The Nature of Macroalgae and Their Interactions on Reefs

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ABSTRACT. What was known about tropical reef algae prior to the use of scuba came largely from dredging studies or drift collections, which usually resulted in highly mutilated specimens and questionable habitat data. Scuba allows a precise determination of ecological conditions and permits in situ photography, two techniques our group has relied on during the past three decades for quantitative studies and field guide production. A goal of this review is to familiarize the scientific diving community with the kinds and roles of algae on tropical reefs, with the hope that seaweeds will be utilized more fully as tools for addressing important ecological questions.

Because of the rapid degradation of tropical reefs worldwide, it is imperative that the role and diversity of macroalgae be studied in a timely, efficient, and scientifically verifiable manner. It is of paramount importance to characterize the world's coral reef environments and to understand the responses of foundation species. The fleshy macroalgal forms are the food of herbivores, and only become abundant when their production rate exceeds the capacity of herbivores to consume them. On healthy oligotrophic coral reefs, even very low nutrient increases may shift relative dominance from corals (Cnidaria) to macroalgae by both stimulating macroalgal production and inhibiting corals. As a result, frondose macroalgae are generally recognized as harmful to the longevity of coral reefs due to the link between excessive blooms and coastal eutrophication.

Reef plant complexity has evolved along very different evolutionary lines. The range of sizes, shapes, life histories, pigments, and biochemical and physiological pathways is remarkable. The biodiversity of coral reef plant life is unequalled. Macroalgae from four evolutionary lines dominate and, in conjunction with coelenterate corals, are the primary producers and builders of coral reef habitats and carbonate architecture. Previously, marine plants were understudied on coral reefs; however, new scuba-based field guides are alleviating this problem. Their rapid growth and short generation time make them ideal subjects for experimental studies.

INTRODUCTION

While extensive taxonomic and distributional data were derived before diving was common in the collection of algae (Boergesen, 1916; Taylor, 1960), scuba has afforded science the opportunity to greatly expand the understanding of the nature of macroalgal diversity with new species, new distribution data, and the mechanisms by which diversity is produced and maintained in reef systems. This of course is true for all three groups of eukaryotic algae—Rhodophyta (red algae), Chlorophyta (green algae), and Phaeophyceae

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(brown algae)—as well as the larger prokaryotic, colony-forming cyanobacteria/Cyanophyta (blue-green algae). These four groups do not have a common ancestor (i.e., collectively polyphyletic) although chloroplasts—common to all the eukaryotes—appear to have had a single blue-green algal (cyanobacteria) origin. The presence of chloroplasts and subsequent capacity for photosynthesis gives marine macroalgae ecological roles as primary producers that are similar to other marine plants, notably sea grasses. Sea grasses are not seaweeds; rather, they are rooted flower- and seed-bearing "higher" plants (Angiosperms).

The macroalgal thallus (i.e., plant body) consists of filaments, sheets and blades (leaflike laminae), reproductive sori (spore clusters), gas bladders (floatation organs on blades in rockweeds, and between lamina and stipes in kelps), stipes (stemlike structures [may be absent]), and holdfasts (with or without haptera, fingerlike extensions anchored to substrates). The stipe and blade combined are known as the frond.

Macroalgae grow attached to stable substrata in seawater (or brackish water) under light levels sufficient for photosynthesis. Seaweeds are most commonly found in shallow waters on rocky shores; however, the giant-celled green algal group Bryopsidales includes rhizoidal forms adapted to proliferating in sedimentary environments. At the shallowest level are algae that inhabit the high-intertidal spray zone whereas at the deepest level are forms attached to the seabed under as much as 295 m of water (Littler and Littler, 1994; see Littler and Littler, this volume: "Coralline Algae," fig. 13,). The deepest macroalgae are calcified crustose coralline species (Rhodophyta).

HUMAN UTILIZATION OF MACROALGAE

Macroalgae have a variety of uses. They are utilized extensively as food by coastal cultures, particularly in Southeast Asia. Seaweeds are also harvested or cultivated using scuba or hookah for the extraction of alginate, agar, and carrageenan—gelatinous substances collectively known as hydrocolloids or phycocolloids. Colloids have great commercial importance, especially in the production of food additives. The gelling, water-retention, emulsifying, and other physical properties of colloids are critical to the food industry. Agar is used in foods such as candies, canned meats, desserts, bottled drinks, and gelatin molds. Carrageenan is used in the manufacture of salad dressings, condiments, and dietary foods, and as a preservative in canned meat and fish, milk products, and bakery goods. Alginates are utilized for many of the same purposes as carrageenan, but are also used in the production of paper sizings, glues, colorings, gels, explosive stabilizers, fabric prints, hydrosprays, and drill lubricants. Macroalgae have long been used as fertilizers and soil conditioners. Seaweeds are currently being investigated as sources of biodiesel and biomethane. Algal extracts are also widely used in toothpastes, cosmetics, and paints.

In the biomedical and pharmaceutical industries, alginates are used in wound dressings and production of dental molds. In diagnostic microbiological research, agar is the culture substrate of choice for pathogens. Seaweeds are also sources of iodine, an element necessary for human thyroid function. The vast array of natural products that algae produce represents a gold mine of potential medicinal compounds and is presently being investigated using both scuba and submersibles.

ECOLOGICAL SIGNIFICANCE OF MACROALGAE

The concepts of top-down and bottom-up controls have long been used (e.g., Atkinson and Grigg, 1984; Carpenter et al., 1985) to describe mechanisms where either the actions of predators or resource availability regulates the structure of aquatic communities. These opposing concepts can be particularly useful in understanding complex coral reef ecosystems. The Relative Dominance Model (RDM; first proposed by Littler and Littler, 1984) predicts that the competitive outcomes determining the relative abundances of corals, crustose coralline algae, microalgal turfs, and frondose macroalgae on coral reefs are most often controlled by the complex interactions of environmental factors (bottom-up controls such as nutrient levels) and biological factors (top-down controls such as grazing).

The study of top-down control of macroalgae by abundant populations of large mobile herbivores is particularly well developed for coral reefs, beginning over five decades ago with the caging study of Stephenson and Searles (1960). As examples, Sammarco et al. (1974), Ogden and Lobel (1978), Sammarco (1983), Carpenter (1986), Lewis (1986), Morrisson (1988), and numerous other researchers (reviewed by McCook et al., 2001) have demonstrated that lowering herbivory usually results in rapid increases in fleshy algae. However, when coral reefs are exposed to increases in nutrients, fleshy macroalgae (Figure 1) may be favored over the slower-growing but highly desirable corals (Lapointe et al., 1997). On healthy oligotrophic coral reefs, even very low nutrient increases may exceed critical levels and shift relative dominances by stimulating macroalgal biomass production while inhibiting corals (Littler and Littler, 1984). Large biomasses/standing stocks of slow-growing perennial macroalgae (e.g., rockweeds) can, given sufficient time, develop even under low inorganic nutrient concentrations (McCook, 1999). Also, *Sargassum* spp. can coexist with corals in oligotrophic waters by utilizing particulate organic sources of nutrients (Schaffelke, 1999). This information suggests that large macroalgal biomasses do not necessarily require, nor indicate, detrimentally abundant dissolved nutrients.

Fleshy macroalgae can outcompete corals (Birkeland, 1977; Bellwood et al., 2006), many of which are inhibited under elevated nutrient levels (reviewed in Marubini and Davies, 1996). Fast-growing macroalgae are opportunists that benefit from disturbances, which release space resources from established, longer-lived organisms. They can also take over space from living

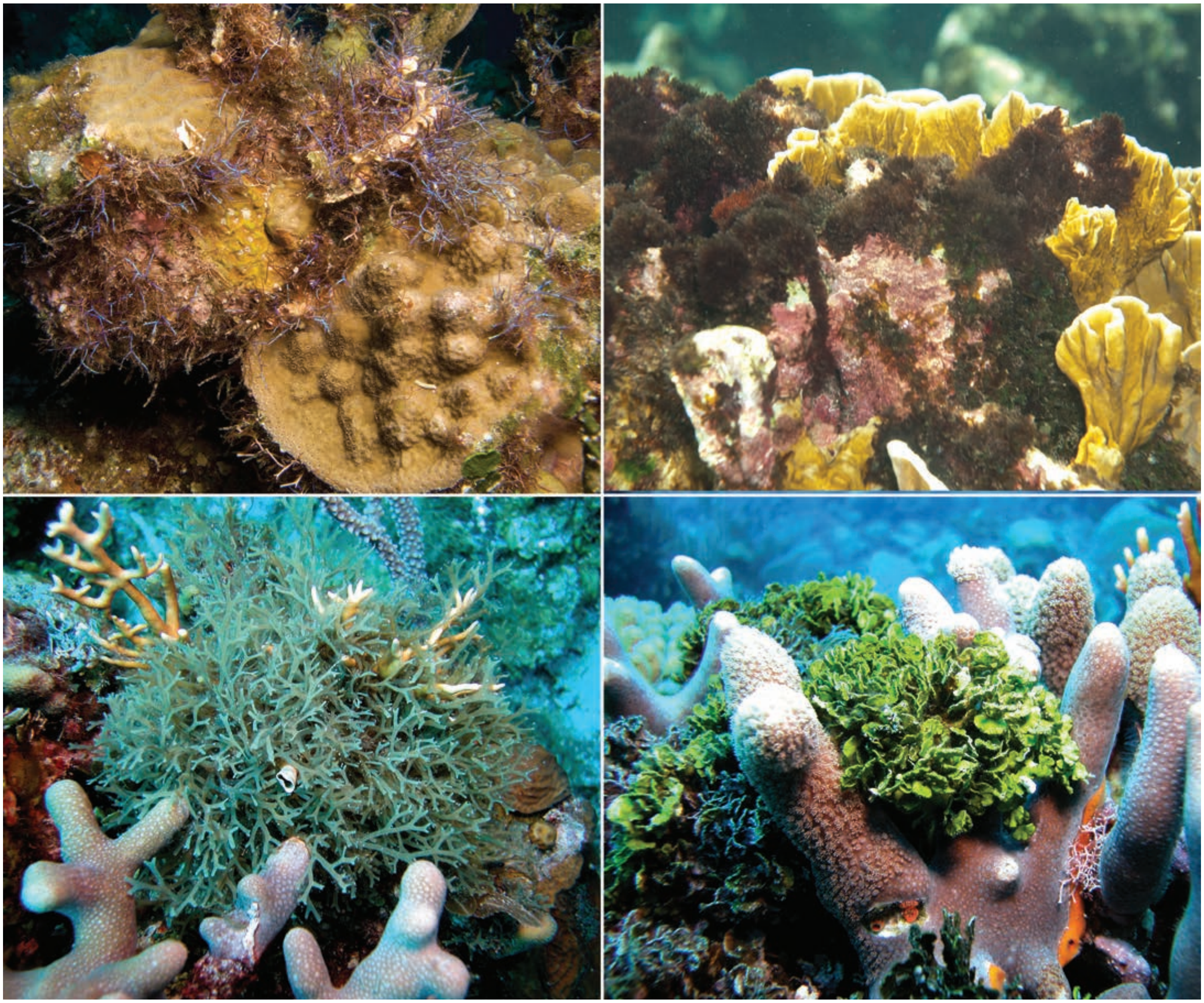

FIGURE 1. Ecological interactions (competition) between coral and algae. Top left: *Coelothrix irregularis*. Top right: *Laurencia obtusa*. Bottom left: *Dictyota cervicornis*. Bottom right: *Halimeda opuntia*. (Photos by D. Littler.)

corals (Birkeland, 1977) when provided with sufficient nutrients. As a result, frondose macroalgae (those that form carpets of horizontal thalli) are generally recognized as harmful to coral reefs due to the link between excessive blooms of these algae and coastal eutrophication (Anderson, 1995). The competitive dominance of fast-growing macroalgae is inferred from their overshadowing canopy heights as well as from inverse correlations in abundances between algae and other benthic producers (Lewis, 1986), particularly under elevated nutrient concentrations (e.g., Littler et al., 1993; Lapointe et al., 1997). Macroalgae, such as *Halimeda* spp. (Figure 2), also can gain competitive advantage by serving as carriers of coral diseases (Nugues et al., 2004). The fleshy macroalgal form group has proven to be particularly attractive to herbivores (see Hay, 1981; Littler et al., 1983a, 1983b) and only becomes abundant where grazing is lowered or swamped by excessive algal growth (chemically defended forms such as cyanobacteria [Figure 3; Paul et al., 2007] are exceptions). Overcompensation with high levels of herbivory may explain some of the reported cases (e.g., Smith et al., 2001) of specific corals surviving high-nutrient coral reef environments.

FIGURE 2. *Halimeda opuntia* overgrowing coral. (Photo by D. Littler.)

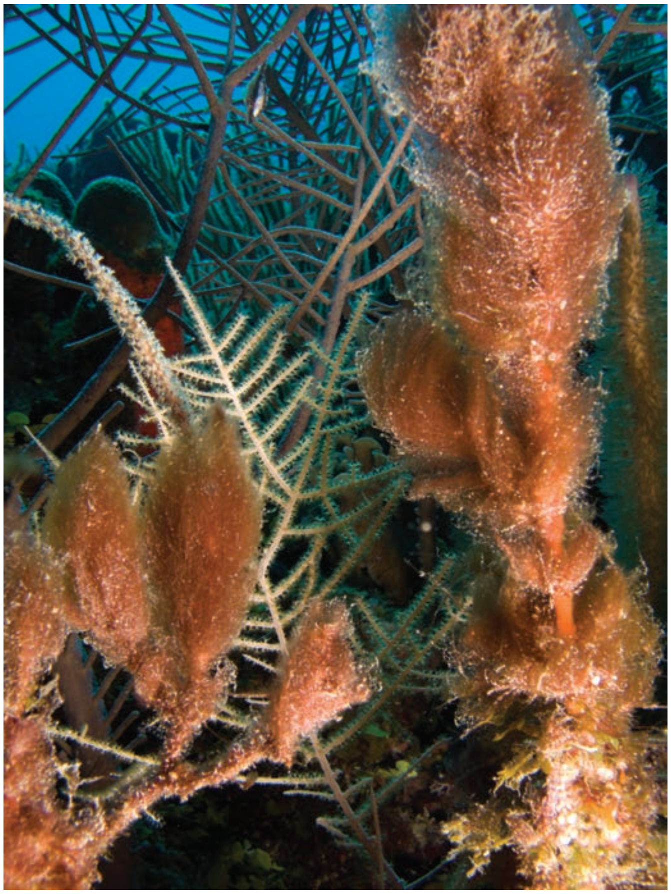

FIGURE 3. *Lyngbya polychroa*, a chemically defended blue-green alga. (Photo by D. Littler.)

MAJOR MACROALGAL GROUPS

What was known about tropical reef algae prior to the use of scuba came largely from shipboard dredging studies or drift collections. These often produced highly mutilated specimens and lacked habitat data since the scope of the dredge cable varied greatly. Scuba allows a precise determination of ecological conditions and permits in situ photography, two techniques our group has relied on during the past three decades for quantitative studies and field guide production. A goal of our three reviews in this volume is to familiarize the scientific diving community with the kinds and roles of algae on tropical reefs, with the hope that seaweeds will be utilized more fully as tools for addressing important ecological questions. The critical role that seaweeds play in reef ecosystems overlaps other fields of marine sciences, such as fisheries resources, marine chemistry, ecology, geology, and coral reef conservation.

RHODOPHYTA (RED ALGAE)

Rhodophyta generally have large quantities of the red pigment phycoerythrin in their photosynthetic cells. This red pigment in combination with various other pigments is responsible for the vast array of colors ranging from translucent pale pink, lavender, purple, maroon, and burgundy to iridescent blue (Figure 4). The pigment phycoerythrin is water soluble; therefore, red algae immersed in hot water will stain the liquid red or pink and the thalli will eventually turn green. Other red-algal cellular characteristics include eukaryotic cells lacking motile gametes (without flagella and centrioles), floridean starch as the food reserve, and (if present) chloroplasts containing unstacked thylakoids without an external endoplasmic reticulum. Pit connections and pit plugs are unique and distinctive features of red algae that form during the process of cytokinesis following mitosis. Most red algae are also multicellular, macroscopic, and reproduce sexually. They display alternation of life-history phases including a gametophyte phase and two sporophyte phases.

The red algae are almost exclusively marine and are the largest and most diversified group of tropical reef plants, with population estimates of up to 10,000 species. The diversity of their forms is astonishing, ranging from small filamentous turfs to some of the larger and most beautifully delicate organisms on coral reefs (Figure 4). Calcareous red algae can dominate some reefs and often surpass corals in reef-building importance (e.g., *Porolithon (Hydrolithon) craspedium*; Figure 5). Most often, corals (Cnidaria) supply the bulk building blocks whereas coralline algae do much of the cementing together of debris. The crustose coralline algae (forms that deposit a type of calcium carbonate [calcite] that is harder and denser than the aragonite of corals) also build the algal ridge (see Littler and Littler, this volume: “Coralline Algae,” fig. 9) on many reef systems. By absorbing wave energy, the raised algal ridge not only protects land masses that would otherwise erode, but also shelters the more delicate corals and other reef organisms.

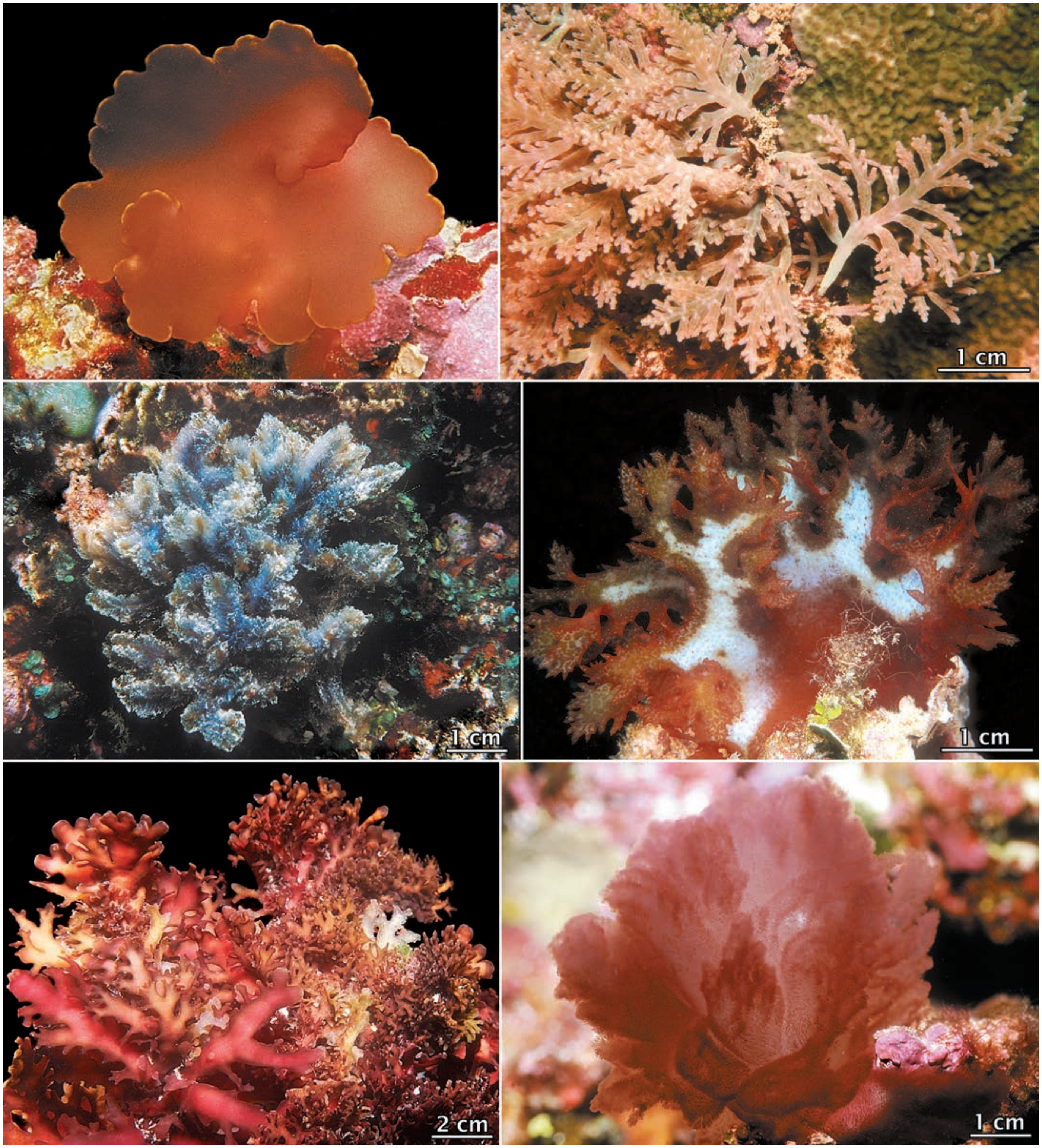

FIGURE 4. Different forms and colors of red algae. Top left: *Halymenia* sp. Top right: *Osmudea pinnatifida*. Middle left: *Dasya iridescens*. Middle right: *Halymenia maculata*. Bottom left: *Carpopeltis maillardii*. Bottom right: *Dudresnaya hawaiiensis*. (Photos by D. Littler.)

FIGURE 5. The reef-building calcareous macrophyte *Porolithon* (*Hydrolithon*) *craspedium*. (Photo by D. Littler.)

PHAEOPHYCEAE (BROWN ALGAE)

Phaeophyceae contain large quantities of the brown pigment fucoxanthin. They have cellulose walls; alginic acid and fucoidin are also important components. Brown algae are unique among macroalgae in their developing into multicellular forms with differentiated tissues, and they reproduce by means of motile flagellated spores. Most brown algae have a life history that consists of an alternation between morphologically similar haploid and diploid plants. *Scytosiphon lomentaria* alternates between four distinct morphological generations, which is considered to be a bet-hedging survival strategy (Littler and Littler, 1983).

The Phaeophyceae comprise about 2,000 species and are almost exclusively marine algae. Tropical brown algae include microscopic filament, sheet, coarsely branched, and crust forms (Figure 6). Nearly all brown algae have fine (microscopic) hairs emanating from their surfaces that may serve to increase surface area for nutrient uptake. Kelps attain their greatest abundance, size, and diversity in cold temperate to polar waters. They occur from the intertidal (Fucales) to 115 m depth (*Sargassum hystrix*; Littler and Littler, 1994) on reefs.

Brown algae are also well represented in coral reef ecosystems, particularly in back-reef areas. For example, *Sargassum* and *Turbinaria* (Figure 7) can form small-scale forests up to several meters high that provide biomass, habitat, and shelter for numerous fishes and invertebrates.

CHLOROPHYTA (GREEN ALGAE)

Chlorophyta generally have predominantly green chlorophyll pigments. The green algae also contain subordinate carotenoid and xanthophyll pigments and are the ancestral relatives of vascular plants (grasses, trees, sea grasses, etc.), which also contain these same basic pigments. Green seaweeds range from microscopic threadlike filaments to thin sheets; can be spongy, gelatinous, papery, leathery, or brittle in texture; and reach up to 1.5 m in length (Figure 8). The green algae store their energy reserves as starch. All produce flagellated spores and gametes, giving them the advantage of motility (Hoek et al., 1995).

Green algae are always present on tropical coral reefs and lagoon floors, often intermixed among sea grass shoots. Chlorophyta are usually the siphonaceous (giant-celled) forms of Bryopsidales, such as *Halimeda, Avrainvillea, Udotea,* and *Caulerpa*, that employ a unique cytoplasmic streaming/blade abandonment mechanism to eliminate epiphytes (Littler and Littler, 1999). Most Bryopsidales have a rhizophytic, rooted growth form and readily take up pore-water nutrients by cytoplasmic streaming (Williams, 1984). The deepest-occurring fleshy upright alga (*Rhipiliopsis profunda*) is a member of this group and was found by submersible attached to bedrock at a depth of 210 m (Littler and Littler, 1994). Many of these same very deep living species were later found by scuba divers in shallower shaded locations. Some genera of filamentous or sheetlike green algae are extremely tolerant of stressful conditions and can be indicators of freshwater seeps, recently disturbed areas (as early colonizers of newly exposed substrates), habitats of low herbivory (high herbivory eliminates palatable greens), and especially areas with an overabundance of nutrients (e.g., bird roosting islands, polluted areas).

Calcified green algae are major contributors to the production of marine sediments. Some genera, such as *Udotea* and *Penicillus*, produce enormous amounts of fine silt and other sediments due to continual sloughing of thalli and the subsequent disintegration. In many tropical locales, the sparkling white sand beaches are mostly bleached and eroded calcium carbonate (aragonite) skeletons of *Halimeda*. *Halimeda* "hash" (i.e., the coarse oatmeal-like accumulations of *Halimeda* segments, Figure 9) has been used in power plants and other fossil fuel industries as a smokestack scrubber/neutralizer to precipitate sulfurous acid and other precursors to acid rain.

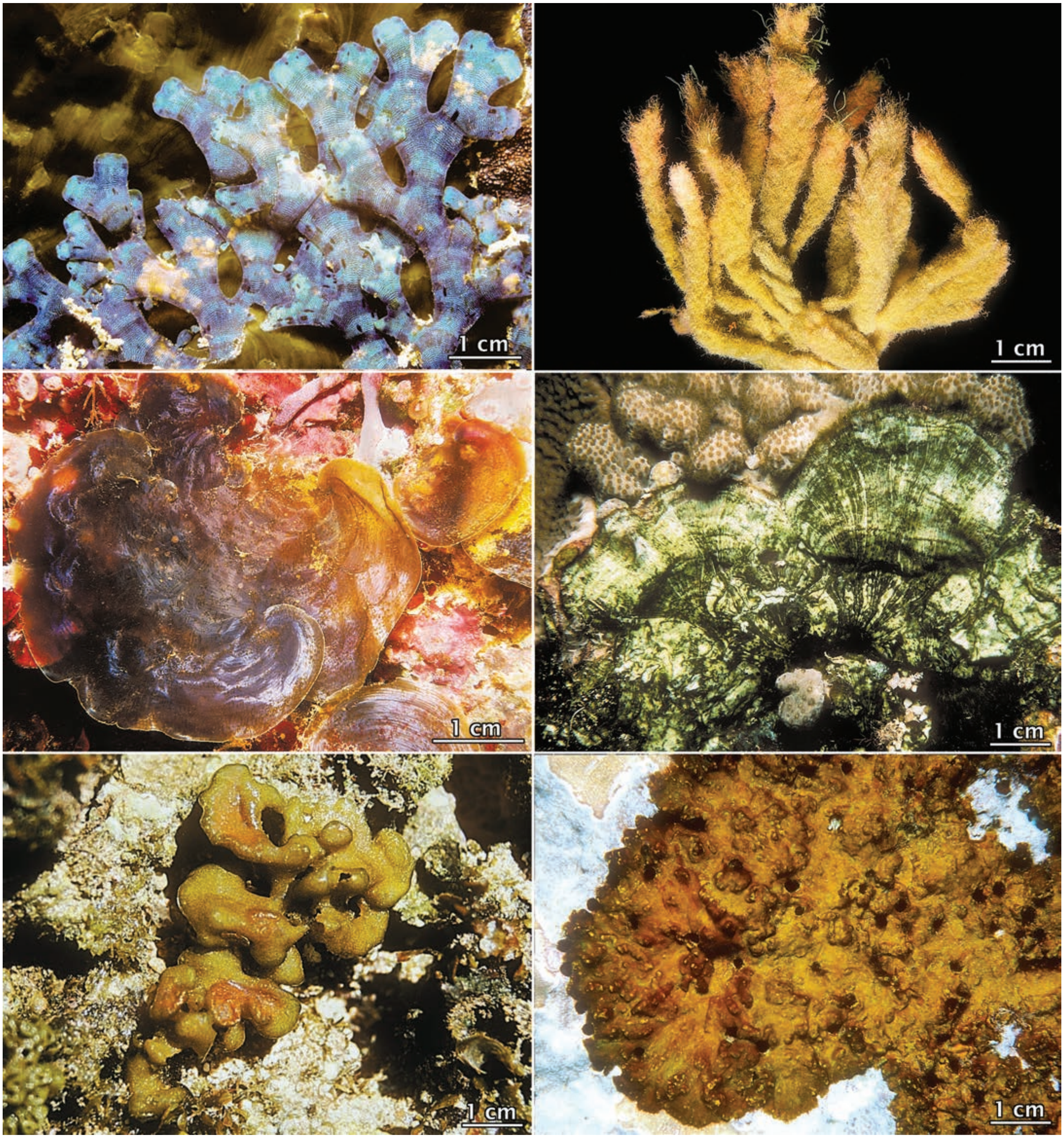

FIGURE 6. Different forms and colors of brown algae. Top left: *Dictyota humifusa*. Top right: *Asteronema breviarticulatus*. Middle left: *Distromium flabellatum*. Middle right: *Cutleria* sp. Bottom left: *Iyengaria stellata*. Bottom right: *Ralfsia extensum*. (Photos by D. Littler.)

FIGURE 7. Top left and middle: *Sargassum hystrix*. Top right: *Turbinaria turbinata*. Bottom: *Sargassum polyceratium* forming vast, dense beds on the windward side of Bonaire. (Photos by D. Littler.)

FIGURE 8. An array of different green algal forms. Top left: *Codium intertextum*. Top right: *Halimeda copiosa*. Middle left: *Ventricaria ventricosa*. Bottom left: *Udotea cyathiformis*. Bottom right: *Caulerpa sertularioides* f. *farlowii*. (Photos by D. Littler.)

FIGURE 9. *Halimeda* "hash" (i.e., dead calcareous segments). (Photo by D. Littler.)

CYANOBACTERIA (BLUE-GREEN ALGAE)

This ancient, highly controversial, and difficult group is prokaryotic, and not a member of the true plants. Cyanobacteria's simple, mostly filamentous, colonial thalli lack sophisticated characters, making their taxonomy highly technical. Saltwater species at scuba depths have seldom been collected and their important roles are only recently being appreciated. Cyanobacteria were the first group to evolve aerobic photosynthesis, the process that generates food for most of the biological world. On tropical reefs, cyanobacteria form masses of microscopic organisms that are strung together into large filamentous clumps or colonies (Figure 10), and they have specific colors, shapes, or growth forms that are distinctive. However, these are lost in preserved specimens, and before scuba went unappreciated by earlier museum/herbarium–bound taxonomists. Most commonly, the color of blue-green algae is some peculiar shade of pink to purple to black—a combination of red from the pigment phycoerythrin, blue from phycocyanin, and green from chlorophyll.

FIGURE 10. An array of different blue-green algal forms. Top left: *Rivularia nitida*. Bottom left: *Schizothrix minuta*. Right: unidentified. (Photos by D. Littler.)

Some filamentous colonies show the ability to differentiate into several specialized cell types: vegetative cells (the normal, photosynthetic cells that are formed under favorable growing conditions); akinetes (the stress-resistant, long-lived spores that form when environmental conditions become harsh); and thick-walled heterocysts, which contain the enzyme nitrogenase for nitrogen fixation (Herrero and Flores, 2008). Many cyanobacteria also produce motile reproductive filaments called hormogonia that glide free from the parent colony and disperse to form new colonies.

High standing biomass of cyanobacteria is usually considered detrimental to the health of both coral reef systems and people. They produce chemical compounds that can be toxic to fish, plankton, and invertebrates. For example, one type of swimmer's itch, a skin irritation that beach-goers commonly experience, can be caused by blooms of the blue-green alga *Lyngbya majuscula* (Figure 11). Black band disease of corals (Figure 12),found throughout all tropical oceans, is caused by blue-green algae and associated microorganisms (Ruetzler et al., 1983). Certain cyanobacteria produce neurotoxins, hepatotoxins, cytotoxins, and endotoxins that can be dangerous to animals and humans (Paul et al., 2007).

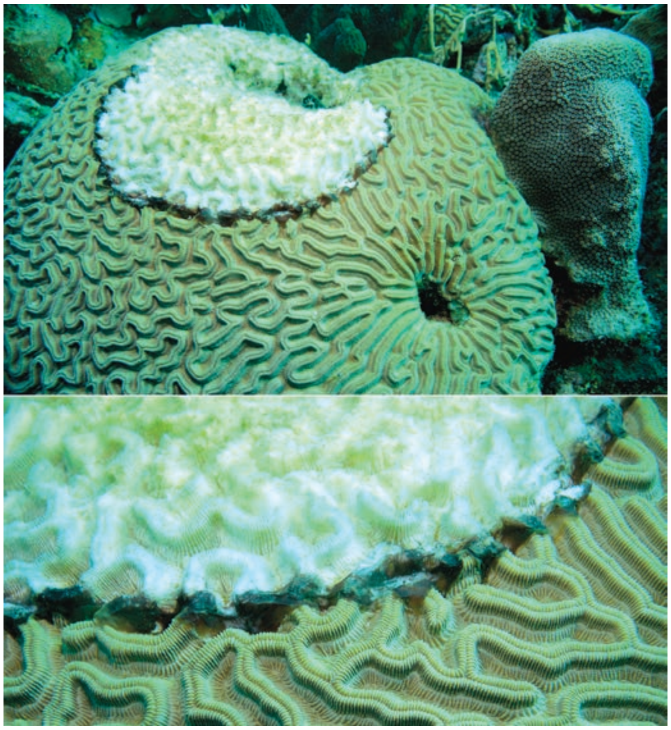

FIGURE 12. Black band disease, *Phormidium corallyticum,* attacking a brain coral. (Photos by D. Littler.)

FIGURE 11. *Lyngbya majustula*, the cyanobacteria (blue-green alga) that causes one type of swimmer's itch. (Photo by D. Littler.)

The nitrogen-fixing capacity of some blue-green algae is extremely important. Heterocyst-forming species bind nitrogen gas into ammonia (NH_3), nitrite (NO_{2-}), or nitrate (NO_{3-}) that can be absorbed by all plants. This role is crucial for tropical reef systems and especially nutrient-depauperate atoll reefs, which are extremely low in fixed nitrogen. Some of these cyanobacteria contribute significantly to global ecology and the oxygen cycle. For example, the marine cyanobacterium *Prochlorococcus* (0.5–0.8 μm diameter) accounts for >50% of the total photosynthetic production of the open ocean and 20% of the planet's atmospheric oxygen (Partensky et al., 1999). Cyanobacteria are the only group of organisms that are able to reduce nitrogen and carbon in aerobic conditions, a feature that may be responsible for their evolutionary and ecological success in certain coral reef habitats.

Blue-green algae are abundant worldwide and ubiquitous on coral reefs, where they often occur under extreme environmental conditions. The universally present black band in the splash zones that make rocks or boat ramps slippery is a layer of microscopic blue-green algae. Such blue-greens can withstand exposure to severe drying, extreme salinity, rain, bright sun, and high heat and still flourish. Cyanobacteria are among the oldest known life forms on Earth. Stromatolites containing fossilized oxygen-producing cyanobacteria date to 1.5 billion years ago (Zhang and Golubic, 1987).

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