Chapter 16
Macroalgae in Tropical Marine Coastal Systems

Astrid Y. Mejia, Gregory N. Puncher, and Aschwin H. Engelen

16.1 Introduction

Tropical marine environments are oligotrophic, warm, and expose primary producers to relatively high levels of photosynthetically active radiation (PAR) that penetrates as far as several hundred meters into the water column. Many tropical marine coastal communities are structurally dependent upon ecosystem engineering organisms such as seagrasses, mangroves, and corals in which the role of macroalgae is fundamentally different from temperate marine systems. This chapter will begin with a brief overview of the abiotic conditions, such as temperature, light, and nutrients, which have a defining influence on algal diversity, distribution, and dynamics with particular emphasis given to coral reef habitats because of the extensive body of research focused on this ecosystem. This will be followed by more detailed information on the role of macroalgae in the three main tropical marine ecosystems. Although they are not the main habitat providers in

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A.Y. Mejia (✉)
Laboratory of Experimental Ecology and Aquaculture, University of Rome Tor Vergata,
Via Cracovia No. 1, 00133 Rome, Italy

Bay Islands Conservation Association (BICA-Roatan), Bay Islands, Honduras
e-mail: aymejia@gmail.com

G.N. Puncher
Molecular Genetics for Environmental and Fishery Resources Laboratory (GenMAP),
Interdepartment Center for Research in Environmental Sciences, via Sant'Alberto,
163-48100 Ravenna, Italy
e-mail: greg@respectnature.com

A.H. Engelen
Centre for Marine Sciences (CCMAR), University of the Algarve, Campus de Gambelas
8005-139, Faro, Portugal
e-mail: aengelen@ualg.pt

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tropical coastal areas, macroalgae are essential to the productivity, structure, and function of each of these communities. Throughout this chapter, the role of macroalgae in regime shifts from systems dominated by the aforementioned habitat providers to ones dominated by algae as well as the factors that bring about these changes will be discussed.

16.2 Abiotic Conditions

Compared to the extreme seasonal changes in temperate regions, the variability of abiotic conditions in the tropical zone is limited, aside from the influence of the rainy season which can reduce salinity, increase water velocity, and decrease PAR.

16.2.1 Temperature

Three types of physiological responses to temperatures determine a species' biogeographical boundaries (Breeman 1988): growth, reproduction, and mortality (see Chap. 3 by Eggert). Pakker et al. (1995) suggested that tropical macroalgae are the most stenothermal macroalgae of any biogeographical region; their growth generally reaching a peak between 25 and 30°C, with those restricted to the tropical western Atlantic surviving a total variation of only 10/13°C. In comparison, macroalgae from colder regions are tolerant of a much wider range of temperatures (see Chap. 3 by Eggert and Chap. 18 by Bartsch et al.). Macroalgae of the tropical to warm-temperate Eastern Atlantic Ocean and Mediterranean Sea show the same temperature limitations as those of the Western tropical Atlantic Ocean and Caribbean Sea. Unsurprisingly, species restricted to the subtidal regions, and thus rarely exposed to extreme variations in abiotic conditions, are least tolerant of high temperatures, generally succumbing to temperatures exceeding 33°C. Furthermore, both subtidal and intertidal species appear to be limited by temperatures lower than 18/20°C.

16.2.2 Nutrients

Seawater in tropical regions is generally low in nutrients due to strong stratification of the water column that prevents vertical mixing of nutrients. Tropical marine habitats that are not exposed to terrestrial effluents are particularly nutrient poor, thereby preventing the proliferation of phytoplankton and macroalgae and increasing the light availability for benthic organisms. Occasionally nutrients become temporarily available through terrestrial runoff during the rainy season or upwelling events, encouraging strong seasonal responses (see also Chap. 21 by Teichberg et al.). After several decades of scientific research it has become clear that nutrients are cycled tightly within tropical ecosystems to prevent losses and enable a high level of productivity. The higher light levels and temperatures of the tropics make continuous productivity possible despite lower nutrient concentrations.

The increased supply of nutrients to the marine environment, resulting from human activities (agriculture, development, sewage, etc.), has been linked to increased algal growth in environments where they were previously a limiting factor (see below). However, the concentration of nutrients in seawater is not always directly related to macroalgal growth rates. For example, under low ambient nutrient conditions, high water motion can also stimulate increased growth rates of macroalgae (McCook 1999). Tropical macroalgae are very efficient nutrient users that are capable of taking advantage of nutrient pulses through surge uptake mechanisms. Additionally, they can store and recycle nutrients in their tissues for extended periods of time (Fong et al. 2003). In tropical macroalgae, small increases in nutrient concentrations can trigger an uptake response comparable to that of bloom-forming species from temperate estuaries responding to much higher nutrient concentrations (Kennison 2008; Fong et al. 2001, 2003). The concept that nitrogen and phosphorus are limiting nutrients in the tropical environment remains a source of controversy (Bell 1992; Lapointe 1997; Bell et al. 2007). Results of nutrient-enrichment experiments using macroalgae taken from coral reef and seagrass habitats indicate that nitrogen limitation is common (e.g., Lapointe et al. 1987; Littler et al. 1991; McGlathery et al. 1992; Delgado and Lapointe 1994; Collado-Vides et al. 2007). Several investigations have reached the same conclusion that phosphorus availability limits the productivity of fleshy macroalgae in oligotrophic reef waters (Lapointe et al. 1987, 1992; Littler et al. 1991). However, alkaline phosphatase activity (APA) enables some macroalgae to fulfill their phosphorus requirements by facilitating the utilization of organic phosphorus. These mechanisms have been well documented in macroalgae growing in the inshore regions of the Great Barrier Reef (GBR) where nutrient supply can be extremely variable and dependent on inshore human activities (Schaffelke 2001).

16.2.3 Light

Light is the most important physical factor affecting primary productivity in the marine realm. At low latitudes, light levels and water transparency are high due to limited suspended sediments, particulate and dissolved organic matter, and phytoplankton. Additionally, very little PAR is lost due to limited scattering and reflection of light on the sea surface. Although light penetrates deeper in the water column in the tropics than in temperate regions, light attenuation with depth still creates a gradient of light quantity and quality (see also Chap. 1 by Hanelt and Figueroa). Light in this way plays a structuring role in the distribution of tropical macroalgae. Rhodophytes, like crustose coralline algae, are common throughout all reef zones, from the intertidal to 80–90°m deep, where the light intensity has been estimated at ~0.2% of the surface radiation (Van den Hoek et al. 1978), and even as deep as 268 m in the Bahamas (Littler et al. 1985, 1986). On Curaçao sparse algal turfs reach their lower limit around 65 m, where PAR levels are as low as 1% of that found at the surface (Van den Hoek et al. 1978). Green macroalgae generally are most common in shallow waters, but have been found forming entire communities consisting of *Udotea, Caulerpa*, and *Halimeda* species at depths of 25 m on Saba Bank (Lesser Netherlands Antilles) (Littler et al. 2010a) as well as *Johnson-sealinkia profunda* colonies found at the extreme depth of 200 m in the Bahamas (Littler and Littler 1988). In addition, the lack of a conspicuous seasonal cycle in photoperiod in the tropics compared to mid and high latitudes provides a relatively constant supply of PAR throughout the year.

Although ultraviolet radiation (UVR) levels are high in the tropics, studies focused on its impact on macroalgae have for the most part been limited to polar and temperate seaweeds due to ozone depletion in these regions (Bischof et al. 2006; see also Chap. 20 by Bischof and Steinhoff). Recently, Figueroa et al. (2009) showed that seaweeds from the Red Sea show dynamic photoinhibition as an efficient mechanism of acclimation to high PAR as well as UV irradiance levels. This is not unique to tropical seaweeds but has been shown for other seaweeds in high light exposed environments (Figueroa et al. 1997). A recent investigation of tropical marine macroalgae collected from Belize at depths of 0.3–26 m depths showed that UVR caused an additional decrease of photosynthetic performance during high light stress which varied according to species, depth of growth, and UV penetration at the site of collection (Hanelt and Roleda 2009; see also Chap. 1 by Hanelt and Figueroa). However, this same study also provided evidence that UVB radiation may not only cause negative effects on cellular processes of seaweeds but may also support recovery processes in high UVR adapted seaweeds (Hanelt and Roleda 2009).

16.3 Vegetation Structure

16.3.1 Succession

Succession patterns depend on the characteristics of vacant space, bottom-up availability of nutrients, and top-down grazing characteristics. Many studies have documented the recovery of coral reef systems after storms and hurricanes and the succession of algae during this process as well as the experimental succession on settlement plates. In general, there is first a dominance of simple turf like green and brown filamentous seaweeds, a midsuccessional stage with thin and finely branched red filamentous seaweeds, and a late stage dominated by coarsely branched and thick canopy-forming seaweeds. The 37-year history of the Tiahura Outer Reef Sector (Moorea) constitutes one of the longest records of coral reef dynamics (Adjeroud et al. 2009). Between 1991 and 1994, the decline in coral cover was accompanied by colonization by turf algae (16.2 ± 5.5% in 1991 to 48.5 ± 2.5%

in 1994). However, instead of a successional sequence of algal growth towards the proliferation of canopy-forming macroalgae, the cover of algal turf decreased after 1994, and returned to the predisturbance levels within a decade (Adjeroud et al. 2009). These results suggest that the availability of vacant space was not sufficient to cause a persistent increase in algal cover, and that other factors, such as a reduction in grazing pressure or an increase in nutrients, may be necessary for a regime shift to macroalgal dominance (McManus and Polsenberg 2006; Mumby 2009; see also Chap. 21 by Teichberg et al.). A similar story emerged from the protracted loss of coral cover in Jamaica following two hurricanes, three bleaching events, a reduction of grazing pressure (overfishing and disease), and a potential pulse of nutrients which all contributed to a dramatic increase of algal cover, from ~4% in 1977 to ~92% in 1993 (Hughes 1994). Experimental studies, like that of Hixon and Brostoff (1996), demonstrate the importance of herbivores on the successional trajectory in tropical marine ecosystems. In conclusion, the impacts that macroalgae can have on tropical marine communities are complex and are dependent upon the identity of the herbivores present as well as the developmental stage of the seaweed community (see Coral reefs below).

16.3.2 Diversity

Tropical marine ecosystems are among the most diverse ecosystems on our planet. While invertebrates have received a great deal of attention during biodiversity surveys and studies in the past, macroalgae have received much less consideration. Some early studies that have assessed macroalgal diversity patterns across latitudinal gradients have arrived at conflicting conclusions, finding high species diversity at low and midlatitudes as well as decreasing diversity towards lower latitudes (e.g., Pielou 1977; Santelices and Marquet 1998). A more recent literature review by Kerswell (2006) revealed distinct gradients in species and genus diversity worldwide. When all macroalgal genera were considered, tropical regions had lower diversity than temperate regions. Only when a more reef associated order like the Bryopsidales was examined, diversity peaked at low latitudes. Furthermore, Konar et al. (2010) confirmed the common trend of higher taxa diversity at midlatitudes compared to low latitudes in the northern hemisphere, particularly in the intertidal.

Until recently, the coral reef seaweed hotspots of the Caribbean Sea were considered to be at Diamond Rock in Martinique and the Pelican Cays in Belize. However, on a recent expedition to the Saba Bank, Littler et al. (2010a) collected between 150 and 200 seaweed species from 17 different dive sites, demonstrating that there is still much to discover. Their checklist of 98 taxa including 43 Rhodophyta, 26 Chlorophyta, 26 Phaeophyceae (Heterokontophyta), and three Cyanophyta contained several unknown species as well as some previously unrecorded seaweed communities. These communities were located at depths of 25–30 m and were dominated by green, brown, or fleshy red macroalgae. In contrast to the predominant idea that abundant macroalgae indicate compromised reef health, no indications were found that conflicted with the existing definition of "pristine" oligotrophic reef systems (Littler et al. 2010a).

Turf algal assemblages can provide the majority of the primary productivity on a coral reef (Adey and Steneck 1985; Fricke et al. 2011). These assemblages are multispecies associations, characterized by undifferentiated upright axes and a rapid turnover (Carpenter et al. 1985). Although inconspicuous, they occur almost everywhere on reefs where space is available (Littler and Littler 1984; Steneck and Dethier 1994). Although they are fast growing, fleshy macroalgae often outcompete with them for limited light and space (Hay 1981). Algal turfs are able to persist under intense herbivory and physical stress in areas where other algae are continuously excluded. Their high productivity rather than their standing crop maintains the high standing stocks of grazers characteristic of coral reefs (Hatcher 1988; Carpenter 1986; McCook et al. 2001). In deep and shallow reef zones, where grazing pressure is low, frondose algae rather than turfs commonly dominate (Van den Hoek et al. 1978; Vuki and Price 1994).

Crustose coralline algae (CCA) play three important roles on coral reefs: (1) limestone formation, (2) the consolidation of loose substrates (Fabricius and Dea'th 2001), and (3) primary production (Littler and Littler 1984). In shallow waters they can build massive carbonate structures on reef crests despite the typically turbulent conditions (Adey and Vassar 1975). Due to their unpalatable nature, coralline algae are more resistant to grazing and therefore survive well in areas where grazing intensity is high.

Fleshy frondose macroalgae are mainly composed of tropical fucoids like *Sargassum*, *Turbinaria*, and *Cystoseira*. They often dominate on shallow reef flats and crests of inner reefs or in deeper fore reef zones and are generally absent from mid and outer shelf reefs (Vuki and Price 1994; McCook 1996). *Sargassum* species are often dominant in terms of biomass and canopy cover, due in part to their high productivity (Vuki and Price 1994; McCook 1996; Schaffelke and Klumpp 1997). Foliose macroalgae are seasonal opportunists and can be found in areas less dominated by canopy-forming macroalgae (Schaffelke and Klumpp 1997). Due to high biomass turnover, reefs with a high cover of large Phaeophyta are often regarded as detritus-driven ecosystems (Schaffelke and Klumpp 1997).

16.3.3 Zonation

The zonation and distribution of macroalgae is highly variable, which complicates extrapolations between similar habitats and across habitat types within regions and between different parts of the world. The distribution and zonation of macroalgae is strongly dependent on the structure of the habitats which is formed by historical (geology: reef types), abiotic (nutrients, temperature, and light), and biotic (grazing and competition) conditions (Berner 1990). We therefore describe the zonation using examples from a Caribbean fringing reef, a Pacific Atoll, and a Barrier reef.

On Curaçao in the Caribbean, van den Hoek et al. (1978) described the vertical distribution of reef macroalgae and distinguished seven different algal communities. The narrow eulittoral zone is inhabited by cyanophytes, turfs, and smaller macroalgae. In the top part of the surf area, the seaweed community is composed of *Ulva* and the brown seaweeds *Giffordia duchassaigniana* and *Sphacelaria tribuloides*, whereas in the deeper part the brown seaweed *Sargassum polyceratium* and the red algae *Hypnea musciformis* and *Laurencia* spp. dominate. In the sublittoral zone on the platform, from the surf area down to 3 m deep is a shallow reef occupied by coral rubble fragments aggregated by the crustose red alga *Porolithon pachydermum* and macroalgal turfs. The foliose brown seaweed *Lobophora variegata* forms a girdle-like vegetation at 30–38 m deep and the erect *Sargassum polyceratium* occurs from 15 to more than 65 m depth. Many shade adapted species are present in this zone reaching to depths of 55–65 m, including the green macroalgae *Udotea* and *Caulerpa* species and numerous red algae. Crustose red algae reach into the deep where the reef terminates and a sandy plateau forms at a depth of 75–90 m.

Womersley and Bailey (1969) described the zonation of macroalgae in the Solomon Islands on four types of coral reefs, with differences in hydrodynamic activity. The seaward rim consists of crustose coralline algae, mainly *Lithophyllum* and corals, and behind this the coralline alga *Porolithon onkodes* dominates. On shallow intertidal rubble near the island shore, crustose and endolithic green algae and cyanobacteria dominate.

Studies of the algal assemblages on the GBR have shown marked latitudinal, cross-shelf, and within-reef variations in composition and abundance (Wismer et al. 2009). In contrast to midshelf and outer-shelf reefs, inshore or coastal reefs typically have abundant and conspicuous macroalgal communities (Diaz-Pulido et al. 2007). The reef flat zone in particular is often dominated by dense and highly productive beds of large fleshy brown macroalgae, predominantly *Sargassum* (e.g., McCook 1997; Schaffelke and Klumpp 1997).

16.3.4 Seasonal Dynamics

Varying weather conditions throughout the year have a strong influence on the abundance of macroalgae in tropical regions. In particular, lower temperatures and the influx of nutrient-rich freshwater during the rainy season can cause a significant increase of algal biomass. For example, in Kenya epiphyte coverage on seagrasses can double or triple during the shift from the NE monsoon (warm temperatures, less rain, and light winds) to the SE monsoon (cool temperatures, heavy rains, and strong winds) (Uku and Björk 2005). In Florida, researchers observed an increase of epiphyte biomass during the rainy season so extreme that it became three times greater than seagrass blade biomass (Lapointe et al. 2004). Of course, the hurricane/cyclone season presents potential for extreme events in the tropical marine environment each year as well. It is widely recognized that these events characterized by intense water velocities, higher freshwater input, and mechanical disturbance can both disrupt and maintain the balance between macroalgae and seagrass, mangrove, and coral reef communities.

Macroalgae within coral reef habitats display a great amount of seasonality as well (Coles and Fadlalah 1991). A very comprehensive overview of seasonality of four major functional groups: canopy, foliose, turf, and CCA was accomplished by Aterweberhan et al. (2006). They monitored biomass of all these groups in four reef zones at two localities in the southern Red Sea. All functional groups showed seasonal variation in biomass, although seasonal variation differed among groups and reef zones. Canopy and foliose macroalgae were highly seasonal, whereas turf algae and crustose corallines showed much less seasonal variability. The biomass variation of *Sargassum* spp. greatly determined the seasonal variation of standing biomass of all algal types on the shallow inner and middle reef flats. On the deeper, outer reef flat, *Turbinaria triquetra* contributed most to the seasonal variation. Foliose algae contribute most to the seasonal variation only where canopy-forming macroalgae were lacking, like on the middle reef flat. Crustose corallines and turf algae only contribute considerably to the total biomass during the hot season when macroalgae are strongly reduced. On the fore reef, crustose corallines contribute most to the biomass throughout the year. In general, turf algae contributed least to the standing biomass during all seasons, at all sites, and all reef zones.

16.4 Macroalgae and Their Roles and Interactions in the Three Main Tropical Ecosystems

16.4.1 Macroalgae and Coral Reef Interactions

16.4.1.1 Herbivory

Herbivory is widely recognized as the main driver affecting the distribution and abundance of macroalgae on tropical coral reefs (Carpenter 1986; Hay 1997; Hughes et al. 2007; Burkepile and Hay 2010). Several experimental studies have demonstrated that coral reef herbivores can remove up to 100% of daily algal production in some coral reef habitats (Duffy and Hay 1990; Hughes et al. 2007). In tropical marine habitats, herbivorous fish and sea urchins are the dominant grazers of macroalgae (Williams et al. 2001; Mumby et al. 2006; Burkepile and Hay 2010). Sparisomid parrotfishes represent more than 80% of the herbivorous fish biomass that is dominant in Caribbean reefs, along with the acanthurids (surgeonfishes, tangs, and unicornfish), kyphosids (sea chubs), and pomacentrids (damselfishes) (Mumby 2009). Herbivorous fish feed on an array of algal types, including fleshy macroalgae, algal turfs, and encrusting coralline algae (Hay 1997; Mumby 2009). Algal turfs are easily digested and have a high energetic and protein value relative to other macroalgae and are thus the preferred food of many herbivorous fish, in both the Caribbean Sea and other tropical habitats (Bruggemann et al. 1994; Kopp et al. 2010). Based on their experiments in the Caribbean (Guadaloupe), Kopp et al. (2010) determined that *Acanthurus coeruleus* (Blue tangs) and *Sparisoma aurofrenatum* (Redband parrotfish) graze preferentially on algal turfs, while *Sparisoma rubripinne (Redfin parrotfish)* and *Sparisoma viride* (Stoplight parrotfish) are more inclined towards *Halimeda* spp. while *Acanthurus bahianus* (Ocean surgeon) prefer Phaeophytes. Their results also revealed the aversion of herbivorous fish towards *Dictyota* spp., a brown macroalgae that uses chemical compounds as a grazing deterrent (Hay 1997; Paul et al. 1990). On the GBR, Mantyka and Bellwood (2007a) report that grazers of macroalgae on the reef crest of Pioneer Bay are composed of six reef fish species (two rabbitfishes, three parrotfishes, and one damselfish) which display species-specific feeding behavior. For example, the rabbitfishes, *Siganus doliatus* feed heavily on *Hypnea* spp. while *Siganus canaliculatus* feed intensively on *Sargassum,* and the three parrotfishes *Chlorurus microrhinos*, *Hipposcarus longiceps,* and *Scarus rivulatus* were the dominant grazers of calcified *Halimeda* spp. (*H. cylindracea*, *H. discoidea*, *H. opuntia)*, and *Amphiroa* spp. During their experiment, *Chlorodesmis fastigiata* and *Galaxaura* spp. were least affected by herbivory, suggesting a reduced palatability owing to their chemical deterrence and calcareous structures (Paul et al. 1990). More recently, Cvitanovic and Bellwood (2009) have reported that the dominance of herbivorous fish over macroalgae species and specific reef areas can show local variability. In an experiment conducted on the Orpheus Islands, they found similar rates of macroalgae removal in three separate bays; however, three different species of herbivores were responsible for the grazing control. They also found that *Kyphosus vaigiensis* (Brassy chub) were responsible for high rates of removal of *Sargassum* spp., although past studies had identified *Siganus canaliculatus* (White spotted spinefoot) and *Platax pinnatus* (Dusky batfish) as the dominant grazers of *Sargassum* spp. in Pioneers Bay *(*Mantyka and Bellwood 2007b). Most recent studies highlight the importance of herbivore richness and diversity (Burkepile and Hay 2010) as well as abundance and biomass (Mumby et al. 2006; Kopp et al. 2010) in maintaining reef macroalgae community structure, reducing fleshy macroalgal blooms and enhancing coral reef recovery and resilience. For example, Burkepile and Hay (2010) determined that complementarity feeding among fish species not only impacted structure of macroalgal communities, but also enhanced coral survivorship and growth on reefs in the Caribbean Sea (Florida Keys, USA). The authors observed that fast grazing by ocean surgeonfish (*Acanthurus bahianus*) and princess parrotfish (*Scarus taeniopterus*) kept macroalgae communities dominated by short, filamentous algae and crustose coralline algae, both algal states that do not suppress coral growth. Conversely, within the established benthic communities, the authors observed that the redband parrotfish (*Sparisoma aurofrenatum*) played a vital role in the removal of upright macroalgae cover which can be detrimental for coral growth and survival. To further investigate the role of herbivory on regulation of macroalgae community structure, numerous herbivory exclusion experiments have been conducted in tropical coral reefs (Lirman 2001; Hughes et al. 2007; Smith et al. 2010a; Hoey and Bellwood 2010). These studies provide evidence of how exclusion of large herbivores is followed by undesirable blooms of upright macroalgal species, which are considered less susceptible to herbivory and capable of causing phase shifts from coral to macroalgae dominated systems. Mork et al. (2009) conducted a 6-week herbivore exclusion study on a moderately disturbed coral reef on the Kenyan coast. Their results show a 77% increase of algal biomass, largely attributed to a 1,000% increase in corticated forms of algae, dominated by *Dictyota* spp. Sotka and Hay (2009) reported similar results from an experiment conducted in the Florida Keys. After 142 days of monitoring, they observed that coral slabs exposed to natural densities of large herbivorous fishes were dominated by crustose coralline algae, short (<0.5 cm) filamentous turf algae, and upright macrophytes, which never exceeded 15% cover. In contrast, herbivore exclusion treatments were subject to 80–100% upright macroalgae cover.

The role of herbivory in regulating macroalgal communities can be severely compromised in overfished and degraded reefs and may result in phase shifts from coral to algae dominated systems (Mumby et al. 2006). In areas suffering from moderate levels of overfishing, a lack of top predators can stimulate an increase of herbivore biomass. However, in severely overfished areas, herbivorous fish are not able to control macroalgae because they too become subject to overfishing and are unable to become sufficiently large in size to regulate algal production, even if they are numerically abundant (Kopp et al. 2010). A significant reduction of fishing pressure of herbivorous fish (Mumby and Harborne 2010) as well as a reduction of confounding disturbances such as nutrient pollution (Smith et al. 2010a) has been suggested as a means of reversing algal phase shifts.

16.4.1.2 Chemical Defenses

Macroalgae defend against herbivory using a number of strategies, including morphological, structural, and chemical defenses as well as associations with other algae or benthic organisms (Hay 1997; Paul and Puglisi 2004; Amsler 2008; Smith et al. 2010b; Fong and Paul 2011; see Chap. 9 by Amsler). Morphological and structural defenses include calcification and toughness, which are characteristics of the *Halimeda, Dictyota,* and *Lobophora* genera (Paul et al. 2001). These species are coarsely branched, leathery, or rubbery and have hard calcium carbonate tissues which are of little interest or nutritional value for herbivores (Schupp and Paul 1994; Hay 1997). Some macroalgae utilize secondary metabolites to help protect against pathogens, fouling organisms, and herbivores (Fong and Paul 2011). A significant quantity of natural products has been extracted and isolated from tropical marine green, red, and brown macroalgae, of which halides like bromine and chloride are very common as well as compounds like terpenoids (Fong and Paul 2011). Chemical deterrents in calcified green algae from the genera *Caulerpa* and *Halimeda* have been well studied and experiments have shown that their chemical composition deters both parrotfishes and sea urchins alike (Schupp and Paul 1994). Brown algae are known to utilize polyphetanolic compounds as deterrents along with terpenoids, which are commonly present in the order Dictyotales (Pereira and Da Gama 2008). Red macroalgae possess a great variety of secondary metabolites and the genus *Laurencia* has been widely studied for this reason (Blunt et al. 2007).

The study of chemical defenses of macroalgae has been widely investigated for over two decades and most of the research has been focused on their utilization against grazers (fishes, sea urchins, and gastropods) and their effect on coral species. For example, from their experiments conducted in the Caribbean and tropical Pacific, Rasher and Hay (2010) provide evidence that five of seven seaweeds (71%) caused bleaching of the coral species *Porites porites* in Panama. While in Fiji, three of eight species (38%) caused bleaching of *Porites cylindrica*. Seaweeds were observed to damage corals via abrasion, shading, or lipid-soluble allelopathic compounds transferred through direct contact. The effects of a lipid-soluble extract from various species of macroalgae (*Ochtodes secundaramea, Dictyota bartayresiana, Lobophora variegata, Halimeda opuntia, and Amphiroa fragillisima* in Panama) caused significant coral bleaching and suppression of photosynthetic efficiency in assays using both intact seaweeds and chemical extracts. The two species that did not cause bleaching in any of the two assays were *Padina perindusiata* and *Sargassum* spp. These results illustrate how overfishing of herbivorous fish, capable of suppressing undesirable macroalgae, will inevitably result in an increase of direct coral–algae contacts and further impair corals through allelopathic interactions. Major gaps still persist concerning the ecological role that macroalgal secondary metabolites play apart from feeding deterrence (Pereira and Da Gama 2008).

16.4.1.3 Providers of Spatial Refuge

Persistence of unpalatable macroalgae on coral reefs can be facilitated by spatial refuges and associational assemblages. An associational refuge is one in which a host species provides protection that enhances the survival of associate species (Bittick et al. 2010). These interactions are becoming increasingly recognized as important drivers of ecosystem function. Smith et al. (2010b) have found that patches of the green algae *Caulerpa sertularioides* found in reef areas of Uva Island in Panama can persist due to their association with an epiphytic cyanobacterium (*Lyngbya majuscula*). The cyanobacterial epiphytes on *C. sertularioides* thalli provide protection from herbivory for both upright assimilators and stolons. Similarly, associational defenses provided by cyanobacteria have been reported to be responsible for the 5-year persistence of the highly palatable alga *Acanthophora spicifera* on the Uva Island reef (Fong et al. 2006). On the coral reefs of Moorea, French Polynesia, Bittick et al. (2010) observed that aggregations of the brown macroalga *Turbinaria ornata* provide mechanical and chemical refuge from herbivory to associated macroalgae. The study showed that aggregations of *Turbinaria* significantly enhanced species richness, especially of fleshy species like *Caulerpa serrulata*, *Dictyota bartayresiana, Sargassum mangarevense, Valonia utricularis,* and *Ventricaria ventricosa.* On the contrary, in coral heads without *Turbinaria,* there was less algal density and these were dominated by crustose coralline algae, filamentous algal turfs, and cyanobacteria. As a result, unprotected coral heads without *Turbinaria* had the lowest diversity of all treatments.

16.4.1.4 Nutrient Enrichment

The influence of excess nutrient supply on the development of reef macroalgae is a topic of major debate between marine researchers (Littler and Littler 2006; Mork et al. 2009; Smith et al. 2010a). Experimental studies have often investigated the effect of nutrient enrichment in the presence and absence of herbivory to determine its role in regulation of macroalgal growth and cover in tropical habitats, especially coral reefs. The available literature is divided between studies that report a significant effect of nutrient enrichment on enhancing growth and abundance of fleshy macroalgae and cyanobacteria in coral reef habitats and others that report no significant effect. For example, Littler et al. (2010b) conducted a 12-month study in a sedimentary lagoon at Carrie Bay Cay in Belize's barrier reef to compare the enrichment effects of dissolved inorganic nitrogen (DIN) and soluble reactive phosphorus (SRP) additions on algal community development. They found that SRP and SRP + DIN treatments stimulated the growth of cyanobacteria (*Spirulina* spp.) and inhibited settlement and colonization of CCA. Meanwhile, the DIN enrichments increased CCA cover, decreased cyanobacteria cover, and had no influence on fleshy macroalgae. Sotka and Hay (2009) reported similar findings related to fleshy macroalgae from a 20-week nutrient-enrichment experiment conducted in the shallow fore reefs of the Florida Keys. They concluded that herbivory is stronger than nutrient abundance in regulating macroalgae abundance and composition on coral reefs. Their results revealed that large herbivorous fish selectively grazed on nutrient-enriched macroalgae. On the contrary, experiments conducted by Smith et al. (2010a) on the reef slope at Puako Reef, Hawai'i found that both fertilization and herbivory exclusion impacted macroalgae community structure at different temporal scales. They observed that reducing herbivory led to rapid changes in benthic communities (1 month), while the effects of nutrient enrichment were only visible after 3–4 months. This can explain the lack of strong nutrient-enrichment effects noted in other studies, as they may be a result of short-term experiments. Vermeij et al. (2010) conducted experiments in Curaçao, Netherlands Antilles, to examine the effects of Caribbean turf algae on neighboring corals and interactions of these algae with nutrient enrichment and grazing. They found that nutrient enrichment significantly enhanced the capacity of turf algae to overgrow the coral *Montrastrea annularis*, since turf algae is also able to overgrow coral at ambient nutrient concentrations when herbivory is excluded or reduced.

16.4.1.5 Competition

Competition is an important force influencing the structure of coral reef communities and its effects can impact all stages of a coral colony's life cycle (Lirman 2001; Nugues and Bak 2006; Foster et al. 2008; Ritson-Williams et al. 2010; Vermeij et al. 2011). Macroalgae are known to compete with corals using different strategies which include the occupation of settlement substrate (Birrell et al. 2005; Vermeij 2006), physical disturbance (e.g., abrasion, shading, smothering) (McCook et al. 2001; Box and Mumby 2007), allelopathy (Gross et al. 2003; Kuffner et al. 2006; Foster et al. 2008), and direct transmission of pathogenic microbes (Vermeij et al. 2009). This competitive interaction is often species specific and capable of causing different levels of stress on coral species, potentially leading to coral mortality (Jompa and McCook 2002, 2003). In the Caribbean, Box and Mumby (2007) determined that *Lobophora variegata* and *Dictyota pulchella* inhibited coral growth on juvenile *Agaricia* spp. and *L. variegata* through shading and abrasion. In Hawaii, Vermeij et al. (2009) found that algal-induced microbes can cause mortality of the planular larvae of *Montipora capitata*. This effect on corals may be related to the ability of some algae to exude organic compounds that enhance rapid microbial growth, causing hypoxia and the reduction of larval resistance via the hampering of the coral's defense mechanisms against opportunistic microbes.

Although competition between macroalgae and corals has received significant attention from marine researchers, more evidence is still required in order to determine if algal growth is a cause rather than a consequence of coral mortality (McCook et al. 2001). More information is also needed concerning the interaction between coral larvae, macroalgae, and microbes in order to improve reef restoration techniques (Vermeij et al. 2009).

16.4.1.6 Facilitation of Coral Recruitment

CCA have been identified as facilitators of settlement and metamorphosis of a variety of marine invertebrate larvae as well as coral larvae (Ritson-Williams et al. 2010; Vermeij et al. 2011). CCA and coral interactions are known to be species specific, since corals have displayed different degrees of specificity in their requirement for CCA to induce successful settlement and metamorphosis. For example, an experiment conducted in the Caribbean (Belize) revealed that both *Acropora palmata* and *Acropora cervicornis* have higher rates of metamorphosis on the top surfaces of the CCA species *Hydrolithon boergesenii* and/or *Titanoderma prototypum* than on *Porolithon pachydermum (*Ritson-Williams et al. 2010). Further observations in the field (after 6 weeks) showed 15% survival of transplanted *A. palmata* recruits on both *T. prototypum* and *H. boergesenii*, and only 13% of A. *cervicornis* recruits on *T. prototypum*. These results suggest that CCA and settling coral polyp interactions can be species specific and also highlight the importance of benthic community composition for successful coral recruitment.

Aside from the positive role of CCA in coral recruitment, Vermeij et al. (2011) have reported that mixed communities of CCA (*Porolithon* spp. and *Hydrolithon* spp.) are capable of suppressing macroalgal growth and recruitment of the green macroalgae *Ulva fasciata,* based on studies conducted on a coral reef area in Hawai'i. Likewise, Birrell et al. (2005) have highlighted the negative impact of the association of macroalgal turfs and sediments have on coral recruitment of *Acropora millepora* found in the Orpheus Islands of the GBR. The results of that study indicated that sediment addition and algal turfs are capable of reducing coral settlement, although the effects of different algal turfs varied. In some cases, algal turfs inhibited coral settlement while other turfs inhibited settlement only when combined with sediments. Their results are suggestive of the need to study the impacts of similar associations to further understand the role of CCA in securing long-term resilience and recovery of coral reefs.

16.4.2 Macroalgae–Seagrass Interactions

In low nutrient environments, seagrasses and slow-growing macroalgae constitute a dominant regime in stable coastal waters. Seagrass habitats are important nurseries for commercially important fish species found within seagrasses and adjacent habitats such as coral reefs and mangroves (Dorenbosch et al. 2005). Within seagrass meadows macroalgae contribute to substrate complexity, act as a vital food resource for grazers, and have a significant influence on the cycling of nutrients. In nutrient-rich locations, macroalgal epiphytes are capable of achieving the same level of productivity as their seagrass hosts (Uku 2005). Some calcareous algae generate such immense quantities of $CaCO_3$ that entire beaches are constructed from the sand that they produce (Muzuka et al. 2005). However, enrichment of coastal waters can encourage the proliferation of algal blooms and initiate a breakdown in the balance of the system, resulting in decreased seagrass coverage (McGlathery 2001; Hauxwell et al. 2003; Lapointe et al. 2004). Macroalgae may provide short-term spatial heterogeneity and an enriched trophic resource, thereby appearing to be beneficial for invertebrate community diversity; however, they are often ephemeral and thus represent a threat to long-term biodiversity, relative to more permanent substrates, such as seagrasses (Cardosoa et al. 2004). Three distinct types of macroalgae (Epiphytic, Drift, and Calcareous Algae) have an important influence on the seagrass environment and thus dictate the structure of the following section.

16.4.2.1 Seagrass Epiphytes

In the tropics, epiphytic macroalgae are abundant and play a major ecological role in several habitats (see also Chap. 11 by Potin). In the Western Indian Ocean, macroalgal epiphytes constitute the most abundant group of epiphytes and can account for as much as 40% of the fresh weight of seagrass shoots (de la Torre-Castro et al. 2008; Uku and Björk 2001). In a Bahamas lagoon, the rates of net primary production (NPP) for seagrass epiphytes (5.2 ± 1.4 gC $kg^{-1}day^{-1}$) have been measured at approximately 40% of the NPP of the seagrasses themselves (Koch and Madden 2001). In highly enriched waters, it is not uncommon for seagrass-associated macroalgae to reach abundances higher than 0.5 kg m^{-2} and obtain canopy heights greater than 0.5 m (McGlathery 2001).

In Kenya, encrusting red coralline algae are the first to colonize seagrass leaves, establishing a purchase upon which subsequent epiphytes may settle, such as the green algae *Cladophora* spp. and red algae *Ceramium* spp. (Uku 2005). This succession of algal groups follows a consistent and predictable community gradient along the vertical length of seagrass leaves, which is likely determined by light exposure (Uku 2005). Of course, leaf colonization by epiphytes inevitably exacts a toll on the host. Dixon (2000) determined that epiphytes covering seagrass leaves can be responsible for reducing as much as 33.1% of available PAR. However, studies in the tropical waters of Eastern Africa provide evidence that shading by epiphytes has no effect on overall photosynthetic output of *Thalassodendron ciliatum* shoots (Uku 2005). It seems that *T. ciliatum* compensate for the lost PAR by maintaining photosynthetic activity in older epiphyte covered leaves while increasing the production of new leaves capable of higher photosynthetic activity.

In the presence of excessive nutrient concentrations, seagrasses may respond to smothering epiphytes by increasing their growth rate (Ferdie and Fourqurean 2004). Nutrient-enrichment studies have revealed decreased carbon reserves in the rhizomes of seagrasses in the presence of excessive concentrations of nitrate and ammonium (Invers et al. 2004). The unbalanced metabolism caused by this type of enrichment can result in a significant loss of nonstructural carbohydrates which allows seagrasses to persist during unfavorable conditions. Koch and Madden (2001) observed surge growth and *N*-storage in macroalgal seagrass epiphytes during enrichment studies, indicating an adaptive trait that allows for a competitive advantage when nutrients are limiting.

Epiphytes constitute an important food resource for seagrass herbivores and omnivores. In Zanzibar, the majority of commercially important fish species found within seagrass habitats, ranging from herbivores, piscivores, and invertebrate feeders, were found to graze directly on seagrasses and epiphytes (de la Torre-Castro et al. 2008). It seems that the higher nitrogen content of epiphytes and their resident invertebrates is an important supplement to nitrogen-poor seagrass diets. Various species of herbivorous parrotfish and surgeonfish collected from the seagrass beds of Curaçao were found to have diets consisting primarily of seagrass epiphytes (filamentous algae) and leaves (Nagelkerken and van der Velde 2004). From their work with manipulative studies in Florida, Baggett et al. (2010) suggest that increased grazing of epiphytes by herbivores (isopods, amphipods, gastropods, and caridean shrimps) compensates for increased coverage during nutrient-enrichment treatments. Recent studies in temperate seagrasses suggest that herbivorous invertebrates exert a strong top-down control of epiphytes on seagrasses (Moksnes et al. 2008). In fact, Spivak et al. (2009) found that the strongest effect during their nutrient-enrichment experiments was an increase in grazer biomass, not epiphytes, indicating an efficient transfer of nutrients through trophic levels. This evidence suggests that removal of large predators (tertiary consumers) is likely to cause trophic cascades, resulting in the increased severity and frequency of algal blooms in the seagrass environment.

16.4.3 Drift Algae Within Seagrass Meadows

In the tropics, drift algae can have a significant impact on the well-being of seagrass communities. Drift algae originate as epiphytes growing within seagrass meadows and neighboring habitats, having been liberated from the substrate during heightened hydrological disturbances. Accumulation of drift macroalgae within seagrass meadows is a function of water circulation characteristics determined by coastal physiography (Kopecky and Dunton 2006) and rates of entanglement in the seagrass canopy (Biber 2007). Transport of drift algae across the seabed is dependent upon substrate complexity, and in the case of seagrasses, it is determined by a meadow's patchiness, blade length, and shoot density. In shallow waters where water velocity is reduced drift algae can become entrained in bare patches. Algae also have a tendency to accumulate where wind or tidal generated water currents are sufficiently reduced to allow deposition out of the water column, be it on the leeward side of a bank or within a protected depression (Kopecky and Dunton 2006). Once entangled, drift algae can rapidly proliferate under favorable conditions generated by freshwater inputs, ideal temperatures, and nutrient loading (Biber 2007). In the Gulf of Mexico, drift macroalgae can reach a biomass exceeding that of the dominant seagrass, *Thalassia testudinum* (Kopecky and Dunton 2006). The adverse weather conditions typical of the tropical hurricane season generate current velocities sufficient for the removal of accumulated algal biomass ($10\ \text{cm s}^{-1}$) (Biber 2007). Drift algae biomass varies by season as well as from 1 year to the next (Houk and Camacho 2010).

It has long been recognized that excessive quantities of drift macroalgae can have serious impacts on underlying seagrasses via competition for nutrients and PAR (Hauxwell et al. 2003). Excessive macroalgal loads can become so dense that they restrict water flow, thereby depriving seagrasses of oxygen and driving up concentrations of sulfides in the subsurface sediments (Holmer and Nielsen 2007). In addition to its impact on seagrasses, light attenuation by blooms of drift algae off the coast of Texas has caused significant reductions in seagrass epiphyte biomass (Kopecky and Dunton 2006). Given that the integrity of seagrasses can be severely compromised during these short-term seasonal blooms, the long-term repercussions of persistent blooms that may arise as a result of climate change demand serious consideration. Climate experts suspect that a changing climate will increase the number of intense storms and decrease those of intermediate intensity (Webster et al. 2005). The consequences of these changing weather patterns on the distribution of drift algae and their persistence within the coastal environment require close monitoring.

16.4.3.1 Calcareous Algae Within the Seagrass Habitat

High densities of seagrasses have the capacity to increase the pH of entire water bodies due to their uptake of CO_2 and release of OH^- (Beer et al. 2006). For example, *Cymodocea rotunda, Halophila ovalis,* and *Thalassia hemprichii* have the capacity to raise water pH from 8.1 to 8.6, 8.8, and 9.2, respectively (Beer et al. 2006). The pH compensation point of each species as well as the inability of seagrasses like *H. ovalis* to tolerate the high pH values and low inorganic carbon concentrations generated by the other two species forces these seagrasses into monospecific tide pools. However, Semesi et al. (2009) determined that calcifying macroalgae, such as *Hydrolithon* spp., *Mesophyllum* spp., and *Halimeda renschii*, can buffer against this increase in pH via intensified calcification. In fact calcification rates of *Hydrolithon* spp. can be five to six times higher in the presence of seagrasses. Similarly, photosynthetic activity of *Mesophyllum* spp. increased by 15% in the presence of seagrasses. Thus, when coexisting these two groups are capable of maintaining high levels of productivity while encouraging higher levels of biodiversity. Monitoring of the balance between these two groups is important as the dominance of one over the other could lead to dramatic shifts in water chemistry and a regime shift. Particularly important are the consequences that ocean acidification may have on this balance.

16.4.3.2 Regime Shifts and Controls Within the Seagrass Habitat

Human development of the coastal zone has often been identified as the source of nutrient pollution that disrupts the balance between seagrasses and macroalgae. In 2008, Houk and van Woesik collected evidence suggesting that seagrass species respond differently to environmental pressures. In a Saipan lagoon they found that increased watershed development stimulated macroalgal proliferation within *Halodule uninervis* seagrass meadows, severely impacting the integrity of the meadows. However, the same study revealed that the growth of a different seagrass, *Enhalus acoroides,* was positively correlated with human development and watershed size. The authors suggest that the physical and/or morphological characteristics of seagrass species determine their susceptibility to macroalgal overgrowth. Similarly, McGlathery (2001) suggests that *Thalassia testudinum* may be more resistant to the pressures of algal blooms because of a proportionately greater allocation of resources to below-ground biomass, allowing them to persist during temporary algal blooms.

The consequences of nutrient enrichment are not always easily predicted. Nutrient addition experiments in Florida resulted in increased seagrass biomass and decreased macroalgal epiphyte coverage offshore. Conversely, the inshore treatment had no effect on two species of seagrasses while macroalgae biomass increased significantly (Ferdie and Fourqurean 2004). In a similar Florida-based study, Armitage et al. (2005) found that enrichment of sediments stimulated highly variable group and site-specific responses by macroalgae. The resulting macroalgal blooms (calcareous green and filamentous red) were ephemeral and had no long-lasting impact on the system. Their results also showed that areas containing a high abundance of macroalgae were exposed to an array of additional chronic pressures including nutrient enrichment, current and erosion pressures, and heavy boat traffic. During nutrient treatments, phosphate (not nitrate) stimulated growth, prompting the researchers to conclude that Florida Bay is phosphate limited, a consequence of the high carbonate content of the sediments, perhaps owing to the calcareous algae contained therein. Results from a similar study in Puerto Rico show that several species of nutrient-depleted nuisance bloom (*Hypnea musciformis*) and mat-forming (*Acanthophora spicifera, Dictyota cervicornis*) macroalgae increased growth rates significantly when exposed to nutrient enrichment. However, enriched algae of the same species had no response to increased nutrient concentrations. Calcareous green algae (CGA) (e.g., *Halimeda incrassata*) did not respond to treatments within the 3-day experiment, suggesting limitation by some other metabolic process, such as calcification (Fong et al. 2003). Therefore, in order to predict the consequences of nutrient enrichment, coastal managers must consider the existing concentration of each relevant nutrient within the system as well as the primary producers contained therein.

Evidence suggests that storms arriving in the late summer cyclone/hurricane season play an important role in maintaining a balance between seagrasses and algae. Frequent disturbances such as large swells and intense currents prevent epiphyte growth and thus maintain seagrasses as the dominant flora (Houk and Camacho 2010). However, the impacts of massive natural disturbances on coastal systems (erosion, mechanical thinning, and burial) can completely transform benthic communities, often irreversibly. Following Hurricane Georges in 1998, Fourqurean and Rutten (2004) observed that while only 3% of *T. testudinum* was removed, 24% of CGAs were lost. CGAs are much more susceptible to hurricane damage because they lack the extensive rhizomes of seagrasses and are thus easily liberated from the substrate during sediment displacement. As the system recovered, CGAs were the first primary producers to recolonize bare patches, although its density did not return to prehurricane levels for another 3 years. This storm-dependent balance within the seagrass–algae complex and the biodiversity that it maintains can be considered within the context of the Intermediate Disturbance Hypothesis (Connell 1978).

16.4.4 Macroalgae–Mangrove Interactions

The vast majority of studies focused on mangroves come out of the Indian and Southwest Pacific Ocean in which water transparency can be low due to high tidal amplitude and intense terrestrial runoff typical of estuaries and deltas (Kristensen 2008). This limits subsurface primary productivity and promotes the development of detrital communities (Kristensen 2008). Studies coming out of Southeast Asia (Thailand, Malaysia) and the Indus Delta describe mangrove forests as nutrient exporting systems that have low epifaunal biodiversity, low macroalgal abundance, and organically rich sediments (Saifullah and Ahmed 2007). In this environment, macrophytes and filter feeding assemblages are extremely limited. As a result, many of the inhabitants are generalists and opportunists with microalgae and allochthonous phytoplankton providing an additional and essential source of nitrogen (Kristensen 2008). However, in the Atlantic Ocean and Caribbean Sea tidal amplitudes are minimal and terrestrial runoff is limited, leading to high water clarity, allowing for the proliferation of macroalgal and filter feeding communities within fringe regions (Kieckbusch et al. 2004). Therefore, the disproportionate amount of research coming out of Asia and Australia has led to a skewed perception of the role of macroalgae within mangrove systems.

16.4.4.1 Abundance and Productivity

The NPP (NPP) of mangrove prop root epiphytes in the Bahamas (8.5 ± 6.4 gC $\text{kg}^{-1}\text{day}^{-1}$) has been measured to rival that of nearby seagrass epiphytes (Koch and Madden 2001). In the Karachi mangroves of the Indus Delta, Saifullah and Ahmed (2007) have estimated that the algal productivity is much higher than that of the mangroves themselves. However, the actual biomass of algae growing within some mangrove systems may be quite low due to light limitation. Nevertheless, their role in coastal food webs is likely to be consistently significant, owing to their nitrogen content, which is 10× higher than mangrove tissues (Alongi 1998). Since decomposition of mangrove tissues is a slow process, due to its high lignin, cellulose, and tannin content, it is likely that algae and bacteria provide a significant amount of nitrogen to the mangrove food web. Therefore, it is probable that any algal tissue appearing within algae-deficient mangrove habitats is likely to be quickly utilized by resident fauna (Alfaro 2008).

In 2001, Koch and Madden attempted to determine the source of nutrients within oligotrophic lagoons in the Bahamas. They found that total nitrogen and phosphorus concentrations were highest within fringe mangrove and seagrass meadow sediment samples directly adjacent to mangroves, relative to sand flats and open lagoon seagrass meadows. On a biomass basis, the gross primary production of prop root macroalgae was twice as high as nearby seagrass epiphytes and their NPP was even comparable to that of seagrasses. At that time they were unable to identify the cause of this nutrient gradient, but they suggested remineralization by bacteria, nutrient mobilization, and even delivery of metabolic wastes by fishes that migrate between habitats during the day.

Recently, a great deal of debate has been focused on whether or not mangrove systems are a source of nutrients for adjacent benthic and pelagic food webs (Kieckbusch et al. 2004; Bouillon et al. 2008). Of course, the retention of organic material within mangroves is completely dependent upon the tidal regimes of the area. For example, from their studies in Thailand, Kristensen (2008) suggests that the main source of organic matter in mangrove systems is derived from the mangroves themselves and that macroalgae contribute very little to the organic pool. Conversely, researchers in the Indus Delta argue that epiphytic algae are an important source of energy within the mangrove environment (Saifullah and Ahmed 2007). However, Bouillon et al. (2002) have provided evidence from studies in India, suggesting that there is very little export of this material to adjacent habitats. According to stable isotope analysis of benthic invertebrates in neighboring habitats, the labile organic matter that is exported from the mangroves is not consumed in significant quantities by faunal assemblages. Instead, grazers outside of the mangrove system prefer to consume local sources of algae which are likely to have a higher content of nitrogen. In fact, they argue that the primary production of mangrove epiphytes in Karachi is higher than that of mangrove trees. Therefore, caution must be taken when reviewing the literature and an understanding that each mangrove system is likely to be unique based upon hydrodynamics and algal communities.

16.4.5 Distribution of Macroalgae Within Mangroves

The mangrove systems of the Atlantic Ocean and Caribbean Sea are quite distinct from those of Asia and Australia, especially in the context of the importance of macroalgae. A recent study revealed that the most abundant epiphytes growing on mangrove prop roots in Panama were sponges and macroalgae (*Caulerpa verticillata* and *Halimeda* spp.) (Diaz and Rützler 2009). Sponges and macroalgae clearly compete for space on prop roots, with algae occasionally dominating where elevated sun exposure tips the balance in favor of algal dominance. In Belize, macroalgae only dominate where deforestation and dredging have recently occurred (Diaz and Rützler 2009). These two disturbances promote the suspension of fine sediments that negatively impact all filter feeders (sponges and ascidians), presenting the resulting macroalgal blooms with a competitive advantage.

Within mangrove habitats, algae growing on vertical surfaces are subject to an array of extremely variable conditions such as submersion and exposure, light, nutrients, temperature, and salinity. These challenging conditions have brought about the evolution of mangrove-specific algae. A survey of macroalgae growing on the pneumatophores of the mangroves of Karachi in the Indus Delta revealed a collection of 14 species belonging to Chlorophyta, Phaeophyta, and Xanthophyta phyla (Saifullah and Ahmed 2007). Within this habitat, algae and cyanobacteria covered 70–81% of the vertical length of mangrove pneumatophores. In Australia, species of macroalgae show a pattern of zonation along the vertical extent of the pneumatophores, likely arising as a result of competition, light exposure, and/or submersion/desiccation tolerance (Melville and Pulkownik 2007). Most algae are positioned above the low water mark where they are able to avoid extended periods of desiccation during the changing tides as well as maximize exposure to sunlight. Melville and Pulkownik (2007) suggest that species are arranged into three distinct ranges within the intertidal region according to their tolerance to desiccation. Low water mark algae are tolerant to submersion and have been suggested to be more aggressive competitors. High water mark algae are tolerant to desiccation and salinity changes (see Chap. 5 by Karsten) and the algae that are found in between these two groups are adaptable to both but have been so arranged as a consequence of competition.

16.4.6 Herbivory Within Mangroves

Studies have shown that many mangrove invertebrates rely on algae as a primary resource and some of them are likely to share symbiotic relationships with algae and/or their photosynthetic components (Bouillon et al. 2008). For example, an opisthobranch found in Indian mangroves feeds exclusively on red and green algae, sequestering the algal chloroplasts into its intercellular spaces in order to yield the products of continued photosynthesis (Bouillon et al. 2008). Grazers of the primary producers within the mangrove habitat (microphytobenthos, macroalgae, and mangroves themselves) are essential for channeling organic matter to higher trophic levels. Littorinids have been suggested as the dominant grazers of macroalgae growing on the vertical surfaces of mangrove prop roots, trunks, and branches and have even been said to have a "strong top-down force" in these coastal ecosystems (Alfaro 2008). Primary and secondary consumers, such as juvenile fishes and invertebrates, which inhabit the fringe of mangroves depend upon the roots of mangroves as a refuge alone and acquire most of their nutritional requirements from algal sources within the mangroves and seagrasses, as well as the seagrasses themselves (Kieckbusch et al. 2004). In 2004, Boyer et al. measured herbivory in three separate habitats dominated by seagrasses (*T. testudinum*), corals, and mangroves (*Rhizophora mangle*) off the northern coast of Honduras. Their results revealed that herbivores in all three habitats are capable of differentiating between food sources based upon nutritive value and thus preferentially grazed on nutrient-rich food items when given the opportunity. Compared to seagrass and coral habitats, overall macroalgae herbivory was lowest in the mangroves (31%, 33%, and 15%, respectively). However, the herbivores within the mangroves displayed the highest capacity for increased grazing (91%) following the nutrient enrichment.

Algae swept into the mangroves from adjacent rocky shore and estuarine habitats can become entangled in pneumatophores, persist, and at times reproduce to establish persistent free living colonies. It is suspected that these drift algae increase the likelihood of colonization by mollusks in mangroves by increasing substrate complexity and possibly serve as an additional food source (Bishop et al. 2009). The complex surface of fucalean macroalgae also represents an additional surface area for the growth of microfilms. Bishop et al. (2009) determined that algae originating from estuaries were capable of attracting more mollusks than algae coming from rocky shores. This is likely due to the typically higher nutrient content of estuarine systems which is capable of enriching algae and increasing its palatability for mollusks.

Some herbivorous fishes living within and adjacent to mangroves depend upon macroalgae growing as epiphytes on mangrove prop roots as a primary food source. For example, in Curaçao, the doctorfish, *Acanthurus chirurgus*, acquires approximately 55% of its macroalgal diet directly from mangrove surfaces (Nagelkerken and van der Velde 2004). The largest herbivorous reef fish in the Atlantic Ocean, *Scarus guacamaia*, is exclusively dependent on the mangrove habitat during its development and has suffered local extinctions where mangroves have been removed (Mumby et al. 2004). Of particular concern is the recent appearance of the invasive predatory lionfish, *Pterois volitans*, in Caribbean mangrove systems and the impacts that it will have on the recruitment of vital herbivorous fish species to adjacent coral reef habitats (Barbour et al. 2010; Albins and Hixon 2008).

16.5 Conclusion

Tropical macroalgae are essential elements of the complex coastal ecosystems they inhabit. They provide a wide range of vital ecological functions, like the stabilization of reefs, retention of nutrients, and provision of habitat and food. Macroalgae are able to provide all of these different functions due to their enormous diversity and habitat-specific adaptations. Over the last few decades, macroalgae have become more abundant across the globe, in coral reef, seagrass, and mangrove habitats, often as a response to human activities. At times, the proliferation of algae has led to regime shifts in these already threatened habitats. These ecosystem shifts have had profound consequences on tropical systems worldwide. In most cases a combination of coral mortality, eutrophication, reductions in grazing pressure due to disease, and overfishing form the basis for these shifts. In the near future, these shifts are likely to be exacerbated and prolonged, resulting in reduced overall habitat complexity and biodiversity.

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