

Coral Reef Algae

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Abstract Benthic macroalgae, or “seaweeds,” are key members of coral reef communities that provide vital ecological functions such as stabilization of reef structure, production of tropical sands, nutrient retention and recycling, primary production, and trophic support. Macroalgae of an astonishing range of diversity, abundance, and morphological form provide these equally diverse ecological functions. Marine macroalgae are a functional rather than phylogenetic group comprised of members from two Kingdoms and at least four major Phyla. Structurally, coral reef macroalgae range from simple chains of prokaryotic cells to upright vine-like rockweeds with complex internal structures analogous to vascular plants. There is abundant evidence that the historical state of coral reef algal communities was dominance by encrusting and turf-forming macroalgae, yet over the last few decades upright and more fleshy macroalgae have proliferated across all areas and zones of reefs with increasing frequency and abundance. Ecological processes that sustain these shifts from coral- to algal-dominated tropical reefs include increases in open suitable substrate due to coral mortality, anthropogenic increases in nutrient supply, reductions in herbivory due to disease and overfishing, and the proliferation of algae with chemical defenses against herbivory. These shifts are likely to be accelerated and the algal state stabilized by the impacts of invasive species and climate change. Thus, algal-dominated tropical reefs may represent alternative stable states that are resistant to shifts back to coral domination due to the strength and persistence of ecological processes that stabilize the algal state.

Keywords Macroalgae • cyanobacteria • chemical defenses • nutrients • herbivory • climate change • invasive species • diversity • coral/algal competition

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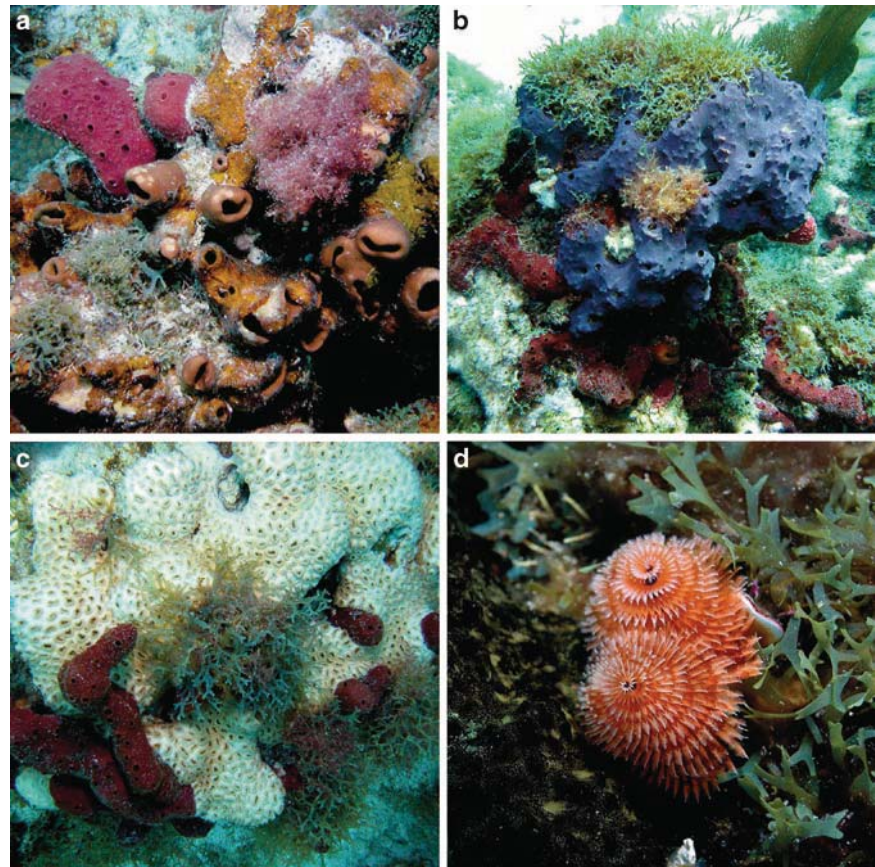
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1 Importance of Coral Reef Algae

Coral reefs are one of the most diverse and productive ecosystems on the planet, forming heterogeneous habitats that serve as important sources of primary production within tropical marine environments (Odum and Odum 1955; Connell 1978). Coral reefs are located along the coastlines of over 100 countries and provide a variety of ecosystem goods and services. Reefs serve as a major food source for many developing nations, provide barriers to high wave action that buffer coastlines and beaches from erosion, and supply an important revenue base for local economies through fishing and recreational activities (Odgen 1997).

Benthic algae are key members of coral reef communities (Fig. 1) that provide vital ecological functions such as stabilization of reef structure, production of tropical sands, nutrient retention and recycling, primary productivity, and trophic support. Macroalgae of an astonishing range of diversity, abundance, and morphological form provide these equally diverse ecological functions. For example, crustose coralline red algae which resemble “pink paint on a rock” are known to make essential contributions of calcium carbonate in the form of calcite “cement” that consolidates the larger volume of less-dense calcium carbonate produced by corals and other animals (Littler and Littler 1988; Littler and Littler 1995). However, the importance of this biotic process relative to submarine lithification has been questioned, especially in deeper reef zones (Steneck and Testa 1997; Macintyre 1997). These same crustose coralline red algae form intertidal ridges at the crest of reefs that protect more delicate forms of coral and invertebrates of the backreef zone from the full force of oceanic waves (Littler and Littler 1988). Calcifying green algae from an entirely different algal division are also important sources of the carbonate that forms key reef habitats. Some genera of siphonaceous (multinucleate but single-celled) green algae form stony plates strengthened by aragonite; this form of calcium carbonate ultimately comprises a large portion of the sandy sediments in backreefs and lagoons. One study found that green algae of the genus *Halimeda* contributed an average of 40% of the volume of sand that comprised

Fig. 1 Algae are key members of coral reef communities: (a) the brown tube sponge *Agelas wiedenmayeri* being overgrown by *Palisada (Laurencia) poiteaui* and *Dictyota* spp. at a depth of 7 m in the Florida Keys, (b) *Dictyota pulchella* and other macroalgae growing on the blue sponge (*Aiolochoxia crassa*) at a depth of 10 m in the Florida Keys, (c) the zooanthid *Palythoa caribbea* being overgrown by *Dictyota pulchella* and other macroalgae at a depth of 7 m in the Florida Keys, and (d) the Christmas tree worm *Spirobranchus giganteus* next to the brown alga *Dictyota* sp. at a depth of 10 m in the Florida Keys (Photographs by Raphael Ritson-Williams)



the barrier reef sediment leeward of a 9-km long emergent reef crest in Belize (Macintyre et al. 1987). When considered globally, carbonate from *Halimeda* spp. accounts for an estimated 8% of total global production (Hillis 1997).

A highly diverse assemblage of tropical reef algae is responsible for a large amount of the nutrient retention and recycling that contributes to the high level of primary productivity typical of coral reefs and provides trophic support to the incredible diversity of consumers. Although tropical reefs generally occur in highly oligotrophic oceanic water, areal rates of primary productivity are comparable to some of the most productive terrestrial ecosystems such as tropical forests (Mann 1982). Shallow reef flats sustain rates of primary productivity over an order of magnitude higher than the surrounding oceanic water and the bulk of this productivity is due to algae (Littler and Littler 1988). These highly productive reef flats are typically covered by crustose coralline red algae and algal turfs comprised of a diverse assemblage of filamentous algae and cropped bases of larger forms. Areas of highest wave energy are often covered by crustose coralline algae, thick and leathery brown algae such as *Turbinaria* and *Sargassum*, and calcified green algae such as *Halimeda* that can withstand wave impact (Littler and Littler 1988). Sand plains surrounding reefs also contain a high

diversity of algae as the relatively flat topography of these regions provides a refuge from herbivores. Tropical reefs have been called “oases of productivity in a nutrient desert,” and this productivity has been attributed to many processes including: (1) high advection rates supplying low concentrations yet high volumes of oceanic water, (2) efficient nutrient uptake by algae of low concentrations of nutrients, (3) extensive nitrogen fixation by cyanobacteria and bacteria, and (4) a highly diverse and spatially rugose set of habitats that dramatically increase the retention and recycling capability of the ecosystem (Littler and Littler 1988).

2 Diversity

Marine macroalgae or “seaweeds” are a functional rather than phylogenetic group comprised of members from two Kingdoms and at least four major Phyla including the Cyanobacteria (prokaryotic blue-green algae, sometimes termed Cyanophyta), Chlorophyta (green algae), Heterokontophyta (including brown algae, Class Phaeophyceae), and Rhodophyta (red algae) (Lee 2008). Coral reef algae have representatives across this wide range of taxonomic diversity. Structurally, coral reef

macroalgae encompass a diversity of forms ranging from simple chains of prokaryotic cells to single-celled yet multinucleate thalli up to a meter in length and upright vine-like rockweeds with complex internal structures analogous to vascular plants. All seaweeds at some stage of their life cycles are unicellular (usually as reproductive stages such as spores or zygotes), and they are viewed as “primitive” photosynthetic organisms because of their relatively simple construction and their long evolutionary history.

Prokaryotic blue-green algae, or Cyanobacteria, are the oldest group with fossils dating back over three billion years (Schopf 2000). Well-preserved fossil cyanobacteria are nearly indistinguishable in morphology from their extant relatives and can be found in intertidal and shallow marine environmental settings like those inhabited by cyanobacteria today. Many of these first algal fossil remains are stromatolites, structures formed in shallow tropical waters when cyanobacterial mats accrete layers by trapping, binding, and cementing sedimentary grains (Lee 2008). Photosynthesis by these early primary producers was responsible for much of the oxygen that eventually built up to the levels that exist today (~20%) (Canfield 1999; Kasting and Siefert 2002; Kerr 2005). Evolution of eukaryotic algae occurred much later, about 700–800 million years ago, though this date is difficult to accurately pinpoint as most groups were composed of soft tissue that would not have been preserved reliably in the fossil record (Lee 2008).

Cyanobacteria are ubiquitous worldwide. On tropical reefs, they are often found forming mats along reef margins or on coral (Smith et al. 2009), may be epiphytic on other algae and other reef organisms (Paul et al. 2005; Ritson-Williams et al. 2005; Fong et al. 2006), rapidly colonize open space opportunistically after disturbances (Littler and Littler 1997), and may bloom in response to nutrient enrichment (Littler et al. 2006; Ahern et al. 2007, 2008; Paerl et al. 2008; Arthur et al. 2009).

Although the marine green algae (Chlorophyta) range from cold temperate to tropical waters, green algae reach their highest diversity and natural abundance in tropical and subtropical regions, with several families such as the Caulerpaceae and Udoteaceae very abundant in coral reef and associated seagrass habitats (Dawes 1998). Often overlooked, but very abundant are filamentous green algae that bore into coral skeleton and proliferate widely, with high rates of productivity (Littler and Littler 1988).

The brown algae (Class Phaeophyceae) are almost exclusively marine and primarily dominant in temperate waters. However, some genera of complex and structurally robust forms such as *Turbinaria* and *Sargassum* dominate in high-energy reef zones (e.g., Stewart 2006). Other groups of fast-growing and more opportunistic genera, such as *Dictyota*, may form seasonal blooms on reefs, covering up to 40% of the benthos in some areas of the Florida Keys (Lirman and Biber 2000; Kuffner et al. 2006).

The Rhodophyta (red algae) are the most diverse group of macroalgae. At present, the approximately 4,000 named species of red algae exceed the number of species in all other groups combined (Lee 2008). The most common forms of red algae on coral reefs include crustose members of the family Corallinaceae as well as a high diversity of small, less-obvious filamentous species that comprise algal turfs. Both groups are ubiquitous across reef zones. However, there are some genera of upright and branching calcifying forms such as *Galaxaura* and branching or flattened foliose red algae in the genera *Gracilaria*, *Laurencia*, *Asparagopsis*, and *Halymenia* that can be quite conspicuous and abundant on reefs under certain conditions because their structural and chemical defenses make them resistant to herbivores.

Communities of tropical macroalgae are often extremely speciose (Littler and Littler 2000, <http://www.algaebase.org>) and field identification of many species proves challenging. This is especially true for members of the Rhodophyta, as they are often differentiated by microscopic reproductive structures (Abbot 1999; Lee 2008). This was the impetus for field ecologists to develop a functional grouping system using morphological forms. The underlying theory was that algae of very similar morphological form may function in a community and ecosystem more similarly than those that are morphologically diverse yet more closely related phylogenetically. Steneck and Watling (1982) first classified macroalgae into seven functional groups based on susceptibility to grazing by gastropods: groups were filamentous, crustose, foliose, corticated foliose, corticated macrophyte, leathery macrophyte, and articulated calcareous algae.

Littler and Littler (1984) proposed a somewhat different set of functional form groups based on a broader set of characteristics such as nutrient uptake rates, productivity, turnover rates, and resistance to herbivory. They argued that algae that share these functional characteristics would perform similarly in response to variation in environmental conditions, regardless of differences in taxonomy. The functional form groups proposed by Littler and Littler (1984) include sheetlike, filamentous, coarsely branched, thick-leathery, jointed-calcareous, and crustose forms (Table 17.1). These groups are arranged in a spectrum from fast-growing opportunistic species that are most susceptible to herbivory (sheetlike) to the slowest growing persists that are not readily consumed (crustose). While functional form groupings have been used extensively over the last 2 decades, there is a burgeoning recognition that macroalgae do not always fit neatly into discreet categories. Using the example of flattened sheetlike algae mentioned above, members of the genus *Dictyota* in the Phaeophyceae should also be included in this category. However, while they are fast-growing nutrient specialists (Fong et al. 2003), and therefore share this characteristic of the functional form group, they are also chemically defended, making some species resistant to even relatively high levels of herbivory.

Table 1 Functional-form groups of predominant macroalgae: their characteristics and representative taxa

Functional-form group	External morphology	Comparative anatomy	Thallus size/texture	Example Genera
1 Sheet-like Algae	Flattened or thin tubular (foliose)	1- several cell layers thick	Soft, flexible	<i>Ulva</i> <i>Halymenia</i>
2 Filamentous Algae	Delicately branched	Uniseriate, multiseriate, or lightly corticated	Soft, flexible	<i>Chaetomorpha</i> <i>Cladophora</i> <i>Gelidium</i> <i>Caulerpa</i>
3 Coarsely Branched Algae	Terete, upright, thicker branches	Corticated	Wiry to fleshy	<i>Acanthophora</i> <i>Laurencia</i>
4 Thick Leathery Macrophytes	Thick blades and branches	differentiated, heavily corticated, thick walled	Leathery-rubbery	<i>Sargassum</i> <i>Turbinaria</i>
5 Jointed Calcareous Algae	Articulated, calcareous, upright	Calcified, genicula, flexible intergenicula	Stony	<i>Galaxaura</i> <i>Amphiroa</i>
6 Crustose Algae	Epilithic, prostrate, encrusting	Calcified, heterotrichous	Stony and tough	<i>Porolithon</i> <i>Hydrolithon</i>

Source: adapted from Littler and Littler (1984)

3 Distribution and Abundance

There is abundant evidence that the historical state of coral reef algal communities was dominance by encrusting and turf-forming macroalgae (e.g., Odum and Odum 1955; Littler and Littler 1984, 1988). Crustose coralline members of the Rhodophyta grow ubiquitously on solid substrates of coral reefs intertidally down to at least 260 m (Littler et al. 1986). Thus, some members of this group are able to tolerate the most extreme low-light conditions found on coral reefs, while others of this same form can tolerate exposure to both extremely high irradiance and desiccation. In general, maximum abundance of crustose coralline algae occurs in shallow turbulent areas. Although crustose coralline algae are both abundant and widely distributed, productivity levels are low relative to other algal groups, suggesting a “persister” life-history strategy. Algal turfs are also ubiquitous on hard substrates throughout tropical reef ecosystems. While turfs are often dominated by filamentous members of the Rhodophyta, they also can include filamentous green algae and cyanobacteria, and cropped bases of larger algae. In contrast to crusts, turfs are characterized by extremely high rates of primary productivity, though biomass is usually very low (<0.27 kg m⁻²), suggesting an opportunistic life-history strategy where success is a result of growing slightly faster than herbivores can consume them (Carpenter 1986; Duffy and Hay 1990, 2001).

Historically, other types of macroalgae with a more upright, foliose morphology were restricted to backreefs, lagoons, or deeper reef areas. Typical standing stocks were 3.0–3.5 kg m⁻², though rarely could be as high as 10 kg m⁻² (Littler and Littler 1988). Calcareous and siphonaceous Chlorophyta usually dominated on rubble or soft-sediment areas of the backreef and lagoon, and often were found in association with sea grasses or mangroves. These are areas unsuited to most other forms of macroalgae due to the lack of hard substrate, but many calcareous green algae have

rhizome-like structures that act as anchors in soft substrates. One genus of calcareous chlorophyte, *Halimeda*, can also be found across most zones of the reef as well as forming extensive meadows in deeper water off the forereef (Littler and Littler 1988; Fukunaga 2008). Natural *Halimeda* populations are commonly 100 plants per square meter, but may reach densities up to 500 plants per square meter. With the exception of a few genera adapted to high wave action, most members of the Phaeophyceae historically reached the highest abundance in backreef and lagoon habitats, where there was sufficient hard-bottomed or rubble habitat with relatively low topographic relief. Historical studies of the distribution and abundance of Cyanobacteria are relatively rare, because cyanobacteria were often considered a component of the turf algae in ecological studies (Littler and Littler 1988). It was believed that, with the exception of cryptic boring algae and members of microalgal filamentous communities, independent, macroscopic Cyanobacteria were largely limited to intertidal or very shallow water habitats.

Over the last few decades, macroalgae of all Divisions have been documented to proliferate across all areas and zones of reefs with increasing frequency and abundance. Green algae such as *Dicytosphaeria cavernosa* have dominated reefs of Kaneohe Bay (Stimson et al 2001). Brown algae in the family Dictyotaceae, including *Dictyota* spp. and sometimes *Padina* spp., *Styopodium zonale*, and *Lobophora variegata*, have become increasingly dominant on the reefs, not just the sand and rubble plains of the backreef (Rogers et al. 1997; Lirman and Biber 2000; Kuffner et al. 2006). Blooms of upright and branching red algae such as *Acanthophora spicifera* and *Gracilaria* spp. are dominating reefs, sometimes lasting years (Fong et al. 2006). Clearly, the distribution and abundance of coral reef macroalgae has undergone rapid change over the last few decades, and those changes appear to be accelerating (although a meta-analysis by Bruno et al. 2009 showed little change in upright fleshy

and calcareous forms of macroalgae over the past decade). Although many investigations into the mechanisms of change and the impacts on coral reef structure and functioning have been conducted and are discussed below, there are still considerable knowledge gaps that must be addressed.

4 Ecological Processes Controlling Algal Populations and Communities

Mechanisms that control distribution and abundance of coral reef algae are the same as for other primary producers: geographic limits for growth are set by temperature and light and for removal by grazing and physical disturbance. Within these geographical limits, biomass accumulation is controlled by many interacting biotic and abiotic factors including availability of suitable substrate, light quantity and quality, nutrients, intra- and interspecific competition, and herbivory.

4.1 Factors Limiting Settlement and Growth: Suitable Substrate

The overwhelming majority of marine algae need little more than “hard” substrata to settle, and thus are able to recruit to a variety of available surfaces throughout depths where enough light penetrates. These surfaces can be abiotic or biotic and include rock, coral rubble, shells of animals live or dead, sea grasses, mangrove roots, and other algae. Microbial biofilms on settlement surfaces may be an important cue for settlement of some algal spores (Amsler 2008b). Some benthic organisms, like many crustose coralline algae, have “antifouling” mechanisms that entail sloughing of outer layers where epiphytes (algae that live on other primary producers) recruit. Others, like corals, slough mucus off their surfaces to rid themselves of algal settlers. Chemical defenses are also employed by marine algae and invertebrates to deter algal settlers and other fouling organisms (Lane and Kubanek 2008; Chadwick and Morrow 2010). Thus, not all hard substrate is equally “available” for algal recruitment.

Not all algae require hard substrata throughout their entire life cycle. As stated earlier, most seaweeds have some form of single-celled swimming or floating stage as part of their complex life cycles, usually a reproductive structure such as a zoospore or gamete. But a pelagic stage is not always limited to single cells. Some macrophytic forms of algae detach and form floating rafts (e.g., Stewart 2006; Bittick et al. 2010) or mats that may drift along the bottom or settle onto benthic communities (Holmquist 1994). These may be very important to dispersal of both the alga and its associated community. They may also have negative effects on the community

upon which they land. For example, species of *Dictyota* in the Florida Keys undergo frequent fragmentation, often as a result of herbivory by fishes (Herren et al. 2006). However, fragments quickly entangle, form holdfasts, and become epiphytic on other organisms including other algae, corals, and sponges (Beach et al. 2003). Negative effects of epiphytic *Dictyota* on other algae include reduced growth due to shading and chemically mediated elevation of respiration.

There are some forms of algae, predominantly siphonaceous green algae, which do not require hard substrata at any stage of their life cycle. They are able to recruit to and establish in soft sediment areas with rhizomes adapted for attachment in soft substrata. These algae include members of the genera *Halimeda*, *Caulerpa*, *Penicillus*, and *Udotea*, which are very important primary producers in backreef and lagoon habitats, and often are associated with seagrass beds.

Algae are rapid and efficient initial colonizers of space on almost any area of coral reefs that has been opened by disturbances. Several examples show how hurricane damage on reefs can lead to rapid colonization by algae (Hughes 1994; Fong and Lirman 1996; Rogers et al. 1997). Within days, coral skeleton bared by hurricane damage was colonized by filamentous green algae that succeeded to turf dominated by filamentous red algae within a month (Fong and Lirman 1996). When openings in otherwise healthy coral colonies were small, areas were recovered by coral in a matter of months; however, larger openings were only partially recovered by coral and the rest remained algal turf. Algae also rapidly colonize dead coral following episodes of coral bleaching and mortality (Littler and Littler 1997; Baker et al. 2008). Of course, algae can also be rapidly removed from reefs when storms or high waves impact reef habitats, which can open up hard substrata for recruitment of other types of algae or corals and other benthic invertebrates (Becerro et al. 2006).

4.2 Factors Limiting Settlement and Growth: Light

Coral reef algae depend on light for use in photosynthesis. Although tropical waters are clear with high-light penetration compared to temperate zones, there are still patterns of light attenuation with depth that change both the quality and the quantity of available light for photosynthesis. Light is reduced exponentially with depth following the Beer-Lambert law, $I_z = I_0 e^{-K_{dz}}$, where I_z is irradiance at depth z , I_0 is surface irradiance, and K_{dz} is the attenuation coefficient for downwelling irradiance. The surface irradiance reaching a reef at a given depth is influenced by properties of the water that affect the attenuation coefficient. Light is attenuated by both absorption and scattering. Scattering of light by water molecules and particulate matter is greatest for the shorter

high-energy wavelengths, while absorption is greatest in longer, lower-energy red wavelengths. Attenuation rate is increased by suspended sediment, detrital particles, dissolved organic matter, and biota. The net result is that most red light is absorbed in the first few meters of depth, while blue and green light penetrate the deepest (Fig. 2).

Coral reef algae have adapted to life at depth, though adaptations to the changes in quality and quantity in light vary across algal divisions. Like all primary producers, algae absorb light for photosynthesis in the visible wavelengths between 400 and 700 nm. This part of the spectrum is called photosynthetically active radiation or PAR. However, not all wavelengths within this active range are equally useful across all algal groups. Each algal pigment has a different action spectrum: an action spectrum is the rate of a physiological activity, in this case, absorption of light, plotted against wavelength (Fig. 2). Peaks in this spectrum show which wavelengths of light are most effective in fueling photosynthesis for each algal pigment.

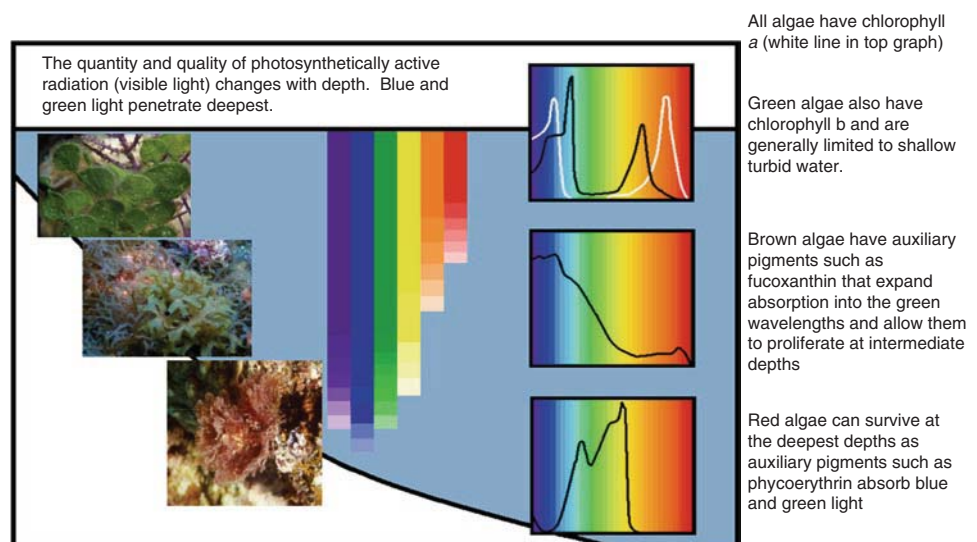
All algae (as well as all terrestrial plants) contain chlorophyll *a*, a pigment that absorbs light maximally in the red and blue wavelengths (Fig. 2) and reflects green light, resulting in a green appearance. Accessory pigments in algae absorb light in different wavelengths than chlorophyll *a* and funnel this energy for use in photosynthesis. The major algal divisions contain a variety of accessory pigments that enable capture of different portions of PAR. Green algae contain chlorophyll *b* as their major accessory pigment. This pigment absorbs maximally in only a slightly different range of wavelengths than chlorophyll *a*, and therefore does not greatly extend the ability to absorb different wavelengths. Thus, based on pigment content alone, one would predict the depth distribution of green algae should be shallower than other divisions. Brown algae have auxiliary pigments such as

fucoxanthins that absorb a broader spectrum of light of blue and green wavelengths than chlorophyll alone; these pigments should enable them to proliferate to deeper depths relative to green algae. Red algae contain phycobilin pigments such as phycoerythrin, which absorb maximally in the blue and green wavelengths that penetrate deepest in clear waters. The red algae therefore have the potential to grow at the deepest depth compared to the other divisions.

It is important to note that the presence of various algal pigments only sets the potential depth distribution of the macroalgae that contain them. Although auxiliary pigments enable algae to extend their ranges deeper, this does not mean that they are limited to those depths. For example, while crustose coralline red algae are the deepest-living marine macroalgae and have been found as deep as 268 m in the very clear waters of the Bahamas (Littler et al. 1986), they are also common across all reefs zones including the intertidal. In addition, while tropical green algae do proliferate in shallow water, some genera, such as *Halimeda*, have been found to form expansive meadows quite deep, down to 75 m in clear water off Malta (Larkum et al. 1967) and to a maximum depth of 118 m in Hawaii (Runcie et al. 2008). Another species of green algae, *Johnson-sealinkia profunda*, is the deepest growing frondose macroalga, recorded at 200 m in the Bahamas (Littler and Littler 1988). In comparison, *Lobophora variegata* only grew down to 100 m in this same area, and was found to proliferate in the 20–30 m range on reefs of Curaçao (Nugues and Bak 2008). Clearly, while pigments control the potential for growth and proliferation of algae at certain depths, other factors such as grazing, wave energy, disturbance, and other adaptations to low light all contribute to algal depth zonation.

Algae can adapt to changing light conditions across a variety of temporal scales, from within minutes to over a season.

Fig. 2 Different divisions of algae have adapted to the varied light regimes that occur along depth gradients in oceanic waters. In clear water, chlorophyll suffices for all groups, as it absorbs blue light that penetrates in all depths. However, in more turbid water, light attenuates more quickly and accessory pigments fill in the “green window,” expanding the potential depth distribution of different divisions of algae (Artwork by Kendal Fong, photographs by Raphael Ritson-Williams and V. Paul)



Light availability can vary over short timescales in response to changes in cloud cover, variation in shading by the macroalgal community during wind or wave events, and changes in light attenuation with sediment resuspension. Although seasonal variability in light regime in most coral reef systems is lower than in temperate zones, irradiance levels do vary across this scale. Algae can adapt very quickly to reduced light levels by increasing pigment content, which increases light utilization efficiency and allows macroalgae to photosynthesize more effectively at low-light levels. There are respiratory costs to the production and maintenance of higher pigment content in low-light plants, so at high irradiances pigment concentrations are typically lower. Algae also react to high-light intensities. Photoinhibition may occur at high irradiances or under high UV stress, and damage to algal photosystems during this process may not be reversible.

4.3 Factors Limiting Settlement and Growth: Nutrients

Coral reefs have long been known to be “oases of productivity in a nutrient desert.” Over 4 decades ago in a seminal paper, Odum and Odum (1955) estimated that supply of allochthonous nutrients to coral reefs of Eniwetok Atoll via advection of oceanic water was not sufficient to sustain the high levels of productivity characteristic of these systems. This finding motivated a plethora of research into how high levels of productivity are supported on coral reefs that was focused on other allochthonous sources of nutrients (e.g., organic and particulate nutrients, plankton, nitrogen fixation, symbiosis), the relative importance of N and P limitation, and efficient uptake, storage, retention, and recycling of water column nutrients by primary producers. Many studies have also tried to quantify the relative importance of nutrient limitation compared to other ecological process in determining the distribution and abundance of coral reef algal communities.

4.3.1 Allochthonous Versus Autochthonous Sources of Nutrients

In theory, the primary source of “new” or allochthonous nutrients to coral reefs should largely depend on the geographic location of the reef system, the type of coral reef (fringing, barrier, or atoll), as well as the type of terrestrial system to which it is coupled. The geographic location of a reef affects many global factors that may influence nutrient supplies, such as currents (Garzon-Ferreira et al. 2004), atmospheric deposition (Muhs et al. 2007), and degree of isolation from major continental sources. Both the type of reef and the type of associated terrestrial system (if any) will

greatly influence the connectivity of the reef system to oceanic versus terrestrial sources of nutrients and therefore their relative importance. For example, nutrient supply to the fringing reef along the shore of Moorea, French Polynesia, a volcanic island with high topographic relief, is likely to be more influenced by watershed characteristics such as rainfall, groundwater, and soil stability than the barrier reef of this same island. And the nutrient supply to both the fringing and barrier reefs of Moorea should be influenced more by the presence of the island than nearby Tetiaroa Atoll, with its low relief set of sandy islands.

Coral reef systems occur across such a large diversity of geographic locations, associated landmasses, and reef types, as well as many other factors, that it is difficult to make generalizations about overall effects on allochthonous nutrient supply. However, recent work across marine systems has suggested that sources of new nitrogen to all marine systems are rapidly increasing globally as a result of anthropogenic alterations of the global nitrogen cycle (for reviews, see Vitousek et al. 1997; Downing et al. 1999), though the importance of these increases in coral reefs is highly debated (for a review, see Fong 2008). Overall, it is likely that coral reef systems more closely associated with terrestrial watersheds will be affected the most by increasing anthropogenic nitrogen supplies compared to open oceanic reef systems.

In situ or autochthonous sources of nutrients to coral reef algae include nitrogen fixation, recycling from other biota, regeneration from deposition of organic matter in any associated sediment areas, and regeneration of nutrients from primary producers during decomposition (Fong 2008). Cyanobacteria abound on coral reefs, and many may fix nitrogen. They are important components of the ubiquitous algal turf communities and live within coral skeletons (Littler and Littler 1988) and epiphytically on other algae (Fong et al. 2006). Recently, blooms were found on coral communities of the reefs themselves (Paul et al. 2005; Smith et al. 2009). Nitrogen fixation on coral reefs may be very high, especially following disturbances that open new substrate for colonization by filamentous cyanobacteria (Larkum 1988). Some measures are equal to the highest rates found in terrestrial systems (Capone 1983). Animals in coral reefs that live in close association with algae may increase local nutrient supplies by releasing nutrient-rich waste products (e.g., Williams and Carpenter 1988). Flocculent material, most likely at least partially of biotic origin, settling on the surfaces of algal thalli has been identified as a source of nutrients to algae in coral reefs (Schaffelke 1999). In tropical reef systems, recycling from sediments may only be a significant contribution in areas subject to long-term nutrient enrichment like Kanoeh Bay, Hawaii (Stimson and Larned 2000). However, in other types of soft sediment and enriched systems, macroalgal interception of nutrient fluxes is ecologically important as it may uncouple sedimentary and water column N linkages

(Valiela et al. 1992, 1997), reducing supplies to other producer groups (Fong et al. 1998). Thus, more research on this source of nutrients is warranted on coral reefs.

4.3.2 N Versus P Limitation of Coral Reef Algae

For tropical marine algae, quantifying the relative roles of nitrogen (N) and phosphorus (P) limitation has been an important focus of research in recent years. In contrast to temperate systems where N limitation is the paradigm (Fujita et al. 1989; Thybo-Christesen et al. 1993; Rivers and Peckol 1995; Taylor et al. 1995; Sfriso and Marcomini 1997; Gallegos and Jordan 1997), many tropical studies have found P to limit productivity and growth more frequently than N (e.g., Lapointe 1987, 1989; Lapointe et al. 1992). Others found stimulation by both N and P (Schaffelke and Klump 1998; Lapointe 1987; Paerl et al. 2008), or dual limitation (Fong et al. 2003). There are several possible explanations why there is high spatial and temporal variability in the relative importance of N and P limitation in coral reef algae. The strength of P limitation has been related to the amount of P-adsorbing carbonate in sediments (Delgado and Lapointe 1994; Lapointe et al. 1992; McGlathery et al. 1994), the habitat or substrate type the algae occupied (Lapointe 1989; Littler and Littler 1988), and the type of island adjacent to the coral reef (Littler et al. 1991). Others have hypothesized that the relative importance of N and P limitation should vary across a nutrient supply gradient, with N increasing in importance in more eutrophic systems due to saturation of the P-adsorption capacity of sediments (Delgado and Lapointe 1994; Downing et al. 1999). Studies in Kaneohe Bay, Hawaii, an area with a history of nutrient enrichment, supported this hypothesis as N limited nine of ten species tested from a broad range of functional forms (Larned and Stimson 1997; Larned 1998). However, Fong et al. (2003) found that several species of macroalgae in Puerto Rico differed in their response to N and P additions depending on their nutrient status; algae from nutrient-replete environments did not respond strongly to either nutrient. Clearly, there is high spatial and temporal variability in the relative importance of N and P limitation in coral reef algae. More research is needed to further our understanding of these patterns of variability.

Three approaches have been used extensively to determine if N and/or P limits productivity of algae, including those on coral reefs. In the first approach, N:P ratios of dissolved inorganic nutrients in the water column have been used as a measure of nutrient availability; water column N:P ratios are compared to nutrient requirements of algae to determine limitation (e.g., Redfield et al. 1963; Lapointe 1989; Duarte 1992). However, different species or functional forms of algae may require nutrients in differing proportions. One study found that one alga was limited by N and another

by P when grown together in seawater of the same N:P ratio (Fong et al. 1993), although this study was conducted with algae from warm temperate, not tropical areas, leaving this an open question for tropical algae. In addition, water column measures provide only a snapshot in time and may not adequately characterize availability in areas where nutrients are supplied in pulses as in the tropics (McCook 1999) or in many estuaries (Fry et al. 2003; Boyle et al. 2004). In the second approach, N:P ratios in algal tissue have been used to predict nutrient limitation (e.g., Lapointe et al. 1992). However, this method also has limitations, because differing uptake and storage capacities of algae may confound the relationship. For example, if both N and P are abundant in the water, and an alga has a greater uptake ability and storage capacity for N than P, then the resultant high tissue N:P ratio would indicate P limitation when limitation by nutrients was not occurring.

The third approach used to determine N or P limitation is factorial enrichment experiments adding N and P alone and in combination, and quantifying responses such as photosynthesis, growth, and changes in tissue N and P content (e.g., Lapointe 1987, 1989; Fong et al. 1993; Larned 1998; Fong et al. 2006). When addition of a nutrient increased any of these response variables, it was considered to be in limiting supply. This approach has been used across a range of scales, from laboratory or field microcosm dose-response experiments (e.g., Fong et al. 2003; Paerl et al. 2008) to large-scale and longer-term field experiments (e.g., Koop et al. 2001). The challenges when using this approach include choice of realistic experimental enrichment levels, effectively scaling up the relatively short-term and small-scale responses from microcosm experiments, and effectively enriching in situ experiments in high-energy environments. The advantages, however, are that the experimental approach provides direct rather than indirect evidence of limitation. Although at present the disadvantages of this approach require careful interpretation and application of experimental results, the strength provided by direct evidence warrants further research and methodological development.

4.3.3 Efficient Nutrient Uptake by Coral Reef Algae

Predicting nutrient uptake rates of coral reef algae from water column sources is complex. For years, nutrient uptake was thought to be a simple function of water column inorganic nutrient concentration that could be described by Michaelis-Menten uptake kinetics (e.g., Fong et al. 1994b), an approach proven successful for phytoplankton (Droop 1983; Sommer 1991). More recently, the recognition that macroalgae are often both relatively stationary in a dynamic flow environment and have significant nutrient storage capacities that reflect past nutrient supplies has focused current research

into the physics of dissolved solute transport across boundary layers as well as the influence of the biological condition of algal thalli on uptake (for a review, see Hurd 2000). Both of these must be incorporated into our understanding of nutrient availability to and uptake by coral reef algae.

Uptake of nutrients from the water column depends on many factors, including the nature and velocity of water flow, water nutrient concentrations of biologically useable substrates, and algal metabolic demand (for a review, see Hurd 2000). For small filamentous or crustose algae completely within the benthic boundary layer, current speeds may be much reduced compared to those that extend into the overlying faster water flow (Carpenter and Williams 1993; Nepf and Koch 1999). Attention to near-bottom flow speeds is essential on coral reefs, as these forms of algae are usually spatially dominant.

Algal morphology also affects uptake of nutrients. Morphology controls the algal height with respect to the benthic boundary layer, and thallus structure may enhance uptake by flexibility in flowing water (Hurd 2000). In addition, some algal growth forms, such as densely packed mats, may reduce uptake by reducing current speeds within the mat (Fong et al. 2001). Morphology also determines the physical surface area of an algal thallus containing uptake sites. Several studies have identified a positive relationship between an alga's surface area to volume ratio and uptake of nutrients (e.g., Hein et al. 1995).

Once nutrients cross the boundary layer and contact the surface of the algal thallus, they must be transported across the cell membrane and then assimilated into organic compounds followed by incorporation into proteins and macromolecules for growth (McGlathery et al. 1996; Cohen and Fong 2004). This process has been best studied for nitrogen (N). Uptake rate varies among the commonly co-occurring forms of N available in coastal marine waters, NH_4^+ and NO_3^- . For example, some algae have strong preferences for NH_4^+ , while others take up either inorganic N source (e.g., Hanisak 1983; Lotze and Schramm 2000; Naldi and Wheeler 2002). Uptake of NH_4^+ is less energetically costly, because NO_3^- must first be reduced to NH_4^+ by nitrate reductase before assimilation (Hurd et al. 1995); thus, energetics may explain preference for NH_4^+ by some macroalgae. However, NH_4^+ storage capacity may be limited due to toxicity (Waite and Mitchell 1972; Haines and Wheeler 1978; Lotze and Schramm 2000), and therefore assimilation rate into inorganic molecules may limit maximum uptake rate of this form of N. The ability of opportunistic macroalgae to take up both forms of N simultaneously may be one mechanism that results in algal blooms (Thomas and Harrison 1987; Cohen and Fong 2004).

Algal demand, a function of algal tissue nutrient status, also influences nutrient uptake rates of macroalgae. Tissue nutrient status reflects the history of nutrient supply to an

alga, as algae subject to excessive or pulses of nutrients may store nutrients for future growth (Wheeler and North 1980; Lapointe and Duke 1984; Fong et al. 1994a, b). Several investigators (e.g., Fujita 1985; McGlathery et al. 1996; Fong et al. 2003; Kennison 2008) found that algae with nutrient-enriched tissues always took up N more slowly than nutrient-depleted algae. These studies demonstrate that algae with higher internal nutrient content will have lower metabolic demand and therefore slower N uptake rates.

Pedersen (1994) separated uptake of N into three phases; although this work was on temperate opportunistic forms of algae, there is reason to believe it is applicable to many coral reef algae with this same strategy. The first phase, surge uptake, is transiently enhanced nutrient uptake by nutrient-limited algae that may last only minutes to hours. Surge uptake has been documented in tropical algae from nutrient-poor sites in Puerto Rico (Fong et al. 2003). Because water column nutrients in tropical systems are characteristically low, experimental nutrient pulses to macroalgae in these experiments were also relatively low ($\sim 20 \mu\text{M N}$), yet the algal response was rapid and of equal magnitude to bloom-forming species from temperate estuaries subjected to nutrients an order of magnitude higher in concentration (Kennison 2008). This suggests that tropical macroalgae may be especially well adapted to take advantage of pulses of nutrients through surge uptake. During the second phase, internally controlled phase of uptake, the rate-limiting step is assimilation of N into organic compounds (Fujita et al. 1988; Rees et al. 1998). This occurs when external N is maintained at a relatively high concentration for enough time that storage pools within algal tissue begin to fill (Fujita et al. 1988; McGlathery et al. 1996; Lotze and Schramm 2000; Cohen and Fong 2004). The third phase of uptake, externally controlled uptake, occurs at low substrate concentrations and is regulated by the rate of nutrient transport across the alga's surface (Pedersen 1994). This is a function of mass transport to the thallus surface as well as diminishing water column nutrient concentration.

The complex and interacting factors and processes affecting nutrient uptake rates of marine macroalgae may mask increasing nutrient supplies to coral reefs as these systems undergo phase shifts from coral- to macroalgal-dominated reefs. As opportunistic algae have rapid nutrient uptake rates, phase shifts to these functional forms may change nutrient dynamics by increasing algal uptake, enhancing sequestering of nutrients within algal tissues, and accelerating recycling of pulses of nutrients within these systems (Valiela et al. 1997). In coral reefs, algae respond quickly to even low levels of nutrient enrichment by enhanced uptake rates (Fong et al. 2001, 2003). Thus, high nutrient uptake in macroalgal-dominated systems may mask increasing supplies by maintaining low water column concentrations, the usual metric to

assess increasing nutrient supplies. This suggests we must rethink our current method for managing water quality in coral reef ecosystems.

4.3.4 Nutrient Storage and Retention by Coral Reef Algae

The capacity to store nutrients, represented by standing stock or biomass, varies tremendously across coral reef algal communities. As an example, consider the tremendous differences in biomass between one study of coral reef turf algae (e.g., 0.03–0.6 kg wet wt m⁻² based on a wet:dry weight ratio of 10:1; Foster 1987) and another of blooms of macroalgae (up to 10 kg m⁻²; Littler and Littler 1988). Although both algal-dominated communities may be highly productive in terms of gross primary productivity, they clearly occupy different ends of a spectrum in terms of biomass accumulation and therefore N storage capacity. Although there are exceptions, in general opportunistic species with simple thallus forms such as those that dominate coral reef turfs often have low levels of biomass despite relatively rapid growth rates due to short life spans, susceptibility to removal by physical disturbance, and grazing by herbivores. In contrast, persisters such as crustose or upright calcified forms often have high standing stocks due to longevity of individual thalli, investment in structure to withstand physical disturbances, and chemical or structural defenses as protection from herbivores. Although more typical of temperate zones, reservoirs of nutrients stored in coral reef algae may also undergo cyclical and/or seasonal patterns (e.g., Lirman and Biber 2000).

4.3.5 Recycling of Nutrients by Coral Reef Algae: Turnover Rates

Algal turnover rates can affect different processes and storage compartments of the nutrient cycle on coral reefs, including rates of microbial transformation, supply of nutrients to other primary producers, and sediment and water nutrient pools. Turnover rates of nutrients stored in algal biomass depend on rates of consumption by grazers, recycling due to death and decomposition, and export. Overall, coral reef algal communities dominated by turfs turnover more rapidly compared to systems dominated by persisters like calcified or fleshy algae (e.g., Fong 2008).

On a global scale, direct consumption of algae by grazers was estimated as 33.6% of total macroalgal net primary productivity, demonstrating the general importance of macroalgae as the base of grazing food webs in all coastal ecosystems (Duarte and Cebrian 1996). However, on pristine, low-nutrient coral reefs this value may be much higher (see below), as there are a multitude of large herbivorous fishes and sea urchins. Experimental and historical evidence abounds to

show that herbivores consume a large proportion of macroalgal productivity (for a review, see Jackson et al. 2001), functioning to accelerate turnover of nutrients stored in tissue.

Death and subsequent decomposition of macroalgal detritus result in release and recycling of stored nutrients. Processing of N through detrital pathways comprises about a third of macroalgal net primary productivity globally (Duarte and Cebrian 1996), while estimates for recycling within coral reef algae are much higher (Duarte and Cebrian 1996). When algae decompose, they release organic N to the water. In addition, recent studies demonstrated that substantial dissolved organic N also “leaks” from healthy thalli (Tyler et al 2003; Fong et al. 2003); healthy macroalgae in growth phase may release 39% of gross primary productivity which is processed via detrital and microbial pathways. Some organic compounds in the water can be taken up directly or are quickly remineralized to inorganic forms that may fuel productivity of other primary producers. If burial in the sediment occurs, remineralization may be slower; thus, sediments may act as a slow release fertilizer and enhance algal productivity when external supplies are low (Stimson and Larned 2000).

Duarte and Cebrian (1996) calculated that a global average of 43.5% of macroalgal net primary production is exported. Export is a function of standing stock, water motion, and algal morphology. For example, *Turbinaria*- and *Sargassum*-dominated reef crests most likely export far more nutrients than those dominated by crustose corallines, despite equally vigorous wave action in both communities, due to their vastly larger standing stock. In contrast, lagoonal systems may export fewer nutrients as there is both less physical disturbance and lower water exchange with oceanic waters to detach and then remove biomass. Thus, algae in lagoons may represent a larger and relatively more stable reservoir of nutrients than those on the reefs themselves.

4.4 Factors Causing Removal: The Importance of Herbivory in Limiting Algal Proliferation

Herbivory on coral reefs can be intense; however, because of overfishing on modern reefs areas of highest herbivory may be limited to remote reefs or those in well-enforced marine protected areas (Jackson 2008). Coral reef herbivores can remove almost 100% of the biomass produced daily by marine algae in certain reef habitats (Carpenter 1986; Hay 1991; Hay and Steinberg 1992; Choat and Clements 1998), and the feeding activities of marine herbivores are an important ecological force controlling the structure and dynamics of algal communities (Ogden and Lobel 1978; Hay 1991; Hay and Steinberg 1992; Paul et al. 2001; Hughes et al. 2007; Amsler 2008a; Bellwood and Fulton 2008). Almost all algal

biomass in the ocean is exposed to consumers because most marine algae do not produce underground parts equivalent to the roots of terrestrial plants, although at least one species of *Caulerpa* is known to absorb nutrients through its underground rhizomes (Williams 1984; Ceccherelli and Cinelli 1997). Experimental studies conducted in the Caribbean in the 1980s showed the importance of fish and sea urchins in influencing the abundance and distribution of algae in different reef habitats (Sammarco 1983; Hay 1984; Carpenter 1986; Lewis 1986; Taylor et al. 1986; Littler et al. 1989).

Herbivores consume food that is relatively low in nutritional value and high in indigestible structural material (Mattson 1980) strategies that enhance nutrient uptake (Cruz-Rivera and Hay 2000). Coral reef fishes may eat many times their required energetic needs in order to gain enough nitrogen from seaweeds (Hatcher 1981). Seaweeds are eaten by diverse vertebrates, especially fishes and turtles in tropical waters, and invertebrate consumers that vary in their selectivity and impact on different algae (Bjorndal 1980; Horn 1989; Choat 1991; Hay 1991; Hixon 1997). Invertebrate herbivores include gastropods (snails, limpets, sacoglossans, sea hares, cephalaspideans, and chitons), sea urchins, crabs, amphipods, isopods, shrimps, polychaetes, and copepods (Hay et al. 1987; Hay and Fenical 1988; John et al. 1992; Hixon 1997). The importance of different herbivore groups varies geographically, herbivore species diversity increases toward the tropics (Gaines and Lubchenco 1982; Horn 1989; Choat 1991; Hillebrand 2004; Floeter et al. 2005). Herbivore diversity in the tropics has for the evolution of seaweeds, as evidenced by the increased diversity of defenses and higher chemical defenses in tropical algae when compared to temperate macroalgae (Vermeij 1987; Steinberg and van Altena 1992; Bolser and Hay 1996; Cronin et al. 1997).

4.5 Factors Causing Removal: Chemical Defenses and Interactions

Seaweeds have several mechanisms for tolerating or resisting herbivory, and these defensive strategies have been discussed previously (Duffy and Hay 1990; Hay 1991). Many seaweeds can deter herbivores by morphological, structural, and chemical defenses or by associating with deterrent seaweeds or other benthic organisms that reduce herbivore foraging (Duffy and Hay 1990; Wahl and Hay 1995). Structural defenses such as calcification and toughness are common in certain groups of green and red seaweeds and have been previously discussed (Paul and Hay 1986; Steneck 1988; Duffy and Hay 1990). Chemical defenses of seaweeds have been reviewed, and it is not our intent to comprehensively review this topic (Paul et al. 2001, 2007; Paul and Ritson-Williams 2008; Amsler 2008a). Often, several defensive mechanisms

may be functioning simultaneously (Hay et al. 1987; Paul et al. 2001) and the importance of multiple defenses may be very significant in herbivore-rich tropical waters. The common co-occurrence of CaCO_3 and chemical defenses in tropical seaweeds has been suggested to be adaptive, because the high diversity of tropical herbivores limits the effectiveness of any single defense (Hay 1997; Paul 1997; Paul et al. 2001). For example, combinations of CaCO_3 and seaweed extracts have been tested as feeding deterrents and both additive (Schupp and Paul 1994) and synergistic (Hay et al. 1994) effects of these combined defenses have been observed.

Many possible defensive functions for algal natural products (often called secondary metabolites) have been proposed including antimicrobial, antifouling, and antifeedant activities (Paul et al. 2001; Paul and Ritson-Williams 2008; Lane and Kubanek 2008). To date, the role of these compounds as defenses toward herbivores has been best studied. Recent studies have clearly shown that many seaweed natural products function as feeding deterrents toward herbivores (e.g., Hay 1997; Paul et al. 2001; Amsler 2008a). However, many compounds may also have other roles or may function simultaneously as defenses against pathogens, fouling organisms, and herbivores, thereby increasing the adaptive value of these metabolites (Paul and Fenical 1987; Schmitt et al. 1995). Some algal secondary metabolites do show antimicrobial or antifouling effects (Paul and Ritson-Williams 2008; Lane and Kubanek 2008).

Thousands of natural products have been isolated from marine red, brown, and green algae, and the majority of these have come from tropical algae (Maschek and Baker 2008; MarinLit 2009). In general, these compounds occur in relatively low concentrations, ranging from 0.2% to 2% of algal dry mass, although compounds such as the polyphenolics in brown algae can occur at concentrations as high as 15% of algal dry mass (Hay and Fenical 1988; Steinberg 1992). Except for metabolites from phytoplankton and cyanobacteria, very few nitrogenous compounds have been isolated from macroalgae (Ireland et al. 1988; MarinLit 2009). Some cyanobacteria, red algae, and a few green algae incorporate halides from seawater into the organic compounds they produce (Fenical 1975, 1982; Ireland et al. 1988; Hay and Fenical 1988). Bromine and chlorine are the most common halides found in marine algae. Halogenating enzymes such as bromoperoxidases and chloroperoxidases function in the biosynthesis of these halogenated compounds (Butler and Walker 1993). The majority of macroalgal compounds are terpenoids, especially sesqui- and diterpenoid. Acetogenins (acetate-derived metabolites), including unusual fatty acids, constitute another common class of algal secondary metabolites (Ireland et al. 1988; Maschek and Baker 2008). Most of the remaining metabolites result from mixed biosynthesis and are often composed of terpenoid and aromatic portions.

Cyanobacteria are often heavily chemically defended. High abundances of *Lyngbya* spp. and *Oscillatoria* spp. have been observed on coral reefs, where benthic mats of cyanobacteria can cover thousands of square meters (Paul et al. 2005; Paul et al. 2007). These benthic, filamentous cyanobacteria produce a wide variety of secondary metabolites, many of which are toxic or pharmacologically active (Moore 1981, 1996; Gerwick et al. 1994; Nagle and Paul 1999; Tan 2007). Their ability to fix nitrogen may explain their production of many nitrogen-containing secondary metabolites including peptides and lipopeptides. Cyclic peptides and depsipeptides are the major types of compounds isolated from marine cyanobacteria (Moore 1996), and some of these compounds have been shown to deter herbivores (Thacker et al. 1997; Nagle and Paul 1999; Cruz-Rivera and Paul 2007; Paul et al. 2007). In contrast, the opisthobranch sea hare *Stylocheilus striatus* specializes on *Lyngbya majuscula* and prefers artificial diets containing compounds produced by cyanobacteria; however, high concentrations of some of these metabolites can still deter feeding by *Stylocheilus* (Paul and Pennings 1991; Nagle et al. 1998; Capper and Paul 2008). The sea hares *S. longicauda* and *Dolabella auricularia* sequester cyanobacterial compounds from their diets, gaining protection from fish and invertebrate predators (Paul and Pennings 1991; Pennings and Paul 1993; Pennings et al. 1996, 1999).

The marine green algae contain a suite of compounds that provide chemical defenses. Most of the compounds isolated from the green algae are terpenes; sesquiterpenes and diterpenes are particularly common (Hay and Fenical 1988). Tropical green algae of the order Caulerpaceae have been especially well studied; members of this group, including species of *Caulerpa* and *Halimeda*, contain acyclic or monocyclic sesqui- and diterpenoids (Paul and Fenical 1986, 1987), which are known to defend against herbivores (Paul et al. 2001; Erickson et al. 2006). Chemical defenses in calcified green seaweeds may be particularly important against herbivores such as parrot fishes and sea urchins that can readily consume calcified foods (Pennings and Svedberg 1993; Schupp and Paul 1994; Pitlik and Paul 1997). In a series of laboratory and field experiments designed to examine differences among fish species in their responses to both chemical and structural defenses in *Halimeda*, Schupp and Paul (1994) found that *Halimeda* diterpenes can limit feeding by the parrot fish *Scarus sordidus*, which is not affected by the levels of CaCO_3 found in *Halimeda* spp. In contrast, the rabbitfish *Siganus spinus* and the surgeonfish *Naso lituratus* were deterred by CaCO_3 in their diets but were unaffected by *Halimeda* diterpenes. In general, combined defenses (CaCO_3 and terpenes) increased the number of fish species that were deterred relative to either single defense, which may explain the abundance of *Halimeda* spp. and other calcified green algae in many reef habitats.

Brown algae are the only seaweeds that produce polyphenolic compounds. Although these compounds may function like terrestrial tannins by binding proteins or other macromolecules, they are structurally different compounds that are complex polymers derived from a simple aromatic precursor, phloroglucinol (1, 3, 5-trihydroxybenzene) (Fenical 1975; Ragan and Glombitza 1986; Targett and Arnold 1998). These metabolites are often termed “phlorotannins” to distinguish them from the terrestrial tannins. Polyphenolics in brown algae may function as defenses against herbivores (Steinberg 1992; Targett and Arnold 1998), as antifoulants (Sieburth and Conover 1965; Lau and Qian 1997, but see Jennings and Steinberg 1997), as chelators of metal ions (Ragan and Glombitza 1986), and in UV absorption (Pavia et al. 1997).

In addition to polyphenolics, brown algae in the order Dictyotales produce nonpolar metabolites such as terpenes, acetogenins, and compounds of mixed terpenoid-aromatic biosynthesis (Maschek and Baker 2008). *Sargassum* species also produce acetogenins and compounds of mixed terpenoid-aromatic biosynthesis (Maschek and Baker 2008). Brown algal compounds, especially compounds from *Dictyota* spp., have been shown to deter a variety of herbivores in temperate and tropical waters (Hay et al. 1987, 1998; Paul et al. 1988; Hay 1991; Pereira and da Gama 2008).

The greatest variety of secondary metabolites is probably found among the red algae where all classes of compounds except phlorotannins are represented and many metabolites are halogenated (Fenical 1975; Faulkner 1984; Maschek and Baker 2008). Red seaweeds from the families Bonnemaisoniaceae, Rhizophyllidaceae, and Rhodomelaceae are rich in halogenated compounds that range from halogenated methanes, haloketones, and phenolics to more complex terpenes (Fenical 1975, 1982; Faulkner 1984; Marshall et al. 1999). The red algal genus *Laurencia*, the subject of extensive investigations, produces over 500 compounds (MarinLit 2009), many of which are halogenated and of unique structural types (Erickson 1983; Faulkner 1984).

Usually, the presence or absence of deterrent secondary metabolites in seaweeds correlates well with the susceptibility of seaweeds toward herbivores. Seaweeds that are least palatable to grazing fishes often employ chemical and structural defenses (Hay 1984, 1997; Paul and Hay 1986; Hay et al. 1994; Schupp and Paul 1994; Meyer and Paul 1995; Paul et al. 2001). The common method of testing for feeding deterrent effects against herbivores has been to incorporate seaweed extracts or isolated metabolites at natural concentrations into a palatable diet, either a preferred seaweed or an artificial diet, and then to compare feeding rates of the grazers on treated foods with those on appropriate controls (Hay et al. 1998). Deterrent effects observed in these assays appear to be based primarily on the taste of the treated food. If a compound is deterrent toward an herbivore, the degree of avoidance is often related to the concentration of the

extract or metabolite in the diet. These methods do not assess toxicity or other physiological effects on the consumers or possible detoxification methods by herbivores (Sotka and Whalen 2008). Predictions about the toxic or deterrent effects of particular secondary metabolites toward natural predators may be difficult to make based upon chemical structures or results of pharmacological assays. Field and laboratory assays with natural herbivores are important for examining these ecological interactions (Hay et al. 1998).

A variety of compounds from all classes of marine algae have now been tested for their effects on feeding by many different temperate and tropical herbivores. Many of these compounds effectively deter feeding by herbivores. However, there is considerable variance in the responses of different types of herbivores to even very similar compounds. There is also considerable variation among different herbivores, even closely related species, in their responses to secondary metabolites from seaweeds. Thus, as diversity of herbivores increases, the probability of having herbivores that are not affected by any particular type of algal defense undoubtedly increases, and in these cases, complex mixtures of secondary metabolites (Biggs 2000) or multiple types of defenses may be particularly important (Paul and Hay 1986; Schupp and Paul 1994; Paul 1997).

Benthic community structure on coral reefs is strongly influenced by the chemical defenses of seaweeds as well as benthic invertebrates. Many macroalgae living on coral reef slopes, where herbivory is most intense, contain structural or chemical defenses that allow them to establish populations in the presence of abundant and diverse herbivores (Hay 1991; Paul 1992; Paul et al. 2001). In studies of algal succession on artificial reefs on Guam, Tsuda and Kami (1973) suggested that selective browsing by herbivorous fishes on macroalgae removed potential competitors and favored the establishment of unpalatable cyanobacteria. It is likely that this same model functions during phase shifts on coral reefs, resulting in establishment of primarily unpalatable macroalgae and cyanobacteria in coral reef habitats experiencing reduced herbivory. The result is the predominance of chemically defended seaweeds, including species of *Halimeda*, *Dictyota*, and *Lobophora*, which are the seaweeds most often implicated in phase shifts on Caribbean reefs (Rogers et al. 1997; McClanahan et al. 1999, 2000).

4.6 Benthic-Community-Level Interactions: Nutrient Supply Shapes Community Structure

The extent to which nutrient supply and thus limitation of coral reef algae shapes the benthic structure of coral reefs is an extremely controversial issue. While some believe nutrients are of key importance, others question whether

algae in tropical systems are usually, or ever, limited by nutrients. To support the latter belief, some reason that if tropical algal turfs are extremely productive even in areas characterized by low water column nutrients (Hatcher 1988; McCook 1999) they cannot be nutrient limited. To support this, Williams and Carpenter (1998) provided evidence that supply of solutes to algal turfs may be more limited by boundary layers than concentration. A second rationale focuses on field studies where water nutrient concentrations do not correlate with algal growth or abundance in the field (e.g., McCook 1999; Thacker and Paul 2001).

Microcosm and in situ field experimental studies of nutrient limitation of tropical algae have had conflicting results, adding fuel to this controversy. Across many systems and scales, effects of nutrient additions have varied from no effects (Delgado et al. 1996; Larkum and Koop 1997; Miller et al. 1999; Koop et al. 2001) to orders of magnitude differences in effects on photosynthesis, growth, and biomass accumulation (Schaffelke and Klumpp 1997, 1998; Lapointe 1987, 1989; Smith et al. 2001). Interpretation of experimental results is limited, in part, by the difficulty of relating results of laboratory or microcosm studies of the effects of nutrient addition to natural growth in high-energy, high-flow environments with variable nutrient supply typical of coral reefs (Fong et al. 2006), and the related methodological challenge of effectively conducting in situ experiments in these same environments (reviewed in McCook 1999). Factors potentially confounding experimental microcosm approaches include, among others, the lack of recognition of the role of nutrient history and status of the experimental macroalgae (Fong et al. 2003). Many experiments are conducted without setting them in the context of the natural spatial and temporal variability inherent in the environment. On the other hand, several processes that are difficult to control in the field may confound in situ enrichment experiments. On the local scale, preferential selection for enriched, fast-growing algae by herbivores may effectively mask the effects of enrichment in small-scale in situ experiments (Boyer et al. 2004; Fong et al. 2006). In addition, sources of nutrients in tropical systems may not be solely from the water column but may flux from sediments (e.g., Stimson and Larned 2000) and therefore not be included in traditional supply estimates. Because of these complex processes and many possible confounding factors, the importance of nutrient limitation for tropical algae is not well understood.

Although we are far from resolving this controversy, it is of paramount importance to continue to our efforts to unravel the complexity. Nutrient supplies to marine systems are certain to continue to increase with coastal development, and interactions with other anthropogenic stressors are equally certain to have complex and often unexpected effects.

4.7 Benthic-Community-Level Interactions: Positive Algal Cues for Coral Larvae

Many marine invertebrate larvae use chemical cues to determine the appropriate habitat for settlement (Pawlik 1992; Hadfield and Paul 2001; Ritson-Williams et al. 2009), and crustose coralline algae are known to induce settlement and metamorphosis for a variety of marine invertebrate larvae (Hadfield and Paul 2001). Settlement is defined as the larval behavioral response that occurs when a pelagic larva descends to the bottom and moves over a substrate with or without attaching to it; it is often considered a reversible process. Metamorphosis includes the subsequent morphological and physiological changes that pelagic larvae undergo to become benthic juveniles. Chemical cues are implicated for settlement and metamorphosis of corals and other coral reef invertebrates; thus, changes in benthic communities can affect the settlement and metamorphosis of many invertebrate larvae (Ritson-Williams et al. 2009; Chadwick and Morrow 2010).

Crustose coralline algae serve as cues for the settlement of coral larvae, although different species of corals display different degrees of specificity in their requirements for crustose coralline algae (CCA) to induce metamorphosis (Morse et al. 1994; Morse and Morse 1991; Harrington et al. 2004; Ritson-Williams et al. 2010). An insoluble, cell-wall polysaccharide (a type of sulfated lipoglycosaminoglycan) is one type of compound that induces the settlement of many species of coral larvae including *Agaricia* spp. in the Caribbean and *Acropora* spp. in the Pacific (Morse and Morse 1991; Morse et al. 1994, 1996). It has been suggested that many different corals require the same type of algal cue for the induction of settlement and metamorphosis (Morse et al. 1996).

Acropora spp. settle and metamorphose in the presence of *Titanoderma prototypum* and *Hydrolithon* spp., but do not require CCA for settlement and metamorphosis (Harrington et al. 2004; Ritson-Williams et al. 2010). Some species of CCA induce very low rates of settlement and metamorphosis of coral larvae, indicating the species-specific nature of these coral-algal interactions (Ritson-Williams et al. 2010). Studies with larvae of *Acropora millepora*, a common Indo-Pacific coral species, and coral larvae collected from natural slicks after mass spawning events also demonstrated the role that coralline algae play in inducing settlement and metamorphosis of acroporid larvae (Heyward and Negri 1999). Chemical extracts of the algae and the coral skeleton were also active with up to 80% of larvae metamorphosing in 24 h. Larvae of the corals *Acropora tenuis* and *A. millepora* in Australia had the highest rates of settlement in response to the coralline alga *Titanoderma prototypum*, which also caused the lowest coral post-settlement mortality of the algae tested. Methanol extracts of *T. prototypum* and *Hydrolithon reinboldii* both induced high rates of metamorphosis at natural concentrations (Harrington et al. 2004).

Coralline algae have been identified as a positive settlement cue for some corals, but it is unclear if the algae themselves or biofilms present on these algae are responsible for the observed settlement behavior (Johnson et al. 1991; Webster et al. 2004). A recent study on Guam found that larvae of the spawning species *Goniastrea retiformis* preferred substrate covered with crustose coralline algae, but the reef-flat brooding coral *Stylaraea punctata* preferred biofilmed rubble (Golbuu and Richmond 2007). Similarly, larvae of the pocilloporid *Stylophora pistillata* did not require coralline algae for metamorphosis (Baird and Morse 2004). Johnson et al. (1991) noted that unique bacteria occur on the surfaces of crustose coralline algae and that they could serve as the sources of inducers for settlement of corals and other invertebrates. Biofilms were isolated from the coralline alga *Hydrolithon onkodes*, and one bacterium alone, *Pseudoalteromonas* sp., was enough to induce settlement and metamorphosis of *Acropora millepora* larvae (Negri et al. 2001). When *H. onkodes* was sterilized in an autoclave, and treated with antibiotics it still induced significantly more settlement and metamorphosis than seawater or terracotta tiles. It is likely that the compounds that stimulate coral larval settlement may be more diverse in reef habitats than previously recognized, and they appear to be associated with only certain species of crustose coralline algae.

4.8 Benthic-Community-Level Interactions: Negative Algal Cues for Coral Larvae

Macroalgae and benthic cyanobacteria can negatively impact the settlement of coral larvae (Kuffner and Paul 2004; Kuffner et al. 2006). The cyanobacterium *Lyngbya majuscula* reduced the survivorship of *Acropora surculosa* larvae and settlement and metamorphosis of *Pocillopora damicornis* in studies conducted on Guam (Kuffner and Paul 2004). In the Florida Keys, USA, two brown algae, *Dictyota pulchella* and *Lobophora variegata*, reduced the total number of settlers of the brooding coral *Porites astreoides*, while the cyanobacterium *Lyngbya polychroa* caused avoidance behavior such that more larvae settled away from the settlement tile (Kuffner et al. 2006). The mechanisms that caused larval avoidance are unclear, but these macrophytes are known to be chemically rich and defended from some herbivores. Baird and Morse (2004) showed similar effects of *Lobophora* sp. on larvae of the corals *Acropora palifera* and *Stylophora pistillata* and suggested that the alga contained compounds that inhibited larval metamorphosis. In contrast, *Favia fragum* larvae had high rates of settlement and metamorphosis onto live *Halimeda opuntia* when offered with coral rubble (Nugues and Szmant 2006).

Filamentous algal turfs, which can trap sediment, were tested alone and in combination with sediments to determine their effect on the settlement of larvae of the spawning Pacific

coral *Acropora millepora* (Birrell et al. 2005). There was reduced settlement in response to one of the algal turfs regardless of the presence of sediment. The other algal turf did not reduce *A. millepora* settlement unless sediment was added (Birrell et al. 2005).

Waterborne compounds from macroalgae have been demonstrated to influence settlement and metamorphosis of larvae of corals and other invertebrates (Walters et al. 1996; Birrell et al. 2008a; Miller et al. 2009). Both positive and negative effects were observed for seawater collected from aquaria that had contained macroalgae for the settlement of larvae of the spawning coral *Acropora millepora* onto fragments of the crustose coralline alga *Hydrolithon reinboldii* (Birrell et al. 2008a). Miller et al. (2009) also saw variability in the responses of larvae of three coral species to macroalgal exudates from different benthic macroalgal assemblages in the Florida Keys. These results underscore the complexity of the effects of macroalgae on coral larval settlement behavior.

4.9 Benthic-Community-Level Interactions: Algal/Coral Competition

Ritson-Williams et al. (2009) and Birrell et al. (2008b) recently reviewed ecological mechanisms affecting coral recruitment and concluded that competition between macroalgae and lar-

val and juvenile coral is a very important ecological force shaping coral reef community structure. Further, Chadwick and Morrow (2010) determined competition between corals and macroalgae occurs through a wide variety of mechanisms, including both physical and chemical processes that can impact all stages of the coral life cycle. Seven mechanisms of competition were identified including preemption of space, shading, allelopathy, attraction of settling larvae to ephemeral algal surfaces, abrasion, basal encroachment, and increased sedimentation. However, a recurring theme of these recent reviews is that the nature and importance of competitive interactions between corals and macroalgae varies greatly across different species of macroalgae (for reviews, see McCook et al. 2001; Birrell et al. 2008b; Ritson-Williams et al. 2009; Chadwick and Morrow 2010). For example, in Roatan, *Lobophora variegata* shading increased mortality of juvenile *Agaricia agaricites*, while the mere presence of the alga reduced coral growth (Box and Mumby 2007). In contrast, shading by *Dictyota pulchella* only affected coral growth. Thus, the diversity, abundance, and spatial placement of the macroalgal community with respect to the coral community must be considered when assessing the importance of competition between these groups (Fig. 3).

Reductions in recruitment in areas that have shifted from coral- to algal-dominated reefs (Edmunds and Carpenter 2001; Birrell et al. 2005) are thought to be due in part to chemically induced mortality or the increased biomass of fleshy algae

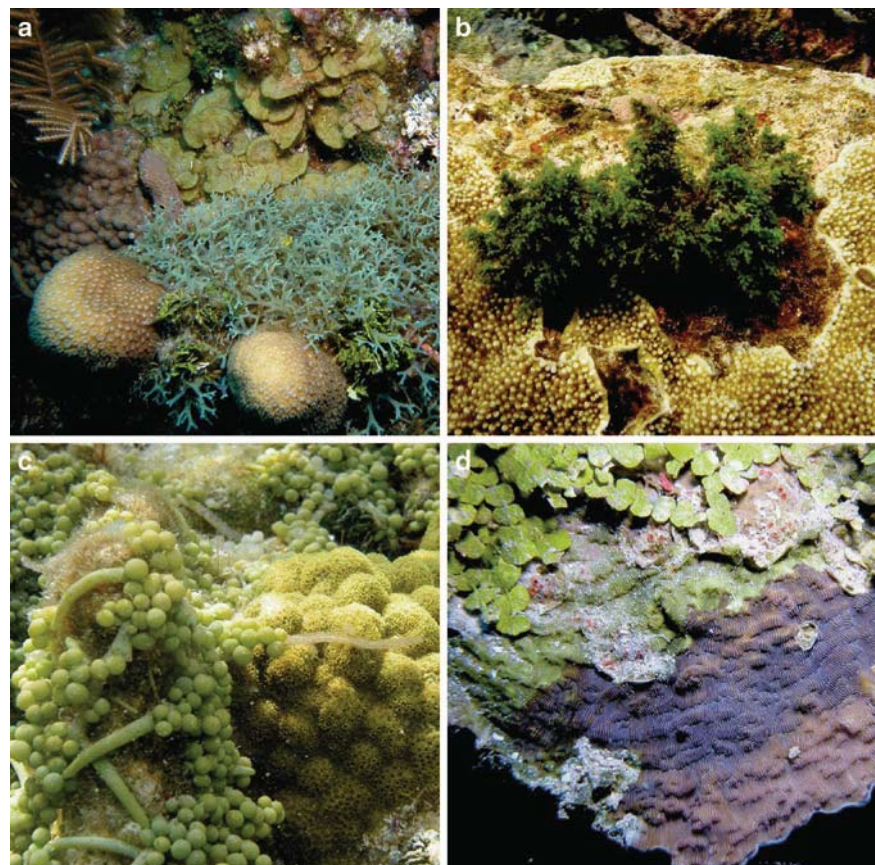


Fig. 3 Examples of algal/coral competition: (a) the algae *Dictyota pulchella*, *Lobophora variegata*, and *Halimeda* sp. growing over the corals *Montastraea* sp. and *Porites astreoides* at a depth of 5 m in Belize, (b) the alga *Laurencia obtusa* growing on top of the coral *Acropora palmata* at a depth of 1 m on the reef crest in Belize, (c) the alga *Caulerpa macrophysa* growing next to the coral *Porites astreoides* on a reef flat in Belize, and (d) the alga *Halimeda copiosa* growing on *Leptoseris cucullata* at a depth of 30 m in Belize (Photographs by Raphael Ritson-Williams)

functioning as a reservoir for coral pathogens (Nugues et al. 2004; Ritson-Williams et al. 2009; Chadwick and Morrow 2010; Rasher and Hay 2010). Bak and Borsboom (1984) proposed that reduction in water flow adjacent to macroalgae could cause increased coral mortality through changes in the flow regime and increased allelochemical concentrations. Most recently, enhanced microbial activity caused by algal exudates has been identified (Smith et al. 2006; Vermeij et al. 2009), and Kline et al. (2006) determined elevated levels of dissolved organic carbon, which can occur in areas of high algal biomass, increased the growth rate of microbes living in the mucopolysaccharide layer of corals. These studies all suggest that the detrimental effect of algae on corals could be mediated by stimulation of microbial concentrations in the vicinity of a coral colony or recruit, but it is not clear at present whether such stimulation occurs by stimulating the microbial community directly through the release of dissolved organic carbon or by lowering the coral's resistance to microbial infections through allelopathy or other mechanisms.

Several studies have identified the role of macroalgal community structure in mediating the outcome of competition between macroalgae and larval and juvenile corals. For example, Vermeij (2006) attributed large reductions in coral recruitment in Curacao over the last 20 years to shifts in macroalgal dominance from CCA to fleshy macroalgae creating a less-suitable habitat for successful coral recruitment. Other recent studies in the Caribbean showed a clear pattern of increased coral recruitment in places where *Diadema* urchin recovery and grazing had reduced fleshy algal abundance and simultaneously increased the population density of juvenile corals (Edmunds and Carpenter 2001; Aronson et al. 2004; Macintyre et al. 2005).

4.10 Benthic-Community-Level Interactions: Invasive Species

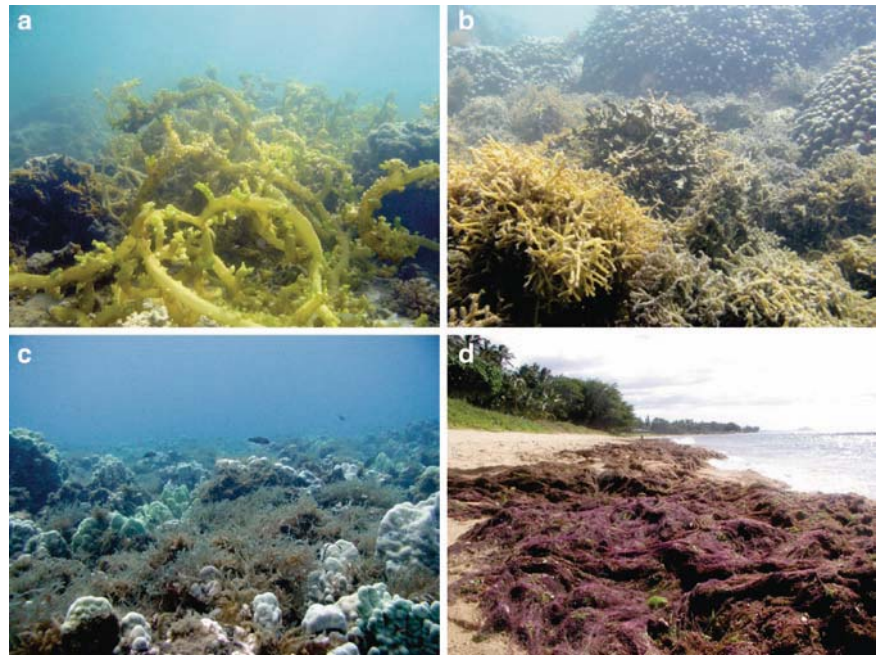
Invasions of nonindigenous organisms into marine habitats have been ranked among the most serious sources of stress to marine ecosystems (Carlton and Geller 1993). During the last century, and especially over the last 3 decades, the frequency of invasions of exotic marine species has increased in temperate coastal regions around the world (for reviews, see Carlton and Geller 1993; Ruiz et al. 1997). Invasions of marine algae are also increasing in frequency, with the total number of introduced seaweeds documented at 277 as of 2007 (Williams and Smith 2007). Invasions of marine algae, especially the invasion of the "killer alga" *Caulerpa taxifolia* into the Mediterranean, represent some of the most dramatic and well-known examples of the strong adverse effects invasive species may have on native populations and communities (Bourdouresque et al. 1992). Although studies of the

frequency and impacts of invasions of marine algae in tropical regions are relatively rare (Coles and Eldredge 2002), global patterns of invasion suggest that the situation will only worsen with time (Williams and Smith 2007).

A recent review identified patterns of invasion of marine algae that varied across algal taxonomic group, morphology, and functional form (Williams and Smith 2007). Although most of the studies summarized were in temperate regions, these patterns can be used to identify which groups warrant future attention by coral reef management groups. Overall, several larger algal families have disproportionately more numbers of invasive species than would be expected by chance. For the green algae (Chlorophyta), the incidence of successful invasive species is high in several families, including the Caulerpaceae, Ulvaceae, and Codiaceae. Each of these families is important in tropical habitats, especially on coral reefs. *Caulerpa* (Bourdouresque et al. 1992) and *Codium* (Lapointe et al. 2005) are two of the most famous invasive genera on coral reefs due to their wide proliferation and strong negative community impacts. Families of red algae (Rhodophyta) that include disproportionately more species of successful invaders include, among others, the Rhodomelaceae, Cystocloniaceae, and Gracilariaceae; these families contain some of the invaders with the greatest known ecological impact on tropical reefs. For example, *Acanthophora spicifera* in the Rhodomelaceae has invaded coral reefs worldwide (<http://www.issg.org/database/species/distribution>), forming stable blooms on coral reefs in Pacific Panama via protection by an associational defense with epiphytic cyanobacteria (Fong et al. 2006). Among the Cystocloniaceae, all invasive species belong to the genus *Hypnea*, identifying the unique invasive abilities of this genus. One of these species, *Hypnea musciformis*, forms widespread and destructive blooms on reefs off the coast of Maui (Smith et al. 2002). The Gracilariaceae contain the highly successful invader *Gracilaria salicornia*, also common in Hawaii (Fig. 4). Although the Areschougaceae does not contain a disproportionately large number of invasive species, it does contain some of the most successful genera, including *Kappaphycus* (Hawaii, Smith et al. 2002; India, Chandrasekaran et al. 2008) and *Eucheuma*. One dominant red algal family on coral reefs, the Corallinaceae (calcifying reds), though speciose, has fewer invasive species than would be predicted by chance, suggesting that it may not have the characteristics that enhance invasiveness.

The success of invasions among algal groups is likely determined by characteristics of both the invader and the invaded habitat. One caveat, however, is that most invasions are only noted when there is proliferation of the large macroscopic form of the alga. Since most algae have bi- or triphasic life cycles, one must keep in mind that the success of some invasions may be due to some unknown characteristics of the diminutive or microscopic phase. In a

Fig. 4 Many species of invasive red algae proliferate on Hawaiian coral reefs including (a) *Kappaphycus alvarezii*, (b) *Gracilaria salicornia*, and (c) *Acanthophora spicifera*. (d) In some areas, such as the coast of Maui, blooms of *Hypnea musciformis* become so prolific that they detach, form floating rafts, and deposit on the beach (Photographs by Jennifer Smith)



global assessment of successful invasions across functional forms (Williams and Smith 2007), invasion success ranked as corticated macroalgae = filamentous > corticated foliose > leathery > siphonaceous > crustose. However, these ranks changed greatly among habitat types. Areas characterized by frequent physical disturbance were successfully invaded more often by filamentous or coarsely branched algae such as those in the genera *Acanthophora*, *Cladophora*, and *Polysiphonia*. In contrast, areas subject to lower disturbance and perhaps higher productivity were more likely to be successfully invaded by corticated or leathery macroalgae such as *Kappaphycus*, *Euचेuma*, and some of the more robust forms of *Gracilaria*. Different levels of herbivory may also play a role in invasion success, because many of the filamentous or coarsely branched forms are not grazer resistant.

A comparison of the most and least successful invasive algal forms may provide some insight as to overall characteristics that enhance invasion success. Some of the most successful algal invaders are siphonaceous green macroalgae in the Order Bryopsidales. Common genera include *Codium*, *Caulerpa*, and *Bryopsis*, all of which are important members of tropical algal communities with broad habitat adaptability allowing them to colonize both hard and soft substrata. Morphologically, these algae are single celled yet multinucleate and range from simple to quite complex pseudoparenchymatous thalli. This thallus construction allows for rapid growth, efficient wound healing, and prolific asexual reproduction via fragmentation. In contrast, articulated and crustose calcareous algae are the least successful invaders; crustose calcareous algae have only experienced a single invasion,

while articulated calcified forms have never been documented to successfully invade a new habitat. Explanations may include relatively specific habitat requirements, narrow physiological tolerances, and a lack of appropriate propagules to disperse via anthropogenic means.

Differences in success of invasions among algal groups may also be strongly influenced by the strength and mode of the invasion vector. However, in 40% of algal invasions globally, the vector is unknown (Williams and Smith 2007). Of those that have been identified, hull fouling and aquaculture account for the majority of successful invasions. Of invaders carried to new habitats on the hulls of ships, over 50% are filamentous or sheetlike. Dispersal via aquaculture can be direct, through escape of cultured algae. In this case, the characteristics of the invaders are determined by the traits that also make them commercially valuable. These are often corticated or leathery macroalgae with copious amounts of agar, carrageenan, or other valuable products. They are also often fast growing and tolerant of a wide range of environmental conditions including herbivores because of their tough or leathery thalli. Dispersal through agriculture may also be indirect, for example, when an invasive alga is brought in accidentally with another aquacultured organism such as an epiphyte attached to shellfish. These are often red corticated algae, though there have been several documented cases of larger leathery forms transported this way (Williams and Smith 2007). In contrast to invasive animals, ballast water of ships account for a relatively small proportion of algal invasions, ~10% globally. It is likely that lack of light in ballast tanks may account for this difference. The aquarium industry accounts for <1% of algal invasions globally, though it

accounts for perhaps the most noteworthy, the invasion of *Caulerpa taxifolia* into the Mediterranean (Meinesz 1999).

The effects of invasive algae on native marine populations, communities, and ecosystems have only been studied in 6% of the cases reviewed by Williams and Smith (2007). Most commonly, negative effects on the abundance of native seaweeds or epiphytes were detected, though this result is hardly universal. Some studies tested the effects on animals, usually whether native herbivores avoided invasive algae. Overall, the findings did not support the “enemy release hypothesis” – invasive species may not be preferred, but were consumed, even the heavily chemically defended *Caulerpa taxifolia*. Yet, herbivores do not seem to effectively control the spread of invasive algae, contrasting with plant invasions on land, in freshwater, or in salt marshes. One explanation is that herbivores may enhance spread of invasive algae through increasing fragmentation. The effect of invasive algae on native algal community structure or ecosystem processes is virtually unstudied. The little evidence that exists suggests that few communities are resistant to invasions, and that both disturbance and nutrient enrichment may enhance invasion success.

Very little is known about introduced algal species in the tropics. This may be due to the lack of historical records and the relative paucity of tropical phycologists. Algal invasions, however, may be of special concern in tropical reefs systems because of the growing aquaculture industry in many of these regions. Many of the most invasive and destructive tropical red algae such as *Eucheuma* and *Kappaphycus* are often cultured right next to coral reefs, and significant negative impacts have begun to be recorded (Smith et al. 2002; Chandrasekaran et al. 2008). Aquaculture near coral reefs is predicted to have a major economic impact in the future (Williams and Smith 2007). Recommendations to limit these impacts include prevention, early detection and rapid responses to eradicate new invaders, and control of present invaders. All of these will require a much more thorough understanding of the processes that control invasion success on coral reefs.

4.11 Climate Change

Climate change is producing a suite of changes in global environmental drivers, including sea-level rise, increased temperature, increased CO₂ in the air and water, ocean acidification, and changes in weather patterns (Parmesan and Yohe 2003). Although perhaps the least studied of all with the highest uncertainties, there are indications that ocean circulation may change (Diaz-Pulido et al. 2007). The IPCC (2007) predicts that CO₂ and temperature will continue to rise with greatest warming at the highest latitudes resulting in further ice melt and rising sea level, putting large deltas

and island nations at greater risk of flooding and coastal erosion. In wetter tropical areas, more heat extremes, heavy precipitation, and higher river run off are predicted, while in drier subtropical areas there will be a decrease in precipitation with more heat waves and drought. Despite this variance in total precipitation across the tropics, the frequency of heavy precipitation events will continue to increase greatly over most areas of the globe, with increased flooding, erosion of terrestrial sediments, physical disturbances, and potentially enhanced nutrient supply to coastal ecosystems. There will be increased tropical cyclone intensity with more poleward shifts in their paths causing major physical disturbances. Tropical regions recognized as particularly vulnerable to this suite of changes include small islands due to their close association with the oceanic environment. Tropical ecosystems noted to be especially vulnerable are mangroves and coral reefs. These global changes will directly affect overall productivity of coral reef algae as well as species distributions, abundances, and diversity. There will also be indirect effects on algae through negative effects on corals. Both direct and indirect effects will result in changes in reef community structure and ecosystem functioning.

Sea-level rise, which is expected to continue for centuries even if green house gas concentrations stabilize today (IPCC 2007), may have relatively minor direct effects on coral reef algae. Even the highest range of predicted rates of rise, 59 cm over the next 100 years (IPCC 2007), are generally not thought to be rapid enough to exceed the ability of coral reef accretion processes to “keep up” (Smith and Buddemeier 1992). One caveat is that these predictions by IPCC do not include rapid dynamical changes in ice cover, which may result in a more rapid and higher rise of up to 7 m. In addition, predictions of reef accretion are based on current or past growth rates (e.g., Smith and Buddemeier 1992; Kan and Kawana 2006), which may be drastically reduced due to other effects of climate change such as acidification (Hoegh-Guldberg et al. 2007). Given these qualifiers, however, for most reefs effects on algae most likely will be limited to minor shifts in patterns of zonation due to increased water depth, with possible losses of the deepest communities. To compensate, rising seas will flood intertidal and shallow subtidal areas and coastal low lands, creating new shallow water habitat that is available for algal colonization and growth (Erez et al. 2010, this volume). In addition, some lagoons that at present lack a good ocean connection may become well flushed and more productive (Smith and Buddemeier 1992). This type of compensation may not always be possible, however, especially for island nations, where low lands are often tightly constrained between the ocean and mountains or are filled with high-density development that may be actively protected (seawalls, filling), limiting the expansion of shallow habitat.

Sea-level rise may have far more significant indirect than direct effects on coral reef algae through interactions with associated terrestrial systems. When reefs are associated with continents or islands, key risks include flooding and coastal erosion (Heberger et al. 2009), which may reduce photic zone depth and reduce suitable habitat for algae, especially on fringing reefs. In addition, erosion of fringing reef flats due to increased wave action as water deepens may reduce the ability of these systems to provide protection from storms (Sheppard et al. 2005), thus forming a positive feedback accelerating erosion and flooding. Because of these indirect effects, the net effect of sea-level rise on coral reef algal communities is difficult to predict, but most likely will be minor relative to the responses to other factors associated with climate change.

The IPCC (2007) predicts sea surface temperatures (SST) will continue to rise in the range of 1.1–6.4°C over the next 100 years, with the greatest uncertainty in predictive ability for the tropics. Paleoclimate records suggest that the tropics are more buffered to temperature changes than other regions (e.g., Smith and Buddemeier 1992), though most agree that the past does not provide an adequate model for anthropogenic climate change. Even if water temperatures remain within the lowest range of predictions, there will be strong effects on coral reef algae, both directly and indirectly through the negative effects on coral. There is a plethora of evidence that corals bleach with high temperature anomalies of as little as 1–2°C over a period of a few weeks and suffer mortality at higher intensities or longer durations (e.g., Hoegh-Guldberg 1999; Hoegh-Guldberg et al. 2007; Hueerkamp et al. 2001; D’Croz et al. 2001). Recent evidence also suggests corals may suffer more outbreaks of disease with thermal stress (Bruno et al. 2007). There is a preponderance of evidence that when corals die they are quickly replaced by algal communities (e.g., Littler and Littler 1997; Hughes et al. 2007). Some evidence suggests that coral reefs subject to higher natural variability in temperature may be more susceptible to climate change (McClanahan et al. 2009), while other studies found variability in response was dependent on the rate and duration of temperature rise (Fong and Glynn 2000; Glynn and Fong 2006). There is little doubt, however, that continued sea surface warming will open a significant amount of space presently occupied by corals for colonization by algae (Hoegh-Guldberg et al. 2007), transforming many coral reefs to algal reefs.

Direct effects of rising SST are also predicted to have strong direct effects on coral reef algal distribution and abundance. Overall, the largest global effect will be poleward shifts in geographic ranges of species that will ultimately alter the composition of all marine communities (for a review, see Hawkins et al. 2008), including coral reef algae. Tropical and subtropical species of algae are predicted to expand their ranges both north and south, while temperate and polar

species undergo a latitudinal retreat. Small and fragmented edge populations may be more susceptible to changes in thermal stress because of inherently lower fitness and lower adaptive capacity due to random genetic drift (Pearson et al. 2009); this may effectively enhance the invasive ability of tropical algae. In addition, in temperate latitudes warming may result in deepening thermoclines and relaxation of cold water upwelling, thus enabling warm water species to more easily jump gaps in distribution, especially along the western margins of major continents. Overall, rising SST is expected to expand the distribution and enhance the abundance of tropical algal communities at the expense of both coral and temperate algal communities. There is some experimental evidence that warming may favor algal turf over crustose coralline algae (Diaz-Pulido et al. 2007). Certain groups of especially thermal tolerant or thermophilic algae such as the Cyanobacteria can be expected to thrive, possibly leading to more frequent harmful cyanobacterial blooms (Hallock 2005; Paul 2008; Paerl and Huisman 2008).

Experimental evidence is beginning to accrue that increased CO₂ concentrations and the resultant acidification of seawater may have strong effects on all primary producers, including coral reef algae. At present, CO₂ concentrations in the atmosphere are ~380 ppm, a level unprecedented in at least the last 650,000 years (IPCC 2007), with predictions of ~500 ppm by 2100 (Hoegh-Guldberg et al. 2007). Experiments with elevated CO₂ and lowered pH revealed strong negative effects on tropical crustose calcareous algae (CCA). In Hawaii, decreased pH treatments decreased growth and benthic cover of CCA by 85% compared to algae in experimental microcosms subject to ambient seawater; rhodoliths actually decreased in weight by 250%, showing a net dissolution of algal-derived CaCO₃ over time (Jokiel et al. 2008; Kuffner et al. 2008). Another study on Australia’s Great Barrier Reef demonstrated that CCA is even more sensitive than coral to elevated CO₂; while CO₂ bleaches both coral and CCA, it has more extreme effects on CCA including net negative primary productivity and dissolution of algal carbonate (Anthony et al. 2008). In a review, Diaz-Pulido et al. (2007) suggested upright calcifying forms of macroalgae may also be affected by acidification and that this may lead to reduction in production of sand and loss of habitat.

Results of aquaculture optimization studies also identified the role of rising CO₂ in changing the growth rates of algae. Overall, increased supplies of CO₂ greatly accelerated growth of algae in the genus *Gracilaria* that cannot utilize HCO₃⁻ as a carbon source (Friedlander and Levy 1995; Israel et al. 2005). CO₂ effects, however, are not uniform across groups. Aquacultured *Porphyra* dramatically decreased growth with increased CO₂, most likely related to increases in dark respiration rates (Israel et al. 1999). Positive effects of increased CO₂ were especially important in low turnover

aquaculture systems (Friedlander and Levy 1995), suggesting that changes in CO₂ may be especially important in highly productive systems with low turnover such as tropical lagoons. Blooms of native and invasive species of *Gracilaria* are already prolific on some coral reefs, and these studies suggest they will only intensify. Thus, rising CO₂ and acidification will change the structure of tropical algal communities by shifting dominance from CCA toward fleshy and invasive species.

How climate change will affect the supply of nutrients to coastal ecosystems with resultant effects on coral reef algae is difficult to predict (Diaz-Pulido et al. 2007). Although complex, the supply of nutrients to surface waters is, at least in part, a function of temperature, and has shown a decreasing trend with increasing temperature over the last 3 decades in the Northern Hemisphere (Kamykowski and Zentara 2005). A strengthening and deepening of the thermocline may cause severe nutrient limitation, especially in coral reef regions where thermocline shoaling may provide a significant source of nutrients such as to the Great Barrier Reef and the Florida reef tract (Leichter et al. 1996; Wolanski and Pickard 1983). Upwelling may be suppressed, limiting oceanic nutrient supplies to some reef systems that are subject to seasonal upwelling such as those in the Gulf of Panamá and the Galapagos Islands (Glynn and Maté 1997). Whether this reduction in supply will be matched or greatly exceeded by changes in terrestrial supplies is highly debated (Jickells 1998; Steneck et al. 2002), but most likely depends on many local factors including accelerating variance in precipitation and the level of watershed development. If supplies are enhanced, then there may be a net increase in benthic algal productivity as well as increases in phytoplankton. However, the net effects of changes in nutrient supply on coral reef algae are likely to vary greatly across tropical regions and to be driven by interactions with local and global changes in other anthropogenically influenced environmental factors.

Current and projected rising sea levels with increased coastal erosion as well as more frequent and intense storms (IPCC 2007) will act to increase the supply of terrestrial sediments to coral reefs; this will only be accelerated by local anthropogenic changes due to coastal development. Sediment particles smother reef organisms and reduce light for photosynthesis (for a review, see Rogers 1990), effectively reducing habitat area by decreasing the depth of the photic zone. Increased sedimentation has been documented to have many negative effects on corals that reduce reef accretion rates and may make them more susceptible to rising sea level. Although studies on the direct effects of sediments on coral reef algae are limited, evidence from the Mediterranean demonstrated that sediment effects vary across algal functional forms. High levels of sedimentation decreased the growth of the dominant algal turfs, facilitating

coexistence with upright macroalgae such as *Halimeda*, *Dictyota*, and *Padina* (Airoldi and Cinelli (1997); Airoldi 1998). However, coral reef turfs are more tolerant of sedimentation than corals as increased sedimentation favored growth of turfs that then reduced recruitment of coral and CCA (Nugues and Roberts 2003). Another study also suggested coral reef turfs may be more tolerant of high levels of sediment than would be predicted from studies in the Mediterranean. Bellwood and Fulton (2008) suggest that sediments provide a refuge from herbivory for coral reef algal turfs, thus facilitating dominance of this functional form as an alternative stable state. As sedimentation is predicted to increase with climate and other anthropogenic factors, it is essential that we further our understanding of the effect of enhanced sediment supply on coral reef algae.

While each of the individual factors that are predicted to change with climate will have significant effects on coral reef algae, evidence is beginning to accumulate that interactions among factors may be even more important. However, interactive effects may be quite complex, limiting our predictive abilities without detailed experiments. For example, while increased temperature and nutrients may increase algal recruitment and growth overall, they should also increase the number of grazers, driving algal communities toward opportunistic species (Lotze and Worm 2002). O'Connor (2009) also found that warming strengthens herbivore–algal interactions, shifting important trophic pathways. Recent multifactorial experiments showed that some stages in the complex life cycles typical of algae may be more sensitive to interactions among climate-related factors, making certain stages important bottlenecks limiting the ability of algal dominants to survive climate change over the long term (Fredersdorf et al. 2009). Aquaculture studies identified an important interaction between rising CO₂ and nutrients, with positive CO₂ effects on growth of *Gracilaria* being accelerated with pulsed nutrient supplies (Friedlander and Levy 1995). Thus, increased storms combined with rising CO₂ will act to facilitate the already prolific blooms of these opportunists on some reefs. Overall, it appears that interacting factors associated with climate change will synergistically enhance algal blooms, and may shift communities beyond a state from which they can return.

In summary, our changing climate may result in irreversible changes in coral reef benthic producer communities. Widespread coral mortality will open space for colonization by algae, producing a shift from coral- to algal-dominated reefs. Sea-level rise may increase algal-dominated areas as well, though these areas may be severely stressed by erosion and sedimentation. Tropical algal distributions will expand poleward, resulting in shifts in community composition due to differential responses of algal species to individual and interactive factors driven by climate change. Upward negative cascades may occur in these newly colonized latitudes

as trophic pathways are altered. On tropical reefs there will be a shift from CCA (reef building) to other types of algae, especially chemically defended species where herbivores are protected, or fast-growing opportunists in areas of reduced herbivory. Shifts toward invasive and/or opportunistic species of algae may also occur as these species have appropriate physiologies to take advantage of changing environmental conditions. If nutrient supplies increase, further shifts toward dominance by nutrient specialists that are disturbance tolerant may occur. These shifts will be most dramatic in lagoons with low turnover or flushing rates and that are associated with developed or developing watersheds. Overall, climate change, with other interacting anthropogenic changes, will synergistically enhance algal blooms on coral reefs worldwide.

5 Phase Shifts, Alternative Stable States, and the Stability of Algal-Dominated Tropical Reefs

There is a preponderance of evidence that reductions in live coral cover have been followed by phase shifts to algal dominance (Hughes 1994; McCook 1999; Diaz-Pulida and McCook 2002; McClanahan and Muthiga 2002; Rogers and Miller 2006), although one meta-analysis suggests that recent increases in dominance by upright algae may have been overestimated (Bruno et al. 2009). Coral reef phase shifts are defined as a transition from a community dominated by reef-building organisms to one dominated by non-reef-building organisms, most often macroalgae (Done 1992). Phase shifts have been attributed to reduced herbivory (Hughes 1994; Hughes and Connell 1999), increased nutrients (Banner 1974; Smith et al. 1981; Lapointe et al. 2005; Fabricius 2005), and reductions in live coral cover due to environmental stress and disturbance (McClanahan et al. 1999; Diaz-Pulida and McCook 2002). Regardless of the cause, reductions in coral dominance can result in increased rates of bioerosion that exceed accretion, leading to gradual destruction of the reef framework and habitat loss (Glynn and Maté 1997).

Though all agree that coral reefs are experiencing high levels of degradation, the relative importance of herbivory and nutrients in regulating phase shifts to algal dominance has been hotly debated (e.g., Aronson et al. 2003; Hughes et al. 2003; Pandolfi et al. 2003; Burkepile and Hay 2006). Though increased nutrients and reductions in herbivory may initiate and commonly contribute to the persistence of phase shifts (Fig. 5), there appears to be increasing evidence that elevated SST due to global warming may be the greatest threat to coral reefs globally (Hoegh-Guldberg 1999; Knowlton 2001; Walther et al. 2005; Hughes et al. 2003;

Hoegh-Guldberg 2004; Pandolfi et al. 2005). Following coral bleaching and mortality events, broad areas of reefs are often overgrown by macroalgae, which can competitively exclude corals once established (Coyer et al. 1993; McCook 1999, 2001; Jompa and McCook 2003; Rogers and Miller 2006; Kuffner et al. 2006). Therefore, the capacity of reefs to weather bleaching events may be determined by the presence of intact herbivore populations and low levels of nutrients, which may help limit the proliferation of macroalgae on reefs. The recent proliferation and persistence of algal dominance on coral reefs requires further study, given the potential interactions between temperature stress and human-initiated changes in top-down and bottom-up forces.

Once established, these algal-dominated phase shifts can be difficult to reverse for many reasons already discussed. Algae that dominate communities following the reduction of herbivory are often chemically defended species such as *Halimeda* and *Dictyota* spp., as well as various filamentous cyanobacteria, which are relatively unpalatable to herbivores (Fig. 6). Studies of phase shifts from coral- to macroalgal-dominated communities have often overlooked filamentous cyanobacteria, which generally have been grouped with turf algae in ecological research (e.g., Steneck and Dethier 1994). Benthic cyanobacteria may play an important role in these phase shifts, as they can be early colonizers of dead coral and disturbed substrates (Tsuda and Kami 1973; Larkum 1988), and in some cases have been observed to overgrow coral branches and kill coral polyps (Littler and Littler 1997). In addition, many types of macroalgae can inhibit the recruitment of corals and other invertebrates through a variety of mechanisms (Birrell et al. 2008b; Chadwick and Morrow 2010), which can lead to the persistence of algal-dominated reef communities.

5.1 The Nature of Transitions to Algal Domination of Tropical Reefs: Phase Shifts Versus Alternative Stable States

Dramatic shifts in populations, communities, and ecosystems worldwide in response to natural and anthropogenic alterations in environmental conditions have focused much attention on the nature of change and the processes that drive them (Scheffer et al. 2001; Beisner et al. 2003; Didham et al. 2005; Jackson 2008). Ecological theory predicts that there are many possible patterns of change for populations and communities. Some studies found ecological communities shifted in a relatively simple, linear, or linearizable manner, where a given change in a controlling environmental variable produced a predictable community response (Fig. 7a). Much recent attention, however, has focused on nonlinear shifts, with extreme nonlinearities occurring in response to both

Fig. 5 An example of multiple stresses causing a partial shift away from a coral-dominated state. This *Pocillopora* reef was treated with nutrient addition and herbivory reduction with cages. The time series is: (a) before manipulation, (b) 6 weeks, (c) 10 weeks, (d) 16 weeks, (e) 22 weeks, and (f) 2 days after end of manipulations. Algal cover developed quickly, but was rapidly grazed down after cages were removed, suggesting that herbivory is a stabilizing force on coral reefs (Photographs by Ranjan Muthukrisnan)

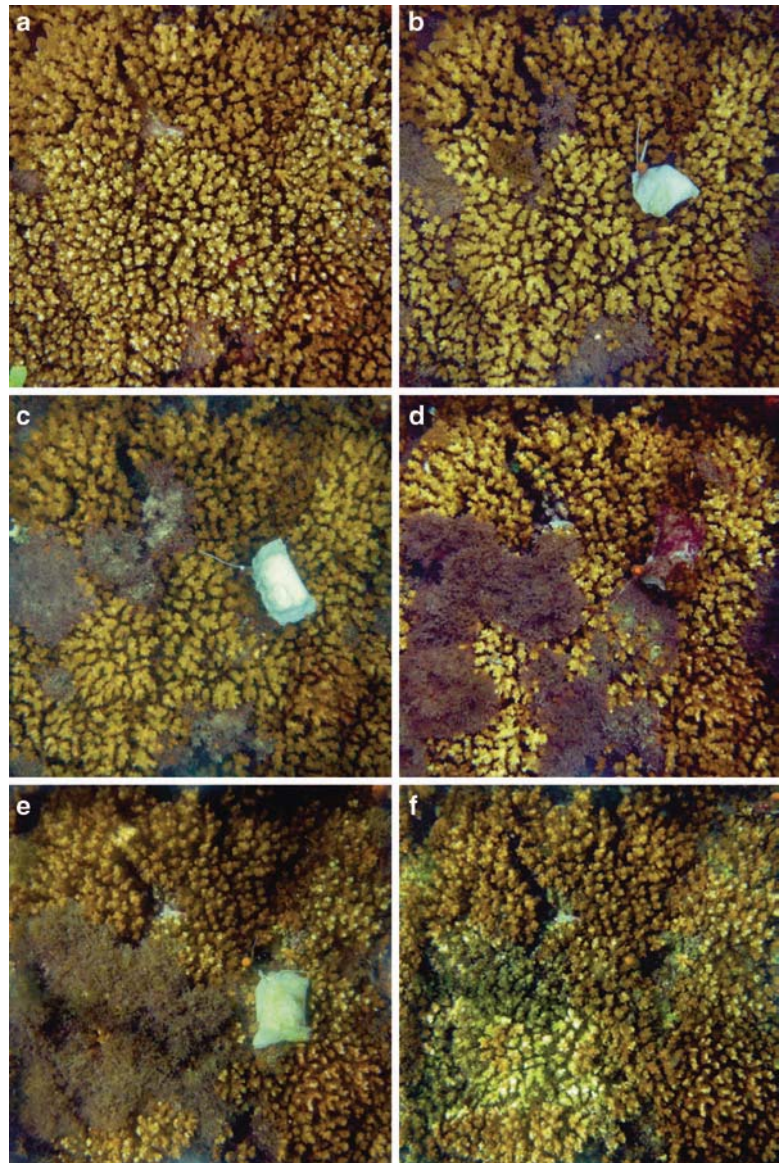
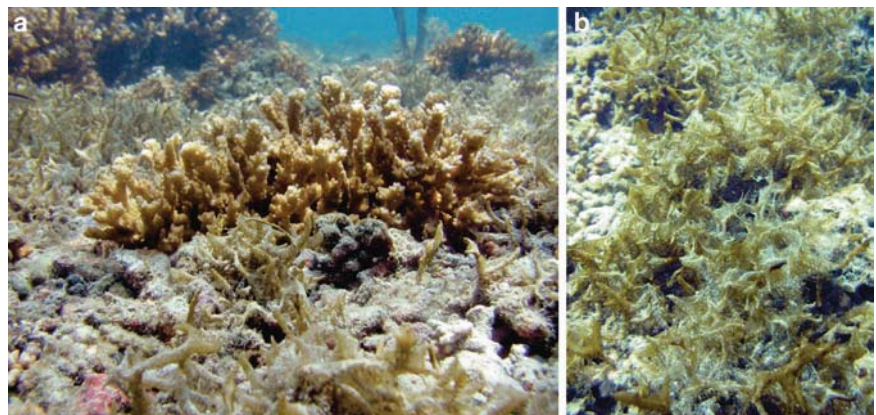


Fig. 6 Blooms of *Acanthophora spicifera* on some reefs of Pacific Panamá were stabilized for at least 5 years by epiphytic cyanobacteria that defended the alga from herbivory: (a) Algal bloom on Uva Island reef. (b) Cyanobacteria coating the algal thalli (Photographs by Tyler Smith)



natural and anthropogenic changes in environmental forcing functions. Examples span a diversity of ecosystems including the collapse of most major marine fisheries (Roughgarden and Smith 1996; Myers and Worm 2003), desertification of the sub-Saharan (Xue and Shukla 1993), and shifts from coral- to algal-dominated tropical reefs (Hughes et al. 2007).

The rising frequency of rapid collapses from one community state to another, often less desirable, state has renewed interest in whether this process is a simple and symmetrically reversible phase shift (Fig. 7b), or if these shifts represent alternative stable states (Scheffer et al. 2001; Beisner et al. 2003; Didham et al. 2005). It is important to distinguish between these two methods of community change because management strategies must be very different for each if the goal is to promote and stabilize the initial, often “desirable” state. For phase shifts, incremental changes of environmental stressors may cause little change until a critical threshold is reached; at that point, shifts from one community dominant to another are rapid and catastrophic over a very short range of environmental conditions. Thus, in the forward direction, the past history of environmental change will not aid prediction of future change. However, backward shifts are equally rapid, and occur predictably at the same level of environmental stress as the forward shift, making management strategies of these systems conceptually straightforward – one must reverse the environmental condition back to the point that caused the forward shift (e.g., Suding et al. 2004).

The clearest, strongest evidence that communities can exist as alternative stable states is to reverse the environmental condition and observe a backward transition at a different point than caused the forward transition, proving hysteresis (e.g., Knowlton 2001). However, these data are often difficult, expensive, or logistically impossible to obtain. Two key aspects of alternative stable state theory that distinguish alternative stable state transitions in communities from phase shifts and can be measured on the spatial and temporal scales appropriate to reefs are the processes that cause transitions among states and those mechanisms that stabilize them (Scheffer et al. 2001). Transitions among community states can be due to either change in the environment or disturbance. Forward shifts from one state to another (e.g., F_1 in Fig. 7c, d) occur at very different points or conditions of the environmental driver than backward shifts (e.g., F_2) that restore the initial state. Thus, there is a range of environmental conditions, between points F_1 and F_2 , where either of two stable states can occur. As a result, there is limited ability to predict the community state based on the current condition of the environment. For alternative stable states, managers would have to reverse the environmental condition far beyond the point of forward shift, to F_2 , to restore the initial community, often a very difficult and expensive management option. The only other way to shift communities between states is to subject them to large disturbances that push the state beyond the unstable

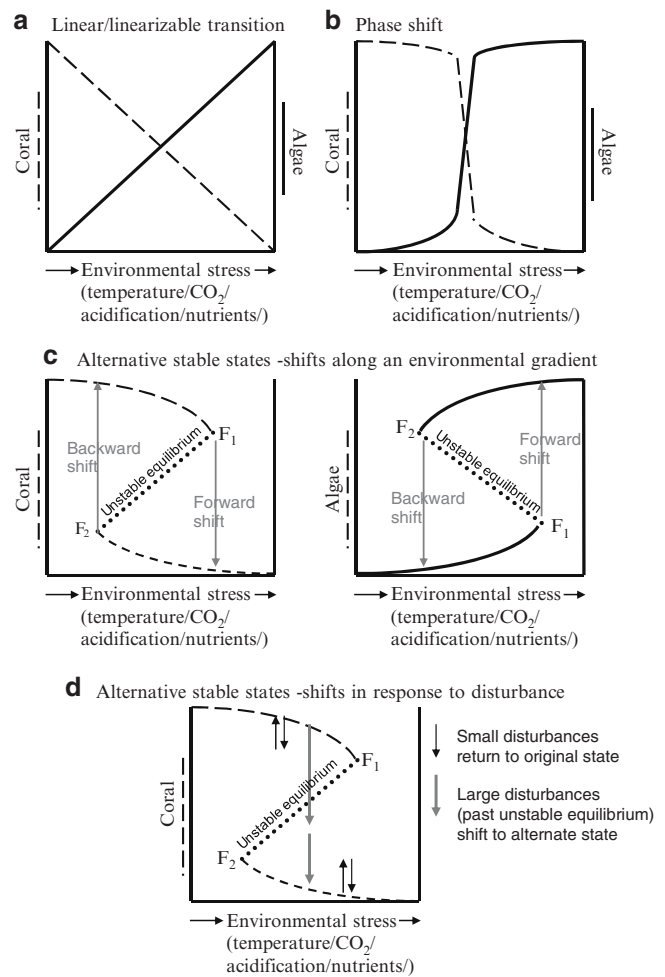


Fig. 7 Conceptual diagram showing the difference between community changes with predictable Y values (e.g., coral or algal cover) for each X value (environmental stresses) such as (a) linear and (b) phase shift relationship and (c and d) alternative stable states where there can be two Y values for a range of X values. One key difference that characterizes alternative stable states is that forward and backward transitions occur at different environmental conditions, thus requiring a greater “correction” of an environmental condition to reestablish the prior, often more desirable state, than it took to degrade it. A second difference that characterizes alternative stable states is that they are maintained by negative, stabilizing feedbacks, which make them resilient to small disturbances, and are only shifted to the other state by large disturbances. Disturbances of varying magnitudes are shown by arrows pushing the community away from the stable equilibrium (Artwork by Kendal Fong)

equilibrium (represented by the dotted lines in Fig. 7c, d). Once past the unstable equilibrium, negative feedbacks will function to stabilize the community in the alternate state.

Another key prediction from theory is that, in order for alternative stable states to exist, negative feedback mechanisms must exist to stabilize each state within the range of environmental conditions, F_1 to F_2 . Stabilizing mechanisms can include abiotic or biotic processes, but must be strong enough to buffer these states across a range of environmental conditions (between F_1 and F_2). The existence of stabilizing

mechanisms provides resilience to small disturbances that only push the community within the basin of attraction of the existing state (does not cross the line of unstable equilibrium in Fig. 7c, d). Thus, at any environmental condition between F_1 and F_2 , theory predicts that small disturbances will result in a return to the stable state. To manage any tropical reef system to maintain the coral state it is key to identify and protect the positive feedback mechanisms that support that state.

Field surveys and experiments that demonstrate rapid transitions among community states are often unable to distinguish between phase shifts and alternative stable states as limited temporal and/or spatial scales usually restrict observations of transitions to single events. The types of evidence that can distinguish between these patterns of change and support that tropical reefs exist as alternative stable states include: (1) persistent dominance by one state or the other across a wide range of environmental stress, and (2) the existence of strong and consistent negative feedbacks that stabilize each state.

There are many examples of rapid, catastrophic collapses from coral to algal dominance, and evidence is accumulating that these algal states may be stable or resistant to reversal. Coral to algal transitions have been documented in response to stressors such as nutrients, overfishing, diseases, and increased sedimentation, as well as large disturbances such as hurricanes and ENSO-associated increases in sea surface temperature (e.g., Hughes 1994; Fong and Lirman 1996; Glynn and Maté 1997; Nugues and Roberts 2003; Rogers and Miller 2006; Hughes et al. 2007; Baker et al. 2008, and many others). A few studies have shown that prior to these transitions, coral states were relatively stable. For example, push cores demonstrated that coral-dominated states were relatively stable over at least 3,000 years on two Caribbean coral reefs (Aronson et al. 2004). However, there is a paucity of evidence for recovery from environmental stressors, which could be due to continued stress (but see Idjadi et al. 2006; Diaz-Pulido et al. 2009). To our knowledge, Kaneohe Bay represents the only recorded case of a backward transition from algal to coral dominance due to a reversal in the environmental stress of eutrophication (Smith et al. 1981). Even in this system, however, more recent phase shifts toward other invasive algae have occurred (Stimson and Conklin 2008). In addition, evidence for recovery (transition back to coral state) from disturbances such as ENSO is very mixed, with areas in the Indian Ocean recovering rapidly, areas of the Pacific with patchy recovery (some reefs recovered rapidly, others did not recover), and a general lack of recovery in the Western Atlantic (Baker et al. 2008). In the Caribbean, this lack of recovery may be due to a recruitment bottleneck when coral abundance is extremely low (Mumby 2009). These patterns are consistent with alternative stable state theory, which predicts both stability across a range of environmental stresses and that recovery from disturbance will

either be rapid or the algal state will become stable depending on the magnitude of the disturbance (Fig. 7c, d).

There is mounting evidence that numerous negative feedbacks stabilize the algal state as predicted by alternative stable state theory. As discussed above, some of the ecological processes that stabilize the algal state include algal defenses, nitrogen fixation by cyanobacteria ameliorating nutrient limitation, and inhibition of coral recruitment by some forms of algae (Ritson-Williams et al. 2009; Birrell et al. 2008b). In addition, algal states often lack the topographic complexity of coral states, thereby reducing herbivory. Herbivory can also be suppressed by sediment deposition that is enhanced by algal turfs, thereby stabilizing this algal state (Bellwood and Fulton 2008). Clearly, it is vital to continue research into the stabilizing mechanisms for both coral- and algal-dominated states, as these may provide some realistic management strategies for future reef conservation and restoration.

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