

Effects of bottom-up and top-down controls and climate change on estuarine macrophyte communities and the ecosystem services they provide

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Abstract

Macrophytes provide important estuarine benthic habitats and support a significant portion of estuarine productivity. The composition and characteristics of these benthic communities are regulated bottom-up by resource availability and from the top-down by herbivory and predation. Human activities in coastal zones have dramatically altered the relative strengths of these controls by delivering nutrients to coastal waters and over-exploiting fishery resources. Here, we review bottom-up and top-down controls and how these may interact to structure estuarine macrophyte communities and the ecosystem services they provide. We further discuss the impacts of climate change on macrophyte communities and highlight the interactions that are likely to occur with our current knowledge of bottom-up and top-down forcings. Future research on the interactive effects of bottom-up and top-down controls and climate change on estuarine ecosystem properties (e.g., diversity, community structure, biogeochemistry, etc.) and the services they provide (e.g., food production, nutrient filtration, etc.) will supply important information for the preservation and management of these critical coastal habitats.

Estuaries are highly productive coastal habitats, typically shallow in depth and with light penetration reaching the benthos. The flora and fauna of estuaries worldwide vary considerably, but primary producer communities generally include phytoplankton, benthic microalgae, macroalgae, seagrasses, and epiphytes growing on the surfaces of macrophytes. The biomass and composition of these producer communities depend on a range of factors, including depth, light availability (or turbidity), nutrient supply, water residence time, grazing, and predation.

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Acknowledgments

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We would like to thank the 2008 Eco-DAS Symposium and its participants for stimulating discussion that aided the development of this chapter. We would like to thank Drs. Paul Kemp and Kate Achilles for organizing the symposium and the proceedings, NSF for funding the symposium, and American Society of Limnology and Oceanography for publishing the proceedings. This chapter was improved by comments from anonymous reviewers. The views expressed in this paper are those of the authors and do not necessarily reflect the views or policies of the U.S. Environmental Protection Agency. This is contribution 1393 from the Gulf Ecology Division.

Publication was supported by NSF award OCE0812838 to P.F. Kemp
ISBN: 978-0-9845591-1-4, DOI: 10.4319/ecodas.2010.978-0-9845591-1-4.129

Seagrass meadows and macroalgal canopies, in particular, are important benthic habitats within estuaries and comprise a significant portion of estuarine primary productivity (Mateo et al. 2006). Carbon fixed by estuarine primary producers can follow several pathways. It can be transferred to consumers, deposited to the sediments, or exported to neighboring systems. Macroalgae, epiphytic algae, and benthic microalgae provide important food resources for a variety of invertebrate and fish consumers. Seagrasses are generally less palatable to consumers than algae since seagrasses have a higher content of carbon-rich structural and storage compounds such as lignin, cellulose, and carbohydrates (Valentine and Heck 1999). However, the value of seagrasses as a food source to consumers is somewhat dependent on latitude. In temperate estuaries, seagrass carbon tends to enter the benthic food web as detritus (Cebrián 1999; Cebrián and Duarte 2001), whereas seagrasses are commonly consumed by invertebrates, fish, and mammals in tropical systems (Hay et al. 1994; Valentine and Heck 1999; Alcoverro et al. 2001; Arnold and Targett 2002; Olsen and Valiela 2010). In both temperate and tropical environments, seagrass production directly or indirectly supports consumers and, potentially, commercially important species (Lubbers et al. 1990; Heck and Valentine 1995; Duarte and Chiscano 1999; Nagelkerken et al. 2002; Heck et al. 2003; Dorenbosch et al. 2004; Spivak et al. 2009a).

In estuaries, macrophytes provide important ecosystem

services by stabilizing coastal sediments (Harlin et al. 1982), modifying biogeochemical transformations (Blaabjerg and Finster 1998; Risgaard-Petersen et al. 1998; McGlathery et al. 2007; Spivak et al. 2007, 2009a), modulating carbon export and burial (Cebrián 1999; Cebrián and Duarte 2001; Morand and Merceron 2005), improving water quality by filtering excess nutrients (Sfriso and Marcomini 1994; McGlathery et al. 2007) and facilitating deposition of suspended particles (Gacia et al. 1999), and providing habitat and nursery grounds to ecologically and economically important animals (Lubbers et al. 1990; Heck and Valentine 1995; Duarte and Chiscano 1999; Madsen et al. 2001; Orth et al. 2006). The delivery of these services is influenced by multiple abiotic factors, including nutrients, light, salinity, temperature, pH, and UV radiation. These factors, or resources, are collectively known as bottom-up controls since they directly regulate primary producer biomass, which forms the base of the food web. Bottom-up controls may alter biomass, species composition, and/or nutritional quality of producers (Jimenez et al. 1996; Valiela et al. 1997; Hemmi and Jormalainen 2002; Fox et al. 2008). Changes in producer community structure at the base of the food web, in turn, affect higher trophic levels (Raffaelli et al. 1998; Deegan et al. 2002; Ware and Thompson 2005; Olsen et al. in press).

Benthic communities can also be regulated from the top down by consumers. Herbivores control primary producer biomass and community composition by selectively grazing on palatable and nutritious algal or plant species (Hay et al. 1994; Jimenez et al. 1996; Heckscher et al. 1996; Lotze and Worm 2000; Hemmi and Jormalainen 2002; Andersson et al. 2009; Olsen and Valiela 2010; Olsen et al. in press). Predators can create “cascading” trophic effects by controlling herbivore abundance, which, in turn, reduces grazing pressure on primary producers (Warwick et al. 1982; Wootton 1995; Davenport and Anderson 2007). Thus, predators can indirectly increase primary producer biomass and ecosystem productivity, altering community composition of producers and consumers and food web structure.

Human activities in coastal zones have drastically impacted controls acting on estuarine primary producer communities by changing resource levels at the bottom of the food web and animal communities at top of the food web. Anthropogenic disturbances such as eutrophication and global climate change alter the relative strength of bottom-up controls (Valiela et al. 1997; Cloern 2001; Orth et al. 2006; Rabalais et al. 2009). At the same time, the composition of animal communities and degree of top-down control are rapidly changing as the result of intense human harvesting of invertebrate, fish, and mammal populations (Jackson et al. 2001; Myers and Worm 2003). Shifts in the relative impact of bottom-up and top-down mechanisms controlling estuarine macrophytes will likely impact the services that these benthic estuarine ecosystems provide. Further, interactions between bottom-up and top-down controls affect biological, trophic, and biogeochem-

ical processes (Fig. 1). Here, we begin with a brief review of the bottom-up and top-down literature, since there are numerous recent articles that have thoroughly analyzed the relative influence of these controlling mechanisms for seagrasses, macroalgae, and estuaries in general (Cloern 2001; McGlathery 2001; Hughes et al. 2004; Burkepille and Hay 2006; Orth et al. 2006; McGlathery et al. 2007; Heck and Valentine 2007; Elser et al. 2007; Gruner et al. 2008). We highlight (1) how the relative influence of bottom-up and top-down controls in estuarine benthic macrophyte communities are altered by anthropogenic disturbances, including increased nutrient inputs and fishing pressure; (2) how climate change might affect carbon flow through these ecosystems; and (3) how these altered pathways might affect some important ecosystem services provided by estuaries.

Bottom-up controls of benthic macrophyte communities

In estuaries, light and nutrients are two of the main bottom-up controls on algae and seagrasses (Moore et al. 1996; Valiela et al. 1997; Livingston et al. 1998; Cloern 2001; Kemp et al. 2004; Orth et al. 2006; Fox et al. 2008). Light penetration through the water column is directly reduced by suspended particles in the water column, including sediments and phytoplankton, and indirectly by increased nutrient supply that stimulates higher water column productivity (Valiela et al. 1992; Taylor et al. 1999; Cloern 2001). Development of coastal watersheds has reduced estuarine water quality by increasing nutrient and suspended sediment loads. Human activities, such as deforestation, suburbanization, dredging, commercial fishing, and commercial and recreational boating, combined with wind and water currents increase suspended sediment concentrations and decrease water clarity (Sanford 1994; Schoellhamer 1996; Yang et al. 2004; Saenger et al. 2008). Humans have also significantly altered inorganic nutrient cycling and availability by increasing nitrogen and phosphorus delivery to rivers and estuaries via runoff, wastewater outfalls, groundwater, and atmospheric deposition (Valiela et al. 1992, 2000; Bricker et al. 2007). Nitrogen likely limits primary production in temperate coastal areas (Nixon and Pilson 1983; Howarth 1988; Oviatt et al. 1995; Teichberg et al. 2009), whereas phosphorus may be more important in tropical environments with carbonate sediments due to adsorption of phosphate to sediments (Lapointe et al. 1992; McGlathery et al. 1994; however see Elser et al. 2007; Teichberg et al. 2009).

Since light and nutrients are two key resources (i.e., bottom-up controls) for growth of algae and macrophytes (Short et al. 1995; Valiela et al. 1997; Burkholder et al. 2007; Brun et al. 2008; Fox et al. 2008), changes in the absolute and relative levels of these resources will influence the biomass and composition of the primary producer communities by altering competitive interactions (Peckol and Rivers 1995; Steen 2004; Worm and Lotze 2006; Fox et al. 2008). Opportunistic, fast-growing phytoplankton, epiphytes, and macroalgae respond quickly to nitrogen and phosphorus supplies in the water column by

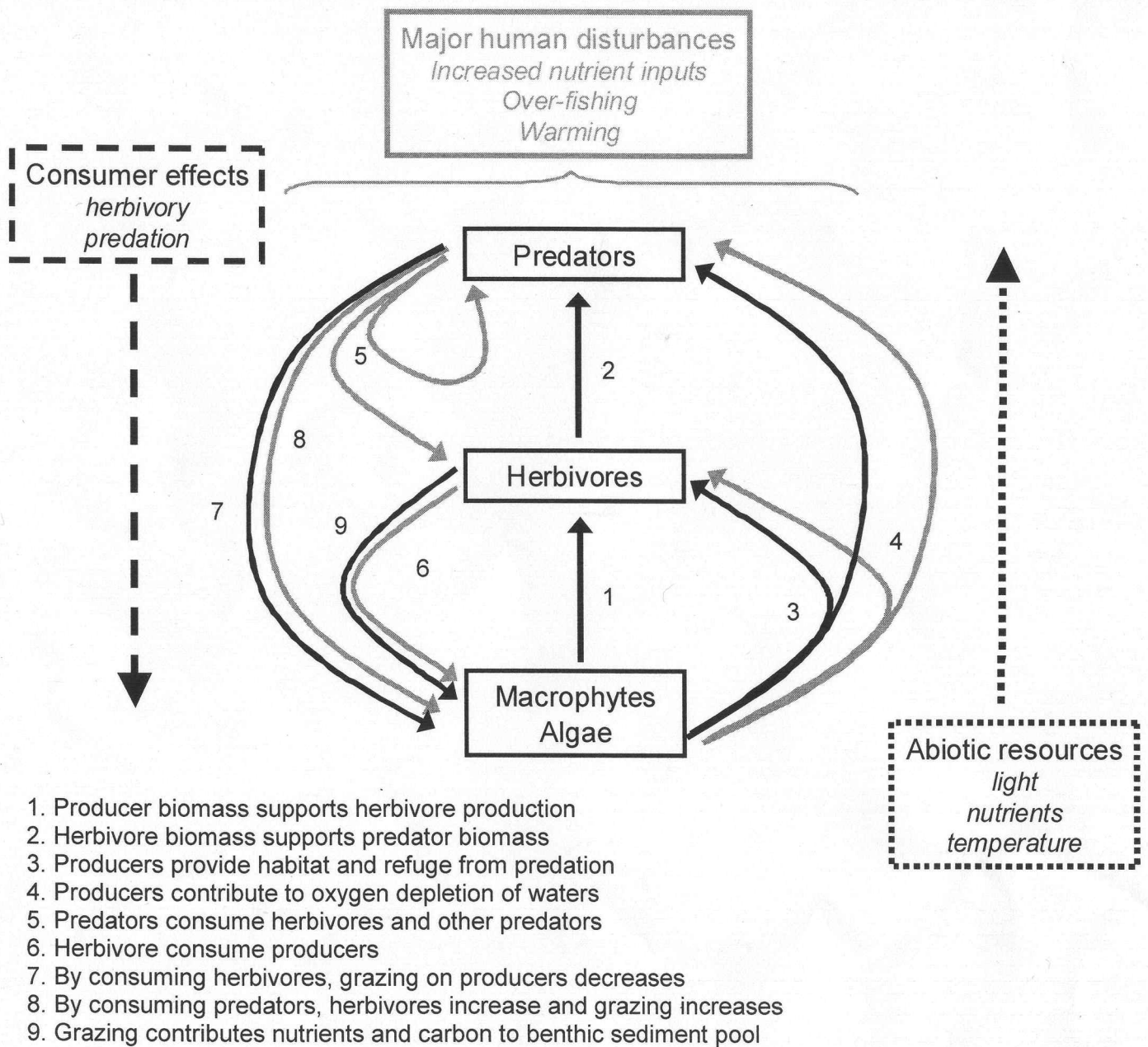


Fig. 1. Schematic diagram of mechanisms of control regulating coastal benthic food webs. Resource effects cascade from the bottom of the food web up, whereas consumer effects cascade from the top of the food web down. Black arrows represent positive interactions, in which abundance at the receiving trophic level is enhanced. Gray arrows show negative interactions in which there is a reduction in abundance at the receiving trophic level. Human disturbances potentially mediate all the interactions drawn.

accumulating biomass (Orth and van Montfrans 1984; Pedersen and Borum 1996; Cloern 2001). Fong and Zedler (1993) found that higher light availability favors the proliferation of free-floating macroalgal biomass. As a result, the larger biomasses of water column algae reduce light availability to benthic macrophytes and algae (Hauxwell et al. 2001; Brush and Nixon 2002; Hauxwell et al. 2003; Frankovich and Zieman 2005). Overall, light limitation by suspended sediments and

algae is believed to be the most serious cause for present-day seagrass decline (Duarte 1995; Short and Wyllie-Echeverria 1996; Hauxwell et al. 2001; McGlathery 2001).

Macroalgal taxa differ in their ability to compete for resources. *Ulva* spp., for example, have high nutrient uptake rates and photosynthetic efficiencies (Pedersen and Borum 1996; Plus et al. 2005), grow rapidly, accumulate high biomass, and outcompete other species (Sfriso et al. 1992; Fong et al.

1996; Pedersen and Borum 1996; Campbell 2001; Steen 2004; Teichberg et al. 2008). Under certain conditions, interactions among species may lead to communities dominated by a few highly competitive taxa (Peckol and Rivers 1995; Worm and Chapman 1996; Fox et al. 2008). However, even when competition is high, groups of dominant species coexist, suggesting that these taxa may have different resource requirements and resource partitioning may occur (Tilman 1988; Peckol and Rivers 1995); for example, nitrogen preferences in coexisting macroalgal species have been suggested (Fox et al. in press; Teichberg et al. 2008). Thus, the relative availability of light, nutrients, and other resources may alter competitive outcomes between estuarine primary producers, thereby influencing producer community biomass and species composition.

Resource supply or availability not only changes biomass and structure of producer communities, but also alters the nutritional quality of benthic macrophytes and algae, because nutrient composition (stoichiometry) of these groups is somewhat flexible (Atkinson and Smith 1983; Duarte 1992; Pedersen and Borum 1996). For instance, when supplies of dissolved inorganic nitrogen and phosphorus are high, plants and algae may take up the available nutrients (Elser et al. 1995; Pedersen and Borum 1996; Hall et al. 2005; Teichberg et al. 2007). The nutrients may then be used to build biomass or be stored until other limiting elements are available or conditions are sufficient for growth (Pedersen and Borum 1996; Romero et al. 2006; Teichberg et al. 2007, 2008). Uptake and assimilation of the available nutrients reduces the carbon-to-nutrient ratio of seagrass or algal tissues, making the primary producers a higher quality food source for grazers (McGlathery 1995; Hemmi and Jormalainen 2002; Boyer et al. 2004; Olsen and Valiela 2010). Light levels may also affect the carbon-to-nutrient ratio of benthic macrophytes and algae, but responses differ and may be species-specific. For example, under low light conditions some freshwater macrophytes and algae may devote their resources to building light-capturing machinery and produce biomass with a high carbon-to-nutrient ratio and a lower nutritional value (Stern et al. 1997; Elser et al. 2002; Frost and Elser 2002). In the macroalga, *Fucus gardneri*, nitrogen content was higher under ambient than under reduced light conditions, and carbon content was not affected by light level (Edwards et al. 2006), so that under low-light conditions nutritional quality of the macroalgae was lower. Alternatively, the macroalga, *Ulva intestinalis*, showed no change in nitrogen content with an increasing light regime (Cohen and Fong 2004). In contrast, high light levels can promote high rates of carbon fixation and production in seagrasses, which can lead to N limitation and nutritionally poor biomass with increased C to N ratios (Abal et al. 1994; Grice et al. 1996). Thus, the identity and relative availability of bottom-up resources may concurrently influence primary producer elemental composition, growth, and community composition.

Bottom-up controls affect the abundance and composition of primary producers, as well as consumers at higher trophic

levels. When nutrient enrichment increases the biomass of easily digestible primary producers, such as epiphytes, benthic microalgae, and ephemeral macroalgae, there are often subsequent increases in herbivore biomass (Raffaelli et al. 1998; Deegan et al. 2002; Spivak et al. 2009a). Increased production at the base of the food web has also been shown to control production at higher trophic levels (Nixon and Buckley 2002; Ware and Thomson 2005). Changes in primary producer biomass and identity may also permeate up the food web by altering the relative availability of food items to consumers (Fox et al. 2009; Olsen et al. in press). Bottom-up controls, therefore, act at all trophic levels with impacts on primary producers propagating up food webs.

Top-down controls of benthic macrophyte communities

Consumers can exert control from the top down on lower trophic levels and primary producers at the base of the food web. Humans, in particular, have dramatically altered estuarine and coastal herbivore and predator communities by overharvesting commercially and recreationally important species. Fishing fleets have removed approximately 90% of the predatory fish stocks worldwide (Myers and Worm 2003; Pandolfi et al. 2003; Mumby et al. 2006). The removal of these organisms has cascading effects on lower trophic levels (Hughes 1994; Heck et al. 2000; Jackson et al. 2001; Mumby et al. 2006; Casini et al. 2009). Because these fisheries are based on organisms that spend some stage of their lives in estuaries, e.g., to seek refuge and to feed as juveniles (Boesch and Turner 1984; Baker and Sheaves 2005; Nagelkerken et al. 2008), overfishing may directly impact estuarine food web structure. Anthropogenic disturbances that alter species diversity and food chain length affect community composition and the distribution of biomass across trophic levels (Heck and Valentine 2007), so that removal of commercially and recreationally important species from estuaries and coastal bays has not only altered trophic interactions, but also the strength of top-down controls in these systems.

The feeding preferences of carnivores and herbivores also alter the strength of trophic controls, as well as the species composition of successively lower trophic levels (Finke and Denno 2004; Byrnes et al. 2006; Halpern et al. 2006). Predators may create "cascading" top-down effects by reducing grazer abundance and indirectly increasing primary producer biomass by releasing them from grazing pressure (Warwick et al. 1982; Wootton 1995; Williams et al. 2004; Casini et al. 2008). For example, in seagrass habitats, the presence of predatory fish and crabs can initiate a trophic cascade by reducing or inhibiting invertebrate grazers, which, in turn, allows algal biomass to accumulate (Duffy et al. 2005; Moksnes et al. 2008; Baden et al. 2010).

Top-down control by herbivores also affects macrophyte biomass and community structure. Reduced top-down pressure has been suggested as a contributing cause of macroalgal blooms in estuaries (Geertz-Hansen et al. 1993; Valiela et al.

1997; Fox et al. in press). In addition, preferential consumption of certain species or functional groups of macrophytes by grazers may alter the structure of the benthic community (Lotze and Worm 2000; Lotze et al. 2001). In seagrass habitats, grazers can promote seagrass growth and survival by controlling epiphyte and macroalgal biomass (Neckles et al. 1993; Hughes et al. 2004; Heck et al. 2006; Baden et al. 2010).

Predicting how changing trophic structure affects estuarine primary producer communities is complicated by the fact that predators induce shifts not only in their prey biomass, but also in prey community structure. Grazer community composition affects the abundance of different primary producers, because herbivores are highly selective in their food choices. In seagrass systems, for example, grazers can consume epiphytic algae, macroalgae, benthic microalgae, and/or seagrasses (Lotze and Worm 2000; Duffy and Harvilicz 2001; Duffy et al. 2001; Goecker and Kall 2003; Tewfik et al. 2005; Valentine and Duffy 2006; Fox et al. 2010). Herbivore control of marine macroalgae, however, is highly variable and depends, in part, on algal palatability (Hay et al. 1994; Heckscher et al. 1996; Lotze et al. 2001; Andersson et al. 2009) and growth rates (Gruner et al. 2008; Andersson et al. 2009; Fox et al. in press). Consequently, the degree of top-down control of herbivores on estuarine primary producers depends on the identity and composition of assemblages of herbivores and predators that are determined by a combination of bottom-up and top-down mechanisms.

Interactions and feedbacks between bottom-up and top-down controls

Bottom-up (i.e., resource) controls can propagate up from the base of the food web to higher trophic levels, and top-down (i.e., consumer) effects are generally strong determinants of biomass distribution across multiple trophic levels (Borer et al. 2006; Burkepile and Hay 2006; Heck and Valentine 2007). The relative magnitude of top-down versus bottom-up controls in coastal benthic food webs is likely a function of multiple factors including resource identity, primary producer, and consumer community composition, and abiotic factors that may vary temporally and spatially. Top-down and bottom-up forcings may have a synergistic effect on the primary producer community (Fig. 1). For example, in the Baltic Sea, higher biomasses of ephemeral bloom-forming macroalgae have been attributed to a combination of anthropogenic factors, eutrophication, and cascading effects of the removal of top-level predators by overfishing (Eriksson et al. 2009). Alternatively, interactions between controls can have an antagonistic effect on the primary producer community (Fig. 1; Hughes et al. 2004; Burkepile and Hay 2006). Understanding how bottom-up and top-down controls, both singularly and interactively, affect estuarine benthic ecosystem properties and processes is important given that human disturbances are simultaneously changing resource availability and abundance and species composition of consumers at higher trophic levels.

Increased nutrient inputs to estuaries result in higher algal biomass and, in some systems, hypoxic events, during which oxygen concentrations in estuarine bottom waters plunge below levels sufficient to support invertebrates and fishes (Baden et al. 1990; Oesterling and Pihl 2001; Fox et al. 2009). This, in turn, can lead to reduced grazing pressure on primary producers and increased algal-derived organic matter delivery to the sediments and export from the system (Valentine and Heck 1999; Cebrián 1999; Cebrián and Duarte 2001; Domning 2001; Heck and Valentine 2007; Fox et al. in press). The ability of herbivores to regulate primary producer biomass depends, in part, on algal growth rates and community composition, which are determined by both resource availability and consumer controls. In seagrass systems, grazers in high densities may be able control algal biomass (Baden et al. 2010), however grazers are often unable to control macroalgal biomass under eutrophic conditions when macroalgal biomass is high (Geertz-Hansen et al. 1993; Hauxwell et al. 1998; Lotze et al. 2001; Worm and Lotze 2006; Fox et al. in press). Thus, the strength of bottom-up forcing in eutrophic systems may thereby overwhelm control from the top down and result in a feedback loop that creates unfavorable hypoxic conditions, which reduce grazer abundances and weaken top-down control of algal biomass.

Bottom-up controls on biomass, species composition, and nutritional quality of the primary producers have implications for coastal ecosystem processes and food webs. For example, nutrient loading to coastal waters can reduce water clarity by increasing phytoplankton, epiphytic, and macroalgal biomass. As a result, the productivity of seagrasses and sediment microalgae may decline and sediment microbial activity may be altered (McGlathery et al. 2007). If the nutrient-stimulated algal biomass is not consumed by herbivores or exported from the system, algal decomposition may lead to lowered dissolved oxygen in the water column (Meyer-Reil and Koster 2000; Cloern 2001). Eutrophication and low oxygen conditions in the water column can, in addition to reducing the survival of benthic invertebrates and fish (Vaquer-Sunyer and Duarte 2008), affect the burial and sequestration of organic matter (Rabalais et al. 2009). Under anoxic conditions and with limited bioturbation from invertebrates, sediments may have slower decomposition rates of refractory organic material, but the organic material deposited under eutrophic conditions will come from more labile sources that are more rapidly decomposed like phytoplankton and opportunistic macroalgae (Kristensen et al. 1995; Kristensen 2000; McGlathery et al. 2007). It is, therefore, difficult to predict the resulting changes in organic matter sequestration.

Top-down and bottom-up controls interact when increased nutrients increase producer nutritional value and alter herbivore feeding habits. Herbivores often prefer and increase consumption rates of nutrient-rich food, as has been shown for invertebrates (Jimenez et al. 1996; Hemmi and Jormalainen 2002), fish (McGlathery 1995; Heck et al. 2000, 2006; Boyer et

al. 2004; Goecker et al. 2005), turtles (Bjorndal 1980), and marine mammals (Preen 1995). Because the stoichiometric requirements of animals are generally more constrained than those of plants and algae, the ability of herbivores to convert algal tissues into biomass depends, in part, on the nutritional quality of algae (Cruz-Rivera and Hay 2000), and the rates of herbivore growth and reproduction are higher when they consume food with a similar nutritional ratio (Acharya et al. 2004). Consumers tend to prefer food of higher nutritional value, because they have to spend energy to excrete unused elements if there is a large imbalance between the nutrient content of the food source and themselves (Anderson et al. 2005).

Quality of primary producers as a food source to herbivore also depends on chemical defenses, including tannins and phenolics (Hay et al. 1994; Arnold and Targett 2002; Goecker et al. 2005), which are influenced by both bottom-up and top-down controls. The degree to which chemical defenses deter grazers is a function of grazing pressure (Toth and Pavia 2007) and primary producer nutrient content (Ruiz et al. 2001). Intense grazing activity increases resistance in algae (Toth and Pavia 2007), whereas increased nutrient availability may lower concentrations of grazing deterrent compounds in producers. When nutrient supply is limited, carbohydrates may be available in excess of what can be metabolized into proteins and instead be allocated to production of nitrogen-free secondary metabolites (Bryant et al. 1983; Buchsbaum et al. 1990). Yates and Peckol (1993) found that defensive compounds were significantly higher in macroalgae from a low-nitrogen site compared with a high-nitrogen site. For seagrasses, similar relationships have been found. Buchsbaum et al. (1990) reported an inverse relationship between tissue nitrogen and chemical deterrents, and Goecker et al. (2005) found that seagrass leaves with higher tissue nitrogen content also had significantly lower levels of defense compounds. Differences in not only nutritional quality, but also biomass and identity of macrophytes and algae lead to preferential consumption of certain taxa by herbivores. The degree of top-down control in structuring primary producer assemblages is thereby mediated by bottom-up mechanisms.

Bottom-up mediated changes in nutritional quality and primary producer composition may also ascend the food web by influencing biomass production at higher trophic levels. Increases in resource availability that lead to higher production of inedible primary producers may weaken herbivore controls on macrophytes and algae. Alternatively, grazer control of primary producers may be strengthened when algal nutritional value is high and chemical defenses are low. Thus, the likelihood that bottom-up controls will increase herbivore abundance is greater if the quantity and quality of primary producer biomass is increased (Cruz-Rivera and Hay 2000). This suggests that the identity of a bottom-up control (i.e., nutrients versus light) and the composition of the primary producer community may determine whether resource effects are propagated to higher trophic levels.

Top-down controls are therefore modulated by shifts in the relative availability of food items following changes in consumer and producer communities. For example, in Waquoit Bay, a shallow temperate estuary, nutrient enrichment resulted in a shift in the availability of food items to omnivores (Fox et al. 2009). Omnivores in this system shifted from a diet that was mainly carnivorous in a noneutrophic estuary, where the preferred small prey were abundant, to feeding mainly as herbivores in a eutrophic estuary, where prey were scarce and macroalgal biomass was high. Similar dietary shifts in small, omnivorous crustaceans have been shown in other systems, where algae or detritus are consumed when preferred prey are scarce (e.g., Edgar 1990; Parkyn et al. 2001; Jephson et al. 2008; Persson et al. 2008). Shifts from seagrass- to algae-dominated producer communities brought about by anthropogenic nitrogen loading may result in consumer diets changing from seagrass- and detritus-based to macroalgae-dominated diets (McClelland and Valiela 1998; Olsen et al. in press).

In addition to altering patterns of biomass and distribution across trophic levels, bottom-up and top-down controls influence benthic ecosystem processes. For example, bottom-up controls that increase algal biomass may also increase gross ecosystem productivity (Spivak et al. 2009a), however, gross ecosystem productivity may be reduced when grazers are present and predators are absent (Spivak et al. 2007). In addition to altering ecosystem metabolism, bottom-up and top-down controls affect biogeochemical cycles. Rooted plants like seagrasses play an engineering role in sediment biogeochemistry and can modify the physical and chemical conditions in the sediments they inhabit, e.g., by releasing oxygen and dissolved organic carbon through their roots (Hemminga et al. 1991; Hemminga 1998). In contrast, macroalgae may reduce oxygen concentrations in bottom waters and decomposition of macroalgal and phytoplankton detritus can lead to sediment anoxia (Krause-Jensen et al. 1999). Thus, top-down and bottom-up forcings that limit seagrass and algal biomass and productivity indirectly lead to oxygen depletion of bottom waters and sediments. Lower oxygen in the sediments leads to more negative redox potential in sediments, which alters bacterial activity and benthic carbon, nitrogen, and sulfur cycling (Marbà et al. 2006). A negative feedback loop impacting benthic macrophytes may be initiated because products of bacterial metabolism under anoxic conditions, such as sulfide, can be toxic to seagrasses and further stress the macrophyte community (Holmer et al. 2006; Calleja et al. 2007; Koch et al. 2007).

Top-down and bottom-up forces can also alter the relative contribution of seagrasses, macroalgae, and plankton to organic matter deposited to the sediments (Canuel et al. 2007; Spivak et al. 2007, 2009b). Algae are preferentially used by bacteria and remineralized more rapidly, probably due to the relatively refractory composition of seagrass detritus (Holmer et al. 2004). A change in the composition of organic matter therefore alters decomposition rates, chemical and physical conditions of the sediment, benthic metabolism, nutrient remineraliza-

tion rates, and benthic nutrient cycling (Eyre and Ferguson 2002; Holmer et al. 2004; Canuel et al. 2007; Spivak et al. 2007, 2009b). Thus, resource and consumer controls that alter the relative biomasses of seagrass and macroalgal relative abundances affect long-term processes, such as carbon supply and burial (Duarte and Cebrián 1996; Cebrián 1999) and organic matter subsidies to nearby ecosystems (Valentine et al. 2007).

In striving to summarize the interactive effects of bottom-up and top-down controls on marine and estuarine habitats, several recent meta-analyses were performed. One such analysis of 54 experiments across multiple marine habitats and geographic locations demonstrated that herbivory and nutrient enrichment interactively affect primary producer abundance (Burkepile and Hay 2006). Further, these trends were widespread and varied with latitude. Top-down controls dominated in tropical environments. In temperate systems, the relative importance of top-down or bottom-up controls depended on system productivity as bottom-up effects were strongest in high-productivity systems, whereas top-down control by herbivores had a stronger influence in low-productivity systems (Burkepile and Hay 2006). Another meta-analysis of 35 studies in seagrass habitats showed that positive effects of epiphyte grazers on seagrass biomass were similar in magnitude to the negative effects of water column nutrient enrichment, suggesting bottom-up and top-down forcings may be of equal importance in some systems (Hughes et al. 2004). Recent experimental work suggests that heavy grazing of algae and epiphytes might be able to offset some of the negative effects of eutrophication on seagrasses (Hughes et al. 2004; Armitage et al. 2005; Heck and Valentine 2007). For example, in nutrient-rich coastal waters, epiphytic algal blooms may be reduced by invertebrate grazers, benefitting seagrasses (Neckles et al. 1993; Duffy and Harvilic 2001; Armitage et al. 2005; Heck and Valentine 2006; Baden et al. 2010).

Climate change, benthic macrophyte communities, and ecosystem services

There is consensus within the scientific community that human activities are altering a myriad of features of the Earth's system. For instance, in the coming decades and centuries, it is expected that human activities will cause air and water temperatures to increase and oceanic pH levels to fall (Parmesan and Yohe 2003; Nixon et al. 2004; Oviatt 2004; Valiela 2006; IPCC 2007). In coastal systems, the impacts of these disturbances will be exacerbated by eutrophication and commercial fisheries. Combined, these global and regional changes will likely alter physical, chemical, and biological drivers in coastal waters. Since many of the expected disturbances affect resource availability, it is likely that bottom-up controls will be more strongly impacted than top-down controls. In addition, synergistic interactions between multiple stressors may affect the relative influence of bottom-up versus top-down controls on production and community dynamics in estuarine benthic macrophyte habitats. As a result, the ability of these systems

to deliver services that are vital to humans, including sediment stabilization, carbon sequestration, water quality improvement, biogeochemical transformations, and habitat to economically important animals, may change (Orth et al. 2006). Reductions in the services estuarine macrophyte communities provide will likely have negative impacts on human well-being and local economies, especially those dependent on fishery and tourism industries (MEA 2005).

Warmer waters are expected to promote growth rates of algae, higher phytoplankton, and macroalgal standing stocks (Bintz et al. 2003; Rabalais et al. 2009), and perhaps increase the frequency of harmful algal blooms (Stachowicz et al. 2002; Tsai et al. 2005; Fig. 2, top). Warming may favor certain taxa, since resource use varies among different primary producer species, and some species may not tolerate the higher water temperatures (Short and Neckles 1999). For example, the competitive dominance of the ubiquitous macroalgae, *Ulva* spp., will likely increase under scenarios of warmer temperatures and higher nutrient supplies since its photosynthetic capabilities increase with temperature and nitrogen enrichment (Longstaff et al. 2002; Bintz et al. 2003; Cabello-Pasini and Figueroa 2005; Plus et al. 2005). Increased water column algal biomass will reduce light availability to seagrass, possibly leading to further declines in seagrass abundance. This may be followed by a loss of ecosystem services provided by seagrass ecosystems, which would lead to increased sediment mobilization (i.e., erosion), lower water clarity (due to suspended sediments and algae), and reduced abundances of fish and invertebrate species that use seagrasses as nursery and foraging habitats. Increasing temperatures will also alter the geographic distributions of species and facilitate the establishment of invasive taxa (Parmesan and Yohe 2003; Valiela 2006; Occhipinti-Ambrogi 2007).

Shifts in the biomass and composition of plant and animal communities will alter nutrient cycling and storage (Cloern 2001), as well as trophic interactions in coastal food webs (Fox et al. 2009; Breitburg et al. 2009). In the sediments, warmer temperatures may increase rates of microbial respiration and decomposition processes; this may alter redox conditions as oxygen concentrations decline and bacterial community metabolism shifts. In turn, rates of organic matter decomposition may slow and sediment carbon sequestration may be enhanced.

Warmer temperatures will also affect animal metabolic rates and, by extension, top-down controls on primary producers (Allen et al. 2005; Lopez-Urrutia et al. 2006; O'Connor et al. 2009). For example, animal respiration rates increase with rising temperature. Shifts in animal carbon demand and usage will alter trophic dynamics since animals must obtain energy from plants or organisms lower in the food chain. Recent models predicted that temperature was a stronger determinant of animal respiration than autotrophic production (Allen et al. 2005; Lopez-Urrutia et al. 2006). As a result, increased temperatures may strengthen top-down controls on

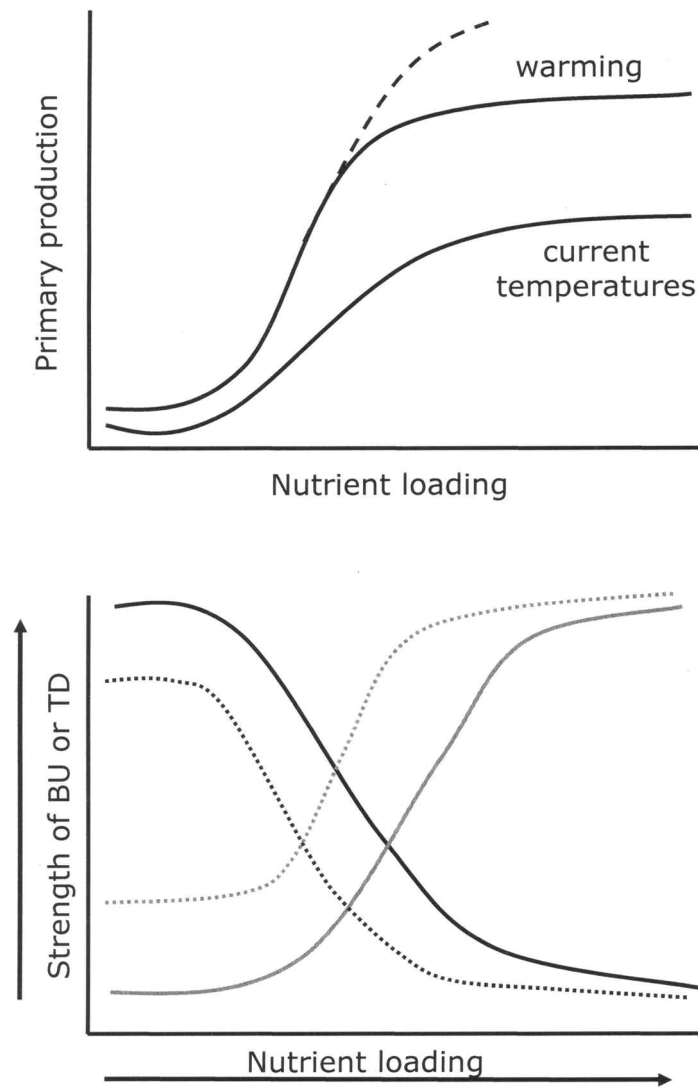


Fig. 2. Strength of bottom-up (BU) and top-down (TD) controls along a nutrient-loading gradient. BU controls (gray lines) tend to be weaker where nutrient loads are lower, and the strength of BU control increases as nutrient-loading increases. TD controls (black lines) tend to be strongest where nutrient loads are lower, and they weaken as nutrient loads increase. The relative importance or strength of BU or TD controls will depend on temperature, so that the position and slopes of the lines under current temperatures (solid lines) may shift with warmer temperatures (dashed lines). The point at which these lines intersect represents the nutrient load at which neither control dominates.

primary producers (O'Connor et al. 2009). In addition, rising temperatures may speed the rates at which animals grow and mature (Harley et al. 2006). Thus, larval invertebrates and fish may spend less time feeding on algae and zooplankton before switching to larger prey items. This will have implications for carbon transfer within the pelagic food web and between the benthic and pelagic food webs. These alterations to trophic structure of coastal communities will further impact top-down control mechanisms. Consequently, shifts in nutrient avail-

ability and temperature may synergistically alter seagrass community assemblages and carbon cycling processes through interacting mechanisms.

Rising coastal water temperatures combined with higher nutrient supply will likely increase water column algal growth and, potentially, the frequency and duration of hypoxic events (Boesch et al. 2007; Rabalais et al. 2009). Periods of low water column oxygen can adversely affect animals, leading to fish kills and reduced benthic organism abundances (Fox et al. 2009; Levin et al. 2009). In turn, this can reduce top-down forcing on lower trophic levels and primary producers (Fox et al. in press). Hypoxia may be exacerbated in the coming decades, since warmer water holds less oxygen because of temperature-dependent solubility of oxygen in seawater (Rabalais et al. 2009). However, recent experimental evidence suggests that interactions between rising temperatures and increased nutrient availability may strengthen top-down control by herbivores on primary producers (O'Connor et al. 2009). Thus in well-mixed estuaries, higher temperatures and nutrient levels may increase the production of high-quality algal biomass that is readily transferred to higher trophic levels

The pH of marine waters is expected to drop from the current level of 8.1 to 7.8 by the year 2100 as atmospheric CO_2 levels rise (Orr et al. 2005). Atmospheric CO_2 dissolution into seawater is followed by an increase in bicarbonate (HCO_3^-), which is readily taken up by primary producers. This is expected to have strong effects on abundances and growth rates of primary producers, corals, calcifying algae, and shell-forming organisms (Harley et al. 2006; Guinotte and Fabry 2008; Doney et al. 2009). For instance, increasing CO_2 is expected to have a positive effect on seagrass productivity and, if water clarity is sufficient, on seagrass extent (Harley et al. 2006; Guinotte and Fabry 2008). Some calcifying invertebrates have also shown positive responses to increased CO_2 and higher water temperatures (Gooding et al. 2009). However, many organisms that depend heavily on their calcified skeletons are expected to be negatively impacted by acidification. For example, calcification rates of mussels and oysters are lower when grown under high CO_2 conditions (Gazeau et al. 2007), and shells of trophically important pteropods were deformed or had evidence of dissolution after exposure to lower pH water (Orr et al. 2005). Lower pH levels can reduce the fitness of calcifying and shell-forming organisms, and will likely have cascading effects on benthic and pelagic food web structure and stability. Reduced pH is also expected to impact the respiration, metabolism, and physiology of marine animals (Portner et al. 2004). As such, it is likely that changes in the community composition of primary producers and animals will follow drops in pH.

Changes in pH levels may also indirectly impact herbivores. Since the carbon to nutrient ratio (i.e., stoichiometry) of algae is flexible, it is possible that increased bicarbonate availability could result in algal cells having higher concentrations of carbon relative to other nutrients. This means that, in lower

pH waters, algal cells may have a lower nutritional value to herbivores (van de Waal et al. 2010). Since the carbon to nutrient ratio of animals is generally less flexible, herbivores may become nutrient limited, resulting in slower growth rates (Urabe et al. 2003). Further, interactive effects between warmer waters and reduced pH may increase the stoichiometric (i.e., C:N:P) mismatch between primary producers and herbivores. This could strongly affect herbivore community composition, favoring species with high carbon to nutrient ratios, and biomass production at higher trophic levels. Alternatively, grazing pressure on algae may increase if herbivores increase their feeding efforts in order to maintain a stoichiometric balance. Because of the complex and understudied effects of pH on plant and animal communities, it is difficult to predict how this stressor will alter bottom-up and top-down dynamics. We suggest that future experimental investigations of benthic macrophyte community responses to pH and interactions between pH and other stressors will be helpful in predicting long-term changes.

With projected increases in human populations in coastal areas (Valiela 2006), it is likely that fishing efforts will intensify. Commercial and recreational fishing that removes top-predators, including fish and invertebrate species, may indirectly reduce predation pressure on herbivores. In turn, grazing pressure on edible primary producers may strengthen and maintain algal biomass at low levels, even in habitats with high nutrient availability (Hughes et al. 2004; Armitage et al. 2005; Burkepille and Hay 2006). This suggests that the negative effects of eutrophication may be alleviated in some areas with high fishing pressure. Therefore, intense grazing, that reduces macroalgal and phytoplankton abundances, may increase water quality and clarity, which are important ecosystem services. Depending on the trophic structure of the food web, overfishing may have the opposite effect. Removal of intermediate predators leads to increased predation pressure on herbivores thereby releasing grazing pressure on primary producers and causing proliferation of algae (Eriksson et al. 2009). It is therefore unclear how overfishing will impact benthic macrophyte communities as alterations to controlling mechanisms progress in the coming decades.

The predicted changes in water temperature and pH, coupled with the expectation that human populations and demands for natural resources will increase, likely mean that coastal systems will face dramatic biological and chemical alterations in coming decades. Research on the interactive effects of temperature, nutrient availability, pH, and diversity in marine environments is needed, especially at the habitat and landscape levels. In addition, effort should be devoted to valuing ecosystem services, predicting how they will change, and identifying ways to sustainably provision these services (MEA 2005). Identifying how bottom-up and top-down control mechanisms affect food production, sediment stabilization, and water quality in estuarine macrophyte communities is a first step.

Looking ahead

Human influences in the coastal zone, including overfishing and increased nutrient inputs, have major impacts on the relative strengths of top-down and bottom-up controls as illustrated by the examples above. Projections suggest that the global human population is likely to increase steadily for several generations to come and that urban sprawl will continue to increase at the expense of natural vegetation and rural areas (Lutz et al. 2001; Valiela 2006). The projected population increase is inevitably linked with increased resource demands, and we will continue to see changes in land use on watersheds coupled to estuaries. Eutrophication status of estuaries is likely to improve in some systems through a combination of research, monitoring, and management, but many estuaries will see worsening conditions. In the 2007 NOAA report on the status of US estuaries, a comparison was made between eutrophic conditions of estuaries assessed in the early 1990s and in 2004 (Bricker et al. 2007). During that time, conditions had improved in 13 estuaries, worsened in 13, and remained unchanged in 32 systems. Of the systems assessed a worsening of eutrophic conditions was predicted for 65% of the nation's estuaries by 2020.

In addition to potential increased nitrogen and phosphorus inputs, these changes will likely lead to losses of wetland area (Lotze et al. 2006; Valiela 2006). Wetlands, e.g., salt marsh or mangroves, intercept land-derived inputs of nitrogen due to high rates of denitrification and nitrogen burial (Valiela 1983). A strong link has been demonstrated between wetland area and seagrass production, which is a good indicator of estuarine health (Valiela et al. 1997; Valiela and Cole 2002). Wetlands are therefore important in regulating nutrient inputs to estuaries and have the potential to mitigate the negative effects of excess nutrients to estuaries.

There is increasing effort to restore estuarine habitats and remediate the negative effects caused by anthropogenic activities. Many restoration schemes are in place worldwide, especially in North America, Europe, and Australia (Ruiz-Jaen and Aide 2005; Elliott et al. 2007). Management actions include restoring tidal flushing to former salt marshes, replanting of seagrass meadows, and improving upper estuarine water quality by increasing flushing times and diverting wastewater outfall pipes. Although restoration techniques have been successful and are worthwhile, restored habitats rarely fully recover to original communities, replace lost habitat, and restore ecosystem services (Elliott et al. 2007).

While evidence suggests that human exploitation of marine resources has altered coastal food webs and thereby increased coastal ecosystems' vulnerability to eutrophication, there are still gaps in our knowledge as to how top-down and bottom-up effects interact. Hughes et al. (2004) point out that experiments manipulating grazers and nutrients simultaneously in macrophyte systems are relatively few, and there is a need to further investigate these interactions to fully evaluate

whether grazers can alleviate symptoms of eutrophication. More investigation is needed to accurately predict how top-down and bottom-up interactions will alter the ability of the macrophyte communities and provision of ecosystem services such as food production, nutrient filtration, and carbon sequestration and burial. One of the major future challenges will be to predict the net result on macrophyte communities of localized impacts of increased inputs of nutrients, contaminants, and sediments and overexploitation of marine fauna and global or large-scale impacts of increasing temperature, frequency and intensity of storms, sea level, and ocean acidity. A better understanding of future interactions is essential for effectively managing coastal resources.

Here, we have illustrated that benthic macrophytes are regulated by a dynamic mix of abiotic and biotic mechanisms that interact in various combinations to structure benthic communities. The floral and faunal communities are susceptible to the many alterations to estuarine habitats that are taking place as a result of human activities on adjacent watersheds, in coastal waters, and in the atmosphere. The human-driven degradation of estuarine water quality and habitats has led to major changes in biogeochemical processing of nutrients and carbon, standing stocks of primary producers and consumers, and trophic transfer of estuarine resources. We emphasize that without a better understanding of the interacting mechanisms that control estuarine benthic communities, we lack the tools necessary to mitigate the powerful changes that are predicted to occur in the coming decades.

Glossary

Bottom-up control: Limitation of the abundance or biomass of an organism by resource availability.

Ecosystem services: Benefits provided by natural ecosystems to humans.

Hypoxia: Low oxygen conditions.

Macrophyte: Macroscopic forms of aquatic vegetation, including seagrasses and macroalgae.

Secondary metabolite: A compound that is not necessary for growth or maintenance of cellular functions. In macrophytes, secondary metabolites may be important for plant defense against herbivory.

Top-down control: Limitation of the abundance or biomass of an organism by predation or herbivory.

Trophic cascades: A change in the rate of consumption at one trophic level that results in a series of changes in species abundances and species compositions at lower trophic levels. Occur when predators in a food chain suppress the abundance of their prey, thereby releasing predation pressure on the next lower trophic level. Conversely predators may decrease in abundance, releasing pressure on their prey, and increasing consumption of the next lower trophic level.

Watershed: The area of land where water from rain and melting snow or ice drains downhill into a body of water.

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