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

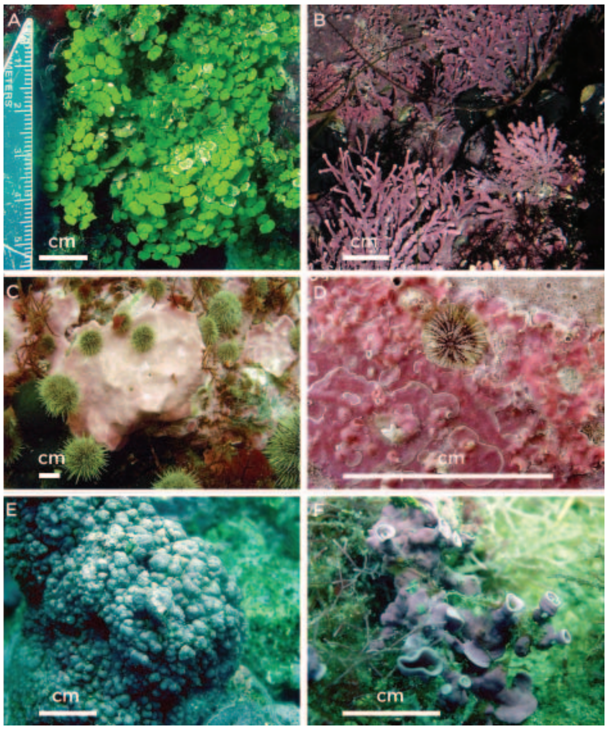

FIGURE 1 Morphological and ecological variety of calcified algae. Bars = 1 cm. (A) Articulated green alga (*Halimeda* from Honduras in the Caribbean) growing on a coral reef. (B) Articulated red algae (*Calliarthron* and *Bossiella* from Monterey Bay, California) growing in low intertidal zone tidepools. (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 scuptus* 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