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Harmful Macroalgal Blooms in a Changing World: Causes, Impacts, and Management

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15.1   Introduction

Macroalgae are loosely defined as multicellular algae that are generally considered to have a simple plant-like body, or thallus, that is macroscopic (visible to the human eye) and ranges from simple to complex in structure (Graham *et al.*, 2016). In freshwaters, where there are very few thalloid macroalgae, the term has been broadened to include filamentous, colonial, tuft-forming, crustose, tissue-like, coenocytic algae, or cyanobacteria that have forms recognizable to the naked eye (Sheath and Cole, 1992; also see, as examples, Burkholder, 2009; Fetscher *et al.*, 2015). That definition is also used to include sheet-like, filamentous, coarsely branched, calcareous, and crustose algae in estuarine and marine environments as well. This review emphasizes macroalgae in U.S. inland, estuarine, and coastal marine waters, but examples from other nations are included to emphasize some points as appropriate. Macroalgae mainly include red, green, and brown taxa (Rhodophyta, Chlorophyta, and Streptophyta; and mostly photosynthetic stramenopiles [Heterokontophyta] – Class Phaeophyceae, respectively) (Graham *et al.*, 2016 and references therein). An increasing number of freshwater, estuarine, and marine habitats also include certain harmful benthic mat-forming cyanobacteria (Cyanobacteria; or blue-green algae, Cyanophyta) as well.

In aquatic ecosystems, macroalgae are largely beneficial by providing important structural habitat for invertebrates and fishes (Dayton, 1985; Marx and Herrnkind, 1985; Holbrook *et al.*, 1990; Pérez-Matus *et al.*, 2008; Pérez-Matus and Shima, 2010; Lapointe *et al.*, 2014), and a source of nutrition for herbivore and detrital food webs (Sammarco *et al.*, 1974; Tenore, 1977; Lewis, 1986). Macroalgae are a natural, common feature of inland waters as well as estuaries, coastal waters, and (to a limited extent) oceanic waters (Bartsch *et al.*, 2012), particularly the Gulf of Mexico, North Atlantic Ocean, and Caribbean Sea where pelagic *Sargassum* is distributed (Lapointe *et al.*, 2014). When excessive growth and biomass accumulation occur from overstimulation by nutrient (primarily nitrogen [N] and phosphorus [P]) pollution and other human-related factors, however, algae are considered harmful because of the potentially severe environmental and economic impacts they can cause. Excessive biomass of macroalgae is commonly referred to as a *bloom*. Although many begin growth in a benthic habit, their mats often become dislodged and growth continues as floating mats, sometimes referred to as *metaphytic* (e.g., Hudon *et al.*, 2014). As the causes and effects of macroalgal blooms are similar in many ways to those associated with harmful phytoplankton species, scientists use the term *harmful algal bloom* (HAB) (ECOHAB, 1995; HARRNESS, 2005) to describe this diverse array of bloom phenomena. The frequency and extent of macroalgal HAB have increased in estuaries and coastal waters throughout North America during the past five decades to now include all coastal states as well as Hawai'i (Figure 15.1); in addition, macroalgal HAB have become common in inland freshwater systems, including lakes, streams, rivers, springs, and reservoirs.
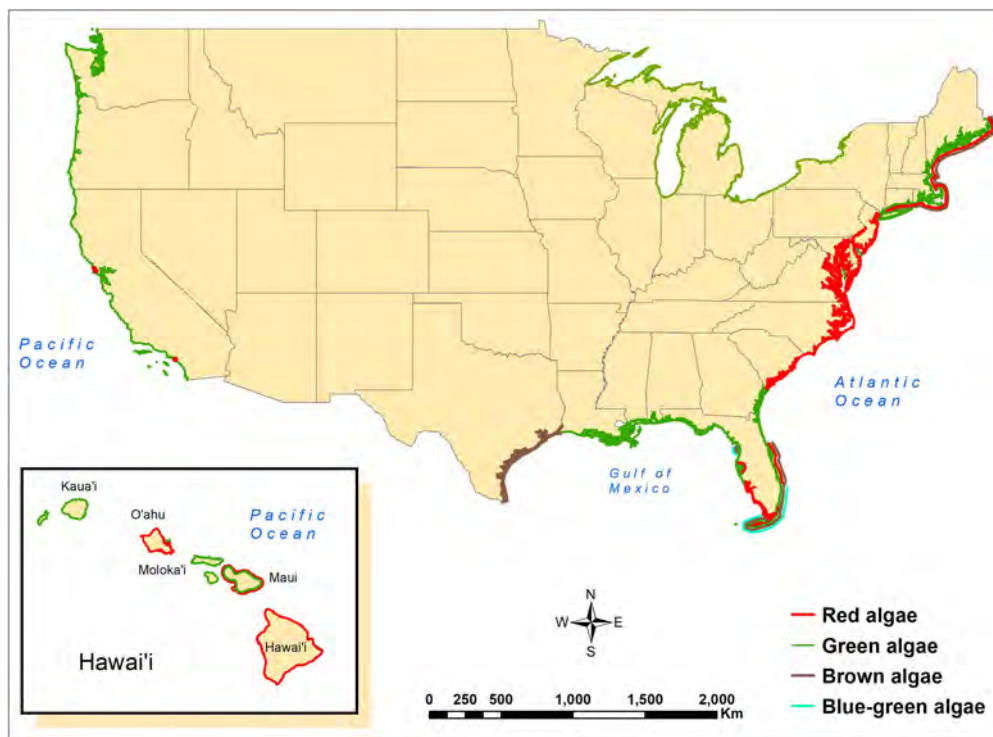
Figure 15.1 Map showing the distribution of estuarine and coastal marine harmful macroalgal blooms (by phylum) in North America and Hawai'i, also including freshwater taxa along the Laurentian Great Lakes.

Here, harmful macroalgal blooms are operationally defined in both ecological and socioeconomic contexts, as in Burkholder (2009). Macroalgal HAB cause undesirable ecological changes in habitats and food webs or, in some cases, produce potent bioactive substances that adversely affect beneficial aquatic life. From a socioeconomic perspective, the excessive biomass also causes undesirable effects for humans, such as decreased recreational uses of beaches and waterways (due to rotting biomass, offensive odors, reduced water clarity, fish kills, and reduced waterfront real estate values, and through provision of habitat for microbial pathogens, mosquitoes, snails as vectors for schistosomiasis, and other noxious species); increased fouling of pumps, filters, and intake pipes; taste and odor problems in drinking water supplies; increased costs of water treatment; increased costs of managing aquatic resources; and, less commonly, direct toxicity to humans and other animals (wild and cultured fish, larvae of commercially important shellfish, waterfowl, livestock, and domestic pets). Socioeconomic impacts also include losses of commercially important finfish and shellfish due to habitat loss and fouling of fishing gear.

15.2 Freshwater and Other Inland Macroalgae

The harmful macroalgae of freshwaters (wetlands, springs, streams and rivers, and lakes and reservoirs) and brackish to highly saline inland waters are low in diversity relative to estuarine and marine macroalgae, but most of the species are so widely distributed among the states that a map of their distribution is not included. Few species of red and brown algae inhabit freshwaters, and they tend to be restricted to nutrient-poor (oligotrophic) habitats (Graham *et al.*, 2016 and references therein). Thus, certain benthic cyanobacteria and green algae are the major macroalgal taxa in freshwaters that form noxious high-biomass blooms or outbreaks (Figure 15.2). In U.S. freshwaters, the noxious benthic bloom-forming filamentous taxa apparently are all native and mainly include the cyanobacteria *Lyngbya wollei*, *Oscillatoria* spp., and *Phormidium/Microcoleus* spp.; the green algae *Cladophora* spp. and *Pithophora oedogonia* (Chlorophyta, Ulvophyceae); and the higher green algae *Spirogyra* spp. (Streptophyta-Order Zygnematales).
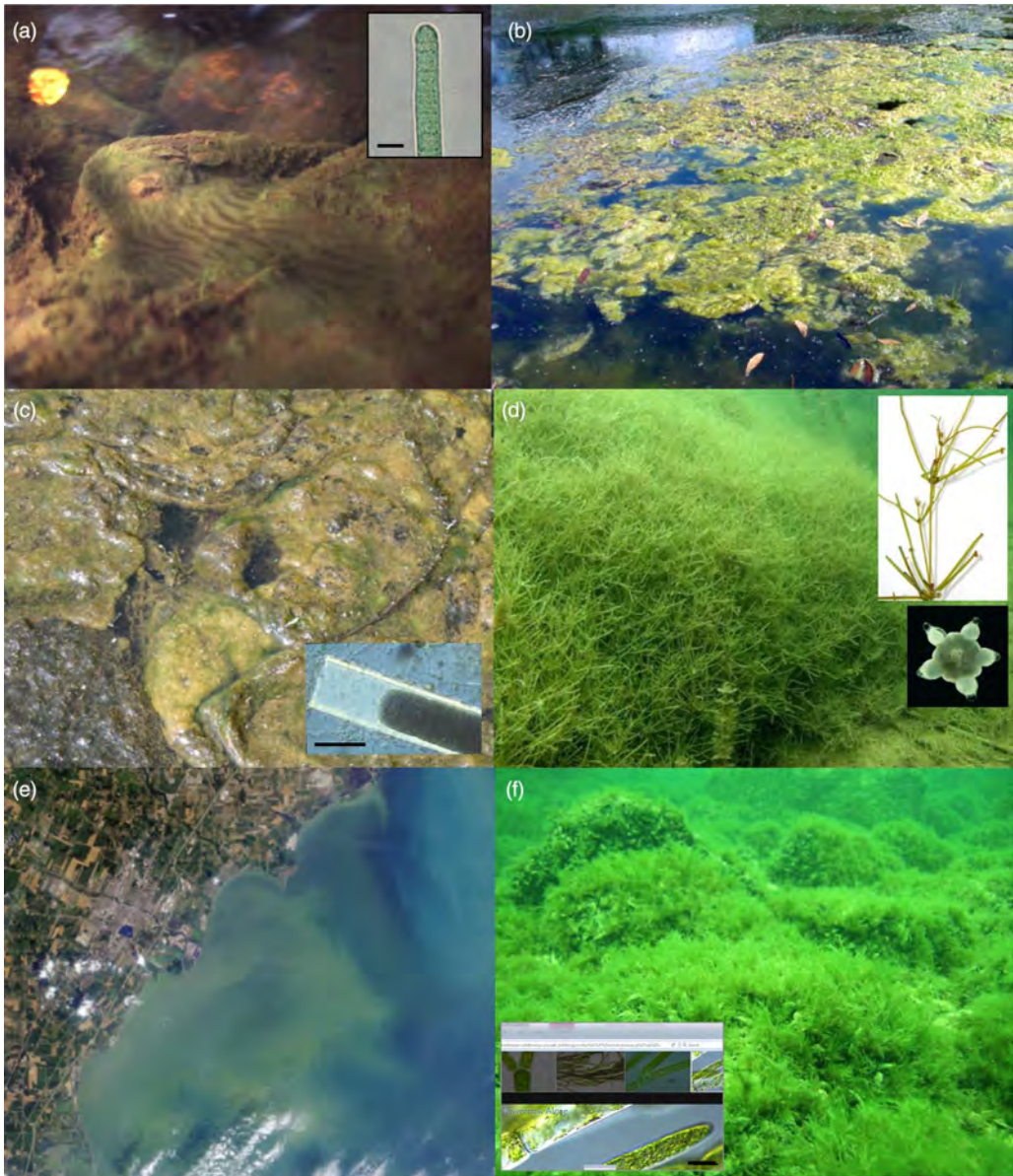
Figure 15.2 Examples of potentially harmful freshwater macroalgae: (a) The cyanobacterium *Phormidium* (both freshwater and marine) – benthic mat in a mildly acidic softwater stream (gold object in upper left is a floating leaf); insert is a light micrograph (scale bar: 20 μm). *Source*: Photos by J. Burkholder. (b,c) The cyanobacterium *Lyngbya wollei*: (b) Floating mats suspended from a benthic habit in a piedmont reservoir, North Carolina, USA. *Source*: Photo by E. Allen, NCSU Center for Applied Aquatic Ecology. (c) Closeup of floating mats mixed with some filamentous green algae (Chlorophyta). *Source*: Reprinted from Burkholder (2009, figure 9l), with permission from Elsevier. Insert is a light micrograph (scale bar: 50 μm). *Source*: Photo by B. Speziale, Clemson University, Clemson, South Carolina, United States, with permission. (d) Invasive starry stonewort (*Nitellopsis obtusa* – Streptophyta, Charales) in an inland lake in Michigan, United States. *Source*: Photo from E. Nat at the Robert B. Annis Water Resources Institute [AWRI], with permission. Courtesy of Ray Van Goethem, http://www.aquaticnuisanceplantcontrol.com/Algae-Album.html. Upper insert is a specimen from the Oneida Lake Education Initiative. *Source*: http://www.seagrant.sunysb.edu/oli/olei-stonewart.htm, with permission from E. Nat at the AWRI. Courtesy of Jeroen Huls, https://www.verspreidingsatlas.nl/2160. Lower insert is a star-shaped rhizoid (diagnostic, 1.5–2 mm in diameter). *Source*: http://deptsec.ku.edu/~ifaaku/jpg/Nat/Nat.html), with permission from the Nationaal Herbarium Nederland, the Netherlands. Courtesy of Emile Nat. (e,f) The filamentous chlorophyte *Cladophora*: (e) Satellite image of a major suspended and benthic bloom in the west basin of Great Lake Erie (Landsat natural color image). *Source*: Courtesy of the National Aeronautics and Space Administration, with permission. (f) Benthic overgrowth in Lake Michigan. *Source*: Photo courtesy of H.A. Bootsma. Insert is a light micrograph (scale bar, 45 μm – at http://www.keweenawalgae.mtu.edu/gallery_images/ulvophyceans/Cladophora_j74-1a_20125z.jpg. *Source*: Photo by J. Oyadomari, with permission.

The major thalloid green macroalgae in freshwaters are (1) the mostly beneficial charaleans (Streptophyta – Order Charales), which grow along shorelines of hardwater habitats (most species) or in mildly acidic softwaters; and (2) *Ulva* (Chlorophyta, Ulvophyceae – now including the former genus, *Enteromorpha*; Hayden *et al*., 2003), found in some brackish and highly saline inland waters, but much more prevalent in marine waters (below) (Burkholder, 2009 and references therein). Charaleans *Chara* and *Nitella* can sometimes become problematic in shallow waters when growth reaches the water surface and impedes human recreational uses (Lembi, 2003). Some *Ulva* spp. can grow in habitats spanning from freshwaters to salt springs and brackish lakes, to the Great Salt Lake, Utah, United States (salinity > 50) (as *Enteromorpha*; Flowers, 1934). A recent bloom of *Ulva flexuosa* (formerly *Enteromorpha flexuosa*) in Muskegon Lake, Michigan, United States, was described as invasive, and covered up to 80% of the littoral zone in some areas, mostly as epiphytic overgrowth (Lougheed and Stevenson, 2004). The affected lake had low grazing pressure, increased salinity from industrial discharge of chlorinated compounds, and a history of nutrient over-enrichment.

Benthic filamentous cyanobacteria, mostly the genera *Lyngbya*, *Oscillatoria*, and *Phormidium/Microcoleus*, commonly form nuisance or potentially toxic growth in inland waters worldwide (e.g., Figure 15.2). They can be both high-biomass and toxic bloom formers. The toxins can include microcystins, anatoxin-a, homo-anatoxin-a, aplysiatoxins, cylindrospermopsin, deoxy-cylindrospermopsin, dihydroanatoxin-a, dihydrohomoanatoxin-a, lyngbyatoxin, and saxitoxin analogs (Quiblier *et al*., 2013; McAllister *et al*., 2016). Five benthic *Phormidium* species and one recently renamed species (*Microcoleus autumnale*, formerly *Phormidium autumnale*; Strunecký *et al*., 2013) have been reported to be toxigenic thus far, including at least four of the six in North America (*M. autumnale*, *Phormidium corium*, *P. favosum*, and *P. tenue*; Tilden, 1910) (Quiblier *et al*., 2013 and references therein). Toxigenic benthic *Oscillatoria* species (e.g., *O. formosa* and *O. limosa*) are poorly identified and easily confused with *Phormidium* spp. (Quiblier *et al*., 2013 and references therein). Similarly, benthic *Lyngbya* spp. (with the exception of *Lyngbya wollei* – see Chapter 16 of this volume) can easily be confused with *Phormidium* and *Oscillatoria* spp., and are usually not identified to species.

Benthic filamentous cyanobacteria thrive in a wide array of habitats ranging from oligotrophic to eutrophic, including wetlands, lake littoral zones, wastewater ponds, hypersaline and geothermal ponds, streams and rivers, deep springs, saltmarshes, and seagrass meadows (Quiblier *et al*., 2013; authors' personal observation). These form cohesive mats that typically consist of a mixture of toxic and nontoxic cyanobacterial strains along with various other microbes (McAllister *et al*., 2016). The mats are often 1 cm or more in thickness (up to 70 cm thick; Dasey *et al*., 2005), so that the environment within the mat biofilm or "microscale ecosystem" (Quiblier *et al*., 2013) becomes distinct and somewhat isolated from that of the overlying water (Stevenson *et al*., 2007; Wood *et al*., 2015a). Although water-column nutrient concentrations (both N and P) during initial substratum colonization can strongly influence establishment and mat formation (Cowell and Botts, 1994; Stevenson *et al*., 2007; Wood *et al*., 2014, 2015b), the interior of the developed mat is characterized by steep chemical gradients that control nutrient uptake and recycling, which are largely independent from nutrient fluxes in the overlying water (Stal, 2012; Wood *et al*., 2015a).

Only sparse information is available about the environmental factors that control toxic, matforming benthic cyanobacteria. Sites with high *Phormidium* coverage in some rivers have been linked to high total N to total P (TN:TP) ratios, usually exceeding 20:1 (Wood and Young, 2012; but see Sabater *et al*., 2003; Vilalta *et al*., 2003). These sites also were characterized by elevated dissolved inorganic nitrogen (DIN = ammonium + nitrate + nitrite) concentrations (> 100 μg/L) and low water-column phosphate (< 10 μg soluble reactive phosphorus [SRP]/L), but had higher loads of fine sediments enriched with biologically available P (McAllister *et al*., 2016).

Harmful filamentous green algae generally thrive in shallow littoral areas of nutrient-rich (eutrophic) habitats (Burkholder, 2009 and references therein), and may be free-floating (e.g., *Pithophora oedogonia* and *Spirogyra* spp.) and/or attached to substrata (e.g., *Cladophora*). The most widely known of these are within *Cladophora* (Figure 15.2), which is the most widely distributed macroalgal genus throughout the world's freshwater ecosystems (Dodds and Gudder, 1992; Higgins *et al*., 2008). These species occur in many alkaline freshwater and brackish lakes and rivers, and in estuarine and marine waters. Some may be grazed when small or dislodged by some fauna, but they generally are considered a poor, nonpreferred food source (Zulkifly *et al*., 2013). These green algae have a relatively high light

optimum for photosynthesis and can rapidly acclimate to low or high light (Graham *et al.*, 1982, 1996; Zulkifly *et al.*, 2013). Maximum biomass or coverage of *Cladophora* has exceeded 900 g dry wt m^{-2}, and its filaments can be 0.5 m or more in length (Burkholder, 2009 and references therein). Worldwide, freshwater *Cladophora* thrives in P-enriched waters with dependable substrata (e.g., large boulders) for attachment (Pitcairn and Hawkes, 1973; Dodds and Gudder, 1992; Zulkifly *et al.*, 2013 and references therein).

The noxious filamentous chlorophyte *Pithophora oedogonia* is restricted to freshwaters and thrives in shallow littoral areas of eutrophic habitats (Lembi *et al.*, 1980, 1988). This species has low affinity for DIN (as nitrate) and SRP in comparison to *Cladophora glomerata*, but generally higher temperature tolerance and wider pH tolerance extending from alkaline to mildly acidic habitats. Spring growth begins in a benthic habit, and then oxygen bubbles trapped within the filaments carry them to the water surface where mats develop. Photosynthetic rates are positively correlated with external concentrations of both N and P (Spencer *et al.*, 1985). This organism is well adapted to low light conditions and even extended periods of darkness, and can survive severe self-shading within the mats where about 95% of the available light is absorbed within the first 5 mm of mat thickness (O'Neal *et al.*, 1985; Spencer *et al.*, 1985). A computer model simulating growth dynamics of *P. oedogonia* in a north temperate lake predicted more biomass reduction from 50% lower nitrate concentrations than from a similar decrease in TP (Spencer *et al.*, 1987).

Filamentous algae within the order Zygnematales are common bloom formers in alkaline and mildly to moderately acidic eutrophic freshwaters throughout the United States (Berry and Lembi, 2000; McKernan and Juliano, 2001 and references therein). Rapid overgrowth by *Spirogyra* spp. sometimes occurs in lakes, ponds, slowly flowing streams, and ditches affected by anthropogenic nutrient sources such as agricultural runoff or sewage effluent (McKernan and Juliano, 2001). Species within this genus can also be abundant in benthic habitats of large lakes; for example, Askari (1992) described a mat of *Spirogyra* that was more than 0.6 m thick washed up on the shores of Lake Huron. *Spirogyra* forms benthic and floating mats, and some species have responded rapidly to N and P enrichment (O'Neal and Lembi, 1988). This alga is less tolerant of low light than *Pithophora oedogonia*, and the mats tend to disintegrate under high temperature and high light, or in darkness (O'Neal and Lembi, 1988; Adrian, 1994; Graham *et al.*, 1995 and references therein). The species *Spirogyra fluviatilis* can withstand current velocities up to 30 cm/sec, if phosphate is available to offset the apparent increase in cellular P demand (Borchardt *et al.*, 1994). It can adjust short-term SRP uptake to compensate for the suboptimal conditions imposed by rapid flow. In Lake Baikal, a World Heritage Site where 3700 species live in the world's oldest, deepest, and most voluminous lake, extensive mats of *Spirogyra* have developed around urban areas as a result of inadequate sewage treatment (Nuwer, 2016). Various other filamentous and colonial chlorophytes can overgrow inland waters and adversely affect other aquatic life and local economies (Burkholder, 2009), exemplified by the taxa discussed above.

15.3 Estuarine and Coastal Marine Macroalgae

Estuarine and coastal marine macroalgae (seaweeds) are a rich, diverse group of macroscopic, multicellular organisms that grow along temperate, subtropical, and tropical coastlines (Taylor, 1960, 1972; Abbott and Hollenberg, 1976; Schneider and Searles, 1991; Littler and Littler, 2000; Gabrielson *et al.*, 2006; Dawes and Mathiesen, 2008). Blooms of macroalgae can occur naturally, but have become increasingly common features of urbanized bays, harbors, and coastal waters where thick submersed mats are formed that can overgrow economically important coastal habitats such as seagrasses and coral reefs. Excessive biomass of these blooms can strand on beaches and along shorelines, where they decompose and become a public nuisance. These blooms transform coastal habitats and have myriad social and economic consequences. The occurrence of estuarine and coastal macroalgal blooms is increasing globally, and now affects virtually all coastal states within the United States, including Hawai'i (Smith *et al.*, 2002; Anderson *et al.*, 2008; Bricker *et al.*, 2008; Table 15.1 and Figure 15.3). Estuarine and coastal macroalgae are eukaryotes within three phyla: the Chlorophyta (green algae), Rhodophyta (red algae), and Phaeophyta (brown algae). The Cyanobacteria (Cyanophyta, or blue-green algae), which are prokaryotic, unlike the other phototrophs included here, are also included because they include filamentous macroalgae, act similarly as other macroalgae from an

Table 15.1 Coastal macroalgal blooms reported for various locations within the continental United States and Hawai'i.

Location	Species	Impacts	Reference(s)
New England, mid-Atlantic U.S.	*Gracilaria vermiculophilla*	Non-native, high biomass, overgrowth of benthos	Freshwater *et al.* (2006), Saunders (2009), Nettleton *et al.* (2013)
New England	*Ulva compressa, Ulva lactuca, Ulva rigida; Codium fragile* subsp. *tomentosoides, Colpomenia peregrina, Grateloupia turuturu*	High biomass, toxin uptake, non-native, loss of shellfish habitat	Sawyer (1965), Thornber *et al.* (2008), Guidone and Thornber (2013), Cheney *et al.* (2014), Ramus (1971), Malinowski and Ramus (1973), Hanisak (1979), Mathieson *et al.* (2003), Green *et al.* (2012), Villalard Bohnsack and Harlin (1997), Mathieson *et al.* (2008)
Massachusetts	*Dasysiphonia japonica*	High biomass on beaches, non-native	Schneider (2010)
Nahant Bay, Massachusetts	*Cladophora* sp., *Pylaiella littoralis*	High biomass on beaches, surf zone	Auer (1982), Wilce *et al.* (1982)
Waquoit Bay, Cape Cod, Massachusetts	*Gracilaria tikvahiae, Cladophra vagabunda*	High biomass, overgrowth of seagrasses, loss of shellfish habitat	Valiela *et al.* (1992, 1997), Peckol *et al.* (1994), Hauxwell *et al.* (1998, 2001a)
Jamaica Bay, New York	*Ulva rigida*	High biomass, loss of shellfish	Wallace and Gobler (2015)
Delaware and Maryland Coastal Bays	*Ulva lactuca*	High biomass, odors	Cole (2002), McGinty *et al.* (2002)
Indian River Lagoon, Florida	*Gracilaria* spp., *Ulva* spp., *Acanthophora, Caulerpa*	High biomass, overgrowth of seagrasses, shellfish and wildlife mortality	Benz *et al.* (1979), Virnstein and Carbonara (1985), White and Snodgrass (1990), Riegl *et al.* (2006), Lapointe *et al.* (2015)
Southeast Florida	*Codium isthmocladum, Caulerpa verticillat, Caulerpa racemosa, Caulerpa brachypus, Lyngbya* spp.	High biomass, overgrowth of coral reefs	Lapointe (1997), Paul *et al.* (2005), Lapointe *et al.* (2005a, 2005b), Lapointe and Bedford (2010)
Biscayne Bay, Florida	*Anadyomene, Dictyota, Halimeda, Laurencia* spp.,	High biomass, overgrowth of seagrasses and corals	Lirman *et al.* (2008), Collado-Vides *et al.* (2011, 2013)
Florida Keys and Florida Bay	*Cladophora vagabunda, Dictyota* spp., *Halimeda* spp., *Laurencia* spp., *Spyridia filamentosa*	High biomass, overgrowth of corals and seagrasses, hypoxia	Lapointe *et al.* (1994), Lapointe *et al.* (2004, 2007), Smith *et al.* (2007), Green *et al.* (2015)
Bermuda	*Cladophora prolifera*	High biomass in Harrington Sound	Lapointe and O'Connell (1989)
Southwest Florida	*Gracilaria* spp., *Hypnea* spp.	High biomass, mass strandings on beaches	Lapointe and Bedford (2007)
Tampa Bay, Florida	*Chaetomorpha, Gracilaria, Ulva* spp.	High biomass, odors, overgrowth of seagrasses	Hagan (1969), Mangrove Systems (1985), Kelley (1995), Johansson (2003)
Texas and Florida	*Sargassum* spp. (drift macroalgae)	High biomass on beaches and coastal waters	Lapointe (1995), Gower *et al.* (2006), Kopecky and Dunton (2006)

Location	Species	Effect	Reference
San Juan Island, Washington	*Ulva lactuca* (reported as *Ulva fenestrata*), *Ulvaria obscura* (reported as *Monostroma fuscum*)	High percent cover, changes in infaunal abundances	Price and Hylleberg (1982), Bulthuis (1995)
Ship Harbor, Anacortes, Washington	*Ulvaria obscura*	Allelopathy (dopamine) – lab experiments	Van Alstyne *et al.* (2014)
Blakely Island, Washington	*Ulvaria obscura*, *Ulva lactuca* (reported as *U. fenestrata*), *Ulva linza* (reported as *Enteromorpha linza*)	Reduction in eelgrass (*Zostera marina*) shoot density, high biomass	Nelson and Lee (2001), Nelson *et al.* (2003)
Penn Cove, Coupeville, Washington	*Ulva lactuca*, *Ulva* spp.	Alterations of seawater pH and oxygen levels, high percent cover	Van Alstyne (2015), Van Alstyne *et al.* (2015)
Puget Sound, Washington	Ulvoid algae	High percent cover, noxious odor, hypoxia	Frankenstein (2000), Nelson *et al.* (2009)
Seahurst Bight Seattle, Washington	*Monostroma grevillei*, *Ulva lactuca* (reported as *U. fenestrata*), *Ulva linza* (reported as *Enteromorpha linza*)	High percent cover (in summer)	Thom and Albright (1990)
Grays Harbor, Washington	*Blidingia minima var. subsalsa*/*Ulva intestinalis* complex	High percent cover	Thom (1984)
Netarts Bay and Yaquina Bay, Oregon	*Ulva linza*, *Ulva lactuca*, *Ulva flexuosa*, *Ulva intestinalis*, *Ulva* spp.	High biomass	Davis (1981), Kentula and Dewitt (2003), Brown *et al.* (2007), Boese and Robbins (2008)
Yaquina Bay and Coos Bay, Oregon	Unspecified macroalgal species	Negative correlation between algal and eelgrass (*Zostera marina*) percent covers	Hessing-Lewis and Hacker (2013)
Coos Bay, Oregon	*Ulva* spp., *Ulva* spp. (reported as *Enteromorpha* spp.)	Negative effects on eelgrass (*Zostera marina*) in riverine, but not marine, sites; high biomass in summer months	Pregnall and Rudy (1985), Hessing-Lewis *et al.* (2011)
Bodega Harbor, California	*Ulva expansa*	Reductions in abundances of phoronids (*Phoronopsis*) and clams (*Macoma*)	Everett (1991)
Tomales Bay, California	*Gracilariopsis* sp.	Reduction of eelgrass (*Zostera marina*) shoot densities and growth rates	Huntington and Boyer (2008)
Elkhorn Slough, California	*Ulva* spp.	High biomass and percent cover	Schaadt (2005)
Huntington Harbor, California	*Caulerpa taxifolia*	Invasive, high biomass	Williams and Grosholz (2002)
Upper Newport Bay, California	*Ulva intestinalis* (reported as Enteromorpha intestinalis), *Ulva expansa*, *Ceramium* spp.	High percent cover	Kamer *et al.* (2001)
Magu Lagoon, Ventura County, California	*Ulva* spp.	Alter macrofaunal distributions and shorebird foraging behavior	Green (2011)
Mugu Lagoon, Tijuana River Estuary, and Upper Newport Bay, California	*Ulva intestinalis*, *Ulva expansa*	High percent cover	Kennison and Fong (2014)

Table 15.1 (*Continued*)

Location	Species	Impacts	Reference(s)
Southern California Bight, California	*Ulva* spp.	High percent cover, high biomass	McLaughlin *et al.* (2013)
Hawai'i	*Gracilaria salicornia*	High percent cover	Smith *et al.* (2002)
SW Maui, Hawai'i	*Cladophora sericea*	High percent cover, overgrowth of coral and other macroalgae	Smith *et al.* (2005)
Maui, Hawai'i	*Ulva lactuca, Hypnea musciformis, Acanthophora spicifera, Hypnea musciformis*	High percent cover	Smith *et al.* (2002), Dailer *et al.* (2012)
Kaneohe Bay, Oahu, Hawai'i	*Dictyosphearia cavernosa, Kappaphycus* spp., *Gracilaria salicornia*	High percent cover, overgrowth of coral reefs	Stimson *et al.* (2001), Conklin and Smith (2005)
Oahu, Hawai'i	*Acanthophora spicifera, Gracilaria salicornia, Kappaphycus* sp.	High percent cover, high biomass	Smith *et al.* (2002, 2004)

ecological standpoint, and are increasingly important macroalgal bloom formers in estuarine and marine systems.

Opportunistic green macroalgae, including the genera *Ulva*, *Chaetomorpha*, *Cladophora*, *Codium*, and *Caulerpa*, are perhaps best known for widespread blooms in urbanized bays and harbors in temperate and subtropical waters (Table 15.1 and Figure 15.3a, 15.3d, 15.3e, 15.3f, 15.3g, 15.3h). For example, extensive blooms of *Ulva* have developed throughout the United States in Boston Harbor (Sawyer, 1965), Narragansett
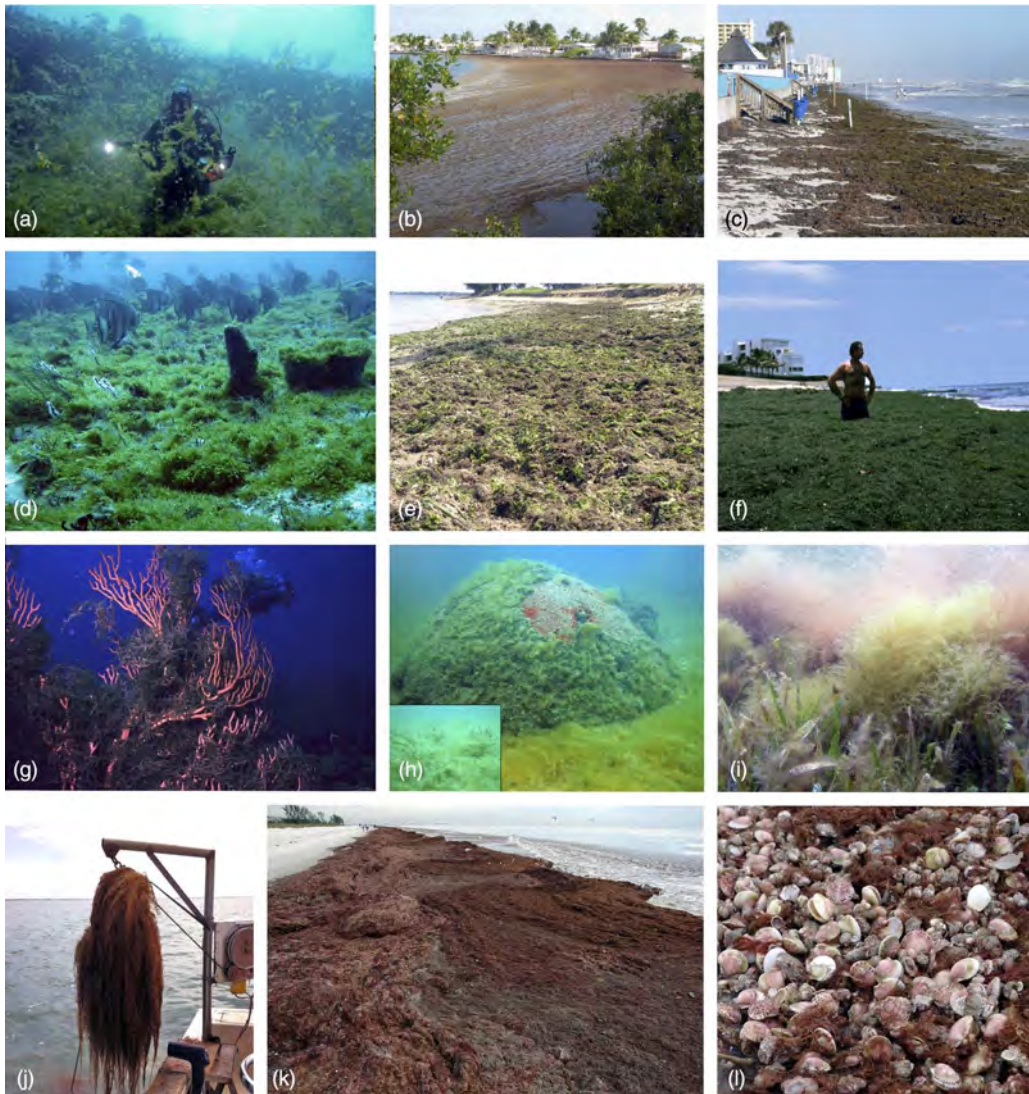

Figure 15.3 Examples of coastal marine harmful macroalgal blooms. (a) The green macroalga *Cladophora* sp. on coastal reefs off Boca Raton, Florida. *Source:* photo by R. Baumberger. (b,c) The brown macroalga pelagic *Sargassum* in the lower Florida Keys and Daytona Beach, Florida. *Source:* photos by B. Lapointe. (d) The non-native green macroalga *Caulerpa brachypus* forma *parvifolia* forming benthic mats on reefs off Riviera Beach, Florida. *Source:* photo by B. Bedford. (e) Mixed bloom of the non-native red macroalga *Hypnea musciformis* and the green *Ulva lactuca* on Maui, Hawai'i. *Source:* photo by B. Lapointe. (f,g) Blooms of the green macroalga *Codium isthmocladum* impacting beaches and coastal reefs off Palm Beach County, Florida. *Source:* photos by B. Lapointe. (h) Blooms of the green macroalga *Cladophora vagabunda* overgrowing a dead brain coral near the Content Keys in the lower Florida Keys. *Source:* photo by B. Lapointe. (i) Drift blooms of the brown macroalga *Dictyota* spp. and the red *Wrightiella blodgettii* overgrowing turtle grass meadows in the lower Florida Keys. *Source:* photo by B. Lapointe. (j) Fouling of stone crab traps by the red macroalga *Wrightiella blodgettii* near Cudjoe Key, Florida. *Source:* photo courtesy of M. Laudicina. (k) Blooms of red drift macroalgae (*Gracilaria* spp., *Hypnea* spp., and *Acanthophora spicifera*) on Sanibel Island beaches in Lee County, southwest Florida. *Source:* photo by B. Lapointe. (l) mortality of scallops by red drift macroalgae blooms at Sanibel Island. *Source:* photo by B. Lapointe.

Bay (Thornber *et al.*, 2008), coastal bays in Delaware and Maryland (McGinty *et al.*, 2002; Cole, 2002), the Indian River Lagoon in east-central Florida (Whitehouse and Lapointe, 2015), Tampa Bay (Hagan, 1969), embayments in southern California (McLaughlin *et al.*, 2014), and the Salish Sea in Washington State (Frankenstein and Redman, 2000; Nelson *et al.*, 2009). In these environments, *Ulva* forms thick mats that overgrow the benthos, resulting in hypoxia and anoxia, offensive odors, and loss of biodiversity. *Chaetomorpha* blooms have also developed in shallow, urbanized estuaries and coastal lagoons where benthic mats form, and they can eventually displace seagrasses as the dominant benthic primary producer (McGlathery, 2001). Blooms of *Cladophora* spp. in estuarine/marine waters have increasingly developed in urbanized bays and coastal waters, including Harrington Sound, Bermuda (Lapointe and O'Connell, 1989); Waquoit Bay, Cape Cod (Valiela *et al.*, 1992; Peckol *et al.*, 1994); as well as coastal waters in southeast Florida (Figure 15.3a), Florida Bay, and the Florida Keys (Dawes *et al.*, 1999; Lapointe *et al.*, 2004; Smith *et al.*, 2007; Figure 15.3d). On coral reefs in southeast Florida, a succession of blooms since 1990 has included the green algae *Codium isthmocladum*, *Caulerpa verticillata*, *Caulerpa racemosa*, and the non-native *Caulerpa brachypus* var. *parvifolia* (Lapointe *et al.*, 2005a; Figure 15.3d). All of these green macroalgal blooms are commonly referred to as "green tides" (Fletcher, 1996; Raffaelli *et al.*, 1998).

Red macroalgal blooms have also been on the rise along developing coastlines for many decades. During the urbanization of the subtropical Tampa Bay area in the 1960s and 1970s, extensive blooms of the red macroalga *Gracilaria tikvahiae* developed (Hagan, 1969), where the excessive drift biomass accumulation overgrew seagrasses and decomposed on shores, causing offensive odors. Similar blooms of drift *Gracilaria tikvahiae* (and other genera of red macroalgae, including *Hypnea*, *Acanthophora*, and *Spyridia*) developed in estuaries and coastal waters of southwest Florida between 2003 and 2007, fouling beaches and shorelines (Lapointe and Bedford, 2007; Figure 15.3k and 15.3l). Similar blooms occurred in the Indian River Lagoon in east-central Florida since the 1970s, where macroalgae now account for greater than threefold biomass compared to seagrasses (Lapointe *et al.*, 2015). Seasonal blooms of *Gracilaria* also occur in the temperate waters of Waquoit Bay, Cape Cod, where thick algal canopies cause light limitation and loss of the seagrass *Zostera marina* (Valiela *et al.*, 1997; Hauxwell *et al.*, 2001a; Hauxwell

and Valiela, 2004). In the subtropical Florida Bay/Florida Keys region, the red drift macroalgae *Laurencia* spp., *Spyridia filamentosa*, and *Wrightiella blodgettii* have formed increasing blooms with increasing urbanization in the Keys and N loading from the Everglades; these blooms are increasingly impacting both seagrasses and coral reefs (Lapointe *et al.*, 1994; Collado-Villes *et al.*, 2007; Green *et al.*, 2015) as well as commercial fishing gear such as lobster and stone crab traps (Figure 15.3i and 15.3j).

Brown macroalgal blooms have also increasingly developed in temperate and subtropical waters. Blooms of a drift form of the brown macroalga *Pilayella littoralis* have fouled the shallow waters and beaches of Nahant Bay since 1903, where they form sludge-like masses that strand on beaches in accumulations up to 0.5 m thick (Wilce *et al.*, 1982). Increasing biomass strandings of the floating, pelagic brown macroalga *Sargassum* have fouled tourist beaches in Texas and Florida for decades (Lapointe, 1995; Gower *et al.*, 2006). In the Florida Keys, blooms of *Dictyota* spp. and *Cladosiphon* have increased since 1990 with increased freshwater flows and nitrogen loading from the Everglades, overgrowing seagrasses (Figure 15.3i) and corals as a consequence of nutrient enrichment and eutrophication (Lapointe *et al.*, 2004).

Over the last decade, estuarine and marine macroalgal blooms have expanded globally to unprecedented spatial scales and biomass levels. In 2007, blooms of *Ulva prolifera* developed in the Yellow Sea, China; by the following summer of 2008, the Yellow Sea region experienced the largest green tides ever, comprising over 20 million metric tons of floating biomass and an area of 13,000–30,000 km^2 (Liu *et al.*, 2009; Gao *et al.*, 2010; Ye *et al.*, 2011). These massive green tides severely impacted the Qingdao area, the site of the summer 2008 Olympic sailing competition, and over 1 million tonnes of *Ulva* biomass were removed by hand (Leliaert *et al.*, 2008). Following the BP *Deepwater Horizon* oil spill in 2010, unprecedented high-biomass strandings of pelagic *Sargassum* (Figure 15.3b and 15.3c) impacted coastal communities beyond the Gulf of Mexico, including the east coast of Florida, Sierra Leone, and the entire Caribbean basin. These blooms were particularly severe throughout the Caribbean region in 2015 (Hu *et al.*, 2016), where widespread and detrimental environmental and economic impacts occurred (Kirkpatrick, 2015; Stasi, 2015; Figure 15.5e). It is uncertain whether these recent *Sargassum* blooms are a short-term response to variable environmental conditions or reflect a

long-term trend of nutrient enrichment and eutro-phication in offshore, oceanic waters on the North Atlantic Ocean.

15.4 Influences on Bloom Development

The ability of a particular alga to become a successful bloom former depends on its physiological responses to local environmental growth-limiting factors. Unlike toxic phytoplankton blooms, macroalgal blooms usually lack direct chemical toxicity, but typically have a broader range of distribution and ecological impacts. These blooms can result in the displacement of indigenous species, oxygen depletion (hypoxia/anoxia), noxious and toxic odors (hydrogen sulfide, dimethyl sulfide, and dimethyl disulfide), habitat loss, alterations of biogeochemical cycles and food webs, alterations in grazing, and die-offs of seagrasses and coral reefs (Jørgensen and Okholm-Hansen, 1985; Lapointe *et al.*, 1994; ECOHAB, 1995; Valiela *et al.*, 1997; National Research Council [NRC], 2000; McGlathery, 2001; HARRNESS, 2005; United Nations Environment Program [UNEP], 2005). Increasingly, macroalgal blooms foul beaches and shorelines important to local tourist economies, impact commercial and sport fisheries, and require ever more expensive biomass removal programs (Harris, 2005; Higgins *et al.*, 2005; Morand and Briand, 1996; Lapointe and Bedford, 2007).

Macroalgal productivity and growth are controlled by interactions of physical, chemical, and biological factors including light, temperature, nutrient availability, salinity, grazing, water motion, water residence time, depth, and desiccation (e.g., Raven, 1992; Lobban and Harrison, 1994; Dawes, 1998; Vis *et al.*, 2008). The physiographic setting, including geomorphology and hydrography, can also be important, as it determines connectivity of macroalgal recruitment, as well as the type of primary production base and biological communities present (e.g., freshwater marshes, submersed freshwater meadows, rocky shorelines, and soft substrata; and, in brackish and marine systems, mangroves, salt marshes, seagrasses, coral reefs, and rocky intertidal, soft-bottom, and planktonic systems). Physical factors such as winds, currents, and tides also influence the transport and accumulation of drift macroalgal blooms.

Of all these factors, however, *the increasing trend of macroalgal HAB results primarily from increased nutrient loading and eutrophication* in many lakes, reservoirs, streams, rivers, shallow bays, estuaries, and coastal waters (Hagan, 1969;

Smith *et al.*, 1981; Lapointe *et al.*, 1994; Morand and Briand, 1996; Valiela *et al.*, 1997; NRC, 2000; Higgins *et al.*, 2005; Stevenson *et al.*, 2007; Vis *et al.*, 2008; Teichberg *et al.*, 2010; Armenio *et al.*, 2016). Thus, many studies have addressed the importance of nutrient loading to the development of macroalgal HAB (below). Compared to the effects of nutrients, other factors associated with global change (e.g., alterations to seawater and air temperatures and seawater pH and carbonate chemistry) on seaweed growth and distribution are poorly known (Harley *et al.*, 2012). These interacting factors could be significant to HAB formation, especially in coming decades.

15.5 Nutrient Pollution

15.5.1 Sources

Although point-source sewage pollution has long been recognized as a cause of HAB (Sawyer, 1965; Hagan, 1969; Smith *et al.*, 1981; Lapointe *et al.*, 2005a; Teichberg *et al.*, 2010), non-point-source inputs of sewage, such as from septic tanks, shallow injection wells, fertilizers, and nutrient-enriched submarine groundwater discharges, can also increase nutrient loading, eutrophication, and the development of macroalgal blooms (Johannes and Hearn, 1985; Lapointe and O'Connell, 1989; Lapointe *et al.*, 1990; Valiela *et al.*, 1990, 1997; Lapointe, 1997; Teichberg *et al.*, 2010). In addition, siliciclastic environments tend toward stronger N-limitation of macroalgal blooms (Hanisak, 1979; Nixon and Pilson, 1983; Lapointe *et al.*, 1992), compared to carbonate-rich waters that tend more toward stronger P-limitation due to adsorption of P in sediments (Lapointe *et al.*, 1992; McGlathery *et al.*, 1994; Lapointe, 1997). In general, human activities are increasing N loading to the biosphere at a greater rate than P loading (NRC, 2000), which will tend toward increasing N:P ratios and P limitation of macroalgal blooms. There is already evidence for this in pelagic *Sargassum* in the Gulf of Mexico, where plants have higher tissue N and N:P ratios than historical baseline values (Lapointe, 1995). This change likely reflects the increasing N and N:P ratios in the Mississippi and Atchafalaya rivers that account for an estimated 90% of the total N load and 87% of the total P load discharged annually to the Gulf of Mexico (Dunn, 1996). Deviations from this general pattern have been reported, however (Larned, 1998; Fong *et al.*, 2001), and underscore

the complexities of eutrophication processes in coastal environments (NRC, 2000).

15.5.2 Indicators of Nutrient Pollution and Nutrient Sources

Among thousands of macroalgal species (Graham *et al.*, 2016 and references therein), relatively few have responded to nutrient pollution (below) by forming high-biomass blooms. Nevertheless, during the past century, macroalgal blooms have increased in frequency and extent in many inland waters and along North America's coastlines (Figures 15.1, 15.2, and 15.3, and Table 15.1) and are now considered a major element of global change (HARRNESS, 2005; UNEP, 2005). As a few of many examples, blue-green *Lyngbya wollei* mats are considered to be an indicator of freshwater ecosystem degradation (Hudon *et al.*, 2014 and references therein). Similarly, in coral reef ecosystems, the presence of massive occurrences of benthic cyanobacteria such as *Lyngbya majuscula* have been suggested to serve as indicators of coral reef health (Golubic *et al.*, 2010). Filamentous chlorophytes (*Cladophora* and others) commonly proliferate in response to nutrients in sewage and animal waste sources that contaminate freshwater streams and rivers (e.g., Stevenson *et al.*, 2012 and references therein). In estuaries and coastal marine systems, the chlorophytes *Ulva*, *Chaetomorpha*, and *Cladophora* spp. are common responders to sewage (Lapointe and O'Connell, 1989; Lapointe *et al.*, 2015 and references therein). The frequency and magnitude of blooms of certain "ephemeral" macroalgae such as *Ulva lactuca* have been considered as an indicator of high nutrient over-enrichment, and seagrass success or failure (Fox *et al.*, 2010; Whitehouse and Lapointe, 2015).

Macroalgal blooms are key ecological indicators of nutrient pollution and coastal eutrophication, and can provide an ideal tool for nutrient monitoring programs. Macroalgae are often attached to benthic substrata (although many blooms can form drift populations) and therefore integrate nutrient availability at a given site over time scales of days to weeks. Opportunistic, fast-growing macroalgae can have rapid nutrient uptake rates, such as the red alga *Gracilaria tikvahiae* (D'Elia and DeBoer, 1978) and the green alga *Ulva lactuca* (Whitehouse and Lapointe, 2015). Accordingly, some macroalgae can be sampled to assess not only relative status of enrichment (nutrient quantity, and the internal tissue percentages of C, N, and P), but also the nutrient source(s) through stable isotope analysis (N [δ^{15}N] and C [δ^{13}C]) of tissues. Macroalgae can be used to discriminate specific nutrient sources in marine ecosystems because there is no fractionation of δ^{15}N values of N sources in N-limited systems (France *et al.*, 1998; Waser *et al.*, 1999; Cole *et al.*, 2004; Savage and Elmgren, 2004; Lapointe *et al.*, 2005b; Deutsch and Voss, 2006; Thornber *et al.*, 2008). Where fractionation has been documented between the N source (groundwater NO_3^-) and macroalgal tissue, enrichment in tissue δ^{15}N was slight (0.2–1.4%; see Umezawa *et al.*, 2002). These measurements allow use of some macroalgae to identify land-based N sources, which can assist policymakers in efforts to reduce nutrient loads through total maximum daily loads and/or basin management action plans (Lapointe *et al.*, 2005a, 2015). For example, studies using macroalgae in Florida have demonstrated utility in discriminating between agricultural and sewage nitrogen sources in estuarine (Lapointe and Bedford, 2007; Lapointe *et al.*, 2015) and coastal environments (Barile, 2004; Lapointe *et al.*, 2004, 2005a). The technique has been used successfully in an array of geographic areas throughout the United States, including Boston Harbor and Waquoit Bay, Massachusetts (France *et al.*, 1998; McClelland and Valiela, 1998); Narragansett Bay, Rhode Island (Thornber *et al.*, 2008); the Florida Keys (Lapointe *et al.*, 2004); southwest Florida (Lapointe and Bedford, 2007); the Indian River Lagoon, Florida (Lapointe *et al.*, 2015); and Maui, Hawai'i (Dailer *et al.*, 2010).

15.6 Uptake/Adsorption of Other Contaminants

Many seaweed species, including those that form blooms, take up inorganic and organic pollutants from the surrounding water or the sediments (Carafa *et al.*, 2007; Cheney *et al.*, 2014; He and Chen, 2014). Brown algae, such as *Sargassum* spp., are known to take up and sequester heavy metals such as lead, copper, cadmium, zinc, nickel, and chromium (reviewed by He and Chen, 2014). These higher uptake rates relative to those of green and red algae are due to the presence of alginate and other cell wall components that have strong affinity for cationic (positively charged) metals (Fourest and Volesky, 1995, 1997). Cations typically are absorbed more quickly by brown algae than anions (negatively charged molecules), and more cationic metals are absorbed in higher pH

waters (Davis *et al.*, 2000). Red and green algae also absorb heavy metals (Rice and Lapointe, 1981; Sfriso *et al.*, 1992; Chakraborty *et al.*, 2014), but generally not as readily as brown algae.

Seaweeds can take up toxic organic compounds from the environment. For example, ulvoid green algae can accumulate polychlorinated biphenyls (PCBs), polycyclic aromatic hydrocarbons (PAHs), and many types of chlorinated pesticides, including dichlorodiphenyltrichloroethane (DDT), dichlorodiphenyldichloroethane (DDD), dichlorodiphenyldichloroethylene (DDE), hexachlorocyclohexane (HCH), and hexachlorocyclobenzene (HCB) (Maroli *et al.*, 1993; Pavoni *et al.*, 2003; Cheney *et al.*, 2014). Sfriso *et al.* (1992) documented seasonal cycles of several persistent organic pollutants in sediments under mats of *Ulva rigida*, which take up and store the compounds. Concentrations of PCBs and nonylphenol polethoxylates in surface sediments markedly increased starting in midsummer as mats of ulvoid algae were decomposing and the organic pollutants in the algae were transferred into the sediments. Thus, the movement of algal mats from a contaminated to an uncontaminated area could also result in the transfer of pollutants that are being absorbed and stored in the algae. Pollutants may also be transferred up the food chain by consumers of the algae that are concentrating the toxins (Cheney *et al.*, 2014). Bloom-forming seaweeds are useful as bioindicators of pollution as they can rapidly absorb heavy metals and organic pollutants (Eide *et al.*, 1980; Chakraborty *et al.*, 2014) and as a means for decontaminating polluted sites (Vieira and Volesky, 2010).

15.7 Impacts on Human Health: Macroalgae as Substrata for Pathogens

Recent research has established that freshwater harmful macroalgae such as *Cladophora* spp. and *Lyngbya wollei* on beaches can concentrate pathogenic fecal bacteria such as *Escherichia coli*, enterococci, and *Clostridium fringens* (Whitman *et al.*, 2003; Paul *et al.*, 2004; Vijayavel *et al.*, 2013). High concentrations of these fecal bacteria were found in *L. wollei* that was growing abundantly in nearshore waters adjacent to a popular recreational beach in Lake St. Clair, Michigan, whereas much lower densities of fecal bacteria were measured in the surrounding water (Vijayavel *et al.*, 2013). A decade earlier, stranded *Cladophora* mats in Lake Erie were found to sustain and nourish the growth of fecal bacteria (Whitman *et al.*, 2003). Samples of *Cladophora* mats along ten beaches in four states bordering Great Lake Michigan were collected in summer 2002, and both *E. coli* and enterococci were ubiquitous (up to 97% occurrence) in the *Cladophora*. The fecal bacteria survived for more than six months in sun-dried mats stored at 4 °C and readily grew upon rehydration at warmer temperature.

Stranded *Cladophora* mats can harbor other human pathogens as well. During a two-year study of the Little Calumet area (Chicago–Lake Michigan and an adjacent ditch), Shiga toxin–producing *E. coli* (STEC) and *Shigella* were detected in 100% and 25% of *Cladophora* samples, respectively, during one year but not the other (Ishii *et al.*, 2006). In addition, the human pathogen *Salmonella* was found in 40% and 80% of ditch and lakeside samples, respectively, with densities as high as 1.6×10^3 cells per gram of *Cladophora*. In addition, there were up to 5.4×10^2 cells of *Campylobacter* per gram of *Cladophora* in 60% and 100% of lake and ditch samples, respectively (Ishii *et al.*, 2006). Such macroalgal repositories for pathogenic microorganisms represent a present-day, potential human health threat along beaches of several Great Lakes where *Cladophora* has again proliferated.

Massive growth of this macroalga, up to 940 g dry mass m^{-2} (median: ~170 g m^{-2}), can extend more than 6 m from shore out into the lake along its northern shoreline, covering up to 100% of the substrata in many locations (Higgins *et al.*, 2005; Stauffer, 2005). Die-off begins in mid-summer and extends into fall each year, wherein *Cladophora* senesces, sloughs from its substrata, and washes ashore. Harris (2005) provided a compelling description:

> The beached algae often accumulate in mats [more than a meter thick] mixed with decaying zebra mussels [*Dreissena polymorpha*], other invertebrates, and fish. The combination results in unsightly, malodorous conditions that drive visitors away from popular beaches and force homeowners to keep their windows shut. . . . Stranded *Cladophora* mats can sustain and nourish the growth of fecal bacteria from gull droppings, sewage overflows, and/or runoff from urban and agricultural areas (Whitman *et al.*, 2003; Paul *et al.*, 2004). Because of its septic odor, the organic mess has been mistaken for manure or sewage from failing septic systems or municipal sewer overflows. In the swash zone, the algae may turn into a

brown-black organic soup with an oily sheen, prompting some people to suspect an industrial waste or oil spill.

Although a number of illnesses occur in recreational users of marine waters (Henrickson *et al.*, 2001), to our knowledge, there are fewer associations between marine macroalgal blooms and human diseases in the United States; however, in the United Kingdom, *Vibrio cholerae* has been found to be associated with macroalgae known to form blooms (*Ulva* spp. and *Polysiphonia lanosa*) (Islam *et al.*, 1994).

15.8 Non-native Invasions

Macroalgae represent about 20% of marine introduced species globally (Andreakis and Schaffelke, 2012), and non-native macroalgal invasions are a major driver of coastal ecosystem change worldwide (UNEP, 2005; Williams and Smith, 2007). Alien macroalgae are increasingly invading coastal waters globally (Grosholz and Ruiz, 1996; Wonham and Carlton, 2005; Miller *et al.*, 2011), and there are more than 120 known introduced species globally (Mathieson *et al.*, 2008). These non-native macroalgae can outcompete native species, reducing biodiversity and leading to alterations of ecosystem structure and function (Vitousek *et al.*, 1997).

To our knowledge, the only freshwater macroalga that has invaded inland U.S. waters is starry stonewort (*Nitellopsis obtusa*) (Figure 15.2d). Thought to be native to Europe, this invader has occurred in various lakes of the upper Midwest (mostly Michigan) and New York since 1978 (United States Geological Survey [USGS], 2016). This charalean species can grow up to 2 m in height at 9-m depths (Pullman and Crawford, 2010). It forms dense mats of vegetation that can completely cover the bottom of shallow lakes and ponds. As its biomass and coverage increase, it covers nearly all of the sediment in a given area and forms irregular, undulating "pillows" of biomass (Pullman and Crawford, 2010). When in decline or dormant, holes open in the starry stonewort mats that resemble the hole pattern of Swiss cheese. Starry stonewort grows well in a wide range of lake types such as clear water or dark water systems, and it is easily transported from lake to lake among aquatic plant debris entangled on boat trailers and anchors. It has shown no apparent preference for shade or full sun (Pullman and Crawford, 2010). Starry stonewort is considered aggressive and has

outcompeted invasive macrophyte species (aquatic vascular plants) such as Eurasian watermilfoil (*Myriophyllum spicatum*), fanwort (*Cabomba caroliniana*), and curly leaf pondweed (*Potamogeton crispus*). Its maximum biomass has been reported at ~260 g m^{-2} (Schloesser *et al.*, 1986; Nichols *et al.*, 1988). This invasive macroalga adversely affects fish spawning habitat by forming a thick mat that impedes access to substrata for nest creation. Its thick growth can completely eliminate spawning activity in the area of infestation (Pullman and Crawford, 2010). On the other hand, there is a strong association between starry stoneworts and invasive zebra mussels, suggesting a mutualistic relationship: the zebra mussels provide nutrients via pseudofeces and feces, and the macroalga provides suitable attachment substrata (Pullman and Crawford, 2010).

Macroalgae that have made transoceanic invasions into coastal waters of North America include the green algae *Codium fragile* var. *tomentosoides* (Fralick and Mathieson, 1973; Malinowski and Ramus, 1973; Carlton and Scanlon, 1985), *Caulerpa taxifolia* (Williams and Smith, 2007), and *Caulerpa brachypus* var. *parvifolia* (Lapointe *et al.*, 2005b); the red algae *Gracilaria tikvahiae* (introduced to Hawai'i; University of Hawai'i, 2001), *Gracilaria vermiculophilla* (Freshwater *et al.*, 2006), *Dasysiphonia japonica* (Schneider, 2010), *Caulocanthus ustulatus* (Miller, 2004), and *Grateloupia turuturu* (Mathieson *et al.*, 2008); and the brown algae *Sargassum muticum* (Scagel, 1956; Aguilar-Rosas and Galindo, 1990), *Sargassum horneri* (Miller *et al.*, 2007), *Colpomenia peregrina* (Green *et al.*, 2012), *Undaria pinnatifida* (Silva *et al.*, 2002), *Lomentaria hakodatensis* (Curiel *et al.*, 2006), and *Cutleria cylindrical* (Hollenberg, 1978). Furthermore, many species that are now considered to be cosmopolitan may owe their broad distributions to transport on the hulls of wooden ships that were transiting the oceans long before the baselines that are used to determine whether a species is native or invasive were established (Carlton, 1996).

Non-native macroalgae are considered harmful when excessive biomass blooms form under certain conditions and environments. Several exotic/invasive macroalgae have invaded coastal waters along the U.S. East Coast. As mentioned above, *Codium fragile* subsp. *tomentosoides* has spread from its native Japan to various parts of the world, including both coasts on the U.S. mainland (Provan *et al.*, 2005 and references therein). Native to Japan, this macroalga is thought to have been carried to New England from Europe on ship hulls

and then spread north to New England in the late 1950s, coincident with the launch of the world's first satellites, the Soviet Union's *Sputniks*. Thus, suspicious New England fishermen called it "sputnik weed," and then "oyster thief," because attachment of its sporelings to oyster (and scallop) shells caused overgrowth and smothering of shellfish aquaculture operations (Trowbridge, 1998 and references therein).

As other examples, *Caulerpa brachypus* f. *parvifolia* was discovered overgrowing deep (25–43 m) coral reef communities off southeast Florida in May 2001, forming dense mats (5–15 cm) covering up to 90% of the reef surface (Figure 15.3d; Lapointe *et al.*, 2005b). Fortunately, this invasive bloom was largely removed by the "twin hurricanes" in summer 2004 (Lapointe *et al.*, 2006), although some re-emergence has since occurred. Along the mid-Atlantic coasts of North America, *Gracilaria vermiculophilla* was first detected in North Carolina in 2000, and in the following years extensive blooms fouled fishing gear and the intake screens at the Brunswick Nuclear Plant (Freshwater *et al.*, 2006).

More than a dozen species of non-native seaweeds have been documented to occur on the U.S. West Coast, but to date none have formed harmful blooms in that region (Miller *et al.*, 2011). These species include algae known to form large, deleterious blooms in other locations, such as *Caulerpa taxifolia* (Williams and Grosholz, 2002), *Codium fragile* spp. *tomentosoides* (Provan *et al.*, 2008), *Undaria pinnatifida* (Thornber *et al.*, 2004), and *Sargassum muticum* (Britton-Simmons, 2004). The lack of spread of the invasive alga *C. taxifolia* in southern California was due to early detection of the introduction and rapid, coordinated eradication efforts by a variety of local, state, and federal agencies in combination with private groups and nongovernmental organizations (Anderson, 2005).

Numerous invasive species have formed harmful blooms in the Hawaiian Islands (Smith *et al.*, 2002; Figure 15.3e). Problematic species have included the rhodophytes *Acanthophora spicifera*, *Gracilaria salicornia*, *G. tikvahiae*, *Hypnea musciformis*, and *Kappaphycus* spp., and the chlorophytes *Avrainvillea amadelpha* and *Dictyosphaeria cavernosa* (Stimson *et al.*, 2001; Smith *et al.*, 2002). Some of these introductions occurred accidentally via transport by boats (e.g., *A. spicifera*), whereas others, such as *G. salicornia*, *G. tikvahiae*, and *Kappaphycus* spp., were deliberately introduced for aquaculture operations (University of Hawai'i, 2001; Smith *et al.*, 2004). The ability of many of these species to spread by vegetative propagation (Smith *et al.*, 2002, 2004), coupled with rapid growth in response to N inputs (Stimson *et al.*, 2001), enable populations of these invasives to rapidly expand, especially in areas where N inputs from sewage and stormwater runoff occur (Lapointe and Bedford, 2011).

15.9 Ecological and Ecosystem-Level Impacts

The ecological impacts of macroalgal blooms depend on many factors, including the level of biomass, duration of bloom, morphology of the species involved, habitat (e.g., seagrass meadow, coral reef, rocky intertidal, or soft-bottom community), and a variety of local physical, chemical, and biological factors. Recent studies have attempted to quantify at what biomass level(s) environmental effects on natural benthic communities occur. Bona (2006) reported effects on benthic habitats at biomass levels of ~90 g dry wt. m^2 and > 70% cover; while Scanlan *et al.* (2007) suggested an "effects" threshold of 70–120 g dry wt m^{-2}, and Green *et al.* (2014) reported significant impacts on benthic invertebrates at 110–120 g dry wt m^{-2} and 100% cover following a month of biomass cover. Additionally, a range of 3–15 g dry wt. m^{-2} was recently suggested as a transition zone from reference conditions in eight California estuaries (Sutula *et al.*, 2014). Given this range of estimates, it is likely that effects vary by geographic location and conditions.

Macroalgal response to nutrient enrichment often translates to rapidly developing canopies ranging from 0.75 m to more than 2 m in thickness (Sfriso *et al.*, 1992; Hauxwell *et al.*, 2001a) with high biomass – for example, 650 g dry wt m^{-2} of *Gracilaria tikvahiae* mixed with other macroalgae known to thrive in nutrient overenriched conditions, such as the chlorophytes *Ulva* and *Cladophora* (Havens *et al.*, 2001). These high-biomass macroalgal outbreaks typically form thick layers or "blankets" on the bottom or over the water surface that impede or outright block oxygen diffusion into the water from the overlying air (also see Section 15.10.1). Thick macroalgal drift assemblages can promote increased hypoxia/anoxia and hydrogen sulfide stress in the water column and sediments below, exacerbated by high macroalgal respiration during the night (Hauxwell and Valiela, 2004; Van Alstyne *et al.*, 2015b). Due to high respiration rates, the macroalgal canopies

themselves commonly become hypoxic or anoxic at night, and sometimes even during the day (Hauxwell and Valiela, 2004). In shallow coastal ecosystems, the respiration of all of that biomass can also deplete the water column of dissolved oxygen, leading to suffocation and death of beneficial aquatic life (Harlin, 1995; Burkholder and Glibert, 2013 and references therein).

Macroalgal-dominated systems sustain inputs of large amounts of labile organic matter when the algae die and decompose periodically due to self-shading, other stressors, and seasonal growth patterns (Havens *et al.*, 2001 and references within). Macroalgae generally release labile (readily biologically available) nutrients rapidly during decomposition, which fuel additional outbreaks when conditions become favorable (Buchsbaum *et al.*, 1991; Havens *et al.*, 2001). Major quantities of DIN (directly used by most algae) and dissolved organic N and P (some forms used by algae, various forms used by bacterial decomposers) are released to the water (up to 850 μmol/m^2) when the algae die and decompose (Havens *et al.*, 2001; Gao *et al.*, 2013 and references therein). Macroalgal die-offs commonly cause a sudden increase in oxygen demand as well (Valiela *et al.*, 1992; Duarte, 1995). A major ecosystem impact that repeatedly has been noted is that harmful macroalgal blooms depress biodiversity (NRC, 2000; Lyons *et al.*, 2014 and references therein). The loss of biodiversity can, in turn, alter bioturbation, nutrient generation, invasion resistance, secondary production, and resource use (Solan *et al.*, 2004; Stachowicz *et al.*, 2007).

Following decades of macroalgal blooms, unprecedented phytoplankton blooms (including a brown tide) developed in 2011 and 2012 in the Indian River Lagoon in east-central Florida (Lapointe *et al.*, 2015). These blooms caused severe light limitation and extensive seagrass loss (> 60%) that coincided with unusual mortality events (UMEs) involving endangered manatees, dolphins, and pelicans. Necropsies of dead manatees revealed stomachs full of macroalgae, especially *Gracilaria* spp., along with severe intestinal irritation and bleeding, suggesting an apparent "toxic shock syndrome." This raised concerns about possible intoxication of the manatees following the phytoplankton HAB events. During the period of unusually high manatee mortalities in the northern Indian River Lagoon in spring and summer 2013, *Gracilaria tikvahiae* and associated drift macroalgal communities, which became a primary food source for manatees following seagrass die-off, were sampled at a manatee mortality "hot spot" at Shorty's Pocket, an embayment along

the Banana River, in May and July of 2013. The mixed macroalgal communities were dominated by red drift algal species including *G. tikvahiae*, *Acanthophora spicifera*, *Hypnea musciformis*, and *Hydropuntia secunda*, but also included conspicuous blooms of the green alga *Chaetomorpha linum*, as well as cyanobacterial mats. The macroalgae in this section of the northern Indian River Lagoon have unusually high N:P ratios, which has been known to cause increased toxicity in some species (Lapointe *et al.*, 2015). As such, toxin dose–response assays of *G. tikvahiae* extracts showed high toxicity activity to mammalian cells (Neuro 2A cells, MCF7 cells) from abundant cyanogenic glycosides (Lapointe and Herren, 2015). Although the drift macroalga *G. tikvahiae* is not generally considered toxic to humans, human intoxication due to consumption of *Gracilaria edulis* (now *Polycavernosa tsudai*) did affect 13 people who ingested the raw seaweed in Guam, three of whom died (Halstead and Haddock, 1992). Similarly, a novel glycosidic macrolide, polycavernoside A, was isolated from the *G. edulis* and was considered responsible for the poisoning (Yotsu-Yamashita *et al.*, 1993). A sewage outfall at 18 m depth, to the north of the reef flat where the *G. edulis* was collected, was considered a possible factor by the Guam Environmental Protection Agency. These seemingly unrelated events suggest that nutrient enrichment and alterations of N:P ratios may increase toxicity of macroalgae to mammals.

15.9.1 Regime Shifts

Many of the ecological and ecosystem impacts caused by macroalgal blooms are relatively short-lived effects from which systems recover as blooms die out or are removed. In some cases, however, changes to ecosystems persist even after the blooms are gone. These regime shifts (also referred to as *phase shifts* or *changes to alternate stable states*) are abrupt, persistent changes in ecosystem structure that typically involve multiple interacting abiotic and biotic drivers (Scheffer *et al.*, 2001; Scheffer and Carpenter, 2003; Rocha *et al.*, 2015).

The following traits are characteristic of regime shifts involving blooms of macroalgae: (1) one of the most common causes of regime shifts in estuaries is excessive nutrient input (Troell *et al.*, 2005; Petersen *et al.*, 2008; Rocha *et al.*, 2015). (2) Multiple causes often interact, such as an invasive species in combination with eutrophication, which can lead to total reorganization of the

food web (Kraberg *et al.*, 2011; Lapointe and Bedford, 2011). (3) Community composition, species dominance, and peak abundance of species can be affected by a regime shift. (4) The new dominant species in the affected ecosystem remains long-term (years), as documented for various macroalgal taxa in coastal lagoons that have undergone a regime shift in response to eutrophication (e.g., Curley *et al.*, 1971; Lee and Olsen, 1985; Valiela *et al.*, 1997). While benthic macroalgae often replace rooted macrophytes (Burkholder *et al.*, 2007; Hastings, 2013 and references therein), shallow macrophyte-free systems have also been shown to undergo regime shifts to undesirable benthic or benthic and floating macroalgae (Genkai-Kato *et al.*, 2012).

Two notable types of regime shifts caused by macroalgal blooms in U.S. waters are ecosystem regime shifts on coral reefs, which have been increasingly impacted by expansion of macroalgae and filamentous algal turfs and loss of hermatypic (reef-forming) corals, and shifts between rooted macrophytes and undesirable benthic or benthic and floating macroalgae in estuaries (Burkholder *et al.*, 2007; Genkai-Kato *et al.*, 2012; Hastings, 2013 and references therein).

Case studies have linked macroalgal blooms to regime shifts and degradation of seagrass habitats in a broad range of environmental settings (NRC, 2000). Early studies in an urbanized estuary (Tampa Bay, Florida) showed that excessive nutrient loading from sewage, especially N, supported extensive blooms of *Gracilaria*, *Ulva*, and *Chaetomorpha* spp. (Hagan, 1969; Guist and Humm, 1976) that averaged up to 195 g dry wt m^{-2} in bay-wide surveys (Mangrove Systems, 1985). These drift blooms not only were harmful to seagrasses and overall biodiversity in Tampa Bay, but also caused noxious odors along shorelines that became unacceptable to the public (Hagan, 1969). Odor was the driving issue that forced improved sewage treatment, including nitrogen removal. Following more than 90% reduction of N loading to Tampa Bay since 1979, macroalgal and phytoplankton blooms have diminished over the subsequent decades and seagrass cover has recently returned to its 1950s level (Greening *et al.*, 2014). Similar excessive macroalgal blooms have developed in other nutrient-enriched seagrass systems, including the Florida Keys, Florida (Lapointe *et al.*, 1994; Green *et al.*, 2015); Waquoit Bay, Cape Cod, Massachusetts (Valiela *et al.*, 1992, 1997; Peckol *et al.*, 1994; Hauxwell *et al.*, 2001b); Narragansett Bay, Rhode Island (Thornber *et al.*, 2008); and the Indian River Lagoon, Florida (Lapointe *et al.*, 2015).

Regime shifts on coral reefs are now happening globally; however, the first example of this came from Kane'ohe Bay, Hawai'i, where the green "bubble alga" *Dictyosphaeria cavernosa* overgrew and killed corals as a result of nutrient enrichment from sewage (Banner, 1974; Smith *et al.*, 1981). Dramatic macroalgal blooms and loss of corals occurred on fringing reefs in Jamaica during the 1980s, and the cause of this regime shift was suggested to be solely due to reduced grazing following the die-off of the long-spined sea urchin *Diadema antillarum* and overfishing of herbivorous fishes; the various fringing reefs that were monitored in the study were all assumed to be unpolluted sites (Hughes, 1994). Other studies, however, had documented elevated N (as NO_3^-) availability from groundwater and river discharges on many of the affected reefs, as well as NH_4^+ at some sites impacted directly by sewage associated with urbanization and tourist resorts (Lapointe, 1997; Lapointe *et al.*, 2011). Following years of scientific debate on this issue, it is now generally accepted that bottom-up (nutrients) and top-down (grazing) operate simultaneously to influence the outcome of regime shifts on a particular coral reef. For example, increasing nutrients combined with overfishing on reefs in Negril, Jamaica, have led to the combination of low cover of corals (5–10%) and turfs (15%) and high macroalgae (65%) (Figure 15.4a); in comparison, increasing nutrients in combination with intense grazing by large, mobile herbivorous fishes (parrotfishes and tangs) at Looe Key Sanctuary Preservation Area (SPA) in the Florida Keys have resulted in equally low coral cover (5–10%), moderate levels of macroalgae (20–25%), and high levels of algal turfs (50%; Figure 15.4b; Lapointe and Thacker, 2002). The escalating nutrients in both Jamaica and the Florida Keys are driving the cover of coral lower and overall benthic algae higher, but the intense grazing at Looe Key SPA maintains relatively lower cover of macroalgae and higher cover of turfs. Additionally, physical disturbance (e.g., turbulence, storm events) can act to keep macroalgal cover at low levels, allowing turf algae to dominate. Recognizing that corals are adapted to oligotrophic conditions, the regime shifts toward less coral and more macroalgae and/or algal turfs that has been occurring throughout the Caribbean since the 1970s appear to be driven by increasing nutrient subsidies from upland watersheds and not solely related to changes in herbivorous fishes (Suchley *et al.*, 2016).
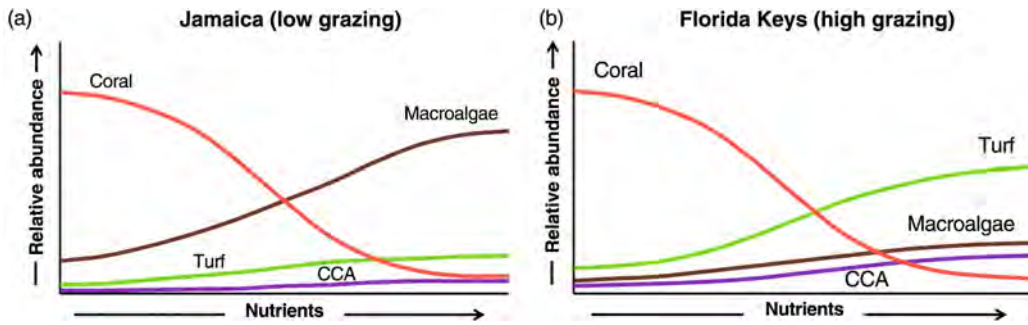
Figure 15.4 Effects of increasing nutrient availability on relative abundance of macroalgae, turf algae, and crustose coralline algae (CCA) on coral reefs. Under conditions of increasing nutrients and low grazing such as the north coast of Jamaica (a), macroalgae become dominant relative to corals, turf algae, or CCA. Under conditions of increasing nutrients and high grazing (or high levels of physical disturbance such as water turbulence) such as the Florida Keys (b), turf algae become dominant relative to corals, macroalgae, or CCA.

15.9.2 Freshwater Macroalgal HAB

15.9.2.1 Filamentous Cyanobacteria

Among the best-known noxious benthic cyanobacteria bloom formers is *Lyngbya wollei*, which is closely related to *Lyngbya majuscula*, a noxious cyanobacterial mat former in marine waters (Speziale and Dyck, 1992). This freshwater species occurs in temperate to tropical, alkaline, or mildly acidic freshwaters in lakes and rivers across North America (Hudon *et al.*, 2014). Blooms of *L. wollei* have been documented for more than 100 years (e.g., Wolle, 1887), but reports of increased abundance are becoming more common in the eastern and southeastern United States (Hudon *et al.*, 2014 and references therein). Thus, this alga is commonly considered as a native species that acts as an opportunistic invader (e.g., PBS&J, 2004; Hudon *et al.*, 2014), or as "an initial aggressive colonizer," for example following natural disturbances (Cowell and Botts, 1994). In situations when other primary producers are limited by unfavorable environmental conditions or are physically removed, *L. wollei* has proliferated (Evans *et al.*, 2007; Hudon *et al.*, 2014). This species is diazotrophic (i.e., it can "fix" nitrogen gas into ammonia), and it can produce an array of aplysiatoxins: cylindrospermopsin, deoxy-cylindrospermopsin, lyngbyatoxin, and saxitoxin analogs (e.g., decarbamoylsaxitoxin and decarbamoylgonyautoxin) (Camacho and Thacker, 2006; Seifert, 2007; Foss *et al.*, 2012).

Initially, *L. wollei* grows attached in a benthic habit, later forming dense free-floating mats in lakes, reservoirs, streams, and springs. Maximal biomass is attained in summer–early fall at a high optimum temperature for growth. Nevertheless, in warm temperate climates such as much of the southeastern United States, *L. wollei* has overwintered while maintaining high biomass (~120–440 g dry wt m^{-2}) (Hudon *et al.*, 2014 and references therein). Other characteristics additionally enable *L. wollei* to proliferate: it is well adapted to low light, and viable populations occur down to 0.05% (15 μEinst m^{-2} s^{-1}) to 1% of incident photosynthetically active radiation (e.g., Speziale *et al.*, 1991; Panek, 2012 and references therein). Photobleaching of external filaments protects the rest of the mat from damage by ultraviolet light. Very low dissolved inorganic carbon (C_i) concentrations can saturate its photosynthesis and growth (Speziale *et al.*, 1991), which would enhance survival in C-limited situations such as the interior of its thick mats. Conditions that enhance photorespiration (e.g., high midday temperatures and high oxygen concentrations) characterize floating mat environments, but photorespiration is minimal in *L. wollei*, probably because it has highly efficient C-concentrating mechanisms and can use bicarbonate as a C source (Beer *et al.*, 1986, 1992 – note that in the latter publication, *L. wollei* was referred to as *L. birgei*).

This benthic cyanobacterium is strongly stimulated by nutrient over-enrichment. Harmful effects have included clogged water intakes, offensive odors, the production of potent toxins, and compromised recreational and potable water use (Hudon *et al.*, 2014 and references therein). Massive mats of *L. wollei* have been reported, such as a mat that was estimated to be 10 m long, 1 m wide, and up to 0.5 m thick, with biomass as high as 1508 g dry wt m^{-2} (Hudon *et al.*, 2014 and references therein). This species has caused major, adverse habitat alteration and aesthetic impairment in various reservoirs of the southeast

(Speziale and Dyck, 1992 and references therein), and in formerly clear, deep Florida springs (Stevenson *et al.*, 2007). Increases have been observed in tributaries that drain agricultural lands in the St. Lawrence River (Hudon *et al.*, 2014); and there has been recent proliferation in western Lake Erie (Bridgeman and Penamon, 2010). A shift in composition of benthic macroalgae in a fluvial lake, from chlorophyceans *Cladophora* and *Hydrodictyon reticulatum* to cyanobacteria *Lyngbya wollei* and *Gloeotrichia*, was related to elevated nitrate from agricultural drainage (Vis *et al.*, 2008).

Wetlands dominated by *L. wollei* have been found to support lower biomass of invertebrates and large fish, lower species richness, and more slowly growing juvenile fish (perch, *Perca flavescens*) than macrophyte (vascular plant)–dominated wetlands (Hudon *et al.*, 2012). Some strains of this cyanobacterium apparently are toxic to certain amphipod species (Camacho and Thacker, 2006; Gélinas *et al.*, 2013). Grazer biomass was significantly lower in areas with abundant *L. wollei*, which apparently was related to reduced food and habitat availability through declines in beneficial macrophytes and associated epiphytes (Lévesque *et al.*, 2012). Replacement of macrophytes by *L. wollei* mats shifted trophic structure, decreased carrying capacity for fish, and significantly altered ecosystem dynamics (Hudon *et al.*, 2014). While mammal deaths have not been linked to *L. wollei*, dog deaths have occurred following ingestion of benthic *Phormidium* mats containing anatoxin-producing strains (Puschner *et al.*, 2008; McAllister *et al.*, 2016). Dogs also reportedly were killed by ingesting toxic benthic *Oscillatoria* mats (Gunn *et al.*, 1992).

15.9.2.2 Filamentous Green Algae
These are common responders to nutrient pollution, often forming massive, slimy growths at or near the water surface in areas affected by sewage and other nutrient over-enriched conditions (Perrin *et al.*, 1988; Mackay, 2006; Benke and Cushing, 2011), and the excessive growth can cause major diel DO fluctuations and "sags" (Pitcairn and Hawkes, 1973; Kirk, 1994). In the western United States, for example, filamentous green algae such as *Cladophora* and *Pithophora oedogonia*, as well as the streptophyte *Chara*, have been listed as among the most consistently problematic aquatic weed species (Anderson, 1990). In the Great Lakes, early post-invasion of zebra mussels was characterized by increased available light and a shift in dominance of benthic algae from diatoms to *Spirogyra* sp., later co-occurring with *Cladophora* (Pillsbury *et al.*, 2002 and references therein).

The best-known harmful macroalgae in freshwaters, *Cladophora* spp. (*C. glomerata* and others), are major responders to P enrichment (Higgins *et al.*, 2008 and references therein; Auer *et al.*, 2010). Rocky substrata in alkaline lakes and streams of the upper Midwest and the western United States provide habitat for *Cladophora* blooms (Lembi, 2003; Sandgren *et al.*, 2005; DiTomaso *et al.*, 2013). In the Illinois River basin, for example, attached *Cladophora* was found to grow optimally under high P enrichment (600 μg TP/L; Leland and Porter, 2000).

Among the most renowned habitats for *Cladophora* blooms are the Laurentian Great Lakes. In the 1960s–1970s, *Cladophora* (*C. glomerata* and others) proliferated in the west basin of Great Lake Erie in response to P pollution, then drifted into shore in rotting masses from major seasonal die-offs that were sometimes measured in tonnes of fresh weight (Higgins *et al.*, 2005, 2008). Major reductions in point-source inputs of P through upgrades in wastewater treatment and detergent P bans led to a dramatic reduction of *Cladophora* during the 1970s and early 1980s, but the Great Lakes soon became a *Cladophora* story of "déjà vu" (Higgins *et al.*, 2008 and references therein). Invasions of zebra mussels followed by quagga mussels (*Dreissena bugensis*) resulted in their domination of nearshore benthic environments by the late 1980s. The increased metabolic wastes from mussels were a major source of internal P loading, and their filtering activity cleared the water and increased light penetration (Hecky *et al.*, 2004; Auer *et al.*, 2010). By the 1990s, the mean peak biomass of *Cladophora* was similar to historic values in Lake Erie during the 1960s–1970s, and has remained so (Auer *et al.*, 2010; Tomlinson *et al.*, 2010); surface mats can extend more than 6.1 m out into the water (Stauffer, 2005). From 1995 to 2002, the northern shoreline of the eastern basin had maximum production of ∼12,000 tonnes dry mass during the spring growth phase and removed an estimated 15 tonnes of P within 30 days (Higgins, 2005; Higgins *et al.*, 2005); shorelines along portions of Lakes Ontario, Michigan, and Huron are also being fouled by rotting *Cladophora* growth (Garrison and Greb, 2005; Higgins *et al.*, 2008).

The Canale and Auer model, later modified as the *Cladophora* Growth Model (CGM) and then as the Great Lakes *Cladophora* Model (GLCM), has been successfully validated on field populations in multiple locations of the Great Lakes (Tomlinson *et al.*, 2010 and references therein). The models indicated that *Cladophora* growth

extended to deeper waters post-*Dreissena*, and that *Dreissena*-induced changes in water quality were responsible for the dramatic resurgence of *Cladophora* (Higgins *et al.*, 2006). While dreissenid mussel abundance is a major factor controlling the magnitude of *Cladophora* production, catchment land cover and nearshore water quality (nutrient levels and suspended solids) are also important (Depew *et al.*, 2011); P from dreissenid mussel wastes apparently is insufficient to produce severe blooms without localized P enrichment (Higgins *et al.*, 2012); and P management from land-based sources "remains the appropriate mechanism for reducing nuisance levels of *Cladophora* growth" (Auer *et al.*, 2010, p. 248).

Most ecological information about freshwater filamentous macroalgae is for *Cladophora*, which has overgrown and displaced beneficial aquatic plants, reduced invertebrate densities and fish spawning, and reduced species biodiversity (Neil, 1975; Ozimek *et al.*, 1991; Zulkifly *et al.*, 2013 and references therein). Decaying mats of *Cladophora* have caused or contributed to anoxia, resulting in kills of other aquatic life (Burkholder, 2009 and references therein), and the mats have retained pathogenic microbes that cause human disease as explained above. The substantial contribution of *Cladophora* (and, more recently, *Lyngbya wollei*) blooms to hypoxia/anoxia zones in Lake Erie has threatened the habitats and food resources needed by sport fish such as walleye (*Sander vitreus*) and yellow perch (*Perca flavescens*) (Arend *et al.*, 2011; Hinderer *et al.*, 2011). Recently, however, it has been increasingly recognized that *Cladophora* also can act as an ecosystem or ecological engineer (i.e., an organism that creates, modifies, and maintains habitat – Jones *et al.*, 1994) by increasing benthic habitat complexity, providing spatial refugia, enhancing sedimentation, reducing current velocity, and shading substrata (Ward and Ricciardi, 2010; Zulkifly *et al.*, 2013; note that similar findings have been reported for *Cladophora* in estuarine habitats – Kraufvelin and Salovius, 2004). This alga also transforms key resources such as P and C from one form to another, thereby controlling resource supplies and cycling on scales that may influence global littoral biogeochemistry (Zulkifly *et al.*, 2013).

15.9.3 Estuarine and Coastal Marine HAB

Seagrass meadows are a common feature of many shallow estuaries and coastal waters in temperate, subtropical, and tropical regions. Seagrasses are highly productive and provide important ecological services, including biodiversity, fisheries habitat, and sediment stabilization, all of which are important to local and regional economies. Like all plants, they require nutrients to grow. In excess, however, nutrients cause decline of seagrass communities (Burkholder *et al.*, 2007; Cabaço *et al.*, 2013) as a result of several factors, including macroalgal blooms. Seagrasses grow relatively slowly in comparison to macroalgae, which can double their biomass in only a few days under nutrient-enriched conditions (Whitehouse and Lapointe, 2015). They also have higher light requirements than many macroalgae, so shading from increased epiphytic fouling, macroalgal overgrowth, and phytoplankton blooms reduces their productivity and growth. Macroalgae can initially grow as epiphytes on seagrasses and eventually break loose, forming thick drift mats that block light from reaching the underlying seagrasses, leading to the loss of seagrass meadows (Burkholder *et al.*, 1992, 2007; Lapointe *et al.*, 1994; Hauxwell *et al.*, 2001b; McGlathery, 2001).

On the U.S. West Coast, nutrient enrichment from upwelling can contribute to the formation of macroalgal blooms that, in some locations, affect the native eelgrass (*Zostera marina*). On the Oregon coast, spatial and interannual variation in macroalgal abundances positively correlates with upwelling (Hessing-Lewis and Hacker, 2013). Although eelgrass abundances were negatively correlated with macroalgal abundances over large spatial scales, there was no temporal correlation. Field experiments conducted in the Coos Bay Estuary, Oregon, demonstrated that ulvoid macroalgae can cause declines in eelgrass abundance at riverine sites, but not at marine sites, suggesting that increased macroalgal growth due to upwelled nutrients along the Oregon coast impacts eelgrasses that experience other physiological stresses such as light limitation (Hessing-Lewis *et al.*, 2011). Because upwelling in this region results in naturally high nutrient concentrations in marine and estuarine waters, it has been suggested that even small anthropogenic inputs of nutrients could cause nutrient levels to exceed a "tipping point," leading to increased algal growth in nearshore waters (Thom and Albright, 1990).

Coral reefs are among the most productive and biologically diverse ecosystems in the world. Coral reefs are distributed in nutrient-poor surface waters in the tropics and subtropics, and increases in nutrient loading can result in regime shifts away from coral to dominance by macroalgae and smaller filamentous algal turfs as noted previously

(Bell, 1992; Lapointe, 1997; NRC, 2000; Fabricius, 2005). For example, in Kane'Ohe Bay, Hawai'i, increased nutrient loading from sewage outfalls in the 1960s led to blooms of the green alga *Dictyosphaeria cavernosa* (Smith *et al.*, 1981). Since then, invasions of non-native macroalgae have led to harmful macroalgal blooms in coastal waters of the Hawaiian Islands, including urbanized areas in Maui where sewage pollution has led to blooms of *Hypnea musciformis* and *Ulva* spp. (Dailer *et al.*, 2012). In highly urbanized southeast Florida, sewage pollution was a primary factor causing a succession of macroalgal blooms and invasions on fringing coral reefs. Spectacular blooms of unattached *Codium isthmocladum* developed during summer months in 1989–1990 on deep reefs (24–43 m) off southern Palm Beach and northern Broward counties (Figure 15.3f and 15.3g); these were followed by blooms of the non-native *Caulerpa brachypus* in the late 1990s (Figure 15.3d). Studies measuring carbon: nitrogen: phosphorus ratios (C:N:P) and stable nitrogen isotopes (δ^{15}N) in macroalgal tissue linked these blooms to nutrient enrichment from sewage outfalls and land-based runoff (Lapointe *et al.*, 2005a, 2005b; Lapointe and Bedford, 2010). Despite a well-funded Water Quality Protection Program since 1991, macroalgal blooms have also increased in frequency and extent throughout the Florida Keys National Marine Sanctuary (Figure 15.3h, 15.3i, and 15.3j). A distinct increase in the frequency and extent of these blooms followed the political decision to increase freshwater discharges and N-loading from the Everglades to Florida Bay between 1991 and 1995 (Lapointe *et al.*, 2004, 2007; Collado-Vides *et al.*, 2007). In response to this increased N-loading, coral reefs in southern Florida Bay were overgrown by thick mats of *Cladophora* spp. (Lapointe *et al.*, 2007), which respond to increasing N enrichment as inorganic N or urea by producing blooms (Zulkifly *et al.*, 2013). Research by Lapointe *et al.* (2004) in the lower Florida Keys indicated that both agricultural runoff and local sewage discharges from septic effluent leachate were significant N sources supporting blooms of the filamentous macroalgae *Cladophora catenata* (Chlorophyta, Ulvophyceae) and *Cladosiphon occidentalis* (Heterokontophyta, Phaeophyceae) in coral reef and seagrass ecosystems, respectively. Similar blooms of *Cladophora* spp. have developed in N-enriched environments in Bermuda (Lapointe and O'Connell, 1989) and Hawai'i (Smith *et al.*, 2005).

Benthic cyanobacterial mats are considered rare on healthy coral reefs, but proliferate on damaged colonies and coral rubble and form loose mats over sandy sediments (Golubic *et al.*, 2010). Highest abundance of these mats has been found on sheltered reefs close to urbanized areas, which has been related to anthropogenic nutrient pollution (Brocke *et al.*, 2015). Reefs with high abundance of benthic cyanobacterial mats have also been characterized by high benthic macroalgal cover and depressed cover of corals (Brocke *et al.*, 2015). Growth of the noxious inhabitant of coral reefs, *Lyngbya majuscula*, has been experimentally stimulated by P, N, and iron enrichment (Ahern *et al.*, 2008).

15.10 Effects of Blooms on the Chemistry of the Oceans and the Atmosphere

Macroalgal blooms consist of high biomass of algae that respire, photosynthesize, and take up and release inorganic and organic compounds from and into seawater, and thus can cause significant changes in seawater chemistry. Large blooms of intertidal and shallow subtidal seaweeds may also affect atmospheric chemistry by emitting volatile compounds either directly into the air or into shallow waters where they eventually cross the sea–air boundary and become airborne.

15.10.1 Changes to Carbonate Chemistry and pH

High macroalgal biomass can affect gas levels in the surrounding seawater through physiological processes (respiration and photosynthesis), by physically altering the air–sea interface, and by promoting bacterial growth. The specific patterns of dissolved gas changes will depend on the size and physiological state of the bloom as well as topographical features of the site and localized water flows.

CO_2 or bicarbonate (HCO_3^-) is removed from seawater during the day by photosynthesizing macroalgae, therefore daytime pH levels near macroalgal accumulations can be dramatically higher than nighttime levels (Middleboe and Hansen, 2007; Saderne *et al.*, 2013). In waters near a small ulvoid algal bloom in Washington State, the difference between daytime and nighttime pH levels exceeded 1.5 pH units during spring–early summer tides (Van Alstyne *et al.*, 2015a), well above the average pH changes expected due to ocean acidification. The high-pH and low-carbon

conditions generated by ulvoid algae in tide pools can reduce photosynthetic rates of other algae (Bjork *et al.*, 2004). Similarly, photosynthetic rates of eelgrass (*Zostera marina*) growing beneath a single layer of *Ulva* were reduced in part because of the high pH caused by algal photosynthesis, but also because of the lower levels of light available to the eelgrass (Mvungi *et al.*, 2012).

15.10.2 Release of Materials and Chemicals into Seawater

Macroalgal blooms are frequently ephemeral and can be a source of particulate matter and dissolved organic and inorganic compounds when chemicals leak through cell membranes of healthy algae or are released as algae senesce or decompose (e.g., Sieburth and Jensen, 1969; Hanson, 1977; Boyer and Fong, 2005). The production of this material can have ecological consequences, including providing a supply of nutrients and carbon for microbial and detritivore communities and moving nutrients from algae into nearby waters and sediments (Nielsen *et al.*, 2004; Hardison *et al.*, 2010).

Some bloom-forming seaweeds also produce and release toxic or allelopathic organic compounds that affect organisms in nearby pelagic or benthic communities. Many red macroalgae have gland cells with inclusions that contain halogenated (bromine, iodine) substances with antimicrobial, antiherbivore, or other allelopathic functions (Paul *et al.*, 2006). Red algae produce the widest variety of toxic secondary metabolites among the algae, including many halogenated terpenoids and even domoic acid (Graham *et al.*, 2016 and references therein).

Many species of ulvoid green algae produce allelochemicals whose effects include reducing densities of barnacles in tidepools (Magre, 1974); causing mortality in crab larvae (Johnson and Welsh, 1985), oyster larvae (Nelson *et al.*, 2003a; Nelson and Gregg, 2013), and juvenile abalone (Wang *et al.*, 2011); inhibiting the growth of planktonic microalgae (Jin and Dong, 2003; Wang *et al.*, 2009; Tang and Gobler, 2011) and benthic macroalgae (Nelson *et al.*, 2003a); and reducing fouling by epiphytic bacteria, algae, and invertebrates (Egan *et al.*, 2000; Nelson *et al.*, 2003b; Harder *et al.*, 2004; Hellio *et al.*, 2004).

The compounds mediating these interactions have been identified in some cases. For example, the bloom-forming ulvoid alga *Ulvaria obscura* releases dopamine into the surrounding seawater when it is stranded during low tide, becomes

desiccated, and is rehydrated during an incoming tide (Van Alstyne *et al.*, 2011, 2013). In seawater, dopamine oxidizes to form a variety of quinones. Dopamine or the quinones resulting from it reduce the growth and germination rates of other seaweeds and increase mortality rates of crab zoeae (Van Alstyne *et al.*, 2014). All ulvoid algae examined to date produce dimethylsulfoniopropionate (DMSP), a small sulfonium compound (Van Alstyne, 2008) that has been shown to inhibit the growth of epiphytic bacteria on *Fucus vesiculosus* (Saha *et al.*, 2014). Although the effects of DMSP from ulvoid algae have not been examined, DMSP may be responsible for mediating many of the allelopathic interactions involving these algae. The invasive bloom-forming macroalga *Caulerpa racemosa* produces several related sesquiterpenes that can have biological activity (Amade and Lemée, 1998). One of them, caulerpenyne, causes decreases in the photosynthetic efficiency of a native Mediterranean seagrass, *Cymodocea nodosa*, at concentrations of 10 ppm (Raniello *et al.*, 2007), which may help the alga outcompete native macrophytes. Fucoid brown algae produce and release phlorotannins, phloroglucinol-based polyphenolic compounds (Amsler and Fairhead, 2005). Phlorotannins from *Sargassum natans* and *S. fluitans* have been shown to inhibit the growth of epiphytic bacteria and invertebrates (Sieburth and Conover, 1965).

Another group of harmful molecules that is released by macroalgae is reactive oxygen species (ROS). ROS are produced as a result of photosynthesis and respiration (Halliwell and Gutteridge, 2015; Lesser, 2006; Bischof and Rautenberger, 2012) and can damage lipids, proteins, and DNA (Fridovich, 1978; Asada and Takahashi, 1987; Halliwell and Gutteridge, 1989), but are also used as signaling molecules in stress responses to changes in temperature, salinity, and desiccation (Miller *et al.*, 2008). Most ROS are scavenged by a variety of enzymatic and non-enzymatic antioxidants (Ledford and Niyogi, 2005); however, when algae are not able to scavenge ROS, which can occur when they are stressed, and the production of ROS increases or antioxidant production decreases (Collén and Davison, 1999a, 1999b, 2001), ROS can diffuse into the surrounding seawater where they can impact other organisms (Collén and Pedersén, 1994; Collén and Davison, 1997; Küpper *et al.*, 2001; Abrahamsson *et al.*, 2003; Choo *et al.*, 2004; Barros *et al.*, 2006; Van Alstyne *et al.*, 2013). The generation and release of ROS during microalgal blooms can be toxic toward fish (see Chapter 7 of this volume). Seaweeds, including species that form large blooms, also release ROS

(van Hees and Van Alstyne, 2013); however, little is known about the effects on nearby organisms.

15.10.3 Release of Volatile Compounds

During low tide, marine macroalgae release into the atmosphere complex mixtures of small, volatile organic compounds (Moore, 1977; Paul and Pohnert, 2011), which can be the source of the characteristic odors of macroalgal blooms. These compounds include a variety of chemical types, such as halomethanes, halogenated hydrocarbons, halogenated and non-halogenated terpenes, aromatic compounds, oxylipins, and small sulfur compounds (Paul and Pohnert, 2011). Several of these compounds, especially isoprene and brominated organic compounds, can affect ozone depletion (Schauffler *et al.*, 1999; Quack *et al.*, 2004). The biogenic production of dimethyl sulfide (DMS) can contribute to acid precipitation and climate change, and has been hypothesized to impact cloud formation in remote environments (Charlson *et al.*, 1987). Whether large growths of seaweeds are important sources of atmospherically significant volatile compounds is not well known. Bromoform and methyl bromide production by kelps (Manley *et al.*, 1992) and the production of halogenated compounds by large seaweed farms (Leedham *et al.*, 2013) have been suggested to be large enough to influence atmospheric chemistry. In contrast, with the exception of the release of volatile sulfur compounds by ulvoid algae, little is known about the potential significance of the release of volatiles by seaweed blooms.

In ulvoid algae, the biochemical cleavage of dimethylsulfoniopropionate (DMSP) to form DMS is triggered by a number of environmental factors, including physical damage from grazers (Van Alstyne and Houser, 2003; Van Alstyne *et al.*, 2009), decreases in salinity, increases in seawater temperature, and especially desiccation (Van Alstyne *et al.*, 2015a). Ulvoid algae respond in a species-specific manner to these stresses. For example, the low intertidal alga *Ulvaria obscura* increases DMS emissions strongly in response to hyposaline conditions, warm (35 °C) temperatures, and desiccation, whereas the high intertidal *Ulva intestinalis* dramatically increases DMS emissions when dried, but does not alter DMS emissions in response to changes in salinity or seawater temperatures (Van Alstyne *et al.*, 2015a). The production of DMS and other volatile sulfur metabolites, including hydrogen sulfide (H_2S), occurs over *U. lactuca* mats in Danish estuaries at low tide and is in the range of

$1–3\ umol\ S\ m^{-2}\ h^{-1}$ (Jørgensen and Okholm-Hansen, 1985). At the end of the growing season, when ulvoid macroalgae senesce or decay, anaerobic bacteria that release H_2S often utilize these algae as substrate (Nedergaard *et al.*, 2002), leading to ecological consequences. For example, H_2S trapped under decomposing mats of *Ulva* is the suspected cause of death for a horse and 30 wild boars on the coast of Brittany, France (Charlier *et al.*, 2007). H_2S is also toxic to many other organisms, including humans as well as beneficial aquatic life (Bagarinao, 1992; Lamers *et al.*, 2013). High sulfide concentrations in the water column have been implicated in mass mortalities of fish and other aquatic life (Bagarinao, 1992 and references therein).

15.11 Management Strategies

Because of the negative environmental and economic impacts that are often associated with harmful macroalgal blooms, government agencies and private stakeholders have increasingly sought various strategies for management and mitigation, although the main historic approaches, physical removal and herbicide treatment, remain common. The strategies used for a given bloom depend on the cause(s) and physical characteristics of the local setting, and can include multiple approaches. For example, herbicides such as copper sulfate have been used for decades to control algal blooms in freshwaters, and are effective for loose mat formers such as *Spirogyra* (Lembi, 2003 and references therein). However, dense mats of the cyanobacterium *Lyngbya wollei* or *Pithophora oedogonia* can block penetration of such chemicals (Lembi, 2003 and references therein), leaving managers with choices such as physical harvest or, if possible, draining ponds followed by application of bleach pellets (e.g., see Poovey and Netherland, 2006; Bishop *et al.*, 2015; note that control efforts of this species have also been impeded by the presence of both surface and benthic mats). Triploid grass carp (*Ctenopharyngodon idella*), restocked as necessary, are effective in removing nuisance charaleans, but their effectiveness in controlling filamentous algal mats is mixed (Lembi, 2003 and references therein). Waterfowl (geese or swans) consume filamentous algae, and charaleans are favored food of herbivorous ducks, coots, and swans; however, waterfowl introduced for macroalgal control are usually flightless, require diet supplements for adequate nutrition, must be protected

from predators, are aggressive in breeding season, and excrete wastes that can accumulate along shorelines and stimulate phytoplankton blooms (Lembi, 2003 and references therein). Overall, Lembi (2003, p. 826) concluded that for freshwater macroalgae, "Methods for direct control . . . are available, but none of them ensure that problems will be solved other than in the short term."

In situations where nutrient pollution from a point source of sewage or other nutrient source has been identified as a controlling factor, *reduction of nutrient loading at the source* is effective at moderating or even terminating the bloom (NRC, 2000). Regarding freshwater *Cladophora* in the Great Lakes, for example, Harris (2005, p. 11) described P supply reduction as "the only feasible option" for biomass reduction, although noting that decreased external P loads may be insufficient to overcome the internal P loading from exotic/invasive dreissenid mussels on *Cladophora* abundance (Bootsma *et al.*, 2004). In Tampa Bay, sewage nitrogen was recognized as a primary driver of eutrophication in the 1970s, including extensive blooms of macroalgae *Ulva*, *Gracilaria*, *Spyridia*, and *Chaetomorpha* in shallow waters of the portion of Tampa Bay known as Hillsboro Bay (Greening *et al.*, 2014). The offensive odors of decomposing macroalgae along the shorelines provided the key impetus for government agencies and stakeholders to develop plans for N removal from the local wastewater treatment plant. In the following decades, a 90% reduction in N loading to Tampa Bay correlated with diminishing macroalgae and phytoplankton blooms and expansion of seagrasses throughout the bay. Today, this highly urbanized subtropical estuary provides a successful case study of how sound science can lead to successful management and termination of macroalgal blooms, and simultaneously leads to recovery of seagrasses (Greening *et al.*, 2014).

Efforts to control harmful blooms in Hawai'i via nutrient reduction have produced mixed results. Diversion of sewage effluents from Kane'ohe Bay, which caused decreases in water-column DIN, was expected to reduce the abundance of *D. cavernosa*; indeed, a marked reduction in algal abundance occurred in the central bay where pre-diversion biomass levels on reef slopes were the highest in the entire bay (Smith *et al.*, 1981). The lack of a response to water-column DIN reductions on reef flats may have been due to the lower biomass levels and the alga assimilating nutrients from the sediments and invertebrate excretions (Stimson *et al.*, 2001). In this system, herbivores did not reduce the abundance of *D. cavernosa* on reef flats because algal species were available that were more preferred as food resources (Stimson *et al.*, 2001).

Physical removal of *Cladophora* accumulations in freshwaters has been described as a short-term mitigation strategy (Harris, 2005). Smaller accumulations have been removed by frequent hand-raking followed by composting or landfilling. Mechanical removal of large accumulations, especially on public beaches, has been successful using front-end loaders, backhoes, or beach-grooming equipment, with the following caveat: the heavy equipment can grind the decaying algae down into the sand, which can stimulate growth of fecal bacteria such as *E. coli* (Harris, 2005). In addition, successful cleanup requires removal of the algal mats as soon as they wash ashore, because they can quickly decay into what has been described as an "organic soup that is extremely difficult to collect and remove" (Harris, 2005, p. 12).

Increasingly, popular tourist destinations have had to develop management strategies to harvest and remove excessive macroalgae from marine beaches. Beaches in Texas, United States, including Galveston, Padre Island, and Port Aransas, have sustained more frequent strandings of *Sargassum* in recent decades. Unlike the Caribbean region, where booms (Figure 15.5e) have been widely deployed to prevent landfall of *Sargassum* on beaches, management in Texas and other areas of the United States has been restricted by the federal Fishery Management Plan for *Sargassum*, which prevents any harvesting within about 161 km (100 miles) of shore (South Atlantic Fishery Management Council [SAFMC], 2002). On Galveston Island, the Galveston Island Board of Trustees rakes with the tractor-towed Barber Surf Rake (Figure 15.5a and 15.5b), which is available in three models. Recent studies comparing raked and unraked beaches at Galveston found no differences in beach height, although the study did not consider horizontal seaward expansion or change in slope of the beach (Williams *et al.*, 2008). The Barber Surf Rake is widely used around the United States, and was used in summer of 2015 to clean *Sargassum* from beaches in Key West, Florida.

In May 2014, unusually large quantities of *Sargassum* washed ashore in Galveston. In situations like this when *Sargassum* mats on the beach become too high for the Barber Surf Rake or other beach-grooming equipment, front-end loaders are used to remove the seaweed to the dune line. In Key West, Florida, the height threshold is 25 cm. When *Sargassum* is higher than this, front-end

loaders are used in combination with dump trucks to transport the *Sargassum* to a desired location. In Port Aransas, this activity required a U.S. Army Corps of Engineers permit to move sand from the beach below the high-tide line. Similar issues are of concern in Florida, where the Florida Department of Environmental Protection does not allow collection of *Sargassum* below the water line. In addition to front-end loaders and dump trucks, graders are used to groom the beach following removal of *Sargassum*. Physical removal of macroalgae from coral reefs in Kaneohe Bay, Hawai'i, by use of the "super sucker" (Figure 15.5c and 15.5d) is labor-intensive and expensive, and tends to produce only temporary reductions in biomass (Smith *et al.*, 2004; Weijerman *et al.*, 2008).

There are few options available to effectively manage *Codium fragile* spp. *tomentosoides* (Global Invasive Species Database, 2016):

> Chemical herbicides are not a viable option of control and end up doing harm. Mechanical removal techniques such as trawling, cutting, and suctioning may reduce density temporarily, but they are expensive and the populations will quickly rebound. Manual removal will not work either. *C. fragile* spp. *tomentosoides* readily reproduces from fragments. There are a variety of naturally occurring organisms that feed on *C. fragile* spp. *tomentosoides*, but no one or combination of species can offer sufficient control [as] these species do not readily discriminate between the native and introduced *C. fragile* subspecies. Preventing the spread of *C. fragile* spp. *tomentosoides* through quarantine measures and public education are [among] the only ways to insure it does not spread.

These examples illustrate the present status, that is, the general difficulty in developing management strategies that are both economical and effective in reducing the biomass of macroalgal blooms, other than as short-term measures.

15.12 Economic Impacts

Harmful macroalgal blooms have been associated with various detrimental social and ecological impacts, such as inhibited recreation, diminished aesthetic enjoyment of the coastal zone, and interference with tourism, fishing, and mariculture (Lyons *et al.*, 2014 and references therein), all of which lead to economic impacts. The toxic H_2S emitted from mats of rotting macroalgae can threaten human health (Chrisafis, 2009; Samuel, 2011). These noxious blooms also depress biodiversity and alter ecological processes as well (Fletcher, 1996; Raffaelli *et al.*, 1998; Lyons *et al.*, 2014), with potential adverse economic effects. Yet, the economic impacts of harmful macroalgal blooms are very poorly tracked, despite general acceptance that these blooms cause major aesthetic loss, adversely affect swimmers and other beachgoers, negatively affect tourism on beaches, and dramatically affect both aquatic ecosystems and recreational/commercial fisheries.

An example of economic impacts due to macroalgal HAB is the Great Lakes *Cladophora* problem. The presence of rotting *Cladophora* mats that sequester fecal bacteria at many beaches along the shores of Lakes Michigan and Erie is believed to have led to beach closures, and closing a Lake Michigan beach was estimated to cause economic losses as high as $37,000 U.S. per day in 2003 dollars (Rabinovici *et al.*, 2004). Moreover, in 2006–2007, only 47% of U.S. beaches along Lake Erie were open for 95% or more of the beach season, and water quality continues to deteriorate (Environment Canada and the U.S. Environmental Protection Agency [EPA], 2009). Massive rotting *Cladophora* mats have led to property depreciation in the Milwaukee region, and financial burdens for industries with water intakes in Lakes Erie and Michigan, such as shutdown of a nuclear power plant because *Cladophora* clogged its emergency cooling pumps (Bootsma *et al.*, 2004). Along the U.S. shores of Lake Ontario, nuisance filamentous algal impacts were noted by nearly half (19 of 42) of business respondents (Limburg *et al.*, 2010). Most of those respondents (18 of 19) described decreased revenues; about half of them (9 of 19) altered some of their goods and services because of the nuisance filamentous algae, such as moving docks, washing boats more frequently, pumping out algal clumps from marinas, and selling beach rakes. Some respondents reported having spent at least $1,000 per season to remove algae, and one marina owner spent $11,200 (Limburg *et al.*, 2010). The regional Great Lakes recreational fishery had an estimated value exceeding $7 billion U.S. annually as of a decade ago (Southwick Associates, 2007), and *Cladophora* blooms have threatened the habitats and food resources needed by sport fish such as walleye (*Sander vitreus*) and yellow perch (*Perca flavescens*) (Arend *et al.*, 2011; Hinderer *et al.*, 2011). The value of real estate on lakefront (Lake Erie) with *Cladophora* mats was reported to average only 80–85% of the value of clean frontage (Ormerod, 1970). Water intakes to

Figure 15.5 Some examples of mechanical methods for mitigating macroalgal blooms on beaches and in coastal waters. (a,b) The Barber surf rake used to remove macroalgae from beaches; *Source:* photos courtesy of H. Barber & Sons, Inc. (c,d) the "super sucker" used for removing invasive red macroalgae from coral reefs in Kane'ohe Bay, Hawai'i; *Source:* photos by B. Lapointe. (e) floating booms used to deflect pelagic *Sargassum* from coastal properties in the Caribbean. *Source:* photo courtesy of D. Jimenez.

power plants have been clogged by *Cladophora*, leading to power outages, and human health and safety on beaches has been threatened by *Cladophora* mats laden with pathogenic microbes as explained above. Unfortunately, despite many years of major impacts, an overall, quantitative economic analysis of *Cladophora*-related economic costs in the Great Lakes is not yet available.

Species of *Cladophora* are also well known in the extensive irrigation systems and aqueducts of the western United States, where they reduce flow rate and canal capacity (Lembi *et al.*, 1988; Lembi, 2003; Ross, 2006 and references therein). Detached mats float downstream and clog pump inlets, irrigation siphons, trash racks, and sprinkler heads (Hansen *et al.*, 1984 in Lembi, 2003). More generally, clogging of rivers, canals, and drainage ditches by *Cladophora* and other filamentous algae can cause flooding events (Lembi, 2003). Yet, only a few dated descriptions of associated economic costs in specific locales are available (Lembi *et al.*, 1988; Lembi, 2003 and references therein).

Macroalgal blooms are having increasing impacts on coastal economies through loss of real estate values and tourism as well as escalating beach cleanup costs. Along Maui's Kihei coast in Hawai'i, over $20 million U.S. per year in tourism revenues and property values have been lost as a result of problems associated with blooms of the rhodophyte *Hypnea musciformis* (Cesar and Van Beukering, 2004; http://www.hawaii.edu/ssri/hcri/ev/kihei_coast.htm). In Maui County, some $250,000 U.S. is spent annually by condominium owners to remove excessive seaweed biomass from the beaches. In the Peel Inlet, Australia, removal of seaweeds cost $160,000 U.S. annually for 13,000 m^3 of macroalgae (Atkins *et al.*, 1993). In France, the cost exceeded 3.6 million francs for 90,000 m^3 of green tides removed from the Brittany coastline in 1992 (Centre d'Etude et de Valorisation des Algues [CEVA], 1993). In Lee County, Florida, costs of beach seaweed removal programs were historically nominal but increased dramatically to $260,503 in fiscal year 2003/2004 with the onset of drift rhodophyte blooms (Lapointe and Bedford, 2007).

Expensive management actions followed the massive *Sargassum* landings on Caribbean beaches between 2011 and 2015. Manual labor activities involving *Sargassum* collection and removal from resort beaches were widespread, and beach management costs up to $33,000 per week were reported to maintain a typical resort with ~1000 ft. of beach. In Cancun and the Riviera Maya, the Mexican government spent up to $10 million U.S. in 2015 on the problem. Funds were used to hire 5000 temporary workers and equipment for *Sargassum* removal, as well as for field tests of methods to prevent *Sargassum* from coming ashore; this involved the Mexican Navy (Alexander, 2015). Booms have been deployed in a variety of locations around the Caribbean, including Mexico, to deflect *Sargassum* from beaches, bays, and coastlines (Figure 15.5e).

15.13 Recycling Macroalgae Biomass

There has been relatively little exploration of freshwater macroalgae for beneficial use in, as examples, fertilizers or biofuels. Focus has mostly been directed toward *Cladophora* spp., which have been described as relatively "easy" to harvest using meshes or mechanical scraping (Zulkifly *et al.*, 2013). The harvested material has been suggested for use in extracting P to supply agricultural fertilizers (Zulkifly *et al.*, 2013). Cellulose extracted from *Cladophora glomerata* has been hydrolyzed to provide glucose for the cultivation of bacteria that have been genetically engineered to produce desirable fatty acid precursors to biodiesel fuel (Hoover *et al.*, 2011). The epiphytic diatoms on *Cladophora* may also be a promising source of fatty acids; it was estimated that *Cladophora*-dominated diatom-rich periphyton grown in wastewater effluent at U.S. wastewater treatment plants could generate about 7.6 billion L (2 billion gallons) of biofuel annually (Graham *et al.*, 2012). Biomass of *Cladophora* spp. may also be a potential source of cyclic tetrapyrrolic photosensitizers for photodynamic therapy (Tang *et al.*, 2012).

Many seaweeds are harvested commercially for use in the food, nutraceutical, cosmetic, agricultural, and biofuel industries (Zemke-White and Ohno, 1999; Dominguez, 2013; Wei *et al.*, 2013; Balboa *et al.*, 2015), and there is much potential for beneficial uses of species that form blooms. Many seaweeds, including *Ulva* spp., are edible (Chapman and Chapman, 1980) and could be used for human consumption, as well as livestock and aquaculture feeds (Bolton *et al.*, 2009; Michalak and Chojnacka, 2009). In general, seaweeds have a number of qualities needed to be good sources of compost, although concentrations of accumulated metals or phytotoxins can be a concern (Han *et al.*, 2014). Due to high C:N ratios, macroalgae are often mixed with other compostable materials to prevent ammonia volatilization (Han *et al.*, 2014). Additionally, macroalgae can be used as feedstocks for the production of biochar, defined as a solid material obtained from the carbonization of biomass used to improve soil conditions (Milledge and Harvey, 2016). Macroalgae can also be used for the production of biofuels, such as ethanol (Huesemann *et al.*, 2010) and biomethane (Langlois *et al.*, 2012); however, most seaweeds are not good candidates for biodiesel production because of low lipid contents. A recent review of energy extraction from macroalgae concluded that it is

too early at the current stage of biofuel development to select definitively what method or combinations of methods for exploiting energy from macroalgae will be commercially feasible (Milledge *et al.*, 2014).

Some bloom-forming species produce specific products that are commercially desirable. For example, brown algae, such as *Sargassum* spp., are typically high in polyphenolic compounds (Amsler and Fairhead, 2005), which are antioxidants (Shibata *et al.*, 2008). Fucoidans, sulfated polysaccharides, are also produced by brown algae and have been reported to have antioxidant, antiviral, and anti-inflammatory activity (Vo and Kim, 2013). Macroalgae are often grown in order to harvest commercially important cell wall components, such as alginate, agar, and carrageenan (McHugh, 1991), and blooms could also be a source of these products.

15.14   Forecast

Given the projected trajectories for increased cultural eutrophication and climate change in the United States and worldwide (Intergovernmental Panel on Climate Change, 2015; World Resources Institute, n.d.), harmful macroalgal blooms ranging from freshwaters to brackish and coastal marine waters are predicted to increase in the coming decades. Considering benthic filamentous cyanobacteria, Quiblier *et al.* (2013) wrote, "As climatic conditions change and anthropogenic pressures on waterways increase, it seems likely that the prevalence of blooms of benthic cyanobacteria will increase." Blooms of benthic filamentous cyanobacteria and filamentous green algae tend to be promoted by higher temperatures and nutrient pollution (Burkholder, 2009 and references therein; O'Neil *et al.*, 2012). While more storms and rainfall would accelerate freshwater delivery of nutrients and flushing, longer drought periods would favor freshwater HAB by decreasing flushing and increase internal nutrient cycling. In coastal areas, predicted sea-level rise would increase the extent of continental shelf areas, providing shallow, stable coastal habitats that could favor macroalgal growth and/or expand suitable habitats inland (Harley *et al.*, 2012; Teichberg *et al.*, 2012 and references therein).

Increasing ocean acidification may also promote the growth of macroalgae and lead to an increase in blooms. As seawater pH decreases, the percentage of dissolved inorganic carbon (DIC) that occurs as HCO_3^- increases. The majority of marine macroalgae studied to date (> 85%) use a C3 photosynthetic process, including use of HCO_3^- as a carbon source (Koch *et al.*, 2013). In nutrient-replete environments, increasing ocean acidification could lead to more rapid growth rates and more frequent or larger blooms of algae that are not DIC-saturated.

Considering the dramatic rise in macroalgal blooms in response to eutrophication in recent years, more research is critically needed on effective methods for harvesting the biomass and recycling for beneficial purposes in mitigating climate change. In the 1970s, fast-growing red seaweeds such as *Gracilaria tikvahiae* were shown to be effective for recycling nutrients from municipal sewage into marine biomass with beneficial purposes, such as hydrocolloids, biofuels, or fertilizers (Ryther *et al.*, 1978). Given the rising energy cost of chemical fertilizers and the increasing opposition to usage because of environmental impacts, research is needed on the potential for conversion of macroalgal biomass into natural, low-cost, sustainable soil additives (N'Yeurt and Iese, 2014). Similar research efforts are needed on production of biofuels and carbon sequestration. For example, the high C:N ratio (50:1) of pelagic *Sargassum* in the Sargasso Sea (Lapointe, 1995), combined with the tendency of this macroalga to sink to the deep-sea floor, makes it an efficient target species to sequester carbon in the oceans compared to phytoplankton, which typically have C:N ratios < 10:1 (Smetacek and Zingone, 2013). The future of harmful macroalgal blooms could be much different if they become regarded as potential crops with beneficial uses rather than excessive biomass that adversely affects the health of freshwater and marine ecosystems.

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