnea*—or many deep red plants and kelp forest understory genera—appear exceptionally complex, with many minor peaks and no green window whatsoever. Overall absorbance can be high, well above 1.0 absorbance units (Fig. 4). There are a series of absorbance maxima in the r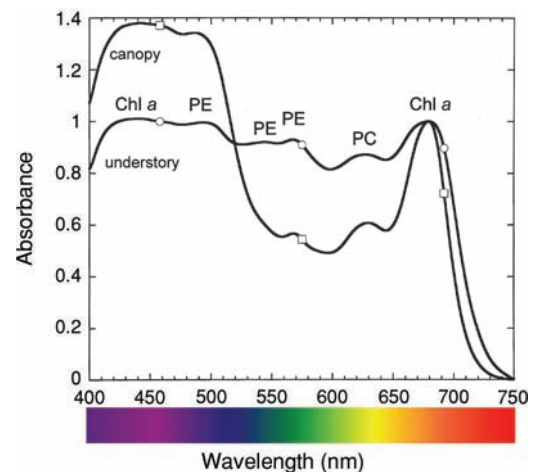ange from 490 to 650 nm, absorbing nearly completely in the green region of the spectrum. This green absorbance arises from two additional pigments not found in green or brown algae: phycoerythrin (PE) and phycocyanin (PC) (Table 1). When phycobilin absorbance is added to the absorbance of Chl *a*, *in vivo* measurements of absorbance are high and effective across nearly the entire visible spectrum. With PE and PC deployed, red algae are very effective at photosynthesis in low levels of ambient light, from deep kelp forest understories to exceptional depths of more than 260 m in clear tropical waters.

PUTTING ALGAL COLOR IN PERSPECTIVE

Dramatic color changes take place when algae grow for extended periods in high-light environments. In many tropical intertidal regions, algae can dominate with a rich assemblage of species and biomass despite the high light stress. The physiological challenges of too much sun, however, are clear. To the human eye, tropical tidal regions are dominated by bright green or golden brown plants. Upon closer inspection, most of these species are actually red algae. They have sunny canopies and shaded bases: such as the golden canopy and purple understory of *Ahnfeltiopsis concinna* (Figs. 5, 6). Our research tool, *in vivo* absorbance spectra, documents remarkable physiological adjustments by the canopies of red algae to life in high-light habitats.

FIGURE 4 *In vivo* absorbance spectra for intertidal and shallow reef red algae *Acanthophora spicifera* (□) and *Hynpea musciformis* (◇). These two red algae can dominate tidal benches or shallow reef regions, adjusting their pigments in response to light levels. Pigments responsible for absorbance maxima indicated by abbreviations. Pigments include chlorophyll *a* (Chl *a*), phycoerythrin (PE), and phycocyanin (PC). Modified from Beach *et al*. (1997).

FIGURE 5 *In vivo* absorbance spectra for *Ahnfeltiopsis concinna* canopy (□) and understory (○). Among red algae, this alga is remarkable in the extent of color change over a short 10-cm distance from canopy to understory portions of the same plant. Pigments responsible for absorbance maxima indicated by abbreviations. Pigments include chlorophyll *a* (Chl *a*), phycoerythrin (PE), and phycocyanin (PC). Reproduced from Beach and Smith (1996) with permission of the *Journal of Phycology*.

FIGURE 6 *Ahnfeltiopsis concinna*, a common intertidal alga, with canopy (yellow) and understory (red) tissues exposed by the photographer who turned over the upper canopy. Tidal benches with this alga are single-species stands where the canopy shades the basal tissue so substantially that the plant synthesizes a full complement of shade pigments to live in near-darkness. Photograph by K. Beach. Reproduced with permission of the *Journal of Phycology*.

In response to high light, *A. concinna* and other red algae turn golden via significant reductions in all shade pigments (Figs. 5, 6) and synthesis of α-carotene, which functions in photoprotection. Remarkably, in the shade of these photoprotected orange canopy tissues, the bases of the same red algae synthesize the full complement of shade pigments, only a few centimeters away from the canopy (Fig. 6). This adjustment can be seen in species of temperate tidal communities from temperate *Mastocarpus papillatus* to tropical *Ahnfeltiopsis concinna* in which golden upper, sunny canopies shade bases of the same plant that lives in extreme shade. No other plant group has been shown to have this range of adjustment to gradients in light; certainly this is one reason that red algae have long dominated tidal shores worldwide and been a source of fascination for marine plant researchers over the decades.

SEE ALSO THE FOLLOWING ARTICLES

Light, Effects of / Photosynthesis

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ALGAL CRUSTS AND LICHENS

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Algal crusts constitute a diverse group of unrelated species that have all adopted a similar encrusting growth form and share a number of ecological characteristics. They are some of the most abundant but most easily overlooked occupants of rocky shores worldwide. They often provide striking coloration to marine habitats, especially the pink and bright red "paint" seen so commonly in pools. While sharing a growth form, algal crusts nonetheless exhibit interesting variation in growth rates, susceptibility to grazers and environmental stresses, and other ecological characteristics.

RECOGNIZING ALGAL CRUSTS

Algal crusts are among the few organisms on a rocky shore that you can step on and not ever notice that you had done so—and that would not be much affected by your having done so. They are constructed like a shag

or pile carpet, composed of microscopic filaments of cells, with the filaments either held together loosely (like a rich shag) or actually glued together (like a commercial carpet) (Fig. 1). The whole body, or thallus, adheres tightly to the rock, except that some species have a raised growing edge. The total thickness of this carpet is usually less than a millimeter. Patches of crust grow laterally as expanding disks; although growth is very slow, many disks may end up running together, or growing for a long time, such that rocky surfaces may end up having wall-to-wall crust carpet.
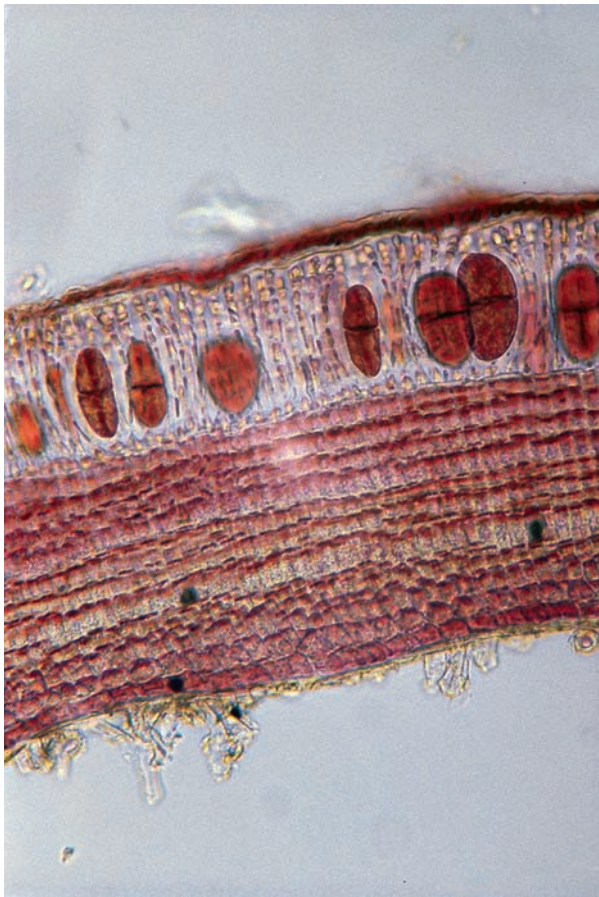
FIGURE 1 Cross section through a reproductive portion of the encrusting red alga *Peyssonnelia pacifica*. Red ovals (tetrasporangia) at the top each produce four spores that can grow into new thalli. Photograph by the author.

This growth form is seen in all the major groups of benthic algae—reds, browns, and greens—and also in cyanobacteria (formerly known as blue-green algae) and in marine lichens. Evolutionarily, this means that the crustose morphology has been converged on by unrelated groups, suggesting that there are some particular advantages

to this growth form. But of course, not all algae are crusts, suggesting that there are disadvantages, too.

FAVORABLE ENVIRONMENTS

Algal crusts can be found in marine communities worldwide, from the tropics to the poles and from the splash zone on the shore down into the subtidal zone. They are probably the most abundant algal form in the ocean, on the basis of the surface area covered (although not on the basis of mass). They are often especially common in the intertidal zone, including tidepools, and in certain other seemingly disparate marine habitats: caves, the very lowest limits of the photic zone, areas scoured by ice, cobbles and boulders that roll around in storms, rock underneath hordes of sea urchins, and surfaces underneath thick canopies of kelp. What do these environments have in common that cause them to be dominated by crusts rather than other marine organisms?

Two environmental factors appear to favor crusts over other algal growth forms, and they are linked logically to the advantages and disadvantages of this morphology. First, crusts are common in areas where algal productivity is limited by stressful environmental conditions, such as where photosynthesis is greatly reduced. These include areas of great desiccation (such as the high intertidal zone) or very low light (such as in caves, the deep photic zone, or underneath algal canopies). Other algal forms, which have higher photosynthetic rates and apparently greater minimum requirements, cannot survive in these marginal habitats. Crusts, however, have very low photosynthetic rates, and this apparently enables them to adopt a slow and steady approach to living in stressful habitats. Crusts are even known to be able to survive being overgrown by other organisms, such as mussel beds, and to persist for years in the apparent absence of light.

The other category of environment dominated by crusts is very different: areas of high disturbance, defined as processes that remove biomass. Disturbance agents can be biological, such as sea urchins or other herbivores, or physical, such as scouring ice or sand, crashing waves, or rolling boulders. The abundance of crusts in such habitats points to one of their main strengths: they are almost impossible to kill. Because they adhere to the rock with almost half their surface area, pulling them off the rock is nearly impossible—in contrast, most algae are attached only by a small holdfast and have a stipe, or stem, that is vulnerable to breakage. Organisms that eat crusts, such as sea urchins and various limpets and other snails, can remove tissue, but they usually only graze the surface, allowing the filaments beneath to regenerate. Even the

occasional grazer that bites all the way through to the rock is unlikely to do so over an entire patch of crust; thus, it leaves behind sections of the thallus, which can regrow. In contrast, a group of hungry urchins can easily wipe out a kelp forest or bed of bushy red algae by biting off the stipes or crawling over and consuming all the blades, leaving little opportunity for regeneration.

The ecological tradeoff for this tolerance of stress and disturbance is that crusts grow very slowly. Only the top cells of each filament are in direct contact with light, gases, and nutrients, greatly reducing potential photosynthetic rates. Lateral growth rates have been measured to be less than a millimeter a year for some species, and even the really "speedy" crusts cannot grow faster than several centimeters a year. In addition, because they grow only flat on the surface, they are vulnerable to being shaded out or overgrown by any alga whose growth form takes it up, not out. Crusts can also be overgrown by sessile invertebrates such as sponges or bryozoans. Thus they are relegated to environments either where larger algae are removed by grazers or other forms of disturbance, or where those better competitors cannot survive because conditions are too stressful. Crusts also compete for space with each other; tidepool observers may see areas of contact between patches of crust in which each edge is growing up, trying to grow over the other (Fig. 2). Often the thicker crust wins.

the latter to expand the thallus out over the rock. Some species with "tight" filaments actually have connections between the cells in adjacent filaments, which in some cases may allow the transfer of nutrients among filaments. One of the most striking morphological variants in crusts is that in some species, most commonly red algae in the order Corallinales, the cell walls contain calcium carbonate. This creates the beautiful pink "paint" that characterizes so many marine communities, and it also creates an algal thallus that is very hard relative to uncalcified seaweeds. This hardness, along with the low digestibility and nutrient content that presumably comes with being calcified, means that coralline crusts are often the last organisms eaten by grazers. As a result, areas with large herbivore populations, such as hordes of urchins in the shallow subtidal zone (Fig. 3) or of limpets in tidepools (Fig. 4) are often dominated by coralline crusts—in fact, these are often the only algae present in such circumstances.

FIGURE 3 An "urchin barren" in the shallow subtidal zone of the Aleutian Islands, Alaska; the only algae present with the abundant urchins are crustose corallines. Photograph by D. Duggins.

FIGURE 2 A field experiment examining competition among species of crustose corallines; note the white edges growing upwards at the zone of contact. Experiment by R. T. Paine, Tatoosh Island. Photograph by the author.

VARIATION

Within the crustose growth form there is quite a lot of variation, including the tightness of the filaments mentioned in the first section. Some species have filaments running not only vertically but laterally, using

FIGURE 4 A small tidepool on the coast of Washington state dominated by limpets and coralline algae. Photograph by the author.

Lichens are another special case, consisting of a symbiotic relationship between photosynthetic cells (of either green algae or cyanobacteria) and fungal hyphae. They may be constructed rather like algal crusts except that the fungal parts are interwoven between the algal filaments, or they may be made of more discrete layers of the different symbionts. The overall form of many intertidal lichens, however, is crustose, with one whole surface tightly adherent to the rock. From a distance, intertidal lichens look like any other crust; that is, they form a solid or patchy band of color on the rock, but the colors are often black, gray, or orange rather than the more common pink, red, or brown of true algal crusts. In addition, they tend to be most common higher on the shore, forming (along with cyanobacteria) the transition zone between truly marine and truly terrestrial habitats.

These maritime lichens, like those that live in other marginal habitats, have a tremendous ability to withstand conditions that would kill other organisms: salinity conditions that change from totally fresh to being covered with salt crystals; long dry periods; and temperatures that change from great heat to great cold. This physiological tolerance is balanced, as for other kinds of crusts, by very slow growth rates and presumably an inability to compete with larger organisms. Most lichens are found only high on the shore, although transplants of some species into areas constantly submerged by the sea show that they can survive and grow there; thus they are probably excluded from lower areas either by competition from other sessile organisms or by herbivores. Limpets, periwinkle snails, and probably other marine grazers will eat some lichens, although experiments with one species whose algal symbiont is a cyanobacterium suggested that it is relatively inedible (many cyanobacteria produce toxic chemicals).

DEFENSES AGAINST HERBIVORES

Because crusts usually grow right on the substrate, they are in some sense more available to a wide range of herbivores than are other algae; chitons, limpets, and sea urchins, for example, seldom climb up erect algae but will readily rasp away at species on the rock surface. As previously discussed, to a great extent crusts can just tolerate this grazing by regenerating from remaining tissue. Others, especially calcified crusts, resist grazing by being very hard. Still others may actually be able to avoid significant losses to herbivores by defending themselves chemically, although this phenomenon has been better studied in noncrustose species. There is evidence

that some brown crusts, like many larger brown algae, produce phlorotannin compounds, which deter various grazers. Some crustose corallines avoid grazing by creating a very bumpy surface (e.g., Fig. 2), making it hard for grazers to consume tissue except off the very tips of the bumps.

Interestingly, many algal crusts appear to actually require herbivores for their survival, or at least they fare much better under moderate grazing. As previously discussed, crusts thrive under various forms of disturbance (including grazing) because disturbing forces remove larger algae that would otherwise outcompete them. Crusts are also susceptible to simply being fouled; that is, having other organisms such as microalgae or small barnacles settle on them, reducing their access to light, nutrients, and gases. For many species, having limpets or other grazers periodically clean their surface is advantageous. An extreme example of this is a limpet-coralline crust association in the North Atlantic that appears to be a mutualism; the limpet gains nutrition (and a nice smooth surface to hold onto) by grazing the surface cells of the coralline. The coralline not only gets cleaned but also may gain a reproductive advantage because the limpet grazing opens up the subsurface pits from which the crust releases its gametes. Other crusts, in contrast, appear to spontaneously slough surface cells, thus keeping themselves clean without benefit of grazers.

There are other examples of grazers, including chitons and limpets, that actually specialize on consuming algal crusts, even the seemingly un-nutritious corallines. Several herbivores, including some abalone, have larval stages that settle preferentially on their crustose food, cued in by molecules released from the surface. Thus, crusts are involved in a variety of positive interactions with other marine organisms.

LIFE HISTORIES

Although all crusts look superficially similar except in color, the foregoing discussion shows that they vary in construction, edibility, and growth rate. The method of reproduction of different crusts follows normal patterns for the taxonomic groups they belong to, although for some species (e.g., the common intertidal red crusts *Hildenbrandia* spp.) no sexual reproduction has ever been seen. All crusts release some kind of propagule, either spores or gametes (e.g., Fig. 1), which allow them to colonize new areas. We know little about dispersal ability of different species, although some seem to recruit readily to new areas whereas others have only

been seen spreading vegetatively from established patches. Life span also varies hugely among species. Some crusts are annuals, passing through their entire lives in only a few months, whereas others are estimated to be decades old (based on measured growth rates and patch sizes). And when we see many meters of rock covered with crust that looks like one patch and is known to grow less than a millimeter a year, we suspect that some live for centuries!

Several crusts are involved in heteromorphic algal life histories, in which one species passes through two very different-looking forms within one life cycle. A number of red and brown algae alternate between one phase (e.g., the haploid) that is an erect alga and another that is a crust. This strategy nicely illustrates some of the tradeoffs involved in different algal forms. The erect form can grow fairly fast, compete for space, and reproduce quickly, but it is susceptible to herbivores and other forms of disturbance. The crustose form grows extremely slowly and is a poor competitor, but it can persist through many sorts of stresses and disturbances in its habitat. Having a crust as part of a complex life history thus may constitute a way for an alga to hedge its bets against conditions encountered in unpredictable marine environments.

SEE ALSO THE FOLLOWING ARTICLES

Adhesion / Algal Life Cycles / Desiccation Stress / Disturbance / Herbivory

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ALGAL ECONOMICS

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Marine macroalgae or seaweeds are ecologically important components of intertidal and subtidal communities that are also economically valuable. Harvesting and cultivation of seaweeds for food and products from them is a multibillion-dollar-per-year industry. Although the value of algae can be estimated in the currency of market economics, their cultural significance, aesthetic appeal, and ecological function in marine environments is no doubt much more valuable but also more difficult to assess.

HARVESTING AND CULTIVATION

Seaweed harvesting from natural populations has been practiced since the fourth century, while cultivation or farming dates back to the seventeenth century. Today over 7.5 million tons of wet seaweed are harvested and cultivated annually, generating ~US$6 billion in revenue each year. The global demand for seaweeds and products from them has increased since the 1950s to the extent that sustainable harvesting of natural populations is often no longer feasible. Although natural harvesting (Fig. 1) occurs worldwide, much of the seaweed supply is now from aquaculture.

FIGURE 1 Kelp-cutting vessel harvesting giant kelp, *Macrocystis,* off the Pacific coast of California. Alginates extracted from the harvested kelp are used in many foods and cosmetics. Photograph by Michael S. Foster.

Some of the most important commercially cultivated genera are *Porphyra* (nori), *Laminaria* (kombu; Fig. 2), *Undaria* (wakame), *Gracilaria,* and *Eucheuma.* Japan, China, and Korea are the leading producers of the first three genera, *Gracilaria* is cultivated in the Indo-Pacific and Chile, and the majority of the world's *Eucheuma* supply comes from the Philippines. The red alga *Palmaria palmata* is also harvested and sold as dulse, but generally on a smaller economic scale and by hand-harvesting natural populations.

FIGURE 2 Ocean cultivation of the kelp *Laminaria* (kombu) seeded on ropes and out-planted in Japan. Photograph courtesy of Michael S. Foster.

ALGAL USES AND PRODUCTS

Macroalgae are consumed as food and are used in a wide variety of applications from fertilizer to fuel. Of the ~US$6 billion per year generated by the seaweed industry, ~US$5 billion is from edible seaweeds. *Porphyra, Laminaria,* and *Undaria* are some of the most important seaweeds in this market and are used locally and exported for use primarily to add flavor and texture to soups, sushi, and other dishes. Algal extracts, including agar and carrageenan (both from red algae) and alginate (from brown algae), account for ~US$585 million. These hydrocolloids are used as thickening and gelling agents and as stabilizers in a variety of products including ice cream, salad dressings, and shampoo. Agarose, derived from agar, is used to make gels to grow bacteria, a technique critical to the biotechnology industry. The very high-grade agar used is one of the most expensive seaweed products.

To a lesser extent, seaweeds continue to be used as fertilizers and soil amendments. Seaweed extracts are used in the cosmetic and diet industry, promising to enhance beauty and facilitate weight loss. These claims, like many of those made for seaweeds as "healthy foods," are typically not validated with rigorous studies or are not made in a cost/benefit analysis with alternatives. The use of seaweeds as a source of biofuel and in wastewater management has also been investigated, but it has yet to be done on a large scale. Their use as biofilters in integrated aquaculture has, however, been successful. When seaweed culture is combined with fish farming, effects of nutrient discharge from fish are minimized. These advances in aquaculture could have positive economic and ecological effects both in open-ocean culture and on land.

CULTURAL VALUE AND INDIGENOUS USES OF ALGAE

Indigenous people throughout the world have used seaweeds as a staple food source. This is particularly true of Asian diets. Typically seaweeds were harvested by hand from local near-shore environments. *Porphyra,* one of the historically most important commercial species, was harvested by hand as early as the fourth century, and primitive shallow-water culture, using bundles of sticks as a substrate for nori to grow on, began in the seventeenth century. The demand for nori was greater than the supply because cultivation was inhibited by the incomplete understanding of *Porphyra*'s life history. Large-scale cultivation techniques were revolutionized in 1949, when Katherine Drew Baker discovered the microscopic phase of *Porphyra*'s life history, which enabled controlled "seeding," leading to vastly increased production and the global increase in nori supply (Fig. 3). The discovery of the microscopic stage was so important to the nori industry that a statue of Baker was erected in Tokyo Bay to honor her contribution to cultivation.

Native Hawaiian diets also historically included seaweeds, known as limu (edible seaweed), although Western influence has reduced the frequency with which seaweed meals are currently consumed. Traditionally, women harvested drift seaweeds from the shore to support their families by collecting and preparing seaweeds for market. Prior to the introduction of Christianity, eating and selling seaweeds was essential to the survival of these women, because they were prohibited from consuming many fish species and local fruits. Today 18 species of seaweeds are still harvested from beach drift and used at home or sold in markets. Typically the limu is prepared with spices and eaten with fish or poi (ground taro root), and is thought to contribute vitamins and minerals to diets.

Indigenous people have also collected and harvested seaweeds for a variety of nonfood uses. During the sixteenth

FIGURE 3 Ocean cultivation of *Porphyra* (nori) gametophytes on nets seeded with spores and out-planted in Japan. Photograph courtesy of Michael S. Foster.

century in the British Isles, brown algae were collected from beach wrack and harvested intertidally for use as fertilizers to grow vegetable crops such as potatoes. Indigenous collections and cultivation of seaweeds for fertilizer are still practiced throughout the world. Organic farmers in Negril, Jamaica, regularly harvest seaweeds, and *Eucheuma,* a source of hydrocolloids cultivated in this region, is essential in the production of a native drink believed to be an aphrodisiac (Fig. 4). French peasants in the seventeenth century harvested intertidal rockweeds (fucoids) for use in glass production and as a pottery glaze. Romans were known to have used algal pigments as dyes for wool.

Many cultures have, and continue to consume seaweeds because of their presumed medicinal properties. The Chinese have relied upon the high iodine content in *Laminaria* to prevent goiter. Asian cultures believed the high potassium chloride associated with a seaweed diet could also prevent hay fever, and in traditional Hawaiian cultures seaweeds were applied to heal open wounds caused by scraping against coral. Finally, seaweeds have spiritual significance for Polynesians, who used them in religious and cultural ceremonies.

Although people in the United States do not cultivate or harvest seaweeds as extensively as is done in other cultures,

they have incorporated algae into their diets and found many creative ways to market and display seaweeds. There is an interesting market niche for pressed algae turned into art. Typically algae are pressed to acid-free paper (techniques similar to those for terrestrial plants) as a means of cataloging and preserving specimens. However, because of their interesting shapes, styles, and colors the seaweeds can be arranged and displayed as unique artistic pieces or bookmarks. Dried seaweeds are also handcrafted into baskets, dolls, rattles, and other decorative items. Specimens used in these applications are typically from sustainable harvest of beach wrack. They produce small revenue and are mostly made for pleasure.

FIGURE 4 A Reef Ranger with Negril Marine Park (A) cultivates and (B) dries *Eucheuma* in Little Bay, Jamaica, for use in the production of traditional island beverages. Photographs by Brian E. Lapointe.

TOURISM: AESTHETIC AND ECONOMIC VALUES

No trip to the shore and rocky intertidal pools would be complete without seaweeds. For better or worse, they provide much of the smell, color, and excitement, with their

funny shapes and often gooey, rubbery, or spiky textures. Although the value of simply existing and enjoying these intertidal features is difficult to assess, it can be related to tourism dollars. The cost of a local trip to the intertidal is generally minimal or free except for vehicle costs, parking, and perhaps state park entrance fees (US$3–10). Considering how low this cost is in comparison to prices for alternative activities such as going to a public aquarium (US$10–20) or the movies (US$8), seeing a sporting event (US$10–100), or visiting a theme park (US$30–50), it is probable that the millions of people visiting coastal areas every year are willing to pay more to enjoy an intertidal experience. This is also likely, considering that tourism in coastal regions around the world is a multibillion-dollar industry. Of course, unregulated coastal access comes at a price to the environment in the form of trampling by tourists, disturbance of marine organisms, and the enormous amounts of trash that must be collected during coastal cleanups each year.

Conversely, it is also possible to assess the negative value of algae and the revenue losses they generate. Macroalgal blooms, for example, are increasingly more common throughout the world and can have tremendous impacts on the environment and the economy. The blooms are often caused by eutrophication; bloom species are typically opportunists and sometimes even invasive species whose life histories enable them to exploit changes in the marine environment. In almost all cases these green (e.g., *Ulva, Codium,* and *Cladophora*) and red (e.g., *Gracilaria, Hypnea, Eucheuma,* and *Kappyphycus*) algal blooms result in massive accumulations of drift that blanket the beaches and shallow bottoms (Fig. 5). The foul smell of degrading

FIGURE 5 Red macroalgal (primarily *Gracilaria* and *Hypnea*) drift accumulation from blooms in Lee County along the Gulf Coast of Florida. Photograph courtesy of Brian E. Lapointe.

seaweeds, physical barriers they create on the beach, and the reduced water clarity and potential health risks associated with them all detract from the appeal of a trip to the shore and have adverse impacts on tourism as well as other near-shore commercial activities. In Hawaii alone it is estimated that over US$20 million per year are lost in tourism and property values along the Maui coast because of algal blooms. Similar impacts are occurring in the Florida Gulf Coast.

Cleanup efforts are often undertaken to eradicate algae from impacted beaches and attract people back to the shore. These efforts, although often done by volunteers, can be costly (more than US$200,000 annually) and are time-consuming. The impacts go beyond tourism losses, because poor water quality associated with the blooms can also reduce fishery and shellfish hatchery yields. Attempts to improve water quality and prevent future blooms by controlling point sources can cost millions of dollars.

ECOSYSTEM SERVICES

As the dominant organisms on rocky intertidal shores, macroalgae contribute greatly to the species diversity of these environments and perform many ecosystem functions. Together with microalgae they are the oceans' primary producers and are an important source of O_2 production. They are useful as CO_2 scrubbers and can act as natural biofilters by absorbing heavy metals from the water column. Because of these functions, as well as their responses to pollution and water clarity, algal populations can serve as indicators of water quality. Marine plants also stabilize sediments, and calcified seaweeds can be important sources of carbonate sand.

Seaweed communities are important structural components of the intertidal zone. They provide food and shelter to a variety of organisms and are favorable recruitment substrates for many invertebrates. Certain calcified red algal species are known to serve as cues for the recruitment of invertebrate larvae such as abalone, and they are recruitment sites for kelps. Many fish and invertebrates take refuge in and amongst macroalgae to escape predators and desiccation during low tides. In some cases invertebrates and fish live permanently in the interstitial spaces created by algal branches and holdfasts. The diversity of organisms living in association with algal habitats is frequently much greater than in habitats without macroalgae. For these reasons, it is arguable that perhaps the most important value of seaweeds is not at all economic, but rather their contribution to productive and diverse marine ecosystems.

SEE ALSO THE FOLLOWING ARTICLES

Algal Blooms / Economics, Coastal / Food Uses, Modern / Kelps / Symbolic and Cultural Uses

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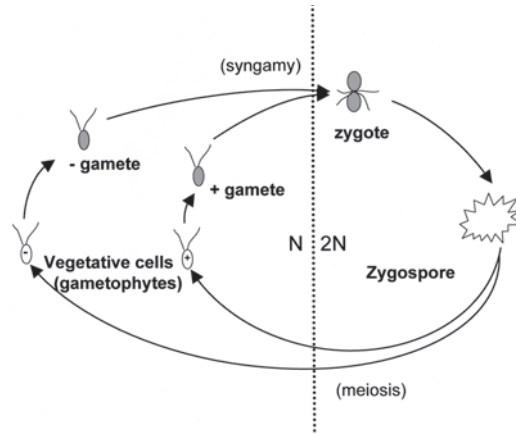
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ALGAL LIFE CYCLES

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Complex life cycles are found in many marine macroalgal (seaweed) species, which include green algae (Chlorophyta), red algae (Rhodophyta), and brown algae (Phaeophyceae). These algal life cycles frequently involve an alternation between two independent, free-living phases that differ in ploidy (the number of copies of each chromosome); one phase is haploid (one copy), and the other is diploid (two copies). Within this basic sequence of haploid/diploid alternation, there is great variability in the size, maximum lifespan, ecological niche, and reproductive biology of each phase. Based upon the general characteristics of the two independent phases, the life cycles of marine algae are frequently categorized into three main types.

TYPES OF LIFE CYCLES

In zygotic or haplontic life cycles the haploid phase is the dominant, frequently macroscopic phase (Fig. 1). Haploid gametophytes produce haploid gametes; these gametes

FIGURE 1 The zygotic-meiosis (haplontic) life cycle of *Chlamydomonas*, a green alga. Zygospore meiosis produces zoospores, which for this species are its vegetative cells. With the proper environmental trigger, the vegetative cells (gametophytes) turn into + or – gametes and fuse to create zygotes. The *Chlamydomonas* life cycle is haplontic because the vegetative cells can persist and self-replicate asexually for (relatively) long periods of time, while the diploid phase is much shorter lived. N represents haploid stages; 2N represents diploid stages.

may be either isogamous (the same size) or anisogamous (different sizes). Gametes fuse to create a diploid zygote, which soon thereafter produces motile zoospores via meiosis. Individual zoospores will then grow into new gametophytes. Algae with this type of life cycle include many green freshwater genera (e.g., *Chara, Coleochaete*) and green unicellular flagellates (e.g., *Chlamydomonas*). Although there are few marine macroalgal tidepool species with truly haplontic life cycles, the tropical marine green algal genus *Acetabularia* is one that has a modified haplontic cycle.

The diploid phase is the dominant, macroscopic phase in gametic (or diplontic) life cycles (Fig. 2); this is also the same basic life cycle found in humans and many
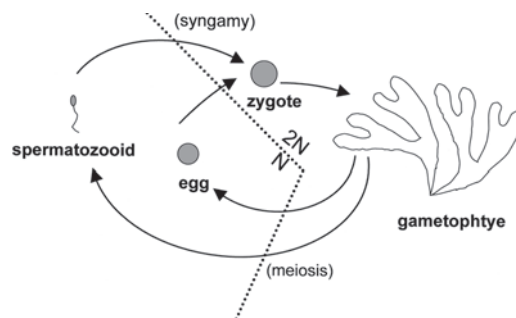
FIGURE 2 A typical gametic-meiosis (diplontic) life cycle of *Fucus*, a brown alga. The macroscopic diploid (gametophyte), when mature, produces gametes that fuse to create new diploids. In *Fucus,* these gametes are called spermatozooids (male) and eggs (female).

animals. Multicellular diploids produce haploid gametes via meiosis; these gametes are released into the water column and fuse soon thereafter to create new multicellular, longer-lived diploid organisms. Gametes are the only haploid stage in this life cycle. Species with diplontic life cycles include the brown algae *Durvillaea* and *Fucus* as well as some benthic diatoms (Bacillariophyceae).

In the sporic (or haplodiplontic) life cycle, the most commonly found in marine macroalgae, both haploid and diploid phases are macroscopic and live independently from one another (Figs. 3–5). This is the most commonly occurring life cycle in marine macroalgae. Multicellular haploid gametophytes produce haploid gametes, which shortly thereafter fuse and create diploid sporophytes.
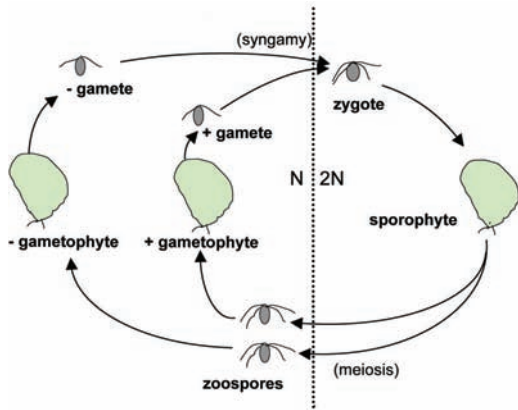

FIGURE 3 The isomorphic sporic (haplodiplontic) life cycle of *Ulva*, a green alga. Gametophytes and sporophytes are both macroscopic and are indistinguishable from one another in the field.
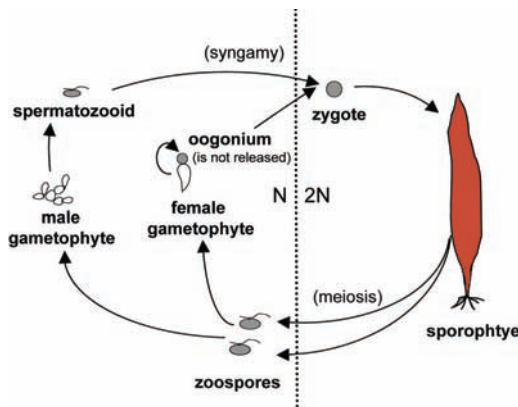

FIGURE 4 The heteromorphic sporic (haplodiplontic) life cycle of *Laminaria*, a brown alga. The sporophyte is macroscopic and much larger than the small, few-celled gametophyte. In kelps, gametes are called spermatozooids (male) and oogonia (female). The oogonium (small gray circle) remains attached to the female gametophyte, so the new sporophyte grows on top of the (then deceased) female gametophyte.
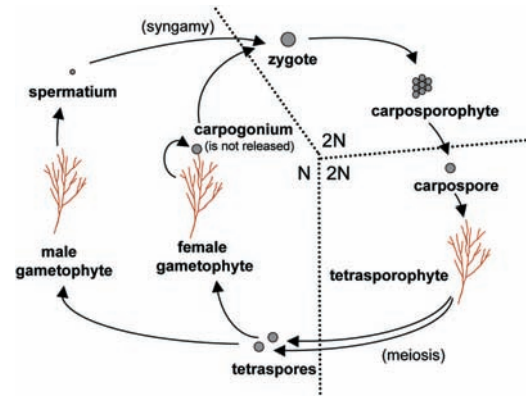

FIGURE 5 The triphasic red algal (class Florideophyceae) sporic (haplodiplontic) life cycle of *Polysiphonia,* an isomorphic red alga. The tetrasporophyte and gametophytes are macroscopic and visually identical, except when reproductive. In this class, gametes are called spermatia (male) and carpogonia (female). The carpogonium (gray circle on top of the female) remains attached to the female gametophyte, so the zygote and carposporophyte grow attached to the female blade. Note the lack of flagella on all stages, which is a red algal characteristic.

Depending upon the species, gametes may be released into the water column or may remain on the gametophyte. When mature, multicellular sporophytes produce haploid spores via meiosis; these spores are released into the water column and subsequently become new haploid gametophytes. The two phases can either be morphologically quite similar (isomorphic, Fig. 3), including *Dictyota* and *Ulva,* or they can be morphologically dissimilar (heteromorphic, Fig. 4, including *Scytosiphon* and *Laminaria*) from one another.

Most red algae (all those in the class Florideophyceae) have a haplodiplontic life cycle, with an additional short-lived phase (carposporophyte, Fig. 5) that may serve to increase reproductive output. In these species, female gametes (carpogonia) remain on the female gametophyte and are fertilized there by male gametes (spermatia). The resulting diploid zygotes quickly grow into small clusters of thousands of diploid spores (carposporophytes) while remaining attached to female blades. These spores are released into the water column and become new free-living tetrasporophytes (so called because they produce spores in packets of four). Species with a triphasic life cycle are either isomorphic *(Polysiphonia)* or heteromorphic (for example, as a haploid blade and diploid crust for *Mastocarpus,* and as a microscopic female haploid and macroscopic male haploid and tetrasporophyte for *Palmaria*) for the two independent phases.

These three life cycle types only partially segregate by taxonomic order; in brown algae, different life cycles exist

in closely related species, indicating multiple evolutionary origins. Also, the distinct, multiple phases found in many algal species can provide unique opportunities for investigating scientific questions on topics ranging from intra-specific population dynamics to theories regarding the evolution of life cycles and sex.

ECOLOGICAL IMPLICATIONS

The life cycle of an algal species can substantially affect its ecological dynamics. Heteromorphic species have two phases with very distinct ecological niches, and the phases may differ in their susceptibility to herbivory, temperature fluctuations, or other physical or biological stressors. By contrast, the two phases of isomorphic species generally have more similar ecological niches, such as similar intertidal location or chemical content, although subtle but important differences may exist between phases, such as per capita fecundity and mortality.

Some algal species have the ability to regulate when switching between different phases will occur. Sporophytes of *Ectocarpus siliculosus,* a common filamentous brown alga with an isomorphic life cycle, produce diploid spores that become new sporophytes during the summertime. This cycle can be repeated several times over the course of a summer, while temperatures are warm. However, during the wintertime, when temperatures are cooler, the sporophytes will produce haploid spores that become gametophytes. This process is not unique to *Ectocarpus;* temperature regulation of life cycles has been demonstrated for other algae, such as the brown alga *Colpomenia sinuosa.*

OTHER METHODS OF REPRODUCTION IN ALGAE

Many other algal species maintain populations exclusively (or nearly so) of either sporophytes or gametophytes, but not both, indicating that they must be able to routinely skip parts of their life cycle. This ability to perform apomixis has been observed in several species and should be considered when studying algal population dynamics, because in some species a particular phase, or stage, may be frequently (or always) skipped. Why certain life stages may be dropped in some algal species and not in closely related others remains an area of active debate.

Some macroalgae can also successfully asexually reproduce via fragmentation or production of stolons or rhizoid production. These processes are more frequently observed in green algae, but they can occur in some brown and red algal species as well.

SEE ALSO THE FOLLOWING ARTICLES

Competition / Dispersal / Kelps / Reproduction

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ALGAL TURFS

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Many rocky and other hard substrata on temperate and tropical shores are covered with an assemblage of algal species that form a cushion or mat. In some environments, these algal assemblages are dominated by one or a few species, although in other environments, they are composed of a diversity of species. These assemblages or communities, collectively referred to as algal turfs, are found in both the intertidal and the shallow sublittoral and can be a major space occupier in some zones. The term *algal turf* is often used to describe two different kinds of algal communities. One type of algal turf is composed of species with simple, filamentous morphologies that form a thin veneer on hard substrata. A different kind of algal turf is formed by much larger (>1 cm), macroscopic algae that grow in a densely packed mat. Although both types of algal turfs occur in a variety of marine environments, the processes that lead to their formation may vary, and both their community structure and function may be very different. Similar to other intertidal and shallow subtidal organisms, the distribution, abundance, and physiology of algal turfs are influenced strongly by both the physical environment and biological interactions with other organisms.

TEMPERATE ALGAL TURFS

On rocky shores in the temperate zone, algal turfs are found on exposed surfaces at low tide, in tidepools, and on shallow subtidal substrata. Algal turfs often develop in the low intertidal zone where they can occupy the majority of rocky surfaces. These algal turfs most often are comprised of larger, macroscopic species with more complex (at the cellular level), branching morphologies. These assemblages often consist of one or a few species with thalli that are packed densely in an interwoven mat (Fig. 1). Some of the more common taxa forming intertidal algal turfs are articulated coralline algae (e.g., *Corallina* spp.) and other red algae (e.g., *Chondracanthus* spp., *Pterocladiella* spp., and *Gelidium* spp.). Turf-forming thalli usually are shorter and more highly branched than thalli of the same taxa growing subtidally.

FIGURE 1 Algal turf assemblage exposed at low tide in a temperate low intertidal habitat (Santa Catalina Island, CA). Photograph by the author.

Intertidal algal turfs are affected most by the rigors of the physical environment in this habitat. Desiccation can be the most important factor that limits the distribution of algae in the intertidal zone. Because a dense mat of thalli traps water and helps to maintain a more humid microenvironment, turf-forming algae experience much less desiccation than single thalli growing in the same habitat. Other limiting physical factors in the intertidal can be high light and temperature. The negative effects of these factors are also mitigated within a dense assemblage of algae, because much of the photosynthetic surface of individual thalli either is self-shaded or shaded by adjacent individuals, and the trapped water reduces temperatures within the turf. Nevertheless, the surface of the turf is exposed to high levels of light and desiccation at low tide and often the apical portions of these turf-forming thalli are bleached (appear white or yellow). Rates of photosynthesis are decreased and respiration increased by the physical conditions during tidal exposure. As a result, growth rates of species comprising intertidal algal turfs are reduced.

Algal turfs growing in tidepools or subtidally are not affected as much by the physical environment (although light still is important) and biotic interactions probably are more critical in determining their distribution and abundance. In this physiologically more benign environment, more species compete for limited space, so the abundance of algal turfs depends, in part, on the outcome of this competition. Competitive interactions often are determined by the relative rates of growth of the competitors, and for algae growth is related (inversely) to the morphological complexity of the thalli. As a result, algae that are simple filaments will have an advantage in competing with other taxa and dense assemblages of these filaments form a second type of algal turf. Another biological interaction that is more common in tidepools and subtidally is herbivory. Released from the constraints of intertidal exposure, herbivores (e.g., snails, sea urchins) can be more common and active in foraging on algae. How algae persist in the face of intense herbivory also depends on how fast they can grow and replace lost tissue. Simple filaments comprising algal turfs quickly regenerate biomass lost to herbivores. So both increased competition and herbivory in tidepool and subtidal habitats favor algal turfs that are diminutive in size, but that grow quickly.

Algal turfs provide food and habitat for a diversity of other species. The trophic importance of subtidal algal turfs in temperate environments probably has been underestimated. Recent studies suggest that rates of algal turf primary production are substantial, yet biomass remains low, indicating that much of this production is removed by herbivores. The structure of intertidal algal turfs also provides a refuge for many associated organisms. Mitigation of temperature and desiccation stress within the turf allows many small crustaceans (e.g., amphipods) and polychaetes to persist despite aerial exposure at low tide. At high tide, the turf may provide a refuge from predation for these same organisms.

TROPICAL ALGAL TURFS

Algal turfs in tropical environments have been studied much more than on temperate shores. Algal turfs in the rocky intertidal are not common in the tropics, most likely due to intense solar heating and the resulting desiccation. However, algal turfs are among the more common space occupiers in subtidal habitats, especially on coral reefs. The most common type of algal turf community in the

tropics consists of many small, filamentous species that generally are <1 cm tall (Figs. 2, 3). These turfs commonly are composed of >10 different species with representatives from each of the major algal phyla (Chlorophyta, Phaeophyta, and Rhodophyta). Coral reef algal turfs are the most productive component of the coral reef and can contribute up to 80% of the total reef primary production. Even more than their temperate counterparts, reef algal turfs are low biomass, high turnover communities with up to 100% of their new biomass production removed by herbivores. As a result of the increased abundance and diversity of herbivores in the tropics, algal turf species are among the few algae able to persist in the face of intense herbivory. As a result of their abundance and high rates of productivity, algal turfs are a very important trophic link in coral reef food webs. Additionally, on some reefs where the reef flat is shallow or may be exposed at extreme low tides, algal turfs include species of cyanobacteria that are able to fix nitrogen. The highest rates of nitrogen fixation measured in any biological community have been associated with these coral reef algal turfs. So in addition to providing carbon to consumers, these algal turfs also contribute large amounts of nitrogen to a community that is nitrogen limited in the oligotrophic waters typical of the tropics.

The algal turfs that are common on coral reefs are too small to provide much habitat for other organisms. Some small crustaceans are associated with these turf assemblages, but likely are subject to frequent disturbance from herbivores.

Intense herbivory in the subtidal zone also may select for turf formation by larger algal species. While much less common than the aforementioned algal turf assemblages, macroalgal turfs also occur in reef habitats. These larger turfs can include both calcified (e.g., *Halimeda* spp.) and uncalcified (e.g., *Dictyota* spp.) taxa and provide some protection from herbivores as a result of the dense packing of branches within the turf. Conversely, herbivory on the apical portions of the algal thalli might promote turf formation by increasing production of lateral branches, much like trimming does to a hedge. Whether it is a cause or effect, it appears that herbivory is the dominant process associated with algal turf communities in the tropics.

Because of their larger size, macroalgal turfs on coral reefs can provide habitat and a refuge from predation for associated mobile organisms. This remains an understudied aspect of these turf assemblages, assemblages that might be viewed as islands of habitat distributed across large areas of reef that experience relatively high predation.

Algal turfs are a multispecific assemblage that represents a functional–form group rather than a defined group of algal species. The environmental factors associated with turf formation in algae are either temperature or desiccation stress (intertidal) or herbivory (subtidal). In each case, turf formation mitigates the negative effects of these factors on algal physiology and growth and promotes persistence in hard substratum habitats in both temperate and tropical environments where they provide food and habitat for other associated organisms.

FIGURE 2 Subtidal algal turf growing on the coral substratum. Washer in photograph is 1.2 cm across. Photograph by the author.
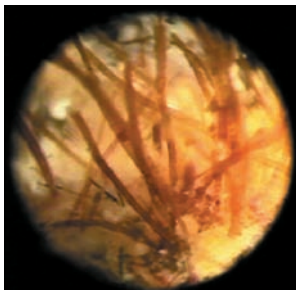
FIGURE 3 Close-up of a coral reef algal turf. Field of view is 3 mm across. Photograph by the author.

SEE ALSO THE FOLLOWING ARTICLES

Corals / Desiccation Stress / Food Webs / Herbivory

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AMPHIPODS, ISOPODS, AND OTHER SMALL CRUSTACEANS

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Although many groups of crustaceans can be found in tidepools and on rocky shores, among the most numerous are the amphipods, isopods, copepods, and ostracods. Most are grazers, living on small macroalgal fragments, microalgae, or detrital particles found on the bottom of pools. All members of these groups found in tidepools are very hardy, being able to tolerate a wide range of physical and chemical conditions. In some cases, the species are not very abundant outside the tidepool environment, and in other cases the species are abundant in tidepools because their preferred food is more common in pools than on the open shore.

TAXONOMY AND MORPHOLOGY

Amphipods and isopods are malacostracan crustaceans usually grouped together as orders in the superorder Peracarida because of their penchant for raising their young in a brood pouch formed by specialized ventral plates on the female. Copepods are a very diverse group of small maxillipodan crustaceans that occupy nearly all marine and freshwater habitats and have a diversity of life habits, including becoming parasitic. Ostracods are small bivalved crustaceans usually allied with the maxillopodans. They are an ancient group, known from the earliest Palaeozoic Era, and can be found in all marine and freshwater habitats. All four groups have species that are well adapted to the wide range of physical and chemical conditions often found in tidepools.

Amphipods have a very characteristic morphology. In many species the body is flattened laterally, making them higher than wide, and as a result they are often seen crawling over the rocks in tidepools, hanging on with the legs of one side of their body. Such a body design may seem to put the animal at a disadvantage, but in fact, amphipods have the most flexible of all crustacean body plans and as a result have been able to exploit a wide variety of habitats. Short, stiff rods, called uropods, are often used to help propel the amphipod away from the substrate in pools. Amphipods living on rocky shores are typically about 0.5 to 2 cm in length.

Isopods have a body design quite different from that of amphipods. They are usually thought of as having a body that is flattened dorsoventrally, but some, in fact, are more cylindrical. Isopods typically have five pairs of pleopods and one pair of uropods on the abdomen. Isopods use their pleopods as the primary source of oxygen uptake, so the pleopods are often well protected under an opercular covering made from the uropods. Isopods of rockpools can be very small, about 0.7 mm in length, but those of the open rock surfaces are often 3–4 cm long.

Copepods are much smaller than the previous two groups, generally only 1–2 mm in length. The body consists of a head with five pairs of appendages to which is fused a varying number (generally one or two) of thoracic somites. The remaining four or five free thoracic somites form a pereon bearing paired swimming legs. Copepods are easy to spot in tidepools by their herky-jerky motion over the substrate, and females always carry their eggs in paired egg strings, called ovisacs, attached to the first abdominal somite.

Ostracods are also generally less than one to a few millimeters in length. The body is encased in an enlarged carapace that is hinged like the two valves of a clam, giving them a bean shape. The thorax is reduced, and, as a result, the enlarged first and second antennae assist with locomotion. When ostracods walk across the substrate, carrying their large carapace, they often rock side to side. In contrast to the other three small crustaceans groups noted previously, ostracods living on rocky shores do not have the capability of swimming in tidepool waters.

FOOD HABITS
Amphipods and Isopods

The primary food sources for both amphipods and isopods are algae and plant detritus, although some species in both groups are capable of capturing and eating small or weakened animals, the exuviae of other crustaceans, or scavenging those freshly dead. Amphipods feed on algae by gripping pieces of the thallus with their

gnathopods and holding it such that bits can be cut off with the bladelike mandible incisors. In some cases, an amphipod will first use the mandibles to scrape all the microalgae, such as diatoms, off the macroalgal thallus, and only when that high-quality food is consumed will they attack the macroalga itself. Isopods, not having their first pereopods modified as gnathopods, appress the mandible directly on the algal thallus and either scrape the surface or consume the macroalga. The large isopod *Idotea granulosa* was seen to prefer the growing tips of *Ascophyllum nodosum*. In very high intertidal pools, the major food source is either microalgae attached to rock surfaces or detrital plant fragments. Small isopods, such as species of *Jaera,* do well in these pools, as does the amphipod *Gammarus duebeni*. In both cases a very wide range of organic particles are eaten, ranging from fresh microalgae scraped from the rock surface, to pollen grains and other terrestrial plant products, to the larvae of tidepool insects.

Copepods and Ostracods

Because of their very small body size, these groups probably consume only microbes and microalgae living on the thalli of larger algal species, on the rock surfaces, or on detritus in the tidepool sediments. Some copepods have evolved specializations of their appendages that allow them to live on the macroalgae from which they are grazing microbes, without being swept away by wave forces. Such specializations include flattening of the body, enlargement of the maxilliped or modification of a walking leg to form a grasping structure, and secretion of encapsulating mucus that the copepod uses to glue itself to an algal thallus. Ostracods rarely have similar kinds of modifications, and they usually live in wave-protected microenvironments at the bases of macroalgae or in tidepool bottom sediments. Here, they feed on diatoms, animal carrion, plant fragments, and detrital products that accumulate in the pools.

ENVIRONMENTAL PHYSIOLOGY

Amphipods and Isopods

Tidepools and rocky shores are sites of extreme physical and chemical environmental conditions. Those animals that are able to live, and in some cases to thrive, in these habitats are usually those that have the ability to tolerate wide variations in temperature, salinity, and dissolved oxygen. For example, the amphipod *Gammarus duebeni* can live in water of 0.2 to 66 parts per thousand salinity. In seawater, *G. duebeni* produces urine that is isotonic with the blood, but when in freshwater the animal can

reduce the amount of excreted salt, with the result that the urine is hypotonic to the blood. In tidepools, as the water becomes saltier through evaporation, the urine becomes hypertonic relative to the blood.

Copepods

Harpacticoid copepods of the genus *Tigriopus* are very common, and highly characteristic, species of high intertidal rockpools. They live in pools that receive salt water only during high spring tides, so the salinity of the pool may vary from near fresh during rain storms to hypersaline during hot dry spells. When the salinity exceeds 90 parts per thousand, *T. fulvus* become quiescent, but resumes normal activity if the salinity drops within about 30 hours. This copepod can tolerate a salinity of 180 parts per thousand for about 3 hours. Lethal temperatures vary with salinity, being lower when the salinity is lower. At a salinity of 4 parts per thousand, death occurs at about 34 °C; but at a salinity of 90 parts per thousand death does not occur until a temperature of nearly 42 °C is reached. *Tigriopus californicus* is quite capable of living in pools lower in the intertidal zone, but because the lower pools contain many copepod predators, ranging from fish to crustaceans to sea anemones, it thrives only in the high pools where conditions are too extreme for the predators. Oxygen can be limiting in high intertidal rockpools, especially at night after the oxygen produced during the day by photosynthesizers has all been consumed. Many copepods do not have a respiratory pigment in their blood, yet at temperatures between 5 and 30 °C *T. brevicornis* is able to maintain a constant rate of oxygen consumption even as oxygen levels become quite low. Under severe hypoxia, these copepods enter a dormant state.

Ostracods

This group of small crustaceans are common inhabitants of algal covered rocky shores. Most live in the sediment at the bases of macroalgae, or on the thalli of macroalgae where there is protection from wave action. A few stray into high rockpools, but most do not have the ability to tolerate the extremes of conditions found in these pools for more than a few days. A few species, however, are well adapted for life in high rockpools, the best known being those from the Baltic shores of Sweden. The salinity in these pools varied from 2 to 8 parts per thousand. One species, *Heterocypris salinus,* could tolerate salinities as high as 32 parts per thousand, but only when temperatures were low. A few other northern European species are also euryhaline, being able to tolerate salinities from 2 to

50 parts per thousand, but most intertidal algal dwelling species are truly marine.

LIFE CYCLES

Amphipods

Typically, tidepool amphipods carry their young in a ventral brood pouch, which then hatch as miniature adults. The period of development varies with temperature. At 18 °C the incubation period is 14 days, but development slows with decreasing temperature, reaching 54 days at about 5 °C. A female may have several broods, especially as the temperature rises through the summer. On hatching, it takes about 23 to 30 weeks to reach maturity at a temperature of 15 to 20 °C. In nature an individual may live for 15 to 18 months. One curious feature of some amphipods is that the sex of the offspring changes with temperature. Under normal North Atlantic conditions, with a salinity of about 10 parts per thousand, all the young will be males if the temperature is below 5 °C a few days before the eggs are deposited in the brood pouch. On the other hand, if the temperature is above 6 °C, all the young will be females. Between 5 and 6 °C, the broods are mixed with respect to sex. Males are usually larger than the females, and some male amphipods carry individual females between their gnathopods for a few days before the eggs are deposited. This is called amplexus, and is a common sight in tidepools during the summer. The female needs to shed her exoskeleton before egg laying and so is vulnerable to predation by other amphipods. She apparently secretes some behavior-modifying substances in her urine, which triggers the guarding behavior in the male and, in particular, curtails his feeding responses. After molting, the male deposits sperm into the brood pouch where the eggs are fertilized. Soon afterward, the female exoskeleton begins to harden and the male is encouraged to leave.

Isopods

Like amphipods, female isopods are brooders, carrying their young in a ventral brood pouch. Although the larger isopods, such as those in the genus *Idotea* that are common among the algae of rocky shores, are good swimmers, at least for short distances, the smaller isopods such as the *Jaera* species are less able. Consequently, for poor swimmers, mates will most likely be other residents of the same rockpool, resulting in relatively high levels of genetic relatedness. Mating among isopods involves depositing sperm into the brood pouch of the female, usually after the female has molted the posterior half of the exoskeleton. At this time (within 2 to 12 hours after

molting) the oviducts are soft and eggs can freely pass into the brood pouch, being fertilized on the way. For many isopods there is a linear relationship between egg number and female size, with the smaller females carrying 11–15 eggs and the larger females about 60 eggs. During development there is a progressive loss of eggs, with brood mortality reaching about 50% by the time of hatching. An isopod hatches from the brood pouch as a manca, resembling the adult in all respects except that the last pair of walking legs is missing. Within three molts, an isopod is a full-fledged juvenile. It is often not known how many additional molts are passed through until sexual maturity is reached, but in many isopods only three to five more molts are required. Laboratory cultures of *Jaera albifrons* produced sexually mature females after 40 to 66 days. One female may produce a new brood every 20 days or so and perhaps four to six broods during her lifespan. Northern Hemisphere females born from April to late summer will produce broods until October and then die; those born in September will overwinter in the pool and produce their first broods the following April.

Copepods

Whether free swimmers or benthic species, copepods hatch from the egg as a nauplius and develop through four or five additional naupliar stages and usually five copepodite stages before maturing to a reproductive adult. One generation for a copepod, then, is the time from production of an egg by a female until that egg develops into another female who produces another set of eggs. As one might expect, generation times vary with temperature, which in many rockpools gradually increases with the onset of summer. For example, at 15 °C, development time of *Tigriopus californicus* is 32 days, but at 25 °C it was only 18 days. Females of *T. brevicornis* produce an average of 25 to 35 eggs during each egg production event, with the higher numbers produced as the pool warms in the summer. These copepods can survive freezing for as long as 70 hours if they are acclimated to colder waters, are moderately well fed, and the rockpool salinity is relatively high.

Ostracods

These small crustaceans either carry their eggs inside the bivalved carapace or attach the eggs to the substrate. Some rockpool parthenogenetic species lay 30 to 40 eggs, usually on small macroalgae or on the rocky substrate. The young hatch as a nauplius (that is, they have only three pairs of limbs), and the adult stage is usually reached in most intertidal species after the eighth and final molt. Many species hatch in the spring and become adults

capable of producing eggs in 35–45 days. In some species, juveniles overwinter in pools, molting to the final adult stage the following spring.

SEE ALSO THE FOLLOWING ARTICLES

Body Shape / Foraging Behavior / Locomotion: Intertidal Challenges / Salinity Stress

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ANEMONES

SEE SEA ANEMONES

AQUARIA, PUBLIC

CHRISTOPHER HARROLD, MARTHA L. MANSON, AND CHRISTINA J. SLAGER

Monterey Bay Aquarium

By recreating the natural world indoors, aquarium exhibits safely introduce visitors to the plants and animals of wave-swept shores (Fig. 1). Communicating the wonder of such dynamic habitats in an exhibit challenges biologists and engineers. Complex systems support tidepool communities in nature; indoors, mechanical systems create wave motion and tide cycles and deliver nutrients. Further, although some plants and animals reproduce in exhibits, others must be collected. Protecting healthy tidepools is vital to conservation-minded institutions; collecting in a sustainable way becomes a logistical and ethical imperative.

FIGURE 1 Aquarium visitors enjoy the Kelp Forest exhibit narration at the Monterey Bay Aquarium in Monterey, California. Over 1 million people visit the Monterey Bay Aquarium every year; 142 million people per year visit aquariums and zoos accredited by the American Association of Zoos and Aquariums. © Monterey Bay Aquarium Foundation.

CREATING ROCKY-SHORE EXHIBITS

Intertidal invertebrates, aquatic plants, and small fishes are adapted to survive in harsh conditions at the edge of the sea. Recreating their habitat in a tidepool exhibit involves a raft of specialists. Fiberglass and concrete artificial rocks create the pools and substrate for plants and animals to attach themselves. Pumps and dump mechanisms generate water motion, simulating natural waves and tides (Fig. 2). Close observation of real tidepool communities guides aquarists in collecting and placing different species. In instances where unfiltered seawater circulates through the exhibit, plants and animals come in with the water and settle. Over time, an exhibit mimicking natural diversity develops.

FIGURE 2 The rocky intertidal exhibit at the Monterey Bay Aquarium. Wave surge, wave crash, and tidal level are all at work in this exhibit. © Monterey Bay Aquarium Foundation.

RECREATING THE PHYSICAL ENVIRONMENT

The aquarist's challenge is to create a physical environment that meets the needs of the plants and animals on display while also creating a compelling visitor experience. The physical parameters of greatest concern are substrate, light, temperature, water quality, and water motion.

Substrate

Artificial substrates in rocky shore exhibits are made of resin and fiberglass, epoxy resin, or reinforced concrete. Substrate texture can be recreated with amazing accuracy and realism using latex molds taken from rock surfaces in nature. With judicious use of molds, dyes and resin, or concrete, exhibit "rockwork" is virtually indistinguishable from the real thing. Benthic plants and animals readily settle, attach, and thrive.

Light

Exhibit lighting is among the most important factors influencing the aesthetic quality of rocky shore exhibits, while helping to create a healthy environment for the plants and animals on display. Exhibit lighting can be natural sunlight or artificial light. Natural lighting is surprisingly problematic, because it usually promotes heavy growth of undesirable fast-growing algae and diatoms, which cover both plants and animals and contribute to turbid water and poor viewing conditions. Artificial lighting is generally provided by fluorescent, incandescent, or metal halide lights. Sometimes theatrical gels are used to adjust the color hue. Some invertebrates, such as tropical corals, tridachnid bivalves, and some temperate-water anemones, host zooxanthellae, which require high light levels in specific wavelengths.

Water Quality

Aquarium life support systems maintain the water quality in rocky shore exhibits. There are three fundamental types of life support systems:

1. In open life support systems, water is pumped from a natural body of water, passed through filters to remove particulate material, piped into exhibits on a once-through basis, and returned to its source. Filtration may be temporarily bypassed to provide food for filter-feeding invertebrates and to encourage the establishment and growth of natural benthic communities.
2. In closed life support systems, water is recirculated through filters and the exhibits many times. In closed marine systems, the seawater composition may be artificially composed or imported from the ocean. The filtration system includes: physical filtration to remove suspended particulate material; biofiltration to detoxify the accumulated nitrogenous waste byproducts of metabolism; and aeration to replace lost oxygen and remove accumulated carbon dioxide.
3. In semiclosed life support systems, water is recirculated and processed as in a closed life support system, and in addition a small proportion of the water volume is continuously replaced with fresh water from a natural body of water.

Temperature

The water temperature of exhibits must be maintained within the tolerances of the plants and animals on display. In open systems, temperature can be maintained by simply providing adequate water flow. In closed or semi-closed systems, temperature may be actively maintained with refrigeration units, heat pumps, or heaters.

Water Motion

Water motion creates a naturalistic exhibit, adequate gas exchange, water quality, and clarity, and it encourages natural growth of organisms on exhibit surfaces.

1. Unidirectional, current-type water motion is generally provided by the entering (incurrent) and exiting (excurrent) water flows required for basic water quality.
2. Back-and-forth, surge-type water motion is created by a wide variety of mechanisms involving pumps, valves, and automated control devices. One example is shown in Fig. 3A.
3. Sudden, breaking-wave crash water motion is simulated by the simultaneous release of hundreds of gallons of seawater into the rocky shore exhibit (Fig. 3B).
4. Long-wavelength tidal cycles are required to maintain intertidal zonation patterns seen in nature. The tidal level in an exhibit can be controlled and varied using a variable-height Hartford loop (Fig. 3C).

RECREATING THE BIOLOGICAL ENVIRONMENT

Most plants and animals from rocky shores are robust and hearty and therefore easily maintained in an exhibit setting. Exhibits are generally stocked with organisms collected from the wild, though natural recruitment into exhibits can occur in open seawater systems. Natural intertidal zonation patterns may develop with suitable wave crash and tidal water motion.

Many aquariums have "live touch" experiences, in which visitors can handle exhibit plants and animals in supervised settings (Fig. 4). Care must be taken to

A

"Suck and Pull" Pipe

Release Sensor

Surge Reservoir

Vacuum Chamber

Air Release

B

Water Inlet

Dump Reservoir (500 gallon capacity)

Second Floor

Indoor Exhibit

Outdoor Exhibit

Acrylic Tunnel

First Floor

C

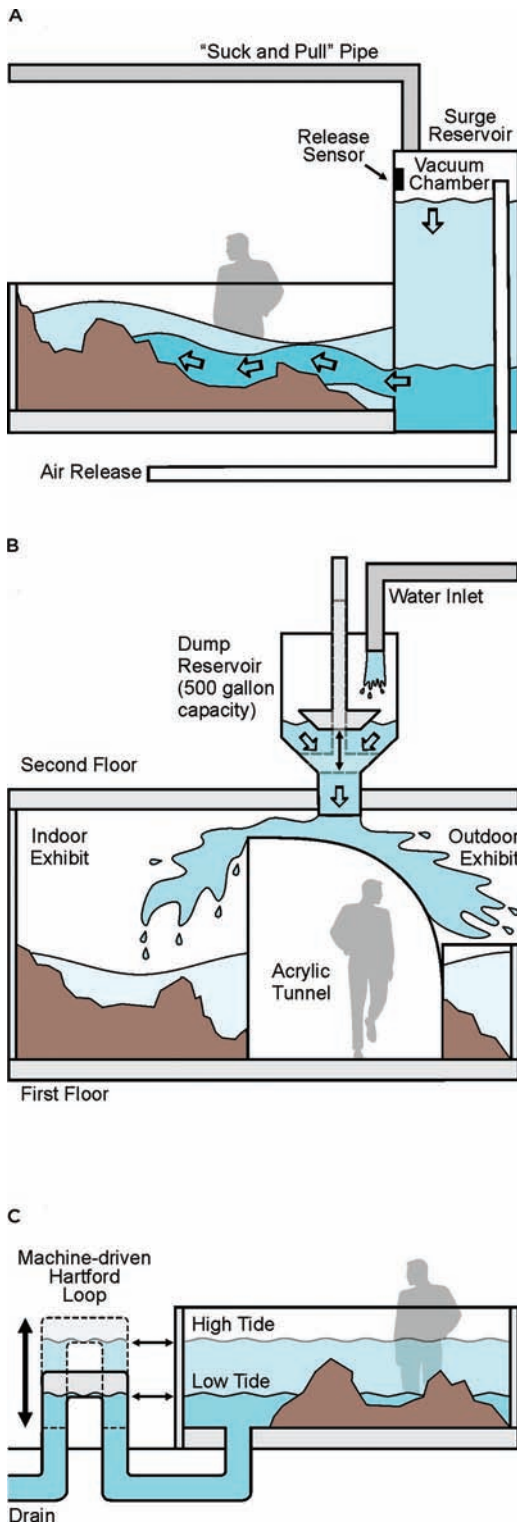Machine-driven Hartford Loop

High Tide

Low Tide

Drain

FIGURE 3 Three mechanisms that generate water motion in a rocky shore exhibit: (A) surge generator; (B) wave crash generator; (C) tide level generator. © Monterey Bay Aquarium Foundation.

FIGURE 4 At this tidepool exhibit, aquarium visitors can hold and touch hardy species of intertidal plants and animals under close supervision by aquarium staff. © Monterey Bay Aquarium Foundation.

maintain high water quality and avoid stressing animals or posing risks to visitors.

Stocking exhibits with living rocky-shore marine life raises two marine conservation issues that aquariums should proactively address. One is the impact of collecting marine life on native populations and habitats. Rocky-shore habitats are increasingly affected by human visitors. Aquariums should play a key role in minimizing or preventing significant human impacts. Collecting impacts can be reduced by minimizing demand (e.g., ensuring maximum longevity of marine life on display, captive breeding) and minimizing impacts (e.g., broadly distribute collecting activity, minimize physical impacts from collecting equipment).

The second conservation issue is the release of exotic or invasive exhibit organisms or their reproductive products into the aquatic environment. Only a few aquariums have systems designed to destroy or neutralize plant and animal reproductive products before discharge. This threat must be taken seriously by the aquarium industry, because the potential for harm is great (e.g., the release and subsequent invasion of the green alga *Caulerpa* in the Mediterranean).

INSPIRING THE VISITORS

Aquariums go to great lengths to recreate and maintain tidepool habitats for public display. They meticulously craft realistic replicas that duplicate rocky coastlines. What are they trying to accomplish with all this effort?

In the broadest sense, aquariums attempt to create a visitor experience that is enjoyable, informative, and that ultimately inspires visitors to preserve natural habitats for future generations. Aquariums want visitors to understand the complexities and adaptations of tidepool life, to

experience the simple pleasure of contact, and to learn how to respectfully visit tidepools and gently handle tidepool animals. Rocky shores and tidepools, like so many other natural environments, are in peril from human impact. Unchecked, waste disposal, habitat destruction, and resource exploitation threaten to forever change or even destroy the world's tidepools and rocky shores.

Worldwide, over 142 million people visit accredited aquariums and zoos every year. People visit for many reasons—to experience the diversity of wildlife up close; to enjoy a safe, family experience; to be dazzled by the beauty of aquatic life; and to learn more about animals and nature. For many who do not live in close proximity to a coastline, an aquarium visit may be their only experience with live ocean animals. Further, typically, visitors believe what they learn during an aquarium visit. A recent Pew Charitable Trusts poll determined that the public considers aquariums and zoos to be reputable and trustworthy sources of environmental information. Consequently, aquariums have a tremendous opportunity to influence people's beliefs and behaviors. If they succeed in creating a sense of wonder about marine life and in educating visitors about the threats to aquatic ecosystems, aquariums can shape a visitor experience that ultimately compels millions of people to conserve our planet's threatened aquatic ecosystems.

SEE ALSO THE FOLLOWING ARTICLES

Education and Outreach / Light, Effects of / Museums and Collections / Water Chemistry

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ARTHROPODS, OVERVIEW

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The largest group of animals is the phylum Arthropoda, and it includes the crabs, shrimps, spiders, scorpions, and insects, as well as millipedes and centipedes. Arthropods are estimated to make up more than 80% of all known animals, in part because of their ability to inhabit sea, land, and air. In the rocky intertidal habitat, there are few representatives of terrestrial and aerial forms, but arthropods are still major members of the tidepool communities in both numbers and species diversity.

WHO THE ARTHROPODS ARE

The classification of the Arthropoda is complex and controversial. Current phylogenies are working to integrate morphological characteristics, including early development and functional morphology of locomotion, with contemporary molecular phylogenetics. The Chelicerata generally include the marine horseshoe crabs and pycnogonids or sea spiders as well as primarily terrestrial arachnids (spiders, scorpions, mites, and ticks). Pycnogonids and mites are the primary representatives of the Chelicerata in the rocky intertidal. The Hexapoda (six-legged insects) and Myriapoda (many-legged millipedes and centipedes) are rare in the rocky intertidal. The Crustacea (crabs, shrimps, barnacles, etc.) amply represent the Arthropoda in this challenging marine habitat.

TIDEPOOL CRUSTACEANS

Crustaceans of the rocky intertidal include a diverse group of large and small organisms. The sessile Cirripedia or barnacles, both stalked and acorn, that settle in the high intertidal are obvious inhabitants, whereas other barnacle species are found lower down in the mid- or low intertidal zones. Parasitic barnacles live on or in other rocky intertidal crustaceans, including hermit crabs and shrimps. Tiny bivalved ostracods and free-swimming or parasitic copepods are present in tidepools or under-boulder sediments, as are the leptostracans, the less obvious and most basal of the Malacostracan group of crustaceans. In their classic book *Between Pacific Tides*, first published in 1939, Ed Ricketts and Jack Calvin (1985) described a typical leptostrachan species *Nebalia* as looking like "a small beach hopper slipped inside a clam shell so small that its legs and hinder parts are left outside." Many species of isopods and amphipods swim in the tidepools, cling to the algae and rocks, and crawl about on other rocky-intertidal invertebrates. Shrimps dart back and forth across tidepools, whereas the largest representatives of the arthropods in this habitat, the crabs, are relatively reclusive. Rapidly moving snail shells are occupied by hermit crabs instead of the original shell makers. When an observer turns over a rock, numerous porcelain crabs *(Petrolisthes)* and grapsids *(Hemigrapsus, Pachygrapsus)* scurry away. The latter can be glimpsed sliding down the side of a rock and out of sight on an overcast, foggy day or on an evening tidepool foray. Bigger boulders often shield larger *Cancer* crab species. Rock holes formed by boring clams, sea urchins, or geological processes are often filled with a variety of crab

species, including anomuran crabs such as *Oedignathus* that protects its soft abdomen with powerful claws to block the entrance of its hole. Beautifully camouflaged kelp crabs, decorator crabs, and umbrella crabs cling to the swaying kelp or walk slowly over the rocks, using the pointed tips, or dactyls, of their walking legs.

KEY CHARACTERISTICS OF ARTHROPODS

The key features of arthropods include paired, jointed appendages or legs (Greek *arthros* = joint, *pod* = foot), a hard, chitinous outer covering or exoskeleton that is molted, and a segmented body plan. The appendages are made up of a linear series of cylindrical sections or articles of hard exoskeleton. Each article is connected to the next by a specialized, flexible region of exoskeleton, and extensor and flexor muscles inside the articles extend across the flexible joints and allow antagonistic movement. The joints of a crab's walking leg, for example, flex in alternating planes, resulting in a limb with a great range of movement. Arthropods have modified the basic jointed appendage into a huge array of specialized structures that function in locomotion, feeding, grooming, sensory input, and reproduction. One individual may have many types of modified appendages, and the functional specialization of arthropod limbs is often referred to as the Swiss Army knife or Leatherman tool approach to evolutionary diversity.

MOLTING

The exoskeleton of arthropods provides protection from predators, abrasion, desiccation, and invading organisms (Fig. 1). It also gives structural support and allows for the antagonistic muscle movement. The rigid nature of the exoskeleton, however, and its location outside the living tissues requires that it must be shed or molted and replaced

FIGURE 1 The hard exoskeleton of the Dungeness crab *Cancer magister* covers its entire body, including claws, feeding appendages, sensory antennae, and even its eyestalks. Photograph by Margaret Ryan.
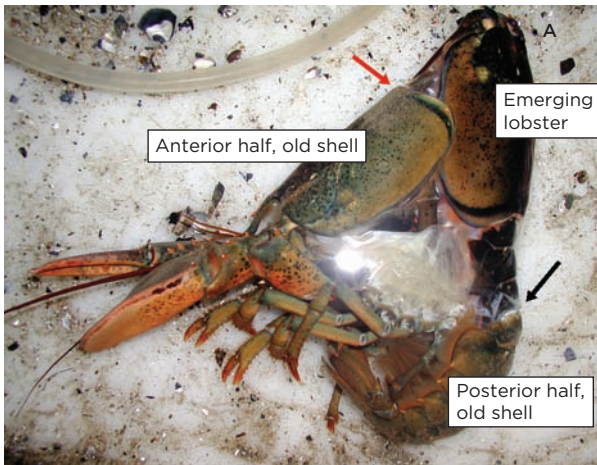
by a new, larger exoskeleton in order for the animal to grow. This process of molting, or ecdysis, is a dangerous yet repetitive part of an arthropod's life cycle. Molting is induced by a family of steroid hormones, the ecdysteroids. Recent molecular studies have indicated that hormonally regulated molting of an exoskeleton or cuticle is present in several other animal taxa. Many biologists now consider the protostome invertebrates to be classified as the Ecdysozoa (animals including arthropods, tardigrades, onychophorans, chaetognaths, nematodes, nematomorphs, priapulids, kinorhynchs, and loriciferans that produce ecdysteroid hormones and periodically molt an exoskeleton) and all other protostomes, the Lophotrochozoa.

Molting requires precise coordination of almost all major organ systems to simultaneously form a new exoskeleton and remove the old one. In many species, molting is closely integrated with the reproductive cycle as well. The sequence of events has been carefully documented and the phases divided into premolt, ecdysis, postmolt, and intermolt. A crustacean remains in intermolt due to circulating levels of neuropeptide hormones, especially a molt-inhibiting hormone (MIH), that prevent synthesis of the ecdysteroid molting hormone. It is generally thought that when levels of MIH decline, ecdysteroid synthesis increases and the animal enters premolt.

Secretion of a crustacean's new exoskeleton begins during premolt while the animal is still stuffed inside the old one, filling available space to capacity. First, proteolytic enzymes are secreted by the cells of the epidermis (sometimes referred to as hypodermis) that lies just inside the exoskeleton. These enzymes digest the inner lining of the exoskeleton to disconnect the extracellular exoskeleton from the living tissues and to make space to build a new exoskeleton. Structural proteins and chitin are then transported across the epidermis into this space to form the layers of the new exoskeleton. After a thin epicuticle is secreted into the extracellular space between epidermis and old exoskeleton, a thicker exocuticle layer appears underneath the new epicuticle. In addition to chitin and cuticular proteins that originate in the epidermal cells, the exoskeleton includes proteins such as cryptocyanin that are synthesized in the hepatopancreas and transported via the hemolymph across the epidermis to the forming exoskeleton. While the old exoskeleton is being partly broken down and the new one forming beneath it, claw muscles, especially in large-clawed species like the lobster, are selectively atrophied so that the claw can fit through the narrow wrist joint at ecdysis. Missing limbs are regenerated during premolt, and calcium from the old exoskeleton is stored in cells of the hepatopancreas in some species.
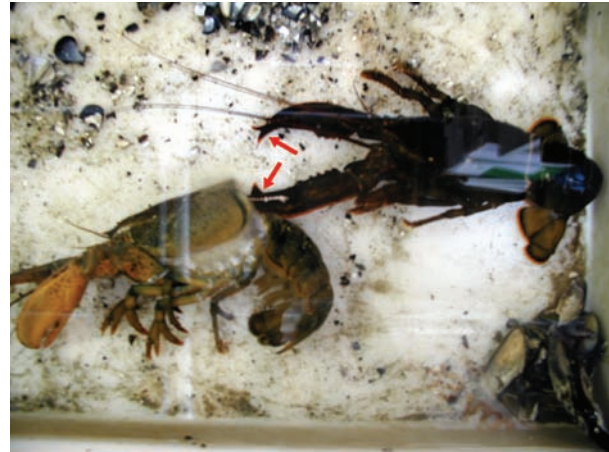
When the new exoskeleton is sufficiently formed, the crustacean needs to escape rapidly from the confines of its loosened old exoskeleton during ecdysis. The animal takes up water to increase internal pressure and split open the old exoskeleton along an ecdysial line between the posterior carapace and abdomen (Fig. 2). The old exoskeleton includes the lining of the foregut, the hindgut, and the covering over the eyes, so once ecdysis is initiated, the animal is temporarily blind with no functional mouth or anus. The new exoskeleton is soft and affords no protection against predators, and although it provides a fluid-filled hydrostatic skeleton temporarily, the animal is relatively floppy and defenseless (Fig. 3). Thus ecdysis must be completed rapidly.

During the postmolt stage, the new exoskeleton must harden—but only after all the limbs have been extracted from the old exoskeleton and after the new layer has expanded to its larger size. Immediately after ecdysis, the crab absorbs huge quantities of water to stretch the new, larger, temporarily flexible exoskeleton. Sclerotization or

FIGURE 3 Immediately after escaping from its old skeleton (ecdysis), *Homarus americanus* is the same size as before molting, and the new exoskeleton is soft. The newly molted lobster is able to move, using its fluid-filled body as a hydrostatic skeleton, but its claws are still small. The claw muscles are too flaccid and the shell is too soft to keep the claw tips rigid and uncrossed (arrows). During the next few hours, the exoskeleton will expand and begin hardening. Photograph by Margaret Ryan.

FIGURE 2 American lobster *Homarus americanus* in midmolt. Old exoskeleton has split at the suture line between posterior end of carapace (red arrow) and anterior end of abdomen (black arrow). Anterior head of lobster (A) and part of abdomen have already emerged from old exoskeleton, but claws and walking legs are still being withdrawn. Photograph by Margaret Ryan.

hardening occurs through a process of crosslinking the proteins and chitin molecules of the new exoskeleton. The enzyme phenoloxidase plays a major role in sclerotization. Synthesis of more exocuticle continues, and then secretion of a third layer, the endocuticle, begins beneath the new exocuticle. The endocuticle layer continues to increase in thickness, while calcification and sclerotization of the exoskeleton progress, until the crab enters intermolt. Replenishment and growth of the claw and other muscles occur during postmolt and especially intermolt, until the

crab enters its next molt cycle (Fig. 4). The length of time from one molt to the next, the intermolt duration, varies with age, nutritional status, and limb regeneration. Juvenile crustaceans molt much more frequently than adults.

Ecdysis and postmolt are dangerous times for crustaceans in the rocky intertidal and elsewhere, because the animals are vulnerable to predators and also subject to life-threatening

FIGURE 4 Old exoskeleton left by recently molted Dungeness crab *Cancer magister*. In addition to the external covering of body and gills, numerous connecting structural elements supported internal organs. Photograph by Margaret Ryan.

mechanical problems if the escape–expansion–hardening processes are not perfectly synchronized. The physiological challenges of rocky-intertidal life, including thermal, osmotic, and hypoxic stress on the rocks and in the tidepools, as well as the dynamics of wave action and surge channels, must be factored into the timing of ecdysis by rocky-intertidal arthropods.

REPRODUCTION

Reproduction and development in arthropods is complex and often includes multiple larval forms. Reproduction is usually closely linked to the molt cycle, with transfer of sperm from male to female usually occurring just after the female has molted, while her new exoskeleton is soft.

Barnacles are unique among the rocky intertidal crustaceans because they are hermaphrodites. Sperm are directly transferred from one barnacle via its remarkably long penis into the mantle cavity of another. Since most adult barnacles are permanently attached to the substrate, settlement in the proximity of other barnacles is obviously a requirement for reproductive success. The fertilized embryos are retained in lamellae in the mantle cavity of the second barnacle until they hatch as free-swimming naupliar larvae. The nauplius undergoes several molts, adding appendages each time, before metamorphosing into a swimming cyprid, the stage that eventually settles onto a hard substrate, glues itself down, and metamorphoses into a juvenile barnacle. The progression through these morphologically and physiologically different developmental stages is referred to as indirect development. The diversity of barnacle types, including sessile, stalked, free-living, commensal, and parasitic, is reflected in differences in the general reproductive pattern.

Crabs and lobsters, like barnacles, undergo indirect development, and reproduction is closely coordinated to the female's molt cycle. During premolt, the female releases pheromones that attract the male. He embraces her until she is ready to molt, releases her when she is ready to shed her old exoskeleton, then embraces her again to insert his sperm into two storage pockets on her soft ventral thorax. He stays with her to protect his investment for several days while her exoskeleton hardens, and then he departs (he molts on his own several months later). Oogenesis and oocyte growth then continue for several months in the female. The oocytes are finally fertilized by the stored sperm as they are extruded from the crab's ovary and pass out onto her ventral surface. She scoops them up with her abdominal appendages or pleopods. The sticky covering added to the fertilized embryos as they were extruded attaches the embryos to the fine processes of the pleopods, and the embryos form a large egg mass or berry on the ventral surface of the abdomen. In a large *Cancer* crab, for example, the berry may include 1–5 million embryos. The female crab aerates the embryos by flexing her abdominal muscles back and forth. After several months of development, the embryo hatches as a swimming zoea. Usually there are multiple zoeal stages, depending on the species, followed by a metamorphosis into a swimming megalopa (Fig. 5). The planktonic megalopa then metamorphoses into a bottom-dwelling juvenile crab (Fig. 6). The first-instar juvenile crab molts within several weeks to a larger, second instar. With each succeeding molt, the interval between molts increases, so that an adult crab usually molts only once per year.

FIGURE 5 The megalopa stage of *Cancer magister*, the Dungeness crab, is an active swimmer that will metamorphose into a first-instar juvenile crab. Photograph by the author.

FIGURE 6 The first instar juvenile stage of *Cancer magister* is primarily a walker instead of a swimmer. Although it has the general shape and full complement of adult appendages, the physiology of the juvenile differs from that of the adult. It will grow and mature with each successive molt. Reproduced with permission of the Company of Biologists.

Amphipods and isopods undergo direct development. The male isopod transfers sperm to the female, after which she releases her oocytes. The fertilized embryos are then deposited into her special brood pouch or marsupium. The marsupium is located on her ventral surface and is a space enclosed by special flaplike extensions of her thoracic limbs that form during her previous molt. The embryo develops within its egg case, gradually acquiring the form of a miniature adult. The newly hatched juvenile, known as a manca, remains in the brood pouch for a short time before crawling away as a young isopod or amphipod.

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