Chapter 21
Bottom-Up Versus Top-Down Control of Macroalgal Blooms

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21.1 Introduction

Macroalgal blooms are increasing worldwide and have many detrimental effects on ecosystems, including more frequent occurrences of anoxia, and loss of seagrasses, coral cover, and ecologically and commercially important species. The increased occurrences of macroalgal blooms have been attributed primarily to increases in the supply of the limiting nutrients, referred to as "bottom-up" control, and decreased grazer abundance due to overfishing and habitat degradation, referred to as "top-down" control. This chapter begins with an overview of the occurrence of macroalgal blooms worldwide and their ecological consequences. It discusses the role of coastal eutrophication and overfishing as the two main global drivers of bloom formations. The relative role of bottom-up versus top-down control in structuring ecological communities is controversial and has been heavily debated within the scientific community. This chapter will provide an overview of the main arguments of this debate in marine coastal waters. Specifically, scientific evidence supporting bottom-up versus top-down controls in shallow estuaries and coastal bays, coral reefs, and intertidal or subtidal rocky shores will be reviewed to understand how systems differ in response to these controls. We will provide an outlook on the future

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trends of eutrophication and overfishing and their impact on algal blooms in combination with other global changes. We will conclude with a discussion on management options to help reduce the escalation of bloom occurrences worldwide.

21.2 Occurrence of Macroalgal Blooms and Their Ecological Consequences

Macroalgal blooms are widespread along the coasts of the world (Table 21.1; Morand and Merceron 2005; Ye et al. 2011), forming dense mats or canopies in shallow estuaries and coastal lagoons (Valiela et al. 1992; Sfriso et al. 1992), accumulating on beaches as wrack (Morand and Merceron 2005), overgrowing corals (Smith 1981; Hughes 1994; Lapointe et al. 2005a, b), and affecting seagrass, soft-bottom, and rocky shore benthic communities (Díaz et al. 2002; Fox et al. 2009). Blooms of green, red, and brown macroalgae are common, although among these there are a few cosmopolitan species belonging to the genera *Ulva, Chaetomorpha, Cladophora*, *Gracilaria*, and *Pylaiella* (Table 21.1). Recent reviews on green algal tides showed bloom occurrences in most marine water bodies adjacent to highly urbanized or agricultural areas throughout Europe, Australia, New Zealand, Asia, and North and Central America (Morand and Merceron 2005; Teichberg et al. 2010; Ye et al. 2011). Some of the most famous examples of macroalgal blooms include the drift mats of *Ulva* spp. in Brittany, France (Morand and Merceron 2005) and Venice Lagoon (Sfriso et al. 1992; Sfriso and Marcomini 1997), *Cladophora* spp. in Peel Harvey Estuary, Australia (Lavery et al. 1991), and the more recent widely publicized *Ulva prolifera* blooms in the Yellow Sea, China during the 2008 summer Olympics with an estimated biomass of approximately 20 million wet tons (Liu et al. 2009; Gao et al. 2010; Ye et al. 2011).

Blooms of macroalgae have become a major ecological and economic problem in coastal habitats (Table 21.1, Fig. 21.1). Seaweed wrack accumulating on beaches can produce foul odors and release toxic hydrogen sulfide gas (Wilce et al. 1982), mats and deep canopies of seaweeds physically obliterate other primary producers including seagrasses (Valiela et al. 1997; Hauxwell et al. 2001; McGlathery 2001) and corals (Hughes 1994; Lapointe 1997; Lapointe et al. 2005a, b), and their decay causes anoxic conditions that lead to fish and shellfish kills (D'Avanzo et al. 1996; Valiela et al. 1997; Diaz 2001). Macroalgal blooms not only affect natural coastal communities and ecosystem function (Duarte 1995), but have high economic consequences by making coastal environments increasingly undesirable for recreational uses and threatening commercially important harvests (Valiela et al. 1992; Raffaelli et al. 1998; Oesterling and Pihl 2001). Often, the macroalgal species that form blooms are nonnative, such as *Gracilaria vermiculophylla*, *Codium* spp., and *Undaria pinnatifida,* and have the ability to quickly adapt to new environments and outcompete native species due to high stress tolerances, rapid nutrient uptake and growth rates, and varying reproductive strategies (Smith et al. 2002; Piriz et al. 2003;

Table 21.1 Examples of macroalgal blooms reported in different parts of the world's coastlines and some of their ecological and economic consequences (adapted from Teichberg et al. 2010)

Site	Seaweed taxa	Some effects	References
North America			
Gulf of California, Mexico	*Ulva, Gracilaria, Cladophora*	Anoxia, loss of species diversity	Ochoa-Izaguirre et al. (2002), Piñon-Gimate et al. (2008)
Nahant Bay, USA	*Pilayella*	Noxious odor, accumulated on beaches, nuisance to swimming and fishing	Wilce et al. (1982), Pregnall and Miller (1988)
Waquoit Bay, USA	*Cladophora, Gracilaria, Ulva*	Replaced seagrasses, anoxia, shell- and fin-fish kills	Valiela et al. (1997), Hauxwell et al. (2001), Fox et al. (2008)
Hog Island Bay, USA	*Ulva, Gracilaria, Codium*	Loss of species diversity	Thomsen et al. (2006)
San Francisco Bay, USA	*Ulva*	Anoxia, replaced benthic fauna	Fong et al. (1996)
Kaneohe Bay, Hawaii	*Dictyosphaeria*	Replaced corals	Smith (1981)
Southeast Florida, USA	*Codium*	Impact coral reefs	Lapointe et al. (2005a, b)
Bermuda	*Cladophora, Laurencia, Codium*	Anoxia, reduced benthic diversity and commercial fisheries	Lapointe and O'Connell (1989)
Southern California lagoons, USA	*Ulva*	Shifts in primary producers, anoxic conditions, cascading effects up food web	Kamer et al. (2001), Fong and Kennison (2010)
Europe			
Laholm Bay, Sweden NW Baltic Sea	*Ulva, Cladophora*	Replaced seagrasses, nuisance to swimming fishing and boating	Baden et al. (1990), Rosenberg et al. (1990)
Maasholm Bay, Germany	*Ulva, Pilayella*	Replaced native macroalgae, lowered benthic diversity and fishery yield, nuisance to swimming, fishing, and boating	Lotze et al. (2000), Worm et al. (1999)
Mondego Estuary, Portugal	*Ulva*	Replaced seagrasses, reduced benthic diversity	Martins et al. (2001), Cardoso et al. (2004)
Venice Lagoon, Italy	*Ulva, Gracilaria, Dictyota,*	Anoxia, fish kills, nutrient re-release, phytoplankton blooms	Sfriso et al. (1992), Sfriso and Marcomini (1997)

(continued)

Table 21.1 (continued)

Site	Seaweed taxa	Some effects	References
South America			
Nuevo Gulf and San Antonio Bay, Patagonia, Argentina	*Ulva, Undaria*	Accumulated on beaches, interferes with recreational uses	Díaz et al. (2002), Piriz et al. (2003), Teichberg et al. (2010), Martinetto et al. (2011)
Asia			
Quingdao, China	*Ulva*	Loss of species diversity, accumulated on beaches and nuisance for recreational activities	Liu et al. (2007, 2009)
Seto Inland Sea, Japan	*Ulva*	Replaced seagrasses	Sugimoto et al. (2007)
Australia			
Peel-Harvey Estuary, Western Australia	*Cladophora, Ulva, Chaetomorpha*	Accumulated on beaches	Lavery et al. (1991)
Tuggerah Lakes Estuary, New South Wales	*Ulva*	Replaced seagrasses, reduced benthic diversity	Cummins et al. (2004)
Africa			
Saldanha Bay, South Africa	*Ulva*	Competed with other commercial use algae	Anderson et al. (1996), Monteiro et al. (1997)

Lapointe et al. 2005a; Thomsen et al. 2006). Invasive macroalgae have often become nuisance species causing major damage to coastal benthic communities, reducing marine biodiversity, and altering food webs (Schaffelke and Hewitt 2007, see Chap. 12 by Andreakis and Schaffelke).

21.3 Coastal Eutrophication

One of the main triggers of macroalgal blooms is increased nutrient loading due to rapid urbanization and development of the coastal zone (Howarth 2008). Coastal eutrophication can be described as the increase in organic matter, including extensive blooms of phytoplankton and ephemeral macroalgae, due to nutrient loading along the coast (Nixon 1995; Cloern 2001). Cloern (2001) provides a detailed review and conceptual model of the rapidly changing problem of coastal eutrophication. This conceptual model describes both direct and indirect responses to increased nutrient loading along the coast, including increases in phytoplankton and macroalgal biomass, and changes in biogeochemistry, water transparency, and

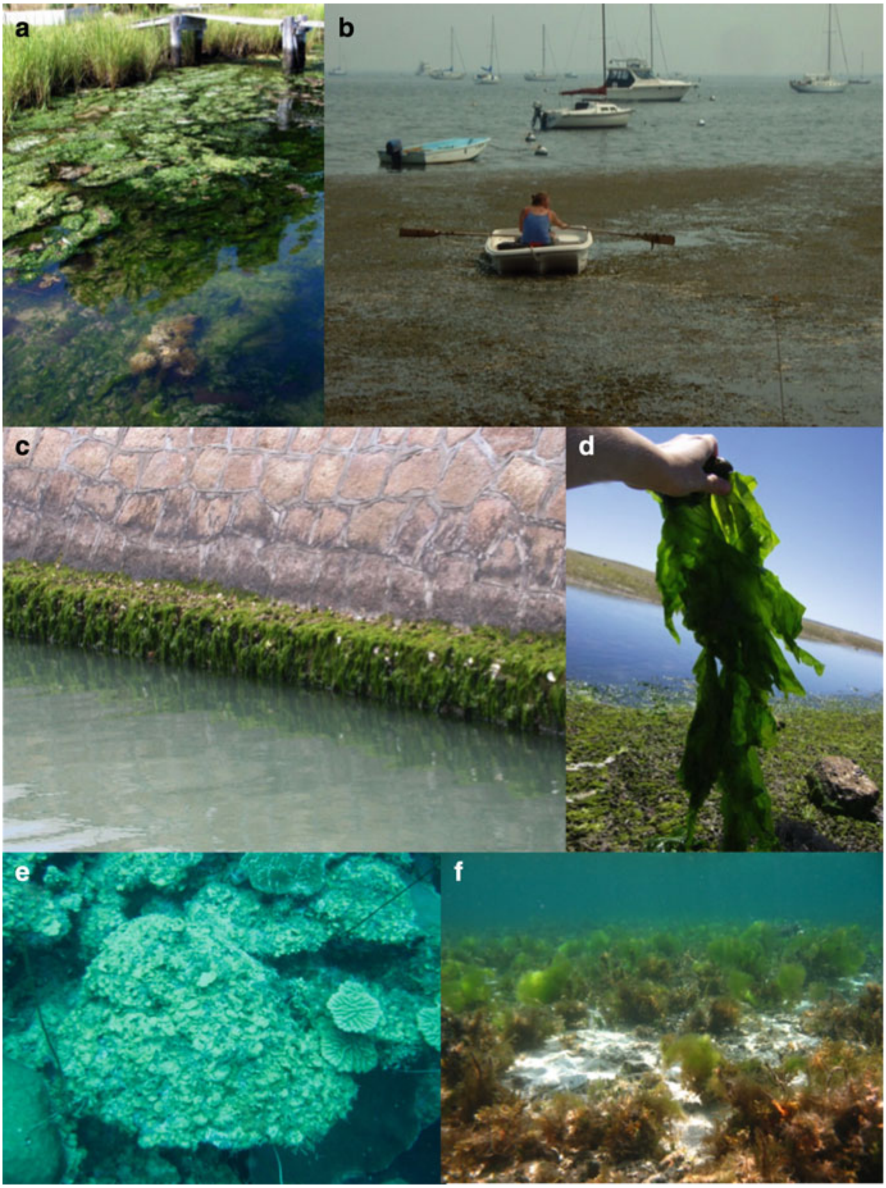

Fig. 21.1 Macroalgal blooms in estuaries and coral reefs habitats: (**a**) blooms of *Ulva lactuca* (photo by Ylva Olsen) and (**b**) *Cladophora variegata* (photo by Gabrielle Tomasky Holmes) along the subestuaries of Waquoit Bay, Cape Cod, USA; (**c**) *Ulva* spp. blooms attached to the walls in Venice Lagoon, Italy (photo by Mirta Teichberg) and (**d**) in the intertidal channel of San Antonio Bay, Argentina (photo by Paulina Martinetto); (**e**) *Lobophora variegata,* overgrowing coral reefs in Curaçao, Netherland Antilles (photo by Anna Fricke); (**f**) blooms of the green and brown macroalgae *Chaetomorpha* and *Dictoya* spp. on reef flats of Spermonde Archipelago, Indonesia (photo by Mirta Teichberg)

habitat quality. Most large occurrences of algal blooms have been associated with increased nutrient enrichment, primarily nitrogen, although phosphorus may also play a role (Howarth 2008; Teichberg et al. 2010). Here, we focus primarily on occurrences of macroalgal blooms reported worldwide that are linked to coastal eutrophication. Ecophysiological uptake and utilization mechanisms of nutrients, nitrogen and phosphorus limitation, assimilation of carbon, and the role of nutrient availability in stimulating macroalgal growth rates are reviewed in the Chap. 4 by Gordillo.

In the USA, approximately 65% of estuaries surveyed showed moderate to high levels of eutrophic conditions, influenced primarily by land-based nutrient loads from human activities (Bricker et al. 2008). In many of these estuaries, extensive chlorophyte and rhodophyte blooms are prevalent and have caused anoxic conditions (Bricker et al. 2008) and changes in the benthic community (Table 21.1). Waquoit Bay, in Cape Cod, Massachusetts, serves as a good example of how increased urbanization has led to drastic changes in the marine community structure over the past six decades (Valiela et al. 1992, 1997; Hauxwell et al. 1998, 2001; Fox et al. 2008). Macroalgal blooms of *Cladophora*, *Gracilaria*, and *Ulva* spp. have been directly linked to increased nitrogen loading rates in the subestuaries of Waquoit Bay predominantly due to increases in wastewater nitrate from septic systems that enters the estuary via groundwater (Valiela 2006; Fox et al. 2008; Fig. 21.1). Along the Florida coast, blooms of green macroalgae, including invasive species of *Codium* and *Caulerpa*, and drift red macroalgae have also been linked to increasing in nutrient inputs from sewage, shown through their high tissue N and P content and heavier nitrogen isotopic signatures that reflect that of wastewater nitrogen (Lapointe et al. 2005a, b; Lapointe and Bedford 2007, 2010).

Outside of North America, frequency of macroalgal blooms driven by high nutrient loads has also been reported (Table 21.1). Most sites where macroalgal blooms reach a remarkably high standing crop are locations where waters are enriched with nutrients as a result of urban growth in surrounding areas. A 20-year study in Peel Harvey Estuary, Australia, showed how large blooms of *Cladophora*, *Ulva*, and *Chaetomorpha* spp. have been caused by high nutrient loading, with interannual differences in biomass associated with nutrient and light conditions (Lavery et al. 1991). In San Antonio Bay, Argentina, high wastewater nitrogen and phosphorus inputs have been linked to high growth rates and biomass of *Ulva lactuca* that forms extensive blooms in the main channel of the bay (Teichberg et al. 2010; Martinetto et al. 2011; Fig. 21.1). Other sites known for macroalgal blooms that have been linked to coastal pollution include Venice Lagoon, Italy and Mondego Estuary, Portugal (Table 21.1, Fig. 21.1). In these sites, *Ulva* blooms persist under high nutrient loads (Sfriso et al. 1992; Martins et al. 2001; Teichberg et al. 2010).

21.4 Overfishing

Drastic changes in consumer abundance due to the overharvesting of commercially and recreationally important fish, mammal, and invertebrate species have occurred in many marine ecosystems throughout history (Jackson et al. 2001). A recent study shows approximately 90% of predatory fish stocks have been removed by fishing fleets worldwide (Myers and Worm 2003) with cascading effects down to lower trophic levels (Hughes 1994; Jackson et al. 2001; Mumby et al. 2006). Here, we focus on the role overfishing plays in the occurrence of macroalgal blooms in marine coastal waters. A classification of the different type of seaweed grazers and an overview of algal–herbivore interactions can be found in detail in Chap. 8 by Iken.

Most cases where overfishing has directly impacted macroalgal growth occur in coral reef and kelp ecosystems. This is due primarily to the number of relatively larger and ecologically important consumers that have been removed from these ecosystems compared to others (Jackson et al. 2001). Overharvesting of herbivorous fish, marine mammals, and invertebrates that directly graze on macroalgae have led to increased occurrence of macroalgal blooms in coral reefs (Hughes 1994; Jackson et al. 2001; Mumby et al. 2006). The opposite trend has occurred in kelp forests, where the removal of large consumers has often led to increases in invertebrate grazer abundance which then reduce macroalgal cover in these systems (Estes and Duggins 1995; Jackson et al. 2001).

It has been argued that shifts in benthic and pelagic communities due to overfishing long predated coastal eutrophication problems in marine systems (Jackson et al. 2001; Lotze and Milewski 2004; Heck and Valentine 2007). A review paper by Heck and Valentine (2007) stressed the importance of overfishing in regulating ecosystem structure by indirectly leading to altered food webs. They support that many of the negative effects on coastal ecosystems attributed to coastal eutrophication may actually be confounded by indirect effects of historical changes in consumer abundances. They state that most manipulative experiments that test the importance of nutrients and consumers on benthic ecosystems today are doing so in ecosystems that have already been long devoid of apex predators and many other consumers lower in the food web. Another study (Eriksson et al. 2009) showed that declines in predatory fish were promoting blooms of macroalgae in the Baltic Sea through cascading effects down the food web. Through surveys they showed that macroalgal cover was highest when abundances of large piscivorous fish were low, which led to higher abundances of smaller fish that feed on invertebrate grazers. Further manipulative experiments supported the notion that these predators when abundant exerted a strong top-down forcing on the food web (Eriksson et al. 2009).

21.5 Bottom-Up Versus Top-Down Control in Marine Coastal Ecosystems

There are an overwhelming number of studies focusing on bottom-up versus top-down controls of primary producer biomass and community structure in marine coastal waters (Hauxwell et al. 1998; Lapointe 1999; Balducci et al. 2001; Lotze et al. 2001; Smith et al. 2010; Martinetto et al. 2011; Fox et al. 2012). Marine communities are, in general, naturally regulated by bottom-up and top-down forces; however, the increase in anthropogenic activities in the coastal zone has influenced the relative strength of bottom-up and top-down controls on these communities. In many instances, increased nutrient inputs seem to be the main driver of macroalgal blooms (Valiela et al. 1997; Hauxwell et al. 1998; Lapointe 1999), while in others changes in grazing pressure are thought to be responsible (Hughes 1994; Smith et al. 2010).

In order to determine the relative influence of these two factors, many experimental manipulations of nutrients and grazing have been carried out in marine habitats under a range of different in situ conditions. Recent metaanalyses by Burkepile and Hay (2006) and Gruner et al. (2008) have compiled the results of these experimental studies to see whether any general patterns can be deduced regarding the relative influence of top-down and bottom-up controls on these ecosystems. They found that in most cases nutrients and grazers independently affected producer biomass, but that the relative role of top-down versus bottom-up control is context dependent, that is, it may differ by latitude, by type of marine habitat, by the functional groups of algae or type of grazers in the system, by the productivity of the ecosystem, or by the sampling method of producer response (Burkepile and Hay 2006; Gruner et al. 2008). They also found that in some cases there were interactive or synergistic effects, in which nutrient enrichment in the absence of herbivores showed the highest productivity and percent cover of macroalgae (Gruner et al. 2008; Burkepile and Hay 2006).

21.5.1 Latitudinal Patterns

Most reports from temperate latitudes addressing the forces behind macroalgal blooms appear to suggest that nutrients were involved (Baden et al. 1990; Valiela et al. 1992; Sfriso et al. 1992; Raffaelli et al. 1998), with the exception of rocky shores (Lubchenco 1978; Lotze and Worm 2000). Similar studies from tropical latitudes place less emphasis on nutrients and suggest large impacts of grazing on macroalgal blooms (Lewis 1986; Hughes 1994), but opinions differ (Lapointe 1997; Littler et al. 2006). The metaanalysis of Burkepile and Hay (2006) showed that in tropical marine habitats, macroalgae responded independently to both nutrient enrichment and herbivore removal by increasing biomass or cover. Nutrient effects were, however, smaller than the grazing effects, and only important when herbivores were absent. This was not the case for temperate marine habitats, which tended to vary in the relative effects of bottom-up and top-down control based on the nutrient status of the system. In high nutrient environments bottom-up effects were stronger, while in low nutrient environments top-down effects were more significant (Burkepile and Hay 2006).

One of the main explanations for these latitudinal differences in the control of macroalgal blooms is the types and sizes of grazers and their grazing rates. Other possible explanations may be the extent of nutrient loading, the macroalgal taxa involved in different systems, the length of the growing season, and the range in light intensity in temperate versus tropical coastal waters.

21.5.2 Dominant Control in Different Habitats

In this section, we provide some key examples from the literature defining the relative roles of bottom-up and top-down controls within different marine habitats, including estuaries and coastal bays, coral reefs, and intertidal and subtidal rocky shores. Through these examples, we show the variation in macroalgal responses to their controls, and also try to include some of the studies, which have paved the way or stimulated the debate in this field.

21.5.2.1 Estuaries and coastal bays

The relative roles of bottom-up and top-down controls in estuarine systems have been thoroughly studied due to the high degree of disturbance found in these ecosystems as a consequence of coastal urbanization and development. This over-development leads to higher nutrient inputs from point and nonpoint sources of wastewater and fertilizers into coastal waters, while wetlands and forests that generally buffer and act as a filter along the coastline are being removed at alarming rates. Most sites receiving high nutrient enrichment generally are found to be bottom-up controlled, whereas undisturbed low nutrient environments are often found to be top-down controlled (Hauxwell et al. 1998; Burkepile and Hay 2006; Fox et al. 2012).

This general model of the relative importance of bottom-up and top-down controls on macroalgal blooms in estuaries is again exemplified by the Waquoit Bay example. Waquoit Bay macroalgal blooms are stimulated by high nitrogen loading to its receiving subestuaries (Valiela et al. 1997; Hauxwell et al. 1998; Fox et al. 2008). In the high nitrogen loaded sites of Waquoit Bay, macroalgal growth rates and biomass were highest (Hauxwell et al. 1998). Additionally, more frequent hypoxic events lowered the abundance of small crustaceans, the dominant grazers, and therefore, grazing rates were too low to compensate for the increase in algal biomass (Hauxwell et al. 1998; Fox et al. 2009, 2012). In contrast, in the low nitrogen loaded site macroalgal growth rates and biomass were lower, grazers were very abundant, and macroalgae were easily controlled by consumption rates (Hauxwell et al. 1998; Fox et al. 2009, 2012).

Another well-studied case of bottom-up and top-down controls of macroalgal blooms is that of Venice Lagoon. In the 1970s and 1980s, the lagoon received inputs of nutrients from urbanized areas in and around Venice from agricultural, industrial, and treated and untreated sewage effluent sources (Sfriso et al. 1992). With high nutrient loading came noticeable changes in benthic community structure driven by large blooms of *Ulva rigida* and other green macroalgae (Sfriso et al. 1987, 1992). Between 1987 and 1998, macroalgal standing crop in Venice Lagoon declined to only 1.6% of what was present in 1987 (Sfriso et al. 2003). This dramatic reduction was initially thought to be due to a combination of changes in climate, sedimentation fluxes, and management of nutrient loading entering the lagoon. Additionally, as macroalgal growth declined, fewer anoxic events allowed for the recovery of invertebrate grazers, which were able to help control macroalgae blooms from the top-down (Balducci et al. 2001).

Other biotic and abiotic factors, however, may affect the relative roles of bottom-up and top-down controls of macroalgal communities in estuarine systems. For example, reproduction and recruitment of early life history stages of macroalgae may respond differently under nutrient enrichment and grazing pressure than adult life stages (Lotze et al. 1999, 2000, 2001; Lotze and Worm 2000). Lotze et al. (1999) found that the bottom-up and top-down controls on early life stages may act as a bottleneck for bloom-forming species of macroalgae in some cases. Lotze et al. (2001), however, showed that total recruit density of ephemeral bloom-forming macroalgae *Ulva* and *Pilayella* spp. in the Baltic Sea was positively influenced by nutrient enrichment, while grazing only limited recruitment and growth of the more palatable of the two species without changing the total recruitment (Lotze et al. 2001).

Macroalgal community structure may also influence the strength of bottom-up and top-down controls. In the presence of canopy-forming macroalgal species, such as *Fucus vesiculosus*, the response of ephemeral algae to nutrients was found to be limited by as much as 90% compared to those without canopies due to a reduction in light availability (Eriksson et al. 2007). In contrast, the presence of epiphytes growing on macroalgae may actually stimulate macroalgal growth if epiphytes are preferentially consumed by grazers (Kamermans et al. 2002; see also Chap. 11 by Potin). Furthermore, on a smaller spatial scale, the presence of grazers within the macroalgal canopy may also be an additional source of nutrients through their excretion (Taylor and Rees 1998, see also Chap. 4 by Gordillo).

Hydrodynamics can also alter the strength of bottom-up and top-down controls on a system. For example, in Mondego Estuary, Portugal, mitigation measures to improve the hydrodynamics of the estuary have been found to alleviate macroalgal blooms occurrences caused by high nutrient loading by increasing the circulation and diverting inflow of nutrient-rich waters (Lillebø et al. 2005). In San Antonio Bay, Argentina, high nutrient loads enter the bay exposing macroalgae to elevated nutrient concentrations during low tide and supporting a large macroalgal biomass (Teichberg et al. 2010; Martinetto et al. 2010, 2011). Additionally, large tidal flushing helps to remove anoxic waters and nutrients from the system, minimizing hypoxia-related stress on grazers and negative cascading effects up the food web (Martinetto et al. 2010, 2011). Therefore, the high biomass of nutrient-rich macroalgae can provide a large quantity of food with higher nutritional quality to grazers and support higher grazer abundances (Martinetto et al. 2010, 2011).

21.5.2.2 Coral reefs

In the last four to five decades, there has been an increasing trend of macroalgal blooms in coral reefs coinciding with a decrease in coral cover (Hughes 1994; McManus and Polsenberg 2004; Nugues and Bak 2008). This shift from coral to macroalgal-dominated reefs, known as coral–algal phase shifts, has stimulated much of the debate in the relative role of top-down and bottom-up controls in marine habitats. Some studies have shown that the removal of the dominant herbivores, through overfishing or natural causes, has been more important as a control on macroalgal growth than nutrient enrichment (Hughes 1994; Hughes et al. 1999; Burkepile and Hay 2006; Sotka and Hay 2009). Others state that recent increases in nutrient inputs from land to coastal reefs have triggered macroalgal blooms (Lapointe 1997; Lapointe et al. 2005a, b). And then there are those studies that support both top-down and bottom-up controls as important influencing factors (McClanahan et al. 2003; Littler et al. 2006; Smith et al. 2001). In this chapter, we do not attempt to provide a comprehensive review of the current extensive literature on coral–algal phase shifts in coral reefs, but rather focus on a few specific studies that examine the effects of top-down and bottom-up controls on macroalgal growth.

In Hughes (1994), one of the first long-term studies of coral reef decline in the Caribbean reported large-scale natural and human disturbances were linked to coral–algal phase shifts. In most of the reefs around Jamaica, the driving factors of these phase shifts were thought to be the increase in human population, which drove an increase in overfishing, followed by the mass mortality of the sea urchin *Diadema antillarum*. Without herbivorous fish and *D. antillarum*, the dominant grazers of macroalgae on the reefs, blooms of filamentous macroalgae began to overgrow corals, which were then replaced by late successional stage species, such as *Dictyota*, *Lobophora*, *Halimeda*, and *Sargassum* spp. These macroalgae inhibited coral reef recovery by effectively competing for open space needed for recruitment of coral larvae (Hughes 1994). Lapointe (1997) introduced another potential trigger of macroalgal blooms on these Jamaican reefs by showing that bottom-up control also played a role. It was demonstrated that dissolved inorganic nitrogen from wastewater entered the reefs through groundwater discharge and elevated reef nutrient water concentrations sufficiently to sustain macroalgal blooms in these habitats (Lapointe 1997). These studies spurred a debate as to the relative role of bottom-up and top-down controls on coral reefs (Hughes et al. 1999; Lapointe 1999).

Since this debate began, a few studies have demonstrated how both top-down and bottom-up controls can be important. Littler et al. (2006) developed a conceptual model, the Relative Dominance Model, to describe the process of bloom formation on reefs under independent and combined factors of nutrients and grazing pressure. Results of manipulative experiments, bioassays, and surveys of communities showed that: (1) under reduced nutrients alone fleshy algae grow when herbivory is low, (2) under high herbivory alone fleshy algae grow when nutrients are high, (3) reduced nutrients and high herbivory prevent blooms of macroalgae (Littler et al. 2006). It has also been found that different controls are important for different groups of algae; for example, McClanahan et al. (2003) found that turf algae were positively affected by nutrients and negatively affected by herbivory, while frondose brown algae grew better under low nutrients and low herbivory. Vermeij et al. (2010) also found that turf algae can overgrow corals under high nutrients, but that herbivores are not able to control their growth under these conditions.

Despite the evidence that bottom-up control does play a role in triggering macroalgal bloom formations on reefs, the majority of studies support that top-down control is the primary driving factor (Thacker et al. 2001; Burkepile and Hay 2006; Sotka and Hay 2009). A recent study in a pristine fisheries management area along a Hawaiian reef revealed that in the absence of herbivores, fleshy macroalgal abundance was higher than in any other treatment, while in the presence of herbivores corals and crustose coralline algae were more abundant (Smith et al. 2010). The effects of nutrient enrichment supported slightly higher macroalgal percent cover than in nonenriched treatments, but the species composition depended on the herbivore treatment. After reexposure to natural conditions, the effects of enrichment and herbivore absence disappeared over a relatively short time frame, supporting the notion that increasing herbivore populations is critical to reduce macroalgal blooms on reefs (Smith et al. 2010).

Based on the variable results of studies examining top-down and bottom-up controls of macroalgal blooms on coral reefs, the relative role of these controls is still not fully resolved. Only through larger scale changes in fishing regulations and better management of nutrient inputs to coastal reefs will we be able to better distinguish which of these or the combination of both is the causal factor.

21.5.2.3 Rocky Intertidal and Subtidal Ecosystems

Much of the knowledge defining the role of top-down controls on macroalgal community dynamics began with the well-known classical ecological studies in rocky intertidal and subtidal communities (Paine and Vadas 1969; Lubchenco 1978, 1983; Estes et al. 1978; Lubchenco and Menge 1978). These studies showed how removal of the dominant grazers or predators influenced macroalgal diversity and community structure directly or indirectly through cascading effects from the top-down. In the experimental study by Paine and Vadas (1969), the removal of the sea urchin *Strongylocentrotus purpuratus* resulted in an increase in the biomass of brown algae (*Hedophyllum sessile* and *Laminaria complanata*) in intertidal pools and subtidally on the rocky coast of Washington, USA. Lubchenco (1978) showed that when snails were removed from tide pools where *Chondrus crispus* dominated, green ephemeral species settled quickly and outgrew *C. crispus*.

Only more recently has the role of bottom-up control, in terms of nutrient supply, been explored in rocky shores (Menge 1992; Nielsen 2003; Bokn et al. 2003; Korpinen et al. 2007a, b). A review by Menge (1992) discusses some of the reasons the role of bottom-up controls on rocky shores has been neglected for so long, including the overemphasis of physical stress in these environments, logistical and methodological constraints of experiments, and different training backgrounds of marine benthic ecologists. Possible explanations of how nutrient enrichment cascades up the food web and affects the community structure of rocky shores were also discussed using a case study along the Oregon Coast. In this environment, nutrient loading from upwelling was thought to increase primary production and lead to higher abundances of filter-feeding prey that then supported higher abundances and feeding rates of predators (Menge 1992). Further studies have also shown that increased phytoplankton due to upwelling events and nearshore hydrography drives this bottom-up regulation of the benthic community (Menge et al. 1997).

The relative effects of bottom-up and top-down control on the rocky shore macrophyte community along the same rocky shoreline were later experimentally tested in intertidal pools by Nielson (2003). Small increases in nutrient supply strongly increased the total percent cover of macroalgae and the diversity of benthic macrophytes under low herbivore abundance, but not under high herbivore abundance. This response in the macrophyte community was primarily due to an increase in the functional group of corticated algae. The results of this study suggest that open-coast marine intertidal communities are more sensitive to fluctuations in nutrient regimes than previously thought, and that nutrient effects are likely to be amplified where consumers are overexploited or naturally low in abundance (Nielsen 2003).

In both the above cases, bottom-up control of intertidal communities was driven by natural sources of nutrients from upwelling events rather than anthropogenic sources. However, other scientists have linked changes in the macroalgal community structure of rocky shores to coastal eutrophication, where macroalgal assemblages nearer to urbanized areas consisted of higher abundances of the opportunistic chlorophyte *Ulva* spp. than in control sites (Díaz et al. 2002; Worm and Lotze 2006). Overall the consensus is that top-down controls are dominant on rocky shores but that bottom-up controls can interact with top-down controls to change patterns in macrophyte community structure and food web interactions.

21.6 Conclusion

There may be no general solution to the bottom-up top-down debate in macroalgal communities, but rather different responses based on species or functional groups, physical and chemical environments, and types of grazers. The fact that so many rigorous experimental studies have found conflicting results shows that both factors are important under different circumstances and often interact simultaneously.

The human population is projected to steadily increase, which will result in further anthropogenic pressure on coastal marine systems. It is likely that nutrient loading rates and fishing pressure will intensify, despite management efforts. The impacts of nutrient loading and overfishing will also be exacerbated by other global changes, such as rising seawater temperatures, sea level rise, and ocean acidification. Nutrients in combination with warmer waters may promote more occurrences of macroalgal blooms, as photosynthesis, growth rates of macroalgae, and recruitment are thought to be positively affected by an interaction of these factors (Longstaff et al. 2002; Lotze and Worm 2002; Bintz et al. 2003; Tsai et al. 2005). Additionally, enhanced CO_2 conditions have been shown to benefit some ephemeral bloom-forming macroalgal species over other slower growing species (Gordillo et al. 2001; Wootton et al. 2008), while negatively impacting many benthic invertebrates (Fabry et al. 2008). Additionally, the increase in invasions by nonnative macroalgal species to new coastal habitats may promote blooms of macroalgae that are better adapted to changing environmental conditions (Thomsen et al. 2006). Cascading effects up or down the food web and, thus, the strength of bottom-up and top-down controls acting on macroalgal communities will likely be altered due to these shifts in species composition and environmental change (Fox et al. 2010).

Management of all aspects (nutrients, fishing, habitat protection, reduction of CO_2 emissions) is important, and choosing one management practice over another will not be successful at controlling macroalgal blooms. The management and removal of nitrogen and phosphorus is necessary as a first step. Wastewater treatment plants and improvements in septic systems have shown significant positive effects on water quality through the removal of the bulk of nutrients prior to entering the coast or groundwater. Reduction of fertilizer use and phosphate-free detergents can also reduce the amount of nutrients entering these systems. Preservation and restoration of wetlands will help to filter nutrient inputs before they enter rivers and coastal waters. Additionally, improving hydrodynamics of low-flow systems by increasing tidal flushing could help to mitigate nutrient effects. Increases in fishing regulations and protected areas with no take zones may help to increase fish and invertebrate populations. This will impact food web communities in multiple ways and will strengthen top-down controls on macroalgal growth.

In many cases, these management practices may not be enough to facilitate recovery of marine habitats to their natural state prior to disturbances, and much is still unknown as to how bottom-up and top-down controls will interact with future global change projections. It is very likely that macroalgal blooms will continue to become more frequent and severe in coastal systems before conditions improve. A better understanding of how these controls will interact under predicted future conditions is critical to develop tools to mitigate these changes.

References

Anderson RJ, Monteiro PMS, Levitt GJ (1996) The effect of localized eutrophication on competition between *Ulva lactuca* (Ulvaceae, Chlorophyta) and a commercial resource of *Gracilaria verrucosa* (Gracilariaceae, Rhodophyta). Hydrobiologia 326(327):291–296

Baden SP, Loo LO, Pihl L, Rosenberg R (1990) Effects of eutrophication on benthic communities including fish: Swedish west coast. Ambio 19:113–122

Balducci C, Sfriso A, Pavoni B (2001) Macrofauna impact on *Ulva rigida* C Ag. Production and relationship with environmental variables in the lagoon of Venice. Mar Environ Res 52:27–49

Bintz JC, Nixon SW, Buckley BA, Granger SL (2003) Impacts of temperature and nutrients on coastal lagoon plant communities. Estuaries 76:765–776

Bokn TL, Duarte CM, Pedersen MF, Marba N, Moy FE, Barrón C, Bjerkeng B, Borum J, Christie H, Engelbert S, Fotel FL, Hoell EE, Karez R, Kersting K, Kraufvelin P, Lindblad C, Olsen M, Sanderud KA, Sommer U, Sørensen K (2003) The response of experimental rocky shore communities to nutrient additions. Ecosystems 6:577–594

Bricker SB, Longstaff B, Dennison W, Jones A, Boicourt K, Wicks C, Woerner J (2008) Effects of nutrient enrichment in the nation's estuaries: a decade of change. Harmful Algae 8:21–32

Burkepile DE, Hay ME (2006) Herbivore vs. nutrient control of marine primary producers: context-dependent effects. Ecology 87:3128–3139

Cardoso PG, Pardal MA, Lillebø AI, Ferreira SM, Raffaelli D, Marques JC (2004) Dynamic changes in seagrasses assemblages under eutrophication and implications for recovery. J Exp Mar Biol Ecol 302:233–248

Cloern JE (2001) Our evolving conceptual model of the coastal eutrophication problem. Mar Ecol Prog Ser 210:223–253

Cummins SP, Roberts DE, Zimmerman KD (2004) Effects of the green macroalga *Enteromorpha intestinalis* on macrobenthic and seagrass assemblages in a shallow coastal estuary. Mar Ecol Prog Ser 266:77–87

D'Avanzo C, Kremer JN, Wainright SC (1996) Ecosystem production and respiration in response to eutrophication in shallow temperate estuaries. Mar Ecol Prog Ser 141:263–274

Diaz RJ (2001) Overview of hypoxia around the world. J Environ Qual 30:275–281

Díaz P, López Gappa JJ, Piriz ML (2002) Symptoms of eutrophication in intertidal macroalgal assemblages of Nuevo Gulf (Patagonia, Argentina). Bot Mar 45:267–273

Duarte CM (1995) Submerged aquatic vegetation in relation to different nutrient regimes. Ophelia 41:87–112

Eriksson BK, Rubach A, Helmut H (2007) Dominance by a canopy forming seaweed modifies resource and consumer control of bloom-forming macroalgae. Oikos 116:1211–1219

Eriksson BK, Ljunggren L, Sandström A, Johansson G, Mattila J, Rubach A, Råberg S, Snickars M (2009) Declines in predatory fish promote bloom-forming macroalgae. Ecol Appl 19:1975–1988

Estes JA, Duggins DO (1995) Sea otters and kelp forests in Alaska: generality and variation in a community ecological paradigm. Ecol Monogr 65:75–100

Estes JA, Smith NS, Palmisano JF (1978) Sea otter predation and community organization in the western Aleutian Islands, Alaska. Ecology 59:822–833

Fabry VJ, Seibel BA, Feely RA, Orr JC (2008) Impacts of ocean acidification on marine fauna and ecosystem processes. ICES J Mar Sci 65:414–432

Fong P, Kennison RL (2010) Phase shifts, alternative stable states, and the status of Southern California lagoons. In: Kennish MJ, Pearl HW (eds) Coastal Lagoons: critical habitats of environmental change, vol 164. CRC, New York, pp 227–251

Fong P, Boyer KE, Desmond JS, Zedler JB (1996) Salinity stress, nitrogen competition, and facilitation: what controls seasonal succession of two opportunistic green macroalgae? J Exp Mar Biol Ecol 206:203–221

Fox SE, Stieve E, Valiela I, Hauxwell J, McClelland J (2008) Macrophyte abundance in Waquoit Bay: effects of land-derived nitrogen loads on seasonal and multi-year biomass patterns. Estuar Coast 31:532–541

Fox SE, Teichberg M, Olsen YS, Heffner L, Valiela I (2009) Restructuring of benthic communities in eutrophic estuaries: lower abundance of prey leads to trophic shifts from omnivory to grazing. Mar Ecol Prog Ser 380:43–57

Fox SE, Olsen YS, Spivak AC (2010) Effects of bottom-up and top-down controls and climate change on estuarine macrophyte communities and the ecosystem services they provide. In: P.F. Kemp (ed.) Eco-DAS VIII Symposium Proceedings, ASLO, pp 129–145

Fox SE, Teichberg M, Heffner L, Valiela I (2012) The relative role of nutrients, grazing, and predation as controls on macroalgal growth in a temperate estuary. Estuar Coasts (in press)

Gao S, Chen X, Yi Q, Wang G, Pan G, Lin A, Peng G (2010) A strategy for the proliferation of *Ulva prolifera*, main causative species of green tides, with formation of sporangia by fragmentation. PLoS One 5:e8571. doi:10.1371/journal.pone.0008571

Gordillo FJL, Niell FX, Figueroa FL (2001) Non-photosynthetic enhancement of growth by high CO_2 level in the nitrophilic seaweed *Ulva rigida* Agardh (Chlorophyta). Planta 213:64–70

Gruner DS, Smith JE, Seabloom EW, Ngai JT, Hillebrand H, Harpole WS, Elser JJ, Cleland EE, Bracken MES, Borer ET, Bolker BM (2008) A cross-system synthesis of consumer and nutrient resource control on producer biomass. Ecol Lett 11:740–755

Hauxwell J, McClelland J, Behr P, Valiela I (1998) Relative importance of grazing and nutrient controls of macroalgal biomass in three temperate shallow estuaries. Estuaries 21:347–360

Hauxwell J, Cebrian J, Furlong C, Valiela I (2001) Macroalgal canopies contribute to eelgrass (*Zostera marina*) decline in temperate estuarine ecosystems. Ecology 82:1007–1022

Heck KL, Valentine JF (2007) The primacy of top-down effects in shallow benthic ecosystems. Estuar Coast 30:371–381

Howarth RW (2008) Coastal nitrogen pollution: a review of sources and trends globally and regionally. Harmful Algae 8:14–20

Hughes TP (1994) Catastrophes, phase-shifts, and large-scale degradation of a Caribbean coral reef. Science 265:1547–1551

Hughes T, Szmant AM, Steneck R, Carpenter R, Miller S (1999) Algal blooms on coral reefs: what are the causes? Limnol Oceanogr 44:1583–1586

Jackson JBC, Kirby MX, Berger WH, Bjorndal KA, Botsford LW, Bourque BJ, Bradbury RH, Cooke R, Erlandson J, Estes JA, Hugues TP, Kidwell S, Lange CB, Lenihan HS, Pandolfi JM, Peterson CH, Steneck RS, Tegner MJ, Warner RR (2001) Historical overfishing and the recent collapse of coastal ecosystems. Science 293:629–638

Kamer K, Boyle KA, Fong P (2001) Macroalgal bloom dynamics in a highly eutrophic Southern California estuary. Estuaries 24:623–635

Kamermans P, Malta E, Verschuure JM, Schrijvers L, Lentz LF, Lien ATA (2002) Effect of grazing by isopods and amphipods on growth of *Ulva* spp. (Chlorophyta). Aquat Ecol 36:425–433

Korpinen S, Jormalainen V, Honkanen T (2007a) Bottom-up and cascading top-down control of macroalgae along a depth gradient. J Exp Mar Biol Ecol 343:52–63

Korpinen S, Jormalainen V, Honkanen T (2007b) Effects of nutrients, herbivory, and depth on the macroalgal community in the rocky sublittoral. Ecology 88:839–852

Lapointe BE (1997) Nutrient thresholds for bottom-up control of macroalgal blooms on coral reefs in Jamaica and southeast Florida. Limnol Oceanogr 42:1119–1131

Lapointe B (1999) Simultaneous top-down and bottom-up forces control macroalgal blooms on coral reefs (Reply to the comment by Hughes et al.). Limnol Oceanogr 44:1586–1592

Lapointe BE, Bedford BJ (2007) Drift rhodophyte blooms emerge in Lee County, Florida, USA: evidence of escalating coastal eutrophication. Harmful Algae 6:421–437

Lapointe B, Bedford B (2010) Ecology and nutrition of invasive *Caulerpa brachypus* f. *parvifolia* blooms on coral reefs off southeast Florida, USA. Harmful Algae 9:1–12

Lapointe BE, O'Connell J (1989) Nutrient-enhanced growth of *Cladophora prolifera* in Harrington Sound, Bermuda: eutrophication of a confined, phosphorus-limited marine ecosystem. Estuar Coast Shelf Sci 28:347–360

Lapointe BE, Barile PJ, Littler MM, Littler DS (2005a) Macroalgal blooms on southeast Florida coral reefs II cross-shelf discrimination of nitrogen sources indicates widespread assimilation of sewage nitrogen. Harmful Algae 4:1106–1122

Lapointe BE, Barile PJ, Littler MM, Littler DS, Bedford BJ, Gasque C (2005b) Macroalgal blooms on southeast Florida coral reefs I nutrient stoichiometry of the invasive green alga Codium isthmocladum in the wider Caribbean indicates nutrient enrichment. Harmful Algae 4:1092–1105

Lavery PS, Lukatelich RJ, McComb AJ (1991) Changes in the biomass and species composition of macroalgae in a eutrophic estuary. Estuar Coast Shelf Sci 33:1–22

Lewis SM (1986) The role of herbivorous fishes in the organization of a Caribbean reef community. Ecol Monogr 56:183–200

Lillebø AI, Neto JM, Martins I, Verdelhos T, Leston S, Cardoso PG, Ferreira SM, Marques JC, Pardal MA (2005) Management of a shallow temperate estuary to control eutrophication: the effect of hydrodynamics on the system's nutrient loading. Estuar Coast Shelf Sci 65:697–707

Littler MM, Littler DS, Brooks BL (2006) Harmful algae on tropical coral reefs: bottom-up eutrophication and top-down herbivory. Harmful Algae 5:565–585

Liu D, Bai J, Song S, Zhang J, Sun P, Li Y, Han G (2007) The impact of sewage discharge on the macroalgal community in the Yellow Sea coastal area around Quingdao, China. Water Air Soil Pollut Focus 7:683–692

Liu D, Keesing JK, Xing Q, Shi P (2009) World's largest macroalgal bloom caused by expansion of seaweed aquaculture in China. Mar Pollut Bull 58:888–895

Longstaff BJ, Kildea T, Runcie JW, Cheshire A, Dennison WC, Hurd C, Kana T, Raven JA, Larkum AW (2002) An in situ study of photosynthetic oxygen exchange and electron transport rate in the marine macroalga *Ulva lactuca* (Chlorophyta). Photosynth Res 74:281–293

Lotze HK, Milewski I (2004) Two centuries of multiple human impacts and successive changes in a North Atlantic food web. Ecol Appl 14:1428–1447

Lotze HK, Worm B (2000) Variable and complementary effects of herbivores on different life stages of bloom forming macroalgae. Mar Ecol Prog Ser 200:167–175

Lotze HK, Worm B (2002) Complex interactions of climatic and ecological controls on macroalgal recruitment. Limnol Oceanogr 47:1734–1741

Lotze HK, Schramm W, Schories D, Worm B (1999) Control of macroalgal blooms at early development stages: *Pilayella littoralis* versus *Enteromorpha* spp. Oecologia 119:46–54

Lotze HK, Worm B, Sommer U (2000) Propagule banks, herbivory and nutrient supply control population development and dominance patterns in macroalgal blooms. Oikos 89:46–58

Lotze HK, Worm B, Sommer U (2001) Strong bottom-up and top-down control of early life stages of macroalgae. Limnol Oceanogr 46:749–757

Lubchenco J (1978) Plant species diversity in a marine intertidal community: importance of herbivore food preference and algal competitive ability. Am Nat 112:23–39

Lubchenco J (1983) *Littorina* and *Fucus*: effects of herbivores, substratum, heterogeneity, and plant escapes during succession. Ecology 64:1116–1123

Lubchenco J, Menge BA (1978) Community development and persistence in a low rocky intertidal zone. Ecol Monogr 48:67–94

Martinetto P, Daleo P, Escapa M, Alberti J et al (2010) High abundance and diversity of consumers associated with eutrophic areas in a semi-desert macrotidal coastal ecosystem in Patagonia, Argentina. Estuar Coast Shelf Sci 88:357–364

Martinetto P, Teichberg M, Valiela I, Montemayor D, Iribarne O (2011) Top-down and bottom-up regulation in a high nutrient-high herbivory coastal ecosystem. Mar Ecol Prog Ser 432:69–82

Martins I, Pardal M, Lillebo AI, Flindt MR, Marques JC (2001) Hydrodynamics as a major factor controlling the occurrence of green macroalgal blooms in a eutrophic estuary: a case study on the influence of precipitation and river management. Estuar Coast Shelf Sci 52:165–177

McClanahan TR, Sala E, Stickel PA, Cokos BA, Baker AC, Starger CJ, Jones SH IV (2003) Interaction between nutrients and herbivory in controlling algal communities and coral condition on Glover's Reef, Belize. Mar Ecol Prog Ser 261:135–147

McGlathery KJ (2001) Macroalgal blooms contribute to the decline of seagrass in nutrient-enriched coastal waters. J Phycol 37:453–456

McManus JW, Polsenberg JF (2004) Coral-algal phase shifts on coral reefs: ecological and environmental aspects. Prog Oceanogr 60:263–279

Menge BA (1992) Community regulation: under what conditions are bottom-up factors important on rocky shores? Ecology 73:755–765

Menge BA, Daley BA, Wheeler PA, Dahlhoff E, Sanford E, Strub PT (1997) Benthic-pelagic links and rocky intertidal communities: bottom-up effects on top-down control? Proc Natl Acad Sci 94:14530–14535

Monteiro PMS, Anderson RJ, Woodbourne S (1997) d^{15}N as a tool to demonstrate the contribution of fish-waste-derived nitrogen to an *Ulva* bloom in Saldanha Bay, South Africa. S Afr J Mar Sci 18:1–9

Morand P, Merceron M (2005) Macroalgal population and sustainability. J Coast Res 21:1009–1020

Mumby PJ, Dahlgren CP, Harborne AR, Kappel CV, Micheli F, Brumbaugh DR, Holmes KE, Mendes JM, Broad K, Sanchirico JN, Buch K, Box S, Stoffle RW, Gill AB (2006) Fishing, trophic cascades, and the process of grazing on coral reefs. Science 311:98–101

Myers RA, Worm B (2003) Rapid worldwide depletion of predatory fish communities. Nature 423:280–283

Nielsen KJ (2003) Nutrient loading and consumers: agents of change in open-coast macrophyte assemblages. Proc Natl Acad Sci 100:7660–7665

Nixon SW (1995) Coastal eutrophication: a definition, social causes, and future concerns. Ophelia 41:199–220

Nugues MM, Bak RPM (2008) Long-term dynamics of the brown macroalga *Lobophora variegata* on deep reefs in Curacao. Coral Reefs 27:389–393

Ochoa-Izaguirre MJ, Carballo JL, Paez-Osuna F (2002) Qualitative changes in macroalgal assemblages under two contrasting climatic conditions in a subtropical estuary. Bot Mar 45:130–138

Oesterling M, Pihl L (2001) Effects of filamentous green algal mats on benthic macrofauna functional feeding groups. J Exp Mar Biol Ecol 263:159–183

Paine RT, Vadas RL (1969) The effects of grazing by sea urchins, *Strongylocentrotus* spp., on benthic algal populations. Limnol Oceanogr 14:710–719

Piñon-Gimate A, Serviere-Zaragoza E, Ochoa-Izaguirre MJ, Páez-Osuna F (2008) Species composition and seasonal changes in macroalgal blooms in lagoons along the southeastern Gulf of California. Bot Mar 51:112–123

Piriz ML, Eyras MC, Rostagno CM (2003) Changes in biomass and botanical composition of beach-cast seaweeds in a disturbed coastal area from Argentine Patagonia. J Appl Phycol 15:67–74

Pregnall AM, Miller SL (1988) Flux of ammonium from surf-zone and nearshore sediments in Nahant Bay, Massachusetts, USA in relation to free-living *Pilayella littoralis*. Mar Ecol Prog Ser 50:161–167

Raffaelli DG, Raven JA, Poole LJ (1998) Ecological impact of green macroalgal blooms. Oceanogr Mar Biol 36:97–125

Rosenberg R, Elmgren R, Fleischer S, Jonsson P, Persson G, Dahlin H (1990) Marine eutrophication case studies in Sweden. Ambio 19:102–108

Schaffelke B, Hewitt CL (2007) Impacts of introduced seaweeds. Bot Mar 50:397–417

Sfriso A, Marcomini A (1997) Macrophyte production in a shallow coastal lagoon: part II coupling with chemico-physical parameters and nutrient concentrations in waters. Mar Environ Res 44:351–375

Sfriso A, Marcomini A, Pavoni B (1987) Relationships between macroalgal biomass and nutrient concentrations in a hypertrophic area of the Venice Lagoon. Mar Environ Res 22:297–312

Sfriso A, Pavoni B, Marcomini A, Orio AA (1992) Macroalgae, nutrient cycles, and pollutants in the Lagoon of Venice. Estuaries 15:517–528

Sfriso A, Facca C, Ghetti PF (2003) Temporal and spatial changes of macroalgae and phytoplankton in a Mediterranean coastal area: the Venice lagoon as a case study. Mar Environ Res 56:617–636

Smith SV (1981) Kanehoe Bay sewage diversion experiment: perspectives on ecosystem responses to nutritional perturbation. Pac Sci 35:279–402

Smith JE, Smith CM, Hunter CL (2001) An experimental analysis of the effects of herbivory and nutrient enrichment on benthic community dynamics on a Hawaiian reef. Coral Reefs 19:332–342

Smith JE, Hunter CL, Smith CM (2002) Distribution and reproductive characteristics of nonindigenous and invasive marine algae in the Hawaiian islands. Pac Sci 56:299–315

Smith JE, Hunter CL, Smith CM (2010) The effects of top-down versus bottom-up control on benthic coral reef community structure. Oecologia 163:497–507

Sotka EE, Hay ME (2009) Effects of herbivores, nutrient enrichment, and their interactions on macroalgal proliferation and coral growth. Coral Reefs 28:555–568

Sugimoto K, Hiraoka K, Ohta S, Niimura Y, Terawaki T, Okada M (2007) Effects of ulvoid (*Ulva* spp.) accumulation on the structure and function of eelgrass (*Zostera marina* L.) bed. Mar Poll Bull 54:1582–1585

Taylor RB, Rees TAV (1998) Excretory products of mobile epifauna as a nitrogen source for seaweeds. Limnol Oceanogr 43:600–606

Teichberg M, Fox SE, Olsen YS, Valiela I, Martinetto P, Iribarne O, Muto EY, Petti MAV, Corbisier TN, Soto-Jimenez M, Páez-Osuna F, Castro P, Freitas H, Zitelli A, Cardinaletti M, Tagliapietra D (2010) Eutrophication and macroalgal blooms in temperate and tropical coastal waters: nutrient enrichment experiments with *Ulva* spp. Glob Change Biol 16:2624–2637

Thacker RW, Ginsburg DW, Paul VJ (2001) Effects of herbivore exclusion and nutrient enrichment on coral reef macroalgae and cyanobacteria. Coral Reefs 19:318–329

Thomsen MS, McGlathery KJ, Tyler AC (2006) Macroalgal distribution patterns in a shallow, soft-bottom lagoon, with emphasis on the nonnative *Gracilaria vermiculophylla* and *Codium fragile*. Estuar Coasts 29:465–473

Tsai CC, Chang JS, Sheu F, Shyu YT, Yu AY, Wong SL, Dai CF, Lee TM (2005) Seasonal growh dynamics of *Laurencia papillosa* and *Gracilaria coronipifolia* from a highly eutrophic reef in southern Taiwan: temperature limitation and nutrient availability. J Exp Mar Biol Ecol 315:49–69

Valiela I (2006) Global coastal change. Blackwell, Massachusetts, p 368

Valiela I, Foreman K, LaMontagne M, Hersh D, Costa J, Peckol P, DeMeo-Anderson B, D'Avanzo C, Babione M, Sham C, Brawley J, Lajtha K (1992) Couplings of watersheds and coastal waters: sources and consequences of nutrient enrichment in Waquoit Bay, Massachusetts. Estuaries 15:443–457

Valiela I, McClelland J, Hauxwell J, Behr PJ, Hersh D, Foreman K (1997) Macroalgal blooms in shallow estuaries: controls and ecophysiological and ecosystem consequences. Limnol Oceanogr 42:1105–1118

Vermeij MJA, Moorselaar I, Engelhard S, Hörnlein C, Vonk SM, Visser PM (2010) The effects of nutrient enrichment and herbivore abundance on the ability of turf algae to overgrow coral in the Caribbean. PLoS One 5:1–8

Wilce RT, Schneider CW, Quinlan AV, Vanden Bosch K (1982) The life history and morphology of free-living *Pilayella littoralis* (L.) Kjellm. (Ectocarpaceae, Ectocarpales) in Nahant Bay, Massachusetts. Phycologia 21:336–345

Wootton JT, Pfister CA, Forester JD (2008) Dynamic patterns and ecological impacts of declining ocean pH in a high-resolution multi-year dataset. Proc Natl Acad Sci 10:18848–18853

Worm B, Lotze HK (2006) Effects of eutrophication, grazing, and algal blooms on rocky shores. Limnol Oceanogr 51:569–579

Worm B, Lotze HK, Bostrom C, Engkvist R, Labanauskas V, Sommer U (1999) Marine diversity shift linked to interactions among grazers, nutrients, and propagule banks. Mar Ecol Prog Ser 185:309–314

Ye N, Zhang X, Mao Y, Liang C, Xu D, Zou J, Zhuang Z, Wang Q (2011) 'Green tides' are overwhelming the coastline of our blue planet: taking the world's largest example. Ecol Res 26:477–485