The Nature of Crustose Coralline Algae and Their Interactions on Reefs

Mark M. Littler and Diane S. Littler

ABSTRACT. What was known about crustose coralline algae (CCA) prior to the use of scuba came mostly from dredging collections. This method usually resulted in damaged specimens and questionable habitat data. Scuba has allowed a more accurate determination of ecological conditions and facilitated in situ photography, two techniques our group has relied on during the past three decades for quantitative ecological studies and field guide production. A goal of this review is to familiarize the scientific diving community with the kinds and roles of CCA on tropical reefs, with the hope that the diving community will more fully appreciate the role of this important group of organisms that is so critical to healthy reef structure and function.

Crustose (nongeniculate) coralline algae occur worldwide from polar to tropical regions, reaching their highest diversity in tropical reef environments. Coralline algae occupy the entire depth range inhabited by photosynthetic organisms, from upper-intertidal regions to depths as great as 295 m. The great abundances of corallines in the poorly known deep-sea realm underscore their widespread contributions to productivity, the marine food web, sedimentology, and reef biogenesis in clear tropical seas. The diversity of CCA forms is astonishing, ranging from small filamentous strands to some of the larger and most beautiful head-forming organisms on coral reefs. The predominant members of this functional indicator group tend to be slow-growing, competitively subordinate taxa that are abundant in most reef systems. As an indicator group they are functionally resilient and able to expedite the recovery and restoration of coral reef systems relatively quickly since some thin forms of crustose coralline algae accelerate colonization and chemically attract and facilitate the survival of coral larvae; the other two fleshy algal functional indicator groups (i.e., turfs and macroalgae) tend to overgrow and inhibit coral settlement, survival, and recovery. Because most crustose coralline algae continually slough off upper surface layers, they play a key cleaning role and physically prevent the settlement and colonization of many fleshy fouling organisms on coral reefs.

INTRODUCTION

Prior to scuba, studies by dredging provided most of the sparse knowledge of crustose coralline algae (CCA), which focused primarily on taxonomy and distributional records. Scuba has enabled studies on ecology, physiology, interactions, etc., that were impossible before its development (Figure 1). Since crustose coralline algae are often overlooked or ignored due to their complex taxonomy and life histories, it is now paramount to understand their fundamental structure and development so that we can utilize

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FIGURE 1. The research team surveying an extensive rhodolith bed at 30 m. (Photo by D. E. Hurlbert.)

this important functional group to answer many questions about marine biology and ecology.

Coralline algae (also "corallines") are red algae (Rhodophyta) characterized by a thallus that is stony because of calcareous deposits contained within and between the cell walls. The extensive crystalline calcium carbonate (calcite) deposits provide a geological history of reefs and an excellent fossil record. These algae are typically pink or other shades of red, but some species can be variations of purple, blue, gray-green, or brown.

Corallines rank among the major reef builders in coral reef systems. Coralline algae are exclusively marine plants and occur throughout all of the world's oceans, attached to substrates by cellular adhesion or root-like holdfasts. Many corallines are epiphytic (on other plants) or epizoic (on animals), and some are even endophytic parasites within other corallines. Despite their ubiquity, all aspects (e.g., taxonomy, biology, ecology) of the coralline algae remain poorly understood, and corallines are often overlooked or intentionally ignored by coral reef scientists.

When they were discovered in 1707 (Sloane), corallines were thought to be animals. In 1837, Philippi recognized that coralline algae were plants and proposed the two generic names *Lithophyllum* (for flat forms) and *Lithothamnium* (for erect, branched forms). However, in an overlooked earlier treatment Bory de Saint-Vincent (1832) had recognized *Tenarea undulosa* as a crustose calcareous alga, making it the oldest species name originally applied to the group in a botanical context. Coralline algae were included in the order Cryptonemiales as the family Corallinaceae until 1986 (Silva and Johansen), when they were elevated to the order Corallinales.

LIFE HISTORIES

Corallines reproduce by sori, which are specialized, volcano-shaped, domed conceptacles containing haploid tetraspores, diploid bispores, or either male or female gametes. Gametes fuse to form the parasitic diploid carposporophyte stage within the female conceptacles, and the resultant carpospores germinate into diploid tetrasporophytes. Haploid tetraspores germinate to produce the male and female gametophytes. Some crustose coralline populations are unusual in that uninucleate bispores (diploid) are commonly the sole means of reproduction. The plant body (thallus) is composed of strands of pit-connected cells (filaments) that may fuse laterally or form secondary pit connections. Pit connections and pit plugs are translocational structures characteristic of red algae (Rhodophyta). These reproductive and vegetative structures provide the critical anatomical characters used in coralline algal taxonomy, but also create major obstacles for researchers, since complicated decalcification techniques and microtome sectioning of infrequently present cryptic features are required.

Articulated (geniculate) corallines are upright or pendulous branched, bushy plants (Figure 2), with shallower and warmer
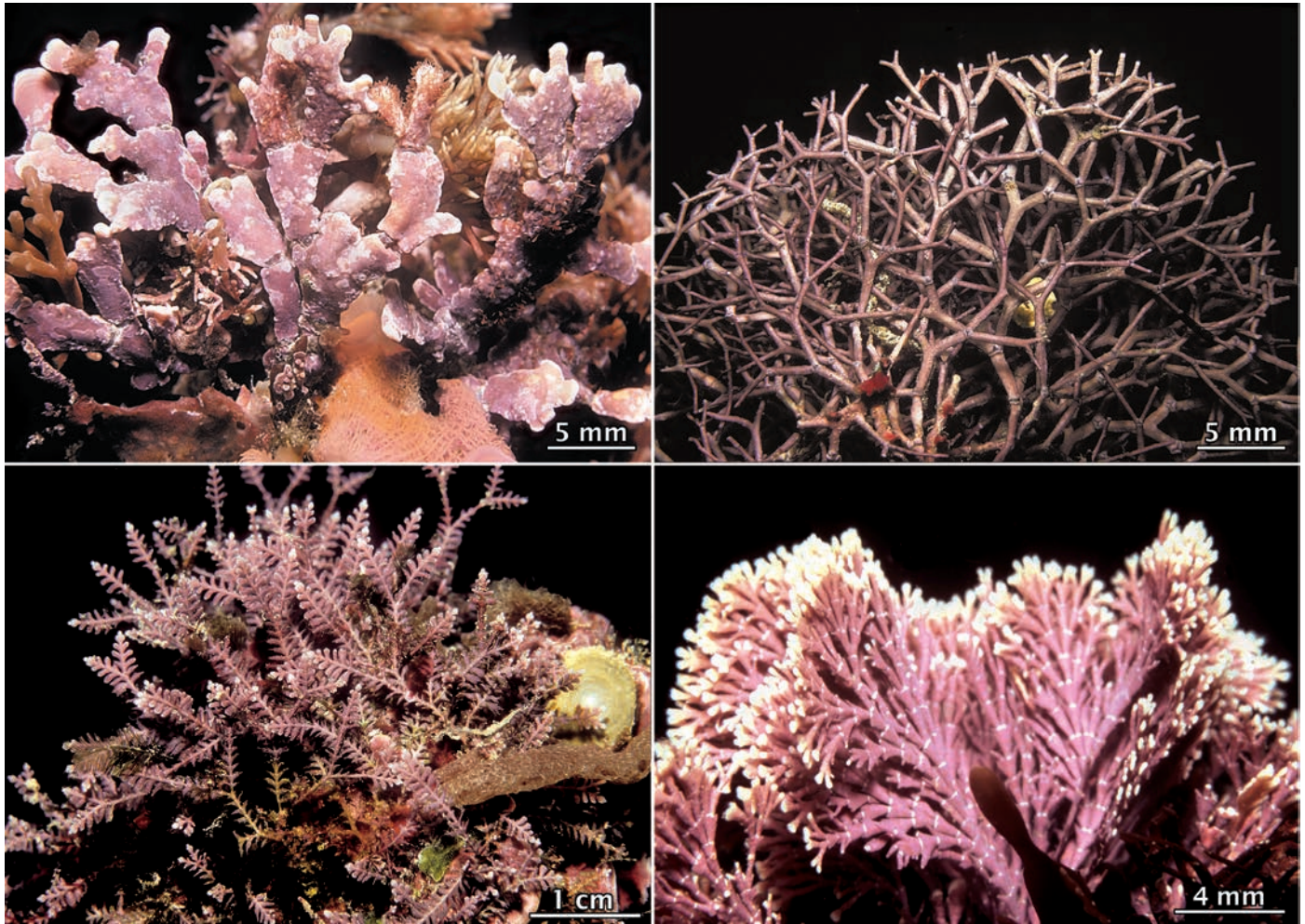
FIGURE 2. Spectrum of articulated (jointed, geniculate) coralline algal forms. Top left: *Amphiroa foliacea*. Top right: *Jania rubens*. Middle left: *Cheilosporum acutilobum*. Middle right: *Amphiroa beauvoisii*. Bottom left: *Corallina berteroi*. Bottom right: *Amphiroa ephedraea*. (Photos by D. Littler.)

distributions than nongeniculate species. The multiple clumped thalli are flexible due to noncalcified zones (genicula, joints) separating longer calcified segments (intergenicula). Many articulated and upright crustose corallines can also form extensive two-dimensional adherent crusts, allowing them to spread laterally, and thereby providing those species with multiple bet-hedging ecological survival strategies (called heterotrichy; Figure 3) (Littler and Kauker, 1984). The upright portions receive relatively more light and nutrients, and are faster growing with increased fertility; horizontal crusts are more resistant to physical forces such as grazing, wave shearing, and sand scouring, and allow the plants to regenerate and invade horizontal primary space.

Crustose (nongeniculate) corallines range in thickness from a few micrometers to many centimeters (Figures 4–7). The thinner forms are faster-growing early colonizers and occur on all

hard substrates and other marine organisms. Crustose corallines span a spectrum of morphotypes from thin, sheetlike crusts to thick, slow-growing massive pavements (Figure 4) and from shelf forms (Figure 5) to upright branched (Figure 6) and columnar coral-like heads and nodules (Figure 7) that contribute to both cementation and bulk. On oceanic reefs, the highest part of the reef is often a massive intertidal algal ridge of crustose corallines in the reef's breaker zone (Dawson, 1961). Thalli of thicker forms often consist of three recognizable layers: an attached lower hypothallus, a middle perithallus, and an upper epithallus. Trichocytes (hair cells, megacells) occur as horizontal plates within the epithallus layer in some genera such as *Porolithon*. The protected meristematic (growing) region is usually located as a layer beneath the uppermost intercalary perithallus cells, a feature which is unusual in the Rhodophyta, whose
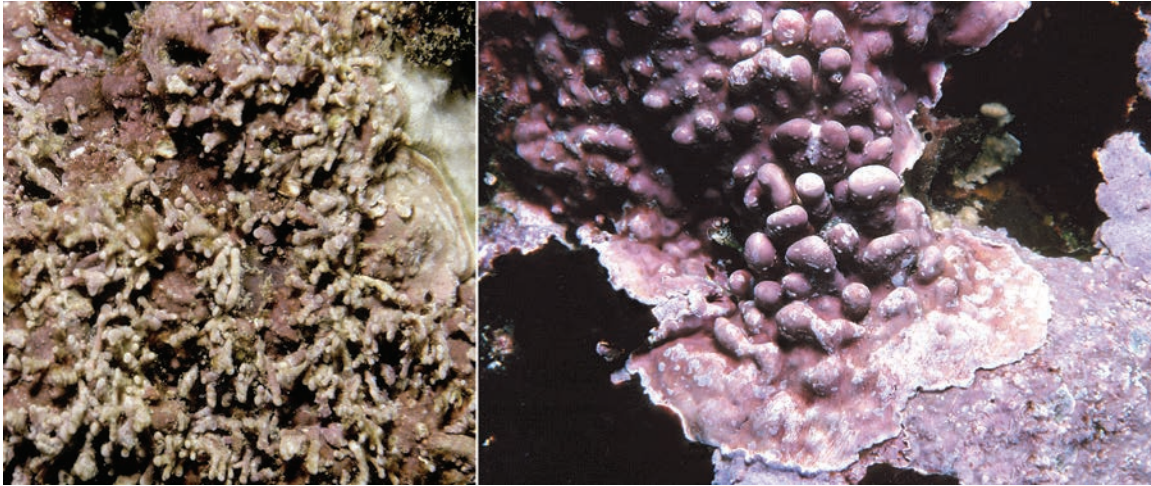
FIGURE 3. Heterotrichy: multiple bet-hedging ecological survival strategies. Left: Jointed corallines with the upright portions receive relatively more light and nutrients and are faster growing, whereas horizontal crusts are more resistant to physical forces and invade horizontal space. Right: Knob-forming coralline with two-dimensional leading crust invading and overgrowing neighboring species. (Photos by D. Littler.)
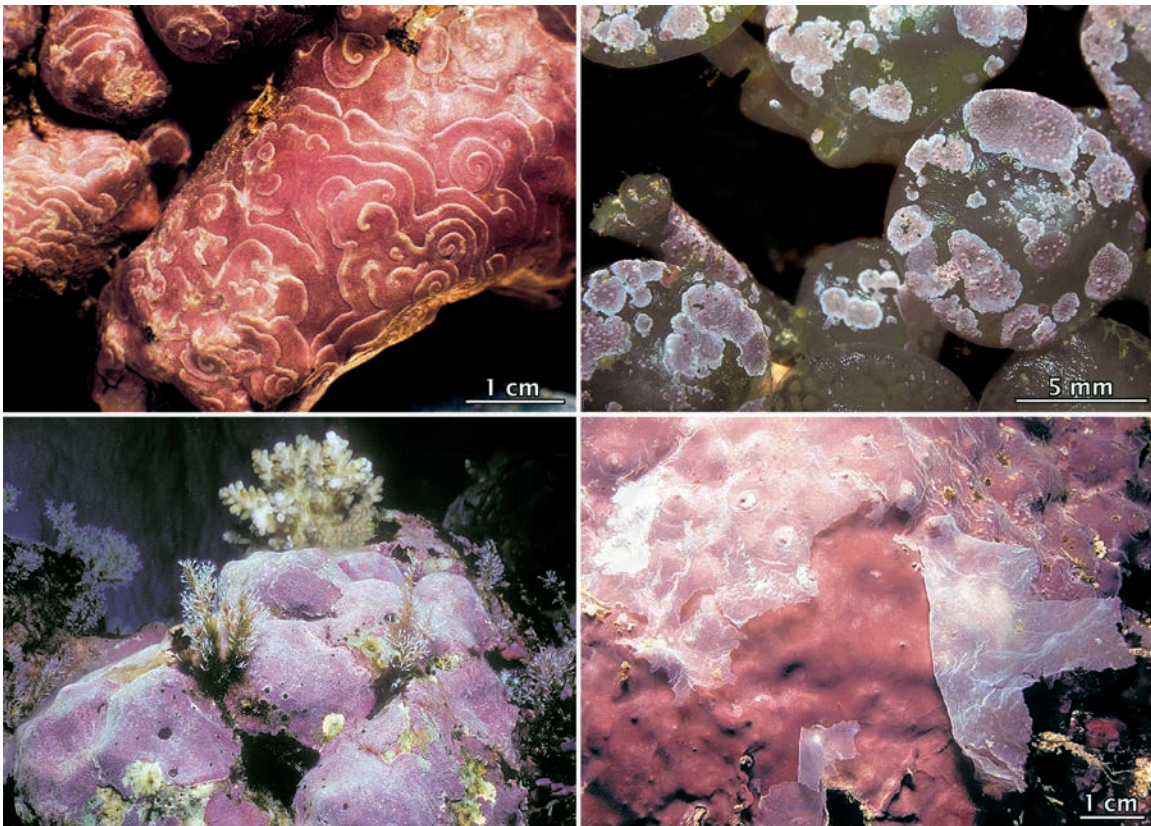

FIGURE 4. Spectrum of simple two-dimensional forms of nongeniculate (crustose) corallines. Top left: *Titanoderma tessellatum*. Top right: *Titanderma pustulatum*. Bottom left: *Porolithon onkodes*. Bottom right: *Neogoniolithon fosliei* showing synchronous sloughing. (Photos by D. Littler.)
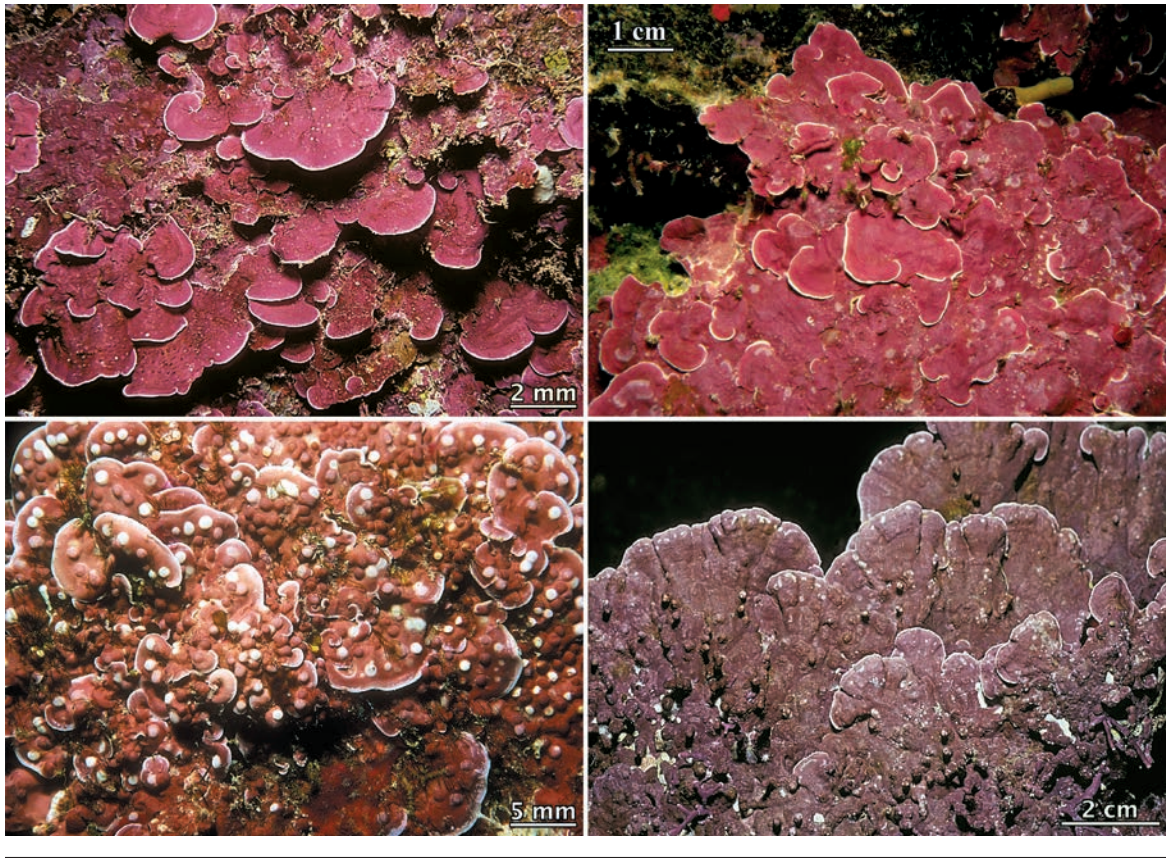
FIGURE 5. Spectrum of shelf-forming crustose corallines. Top left: *Mesophyllum funafutiense*. Top right: *Mesophyllum mesomorphum*. Bottom left: *Mesophyllum* cf. *lichenoides*. Bottom right: *Mesophyllum* sp. Note abundant examples of conceptacles in bottom left image. (Photos by D. Littler.)

members (except for Delesseriaceae) typically show strictly apical cell growth. Because of the upright branched head formers (Figures 6, 7), some specialists prefer the term nongeniculate over crustose; however, all have extensive crustose bases and whether branched or simple they are still elaborations of crusts.

RHODOLITHS

In the absence of hard substrates, many nongeniculate species can propagate as free-living rhodolith nodules colonizing sedimentary seafloors (Figure 8). Some of the attached crustose corallines break free and then continue spherical growth as they are tumbled by wave action and bioturbation to ultimately cover vast areas as free-living rhodoliths (also called nodules, rhodolites, maërl, red algal balls, algaliths). Rhodolith beds have been found throughout all of the world's oceans. Globally, rhodoliths fill an important niche in marine ecosystems, serving as transitional habitats between rocky substrates and barren sedimentary areas (Littler and Littler, 2008). Under favorable preservation conditions, rhodoliths can be the predominant contributors

of carbonate sediments, often forming rudstone or floatstone depositional beds consisting of large fragments of rhodoliths contained in grainy matrices. Although they can be rolled by infrequent tropical storms, stationary rhodoliths nevertheless provide a three-dimensional microhabitat by intercellular translocation onto the lower shaded layers that continue to expand. A wide variety of species attach to rhodoliths, including other algae, corals, and commercial species such as clams, oysters, and scallops. Rhodoliths are a common feature of modern and ancient carbonate shelves worldwide. Fossil rhodoliths commonly are used to derive paleoecological and paleoclimatic information, and rhodolith communities contribute significantly to the global calcium carbonate budget.

Quantitative submersible studies in conjunction with scuba-based research (Littler et al., 1985, 1986, 1991; Littler and Littler, 1994) on deep-water rhodolith development, distribution, abundance, and primary productivity, at sites of both active formation and breakdown, provided the following detailed case study. The 1.27 km^2 upper platform (67 to 91 m deep) of a ~1,000 m high Bahamian seamount (San Salvador Seamount) averaged 95.8% cover of rhodoliths, contributing an impressive 391 tons of organic
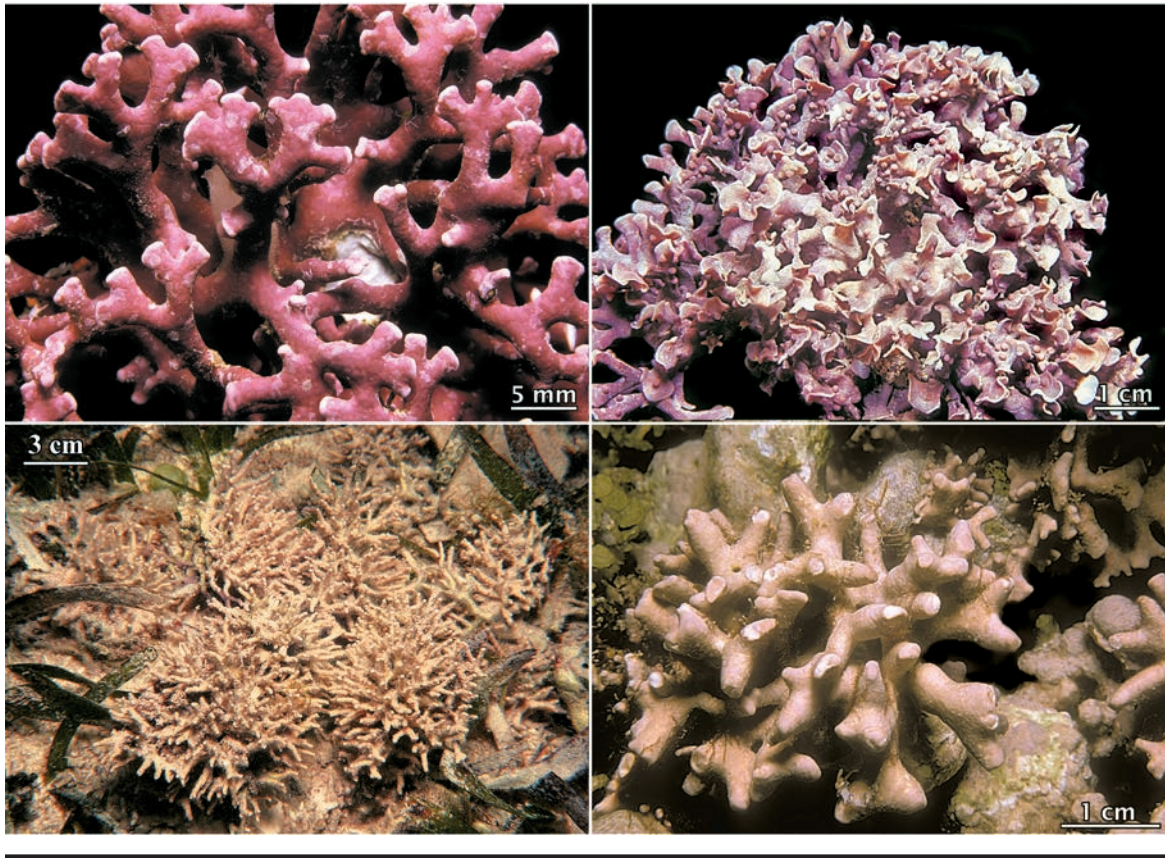
FIGURE 6. Spectrum of head-forming crustose corallines with upright branched excrescences. Top left: *Lithophyllum bamleri*. Top right: *Mastophora pacifica*. Bottom left: *Neogoniolithon spectabile*. Bottom right: *Lithophyllum pygmaeum*. (Photos by D. Littler.)

carbon per year to deep-sea productivity. The predominant crustose coralline alga was acclimated to extremely low light ranges, with an extremely narrow photosynthesis versus irradiance (PI) curve of net primary productivity (0.005 to slightly beyond 0.24 μmol per meter square per second of photosynthetically active radiation). Horizontal platform areas contained accumulations up to five rhodoliths deep (about 45 cm thick), with their visible planer (two-dimensional) crustose algal cover (68.5%) being composed of 41% *Lithophyllum* sp., 14.9% mixed crustose corallines, and 12.6% *Peyssonnelia* sp. The platform rhodoliths also contained an average 25% cover of the foraminiferan *Gypsina* sp.; by contrast, *Gypsina* cover was minimal on the slope rhodoliths. Rhodoliths that had spilled down from the relatively flat platform tended to be concentrated in fan-shaped deposits that were more prevalent near the tops of the slopes. Cover of living crustose algae on the deeper slope rhodoliths averaged only 22.8% and was made up of 14.8% unidentified crustose corallines, 6% *Lithophyllum* sp., and 2% *Peyssonnelia* sp.

Throughout platform depths from 67 to 91 m, rhodoliths were fairly uniform in composition and abundance. They ranged from 4 to 15 cm in diameter, with an average diameter of about 9 cm, and were roughly spherical with smooth living surfaces. The rugose rhodoliths spilling down the steep slopes of the seamount to depths below 200 m were characteristically smaller (about 5 cm average diameter), much rougher, and pitted by boring organisms. Cross-sections through the centers of upper platform nodules showed relatively thin (1–3 cm thick), well-preserved, outer envelopes overlying dead laminated crustose layers. These layers surrounded much thicker cores of biotically altered carbonates (comprised mostly of corallines, foraminiferans, and corals) that had been extensively reworked by boring sponges, boring algae, polychaetes, and pelecypods. Radiocarbon dating indicated that the outermost unaltered envelopes beneath actively growing platform crusts averaged 429 years old (range = 112 to 880 ybp), while the innermost unaltered layers showed an average age of 731 ybp (range = 200 to 1,100 ybp).

GEOLOGY AND EVOLUTION

Crustose coralline algae appeared in the early Cretaceous and have been important components of shallow marine communities

FIGURE 7. Spectrum of crustose coralline that form knoblike branched excrescences. Top left: *Mesophyllum erubescens.* Top right: *Lithothamnion proliferum.* Bottom left: *Hydrolithon reinboldii.* Bottom right: *Lithophyllum congestum.* (Photos by D. Littler.)
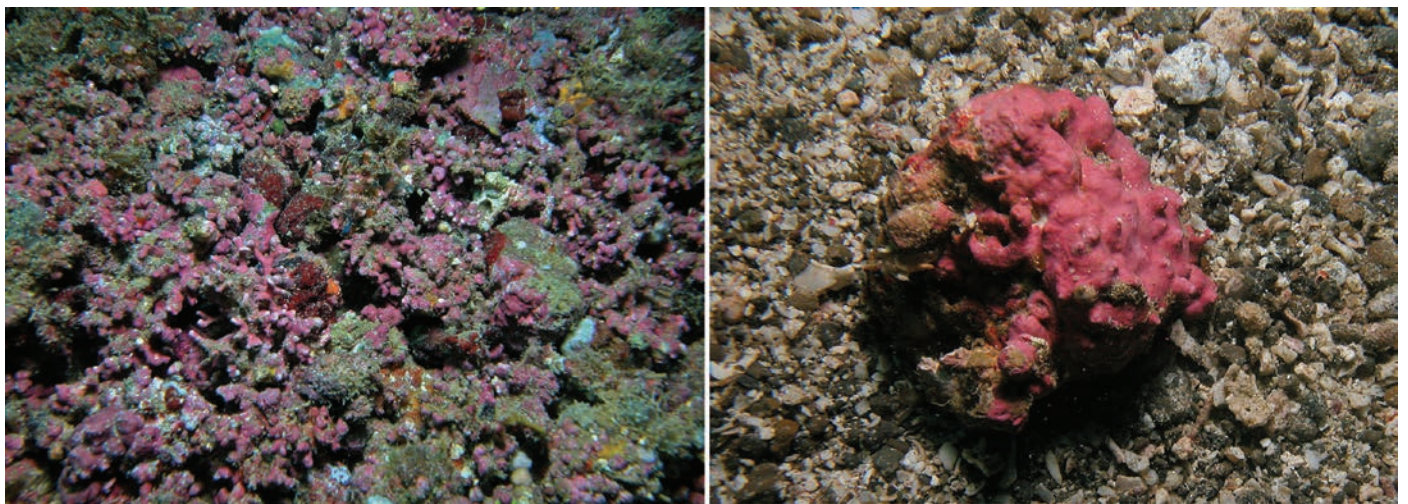

FIGURE 8. Examples of coralline algal rhodoliths. (Photos by D. Littler.)

throughout the Cenozoic, mostly showing long-term increases in species richness during much of their history. There are currently over 1,600 described species of crustose coralline algae (Woelkerling, 1988) and ~649 fossil species (Aguirre et al., 2000). Interestingly, Miocene coastal carbonate habitats are characterized by a worldwide bloom of coralline red algal deposits (termed rhodalgal facies). These extensively developed facies (i.e., characteristic sedimentary deposits) temporarily replaced corals throughout the tropics and subtropics as dominant carbonate producers (e.g., Esteban, 1996). By calibrating modern carbonate assemblages to local oceanographic conditions in the Gulf of California, Halfar et al. (2004) demonstrated that the predominance of rhodalgal facies occurred under mesotrophic to slightly eutrophic conditions. In the Mediterranean region, early to middle Miocene carbonates contain more rhodalgal components than coral reef deposits (Esteban, 1996). In addition to being widespread globally, fossil coralline algae also exhibited their greatest species richness during the early and middle Cenozoic (early Miocene peak of 245 species; Aguirre et al., 2000), with a collapse to a late Pleistocene low of 43 species. In reviewing 37 representative late-Pliocene studies, Halfar and Mutti (2005) concluded that although rhodalgal facies were clearly the dominant components at specific study sites, they often were not emphasized as extensively as the much better known coral assemblages. A number of the above studies focused mainly on coral reef components although rigorous reanalyses of the facies studied actually indicated a relatively low percentage of corals and a predominance of rhodoliths. Esteban (1996) noted a similar bias in a review of Miocene Mediterranean coral reefs and rhodalgal facies. Such discrepancies can be attributed mostly to poor knowledge of coralline red algae and rhodolith facies in conjunction with the tendency for researchers to apply classic coral reef depositional models, even in settings where corals were sparse.

Throughout the world's oceans during the late-early to early-late Miocene, while many phototrophs declined globally, coralline red algae radiated and diversified greatly. In fact, corallines have shown a long-term overall increase in species richness throughout most of their history. Despite this, coralline species diversification was not sustained after the Miocene (Aguirre et al., 2000) and coralline algae suffered a series of extinction events, each of which eliminated at least 20% of the species. In fact, during the two largest extinction events of the late Cretaceous and late Miocene–Pliocene, about 66% of all coralline species were lost. Each extinction event was followed by substantial episodes of rapid radiation and speciation, particularly in the early Paleocene and Pleistocene.

The conspicuous Miocene shift from coral- to rhodolith-dominated carbonate communities has been attributed to global climate changes. Halfar and Mutti (2005) argued that the prevalence of rhodolith facies, which developed under broader nutrient and temperature ranges than did the coral reef facies, was initially triggered by a global enhancement of nutrient resources. In the middle Miocene, nutrient availability was apparently augmented by increased upwelling- and erosion-related nutrient inputs into coastal ecosystems. These nutrient increases together with declining temperatures following the early to middle Miocene climatic optimum led to further expansion of rhodalgal facies. Hence, a global phase shift in dominance occurred in nearshore shallow-water carbonate producers from corals to coralline species that were tolerant of the higher nutrient levels (in accordance with the Relative Dominance Model [RDM]; Littler et al., 2006). Geological deposits of coralline algae contain organic carbon compounds such as cellulose (due to photosynthesis), as well as massive calcareous compounds due to calcification (precipitation of inorganic $CaCO_3$). The resultant carbon stores may be among the most important in the biosphere as neutralizers of global oceanic acidification and as reservoirs of excess greenhouse CO_2.

A striking geological pattern is an inverse relationship in the species richness of two of the families of Corallinales. From the Cretaceous to Pleistocene, Corallinaceae (both warm- and cold-water species) increased, while the tropical Sporolithaceae declined. This climatic link for Sporolithaceae and Corallinaceae was supported by both direct and inverse correlations, respectively, between species diversity and documented Cretaceous to Cenozoic paleotemperatures. Coralline diversification since the Cretaceous (Steneck, 1983, 1985) may have been driven by simultaneous coevolutionary increases in herbivores (mainly limpets, echinoids, and grazing fishes) that physically scrape and remove fleshy algal competitors, though that remains to be more firmly established.

DISTRIBUTIONAL PATTERNS AND FUNCTIONAL SIGNIFICANCE

Crustose (nongeniculate) coralline algae occur worldwide from polar to tropical regions, reaching their highest diversity in tropical reef environments. Three subgroups of Corallinales show characteristic distributions (Aguirre et al., 2000): (1) Sporolithoideae, low latitude/mainly deep waters; (2) Melobesioideae, high latitude/shallow waters to low latitude/deep waters; and (3) Lithophylloideae/Mastophoroideae, mid to low latitude/shallow waters.

The abundant occurrence of crustose corallines (and corals) in Indo-Pacific reefs was initially recognized by Darwin (1842); however, their important role as reef builders was first emphasized by Agassiz (1888). Most often, corals (Cnidaria) supply the bulk building blocks whereas coralline algae do much of the cementing together of debris. Barrier, fringing, and atoll reefs are complex ecosystems that depend on calcareous coralline algae for the development and maintenance of wave-resistant outer fronts (Figure 9). The crustose coralline algae, which deposit a type of calcium carbonate (calcite limestone) that is harder and denser than the aragonite of corals, build this raised algal ridge (Dawson, 1961). The intertidal–outer algal ridge habitat, to which crustose corallines (mainly species of *Porolithon*) are crucial for constructing the framework, characterizes surf-pounded
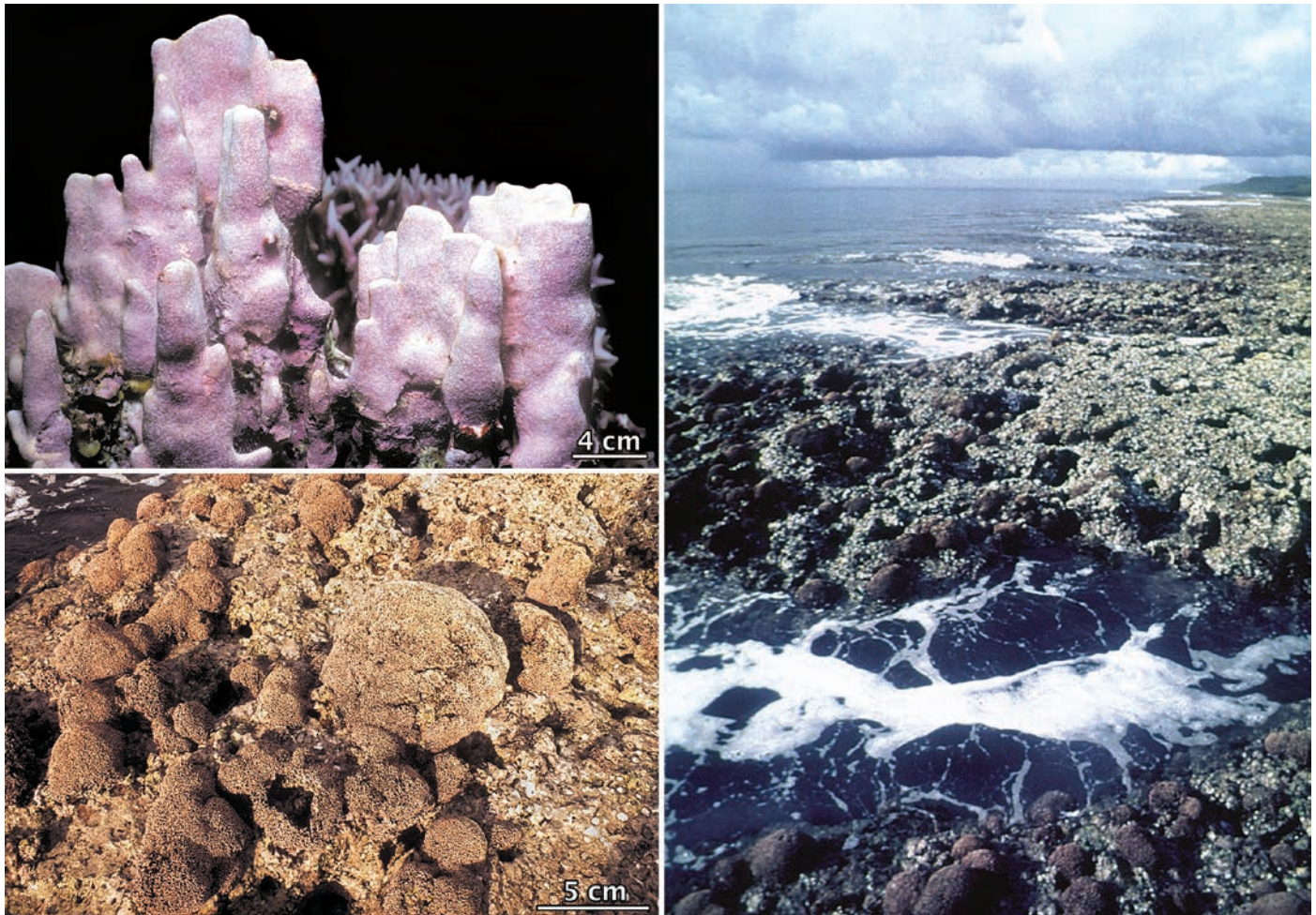
FIGURE 9. Right: A well-developed algal ridge from windward Guam. Top left: close-up of the pink crustose *Porolithon craspedium*. Bottom left: close-up of the head-forming *Lithophyllum kotschyanum*. (Photos by D. Littler.)

windward coral reefs of tropical Indo-Pacific and, to a lesser extent, Atlantic regions. The Pacific algal ridge builder *Porolithon onkodes* fixes a remarkable 3.2 mg of organic carbon per square meter per hour and 1.9 mg calcium per square meter per hour during an average-daylight day (Littler, 1973). By extending above the waterline, the algal ridge absorbs tremendous wave energy, not only protecting coastal shorelines that would otherwise erode, but also sheltering the more delicate corals and other reef organisms. Algal ridges develop intertidally and, therefore, require intense and persistent wave action to form, so are best developed on windward areas where there are consistent trade wind conditions.

Some of the coralline algae that develop into shelf-like crusts (Figure 5), upright branches (Figure 6), or thick knobby crusts (Figure 7) provide microhabitats for countless vulnerable invertebrates that would otherwise suffer increased mortality due to fish predation. Coralline algae also constitute a food source in the energy webs of coral reefs. Sea urchins, parrotfishes, surgeonfishes, limpets, and chitons all readily feed on coralline algae, which are usually not destroyed due to sunken, intercalary meristems that replenish the upper, damaged areas. Crustose corallines accelerate colonization by chemically attracting and facilitating the survival of coral larvae (Harrington et al., 2004), as well as the larvae of certain grazing invertebrates. This is beneficial for the corallines because the herbivores then remove epiphytes that might preempt available light or otherwise smother the crusts. Because of their stony texture, indigestible acid-neutralizing $CaCO_3$, and covered intercalary meristematic layer, corallines are uniquely resistant to considerable levels of grazing. As examples, the most common Indo-Pacific crustose coralline, *Porolithon onkodes*, often forms an intimate relationship with the chiton *Cryptoplax larvaeformis* (Littler and Littler, 1999), as does the Atlantic coralline *H. pachydermum* and the chiton *Choneplax lata* (Littler et al., 1995). The chitons live in
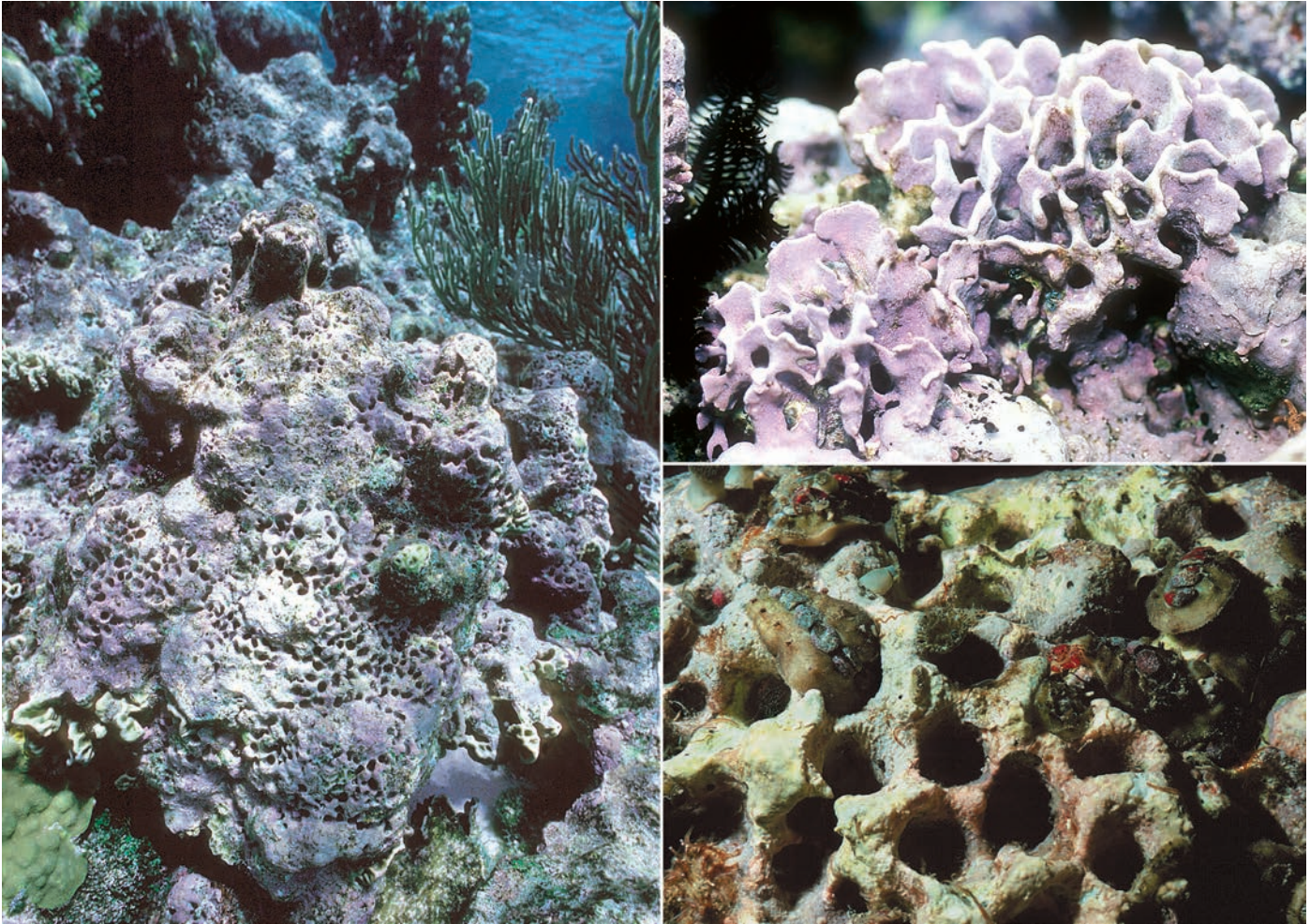
FIGURE 10. Castle forms of the crustose corallines created by their association with herbivorous chitons. Left and top right: *Hydrolithon pachydermum*/*Choneplax lata* (Pacific). Bottom right: *H. onkodes*/*Cryptoplax larvaeformus* (Atlantic). (Photos by D. Littler.)

burrows that are overgrown by *Porolithon* and graze nocturnally on the surfaces of the corallines (Figure 10). The pattern of grazing causes rapid meristematic differentiation and redirection in which the coralline produces an abundance of vertical, blade-like lamellae, resulting in a spectacular growth form resembling castles. This type of relationship is unique in the marine environment, whereby the predator actually increases the biomass, surface area, and reproductive capacity (i.e., fitness) of its principal prey (Littler et al., 1995).

PATHOGENS

Instances of coralline algal pathogens were unknown until 1993, when Coralline Lethal Orange Disease (CLOD) was first discovered using scuba (Littler and Littler, 1995) on Aitutaki Atoll, Cook Islands (Figure 11). The occurrence of CLOD at 25 Great Astrolabe, Fiji, sites increased from 0% in 1992 to 100% in 1993, indicating that the pathogen was in an early stage of virulence and dispersal. The bright orange bacterial pathogen grows as fan-shaped or circular bands at a mean linear rate of 1.5 mm per day, totally consuming host corallines that are in its path. All species of articulated and crustose species tested to date are easily infected by CLOD, and it has now become circumtropical throughout all coral reef habitats. In recent years, a white CLOD-like pathogen has become even more abundant worldwide; this is in addition to the recently recorded dispersion of a virulent black fungal pathogen (Figure 12) of coralline algae first found in American Samoa (Littler and Littler, 1998) and an unknown species of target-shaped coralline pathogen (Figure 13) first reported from the Great Astrolabe Reef (Littler et al., 2007). Without scuba, none of the above pathogens would have been discovered.
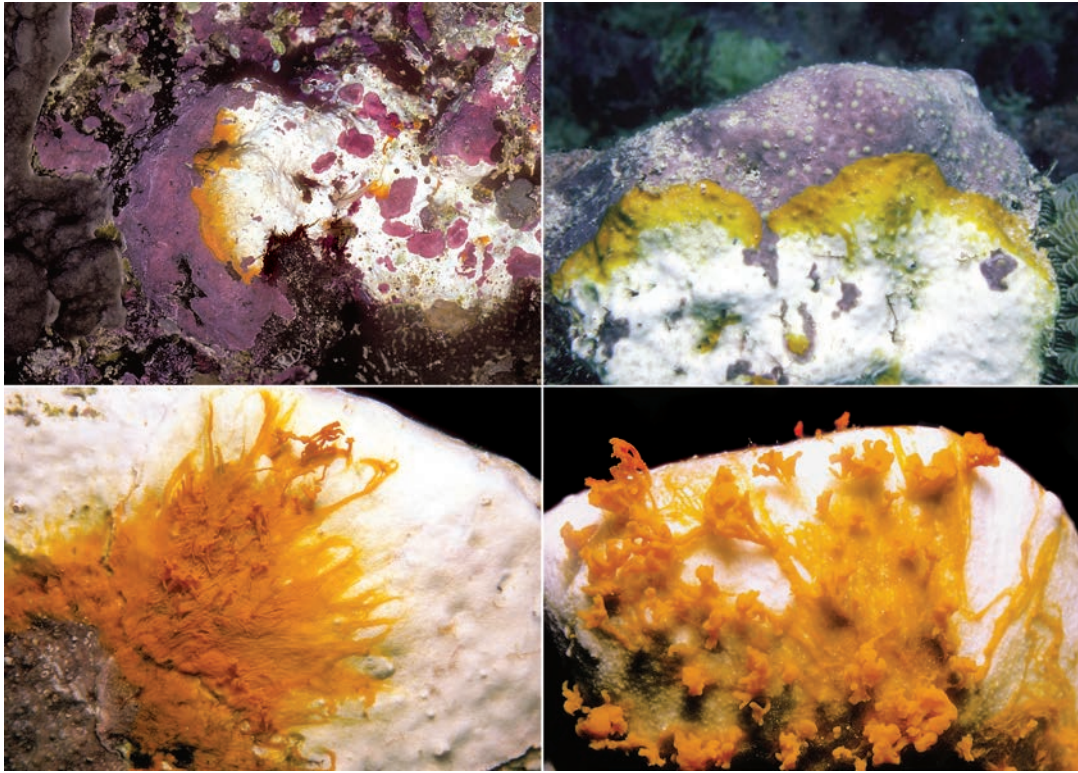
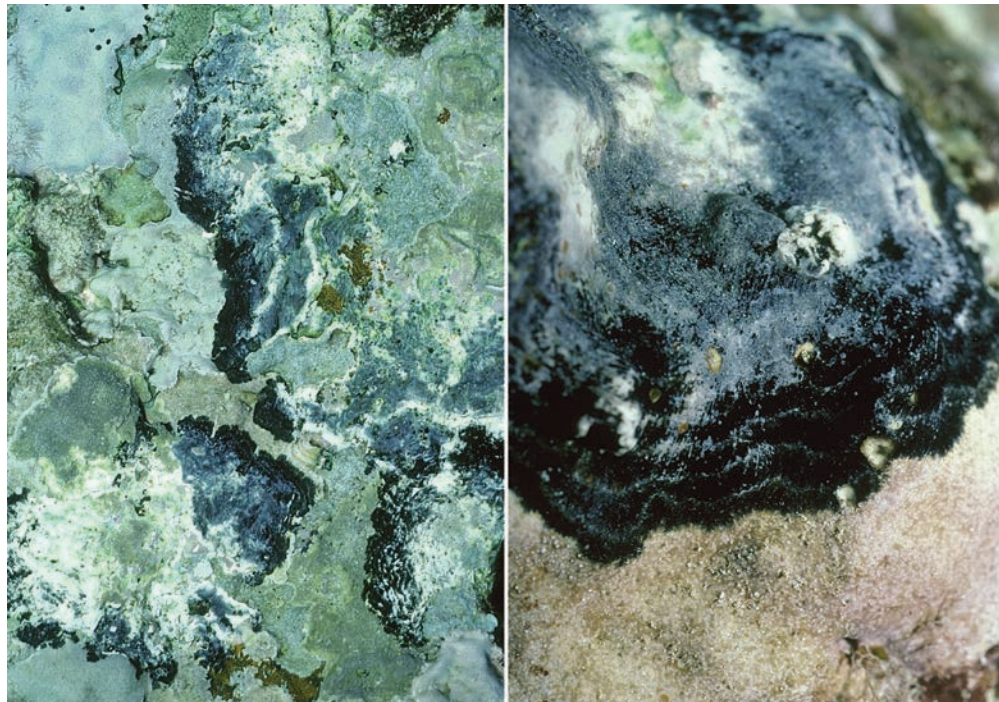**FIGURE 11.** In situ images of the worldwide CLOD pathogen. (Photos by D. Littler.)

FIGURE 12. In situ images of black fungus disease in the Pacific. (Photos by D. Littler.)

FIGURE 13. In situ images of target pathogen in the Pacific. (Photos by D. Littler.)

IMPORTANCE AND ROLE

The findings reviewed here are based mainly on extensive scuba research. Crustose (nongeniculate) coralline algae occur worldwide from polar to tropical regions, reaching their highest diversity in tropical reef environments. Coralline algae occupy the entire depth range inhabited by photosynthetic organisms, from upper-intertidal regions to depths as great as 295 m (Figure 14; Littler and Littler, 1994). The great abundances of corallines in the poorly known deep-sea realm underscore their widespread contributions to productivity, the marine food web, sedimentology, and reef biogenesis in clear tropical seas. The diversity of coralline algal forms is astonishing, ranging from small filamentous strands to some of the larger and most beautiful head-forming organisms on coral reefs (Figures 4–7). The predominant members of this functional indicator group (Littler and Littler, 2007) tend to be slow-growing, competitively subordinate taxa that are abundant in most reef systems. As an indicator group they are functionally resilient and able to expedite the recovery and restoration of a particular coral reef system relatively quickly since some thin forms of crustose coralline algae accelerate colonization and chemically attract and facilitate the survival of coral larvae (Harrington et al., 2004); the other two fleshy algal functional indicator groups (i.e., turfs and macroalgae) tend to overgrow and inhibit coral settlement, survival, and recovery. Because most crustose coralline algae continually slough off upper surface layers (bottom left, Figure 4), they play a key cleaning role and physically prevent the settlement and colonization of many fleshy fouling organisms on coral reefs (Littler and Littler, 1997).

Crustose corallines, because of their slow growth, tolerate a wide range of nutrient levels and generally are conspicuous, but not as predominant as corals, under low concentrations of nutrients and high levels of herbivory (Littler and Littler, 2007). Accordingly, they do well in the presence of both low and elevated nutrients (i.e., most are not inhibited by nutrient stress and many are maintained competitor free by surface cell-layer shedding [Johnson and Mann, 1986], even at lower levels of grazing [Littler and Littler, 1997]). Therefore, crustose coralline algae do not require elevated nutrients as might be inferred (Littler and Littler, 2007); instead, the degree to which they rise to dominance is largely controlled indirectly by the factors influencing the abundances of other functional groups, primarily the corals and fleshy macroalgae. The key point is that crustose corallines dominate mainly by default (i.e., under conditions of minimal competition) where corals are inhibited (e.g., by elevated nutrients or by strong wave action) and where fleshy algae are removed by intense herbivory. The wave-pounded intertidal algal ridges are built predominantly by *Porolithon (Hydrolithon) onkodes*, *P. gardineri*, *P. craspedium*, and *Lithophyllum kotschyanum* in the Indo-Pacific and by *P. pachydermum* and *L. congestum* in the Atlantic; all are coralline species that appear uniquely tolerant of aerial exposure. The transition from frondose- to turf- to coralline-algal communities has been reported (Steneck, 1989) to closely correlate with increasing herbivory gradients on coral reefs.

In addition to their protective reef-building nature, coralline algae provide a number of other goods and services. Since the eighteenth century, unattached corallines (maërl) have been harvested as acid-soil pH conditioners. In Britain and France, hundreds of thousands of tons of *Phymatolithon calcareum* and *Lithothamnion corallioides* continue to be dredged annually. Enormous maërl beds several km² in area, mainly composed of species belonging to the genera *Lithothamnion* and *Lithophyllum*, are present off the coast of Brazil and have begun to be
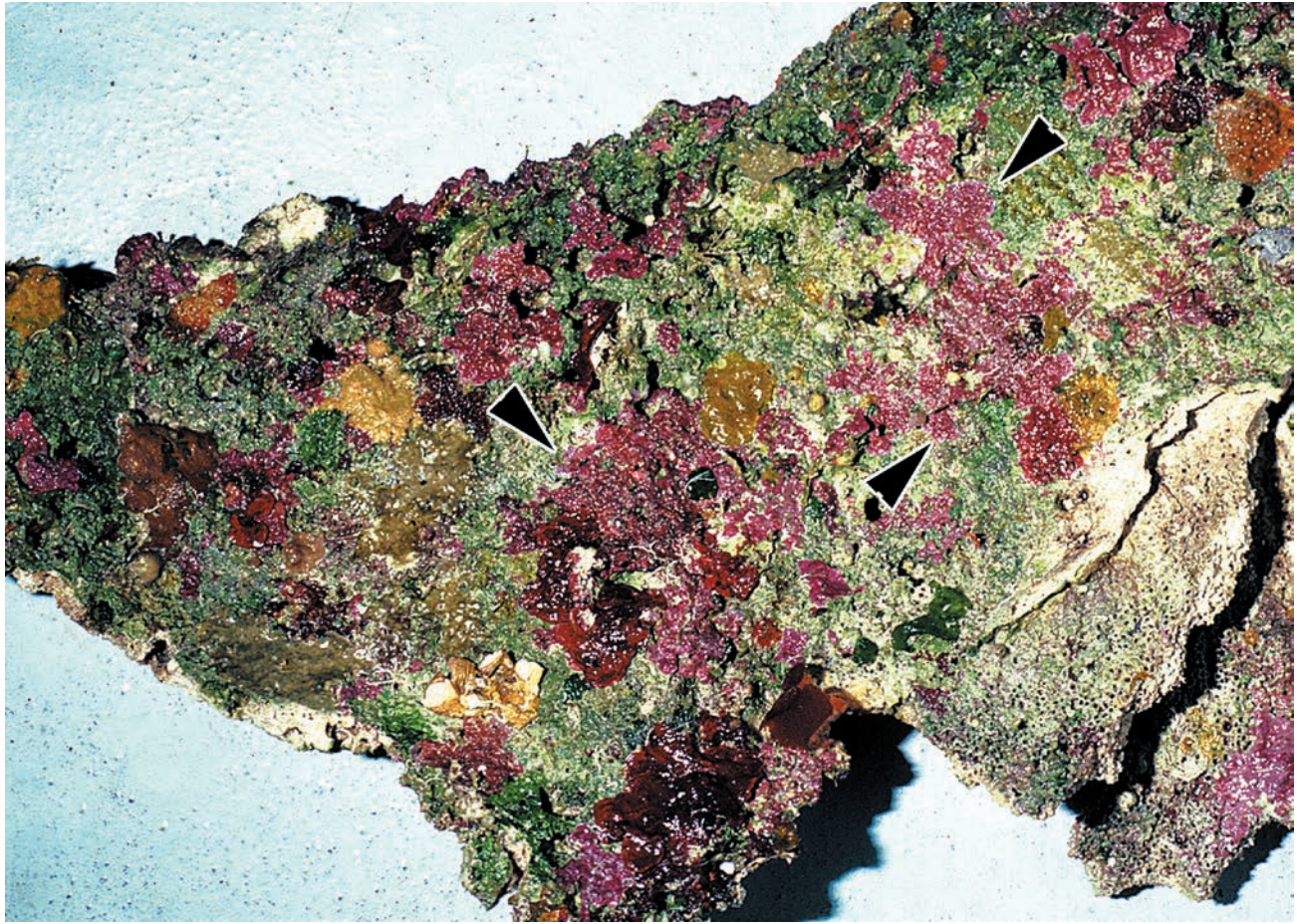
FIGURE 14. Rock taken by submersible from >200 m depth off San Salvador Seamount, Bahamas, showing the deepest plant life (a crustose coralline alga) on Earth. (Photo by D. Littler.)

commercially harvested. Maërl is also used as a mineral food additive for cows, hogs, and other livestock, as well as in the filtration and neutralization of acidic drinking water. Corallines are used in modern medical science in the preparation of dental bone implants (Shors, 1999). The cellular carbonate skeleton provides an ideal matrix for the adherence and regeneration of bone and tooth structures. Coralline algal fossils have proven to be extremely beneficial in deriving paleoecological and paleoclimatic information, and also have been employed as stratigraphic markers of particular significance in petroleum geology. As a spectacularly colorful component of live rock for the flourishing marine aquarium trade, coralline algae are highly desired for their architectural and attractive aesthetic qualities. However, the most important contribution of coralline algae worldwide may well prove to be in ameliorating the greenhouse CO_2 buildup associated with global climate change. It is the balance between calcification and respiration—which produces carbon dioxide—and the consumption of CO_2 by photosynthesis that will determine whether corallines act as a "sink" (absorbing CO_2) or as a source of CO_2. Experiments that studied how various calcifying systems take up and give off carbon dioxide have shown that the rise in CO_2 produced by calcification is mitigated by its removal through increased photosynthesis (Ohde, 1999; Iglesias-Rodriguez et al., 2008), with a net effect that is unlikely to either greatly contribute to or significantly reduce the rise in atmospheric CO_2. However, rising levels of CO_2 and concomitant acidification of seawater inhibit all reef builders, including coralline algae (Kleypas et al., 1999). By binding vast accumulations of $CaCO_3$ during calcification and photosynthesis, corallines may play a role in slowing future acidification of marine habitats such as coral reefs.

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