CHAPTER SEVEN

Bottom-up and top-down interactions in coastal interface systems

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General introduction of rocky intertidal and salt marsh systems
The land–sea margin encompasses a variety of hard and soft-bottom habitats where organisms are exposed to a dynamic range of aquatic and atmospheric

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conditions dependent on a rhythm set by the tides. In this chapter, we focus on rocky intertidal and salt marsh ecosystems, which have been extensively studied on many continents. Both rocky shore and salt marsh communities exhibit strong and consistent patterns of intertidal zonation over relatively compressed spatial scales, making them excellent systems for understanding the context-dependency of species interactions. Hard-bottomed rocky intertidal communities are dominated by marine macroalgae and sessile marine invertebrates extending their reach to the furthest edge of the influence of sea spray, while soft-bottomed salt marsh communities are anchored by terrestrial plants with adaptations or tolerance to inundation by salty and brackish waters. Rocky shore communities may be battered by the full force of large ocean waves or gently lapped with seawater on more protected shorelines. In contrast, salt marshes are restricted to quiet waters where sediment accretion by plants is the main mechanism for habitat creation. Both communities may experience very large tidal excursions or only minimal ones, depending on the local dynamics of the tides, with corresponding consequences for the spatial extent of these communities across the shoreline. The steep environmental gradients and distinctive biological zonation patterns that characterize both rocky shore and salt marsh ecosystems (Fig. 7.1) have provided ecologists with accessible and highly tractable ecosystems for investigating the role of bottom-up and top-down factors along environmental gradients.

Bottom-up and top-down interactions in rocky intertidal systems

Introduction to rocky intertidal systems
Rocky intertidal communities have been the subject of intensive study worldwide, especially at temperate latitudes. The typically broad tidal range and relatively moderate atmospheric conditions create a wide zone of intertidal habitat that is generally hospitable to rocky intertidal species, while also readily accessible to investigators for hours at a time during periods of low tide and calm sea state. The effects of consumers, or top-down factors, have been documented over decades (Robles and Desharnais, 2002), while the role of nutrients and other influences on the base of the food web have only more recently been a focus of exploration (Menge, 2000). The marine invertebrates and macroalgae that dominate this ecosystem have adapted to living on hard substrates that are periodically exposed to air during low tides, while surfgrasses (Phyllospadix spp.), the only true plants found in the rocky intertidal, have adaptations that allow them to thrive while submerged in saltwater. Rocky intertidal communities display distinct patterns of zonation that are associated with steep environmental gradients, typically over scales of a few centimeters to several meters (Fig. 7.1). Tidal range varies dramatically in different regions of the world, which is a primary constraint on the extent of the intertidal zone (together with the steepness
The character (i.e., diurnal, semidiurnal, mixed) and timing of tidal cycles with respect to daily, seasonal, and even celestial cycles are also important to local species distributions (Denny and Paine, 1998). These tidal rhythms set the stage for the degree of exposure to potentially stressful atmospheric conditions (e.g., intense light, high or low temperatures, wind, rain, ice), especially for those organisms living higher on the shore. Even organisms living in tidal pools experience a wider range of physical conditions (e.g., temperature, pH, salinity) than is typical for marine organisms, as they can be isolated from the ocean for periods ranging from hours to days, depending on the tidal height of the pool.

Most rocky intertidal species have complex life histories that include propagules (larvae or spores) that are dispersed by ocean currents. Dispersal distances may be very short (1–10 cm) or long (100s of km), depending on pelagic larval duration (ranging from minutes to months), their behavior, and prevailing
ocean currents (Kinlan and Gaines, 2003). As a result, the scale at which intertidal communities are considered determines whether interacting species can be thought of as sharing open or closed population dynamics (Kinlan and Gaines, 2003). For example, over \(\leq 1\) km scales, individual subpopulations (or “local” populations) of barnacles on a rocky shoreline are open (i.e., offspring may not return to their population of origin; instead, they disperse and populate a different population). However, over scales of 100s of km, they can be viewed as part of a larger (closed) metapopulation (Hanski and Gilpin, 1991). These characteristically diverse life histories and scaling of population dynamics distinguish marine communities from terrestrial communities and have important, and sometimes surprising, consequences for conceptualizing and modeling the influence of top-down and bottom-up processes on rocky intertidal populations, communities, and ecosystems.

Rocky intertidal communities occur on the most wave-exposed headlands of the open coast, where the intertidal zone is broadened by the reach of wave run-up and splash, and on the low energy shores found in wave-protected coves of the open coast or straits and bays, where the intertidal zone is more compressed in space (for shores of similar slope). Disturbances by waves that free up limited space on open-coast rocky intertidal zones have a predictable, seasonal rhythm. These disturbances enhance diversity by creating a mosaic of patches in different stages of succession (Paine and Levin, 1981). The life histories of some species are even tuned to take advantage of the seasonal disturbance pattern (e.g., Paine, 1979). Organisms attached to sedimentary rocks are more easily dislodged by waves than those attached to igneous rocks, thus the type of rock itself can have a strong influence on community susceptibility to disturbance. Episodic scouring or burial by sand or ice is another common disturbance in this ecosystem. Seasonal ice scour is a common disturbance at higher latitudes (e.g., Wethey, 1985; Scrosati and Heaven, 2007). Large rocky boulders and smaller benches (flat, narrow, wave-cut areas often at the base of a seaside cliff) are often interspersed in a mostly sandy shoreline, resulting in so-called psammophilic (sand associated or tolerant) species assemblages (e.g., Díaz-Tabia et al., 2013).

**Historical development of top-down and bottom-up perspectives**

Early and influential field experiments from rocky intertidal ecosystems (Connell, 1961; Paine, 1966; Dayton, 1975; Menge, 1976; Lubchenco, 1978) closely paralleled, and contributed to, emerging ecological theories on the role(s) of energy flow and species interactions in determining community structure (Bertness et al., 2014). Initially, zonation of rocky intertidal communities was thought to be determined by the limitations of organismal physiology and biomechanics to atmospheric conditions and wave forces, respectively (Colman,
1933; Stephenson and Stephenson, 1949; Lewis, 1964). However, field experiments revealed that competition and consumption often determined the lower limits of species distributions, while physical factors prevailed in controlling their upper distributional limits (Connell, 1961; Paine, 1966).

Paralleling these mechanistic insights, early trophic and energetic theories of ecology (Lotka, 1925; Volterra, 1926; Elton, 1927; Lindeman, 1942) were being integrated into models of community structure and dynamics (Hairston et al., 1960; Oksanen et al., 1981; Fretwell, 1987; also, see Chapter 1). Importantly, these models also provided insights into where competition or trophic interactions should be expected to regulate species abundances. Menge and Sutherland (1976), using evidence from rocky shores, expanded on these ideas to explain patterns of species diversity. Niche theory, previously thought to be the dominant process defining the structure of communities (reviewed by Vandermeer, 1972), was largely abandoned by rocky intertidal ecologists as more compelling evidence emerged from field experiments clearly demonstrating the importance of predation and disturbance (Robles and Desharnais, 2002).

Focused research on the influence of consumers further revealed the importance of indirect effects (e.g., Wootton, 1993; Menge, 1995) and the context-dependency of species interactions (e.g., Menge and Sutherland, 1987; Menge and Olson, 1990). Variation in the ability of rocky intertidal consumers to influence the abundance of their prey and community structure began to be seen in the context of open rather than closed population models (e.g., Gaines and Roughgarden, 1985; Menge, 1991). Most rocky intertidal predators have open (local) populations with complex life histories and dispersing larvae, but some are direct developers (e.g., the whelks Nucella spp. and Acanthina spp.) or brooders with closed populations (like the sea stars Leptasterias spp.). The omnipresent mussels and barnacles also have dispersing larvae. Incorporating variation in the scaling of demographic processes is an important consideration for modeling marine community dynamics in general, and is explicitly considered in marine conservation models (i.e., networks of marine protected areas; e.g., Gaines et al., 2010).

Models incorporating open population dynamics have focused on space-occupying invertebrates and their predators (e.g., Wieters et al., 2008), sometimes treating sessile heterotrophs as the base of the food web and disregarding phytoplankton. In contrast, investigations of benthic autotrophs and consumers continued to emphasize the relative rates of algal growth and consumption by invertebrate herbivores (e.g., Cubit, 1984). As argued by Menge (1992), the potential role of nutrient supply, or bottom-up factors, had been largely overlooked by benthic marine ecologists, in striking contrast to the perspective held by pelagic marine ecologists (i.e., biological oceanographers) that nutrient dynamics structured pelagic ecosystems.
Since the early 1990s, a more balanced appreciation of the interplay between bottom-up and top-down processes in rocky intertidal communities has emerged, but studies typically focus on one or the other of the two major food webs: (1) phytoplankton, sessile, suspension-feeding herbivores, and mobile predators, or (2) benthic algae, mobile grazers, and mobile predators (Fig. 7.2). Below we discuss each of these “sub-webs” along with more recent work that integrates the roles of nutrients (bottom-up factors), consumers (top-down factors), and scales of connectivity among ecosystems (i.e., meta-ecosystem dynamics, sensu Loreau et al., 2003) across both to shape the structure and dynamics of rocky intertidal ecosystems. But first, we consider the roles of consumers and nutrients generally.
Consumers
Top-down effects of consumers are commonly observed in rocky intertidal ecosystems (Menge, 2000). These may result from consumption, consistent with the mathematical foundation of classic food chain models, or through non-consumptive effects whereby prey behavior or traits are altered by limiting foraging excursions or inducing the production of defensive structures or chemicals (e.g., Raimondi et al., 2000). If these modified behaviors or traits influence additional species, they are referred to as trait-mediated indirect effects (of consumers). For example, waterborne predator cues may inhibit the activity of lower level consumers, reducing their consumption of prey (e.g., Raimondi et al., 2000; Trussell et al., 2002). Omnivory is not unusual among rocky intertidal consumers. The adults of benthic predators and even so-called herbivores often feed on more than one trophic level, while larval stages range from planktotrophic to non-feeding. Ontogenetic and adult omnivory may also augment the influence and effectiveness of invertebrate consumers in structuring rocky intertidal communities (Menge and Sutherland, 1987). Furthermore, highly mobile, vertebrate consumers from adjacent ecosystems such as surf zone fishes (e.g., Paine and Palmer, 1978; Menge and Lubchenco, 1981; Ojeda and Muñoz, 1999; Taylor and Schiel, 2010; Vinueza et al., 2014) and shorebirds (e.g., Marsh, 1986; Wootton, 1997; Ellis et al., 2007) forage during high and low tides, respectively. Conversely, the effects of consumers on the abundance of lower trophic levels may be minimized when prey recruitment rates are high, or when their activities are curtailed by environmental stress (Menge and Sutherland, 1987).

Direct exploitation of intertidal animals and plants by humans is ubiquitous, but the intensity of top-down effects varies geographically and historically with cultural and economic context. Prehistoric middens filled with the hard remains of intertidal organisms are common worldwide (e.g., Hockey, 1994; Moreno, 2001; Fa, 2008). Mussels, abalone, and other gastropods, chitons, barnacles, crabs, urchins, and tunicates are all gathered and eaten. Macroalgae, including the rhodophytes Porphyra spp. (e.g., nori in Japan, laver in Wales, luche in Chile) and Chondrus crispus (Irish moss), many kelps (e.g., Laminaria, Undaria, Alaria, Durvillaea, and Postelsia), and sea lettuce (a chlorophyte) are all eaten, and some intertidal algae (including Fucus, Ascophyllum, Lessonia, and Chondrus) are used industrially or agriculturally (Thompson et al., 2010). Human impacts can be substantial (e.g., Castilla and Duran, 1985; Roy et al., 2003; Salomon et al., 2007), but have been treated within the more applied contexts of ecosystem-based management and marine conservation biology, rather than as consumers in natural ecosystems (McLeod and Leslie, 2009; also, see Chapter 14).

Nutrients
Bottom-up inputs of inorganic nutrients that fuel the growth of benthic macrophytes (macroalgae and surfgrasses) and nearshore phytoplankton production
provide a direct connection between intertidal communities and adjacent coastal oceans. These inputs generally originate from physical oceanographic processes such as coastal upwelling and tidal mixing. For some systems, anthropogenic nutrient inputs via river runoff, groundwater discharge, and atmospheric deposition can further represent important contributions. Macroalgal uptake rates can be very high, and this is accentuated high on the shore where nutrient uptake is limited to periods of high tide inundation (Bracken et al., 2011). Nutrient uptake occurs over the entire macroalgal thallus and primarily via leaves in surfgrasses (Terrados and Williams, 1997), instead of, as in terrestrial systems, being taken up by roots embedded in a matrix of soil where microbial processes and physical conditions affect rates of nutrient cycling. In rocky intertidal systems, recycling of nutrients is very limited relative to physically mediated inputs, but ammonium excreted by mussels can be important in isolated tidepools and for macrophytes in close association with mussel beds (Bracken and Nielsen, 2004; Aquilino et al., 2009; Pather et al., 2014). Excretion by small macroinvertebrates may also affect surfgrass growth (Moulton and Hacker, 2011). Interestingly, despite the very high nutrient uptake capacity of macrophytes, local nutrient depletion is rare (in contrast to soil nutrient pools in terrestrial ecosystems), with the exception of isolated tidepools or environments with low water flow (Hurd, 2000; Nielsen, 2003). Due to the typically high seawater flow rates in this ecosystem, nutrient availability is largely independent of the uptake capacity of macrophytes and instead reflects the dynamics of the pelagic subsidy. This stands in sharp juxtaposition to the well-known phenomenon of nutrient draw-down by pelagic phytoplankton, the other major source of primary production for intertidal ecosystems. Phytoplankton may thus reduce (or pre-empt) pelagic nutrients before they reach intertidal macrophytes, and be nutrient-limited themselves. In summary, rocky intertidal ecosystems rely almost exclusively on allochthonously sourced nutrients (from adjacent ocean and terrestrial ecosystems) with almost no internal (re)cycling or local nutrient pool depletion. These are not standard assumptions of classic food chain models (Oksanen et al., 1981; Oksanen and Oksanen, 2000), and this has consequences for the influence of bottom-up processes on higher trophic levels, as illustrated below (also, see Chapter 1).

Effects of consumers and subsidies on food webs

Sub-web #1: effects of consumers and pelagic subsidies on sessile invertebrates

The effects of predators have been intensively studied within the most experimentally tractable sub-web of the community: mussels and barnacles, and the sea stars and carnivorous snails that prey on them. In this sub-web, the effects of predation on community structure are consistently evident (Navarrete and Castilla, 2003; Menge and Menge, 2013), except where recruitment rates of prey
are very high or predation rates are very low (e.g., Menge, 1976; Menge and Menge, 2013), or where environmental stress, such as desiccation from winds, is extreme (Bertness et al., 2006). The effects of individual predators (on a per capita or per population basis) can vary substantially both within and among sites, and among species (Navarrete and Menge, 1996; Navarrete and Castilla, 2003). Variation in pelagic subsidies, in the form of juvenile mussels and barnacles and their primary food source, phytoplankton, can strongly influence rates of predation (i.e., individuals eaten per day), the pace of succession, and ultimately community structure (Fig. 7.3; Menge et al., 2003; Menge and Menge, 2013). For example, in a synthesis of many studies from the west coast of North America and New Zealand’s South Island, Menge and Menge (2013) found that increases in phytoplankton availability were strongly associated with increases in rates of predation (primarily by sea stars) on, competition among, and abundances of sessile invertebrate herbivore populations (mussels and barnacles). One interpretation is that this represents an interaction between bottom-up and top-down forces (Menge et al., 1997). An alternate interpretation is that physical oceanographic processes that mediate the supply of ecological subsidies (i.e., propagules, nutrients, and organic matter) over larger spatial scales play the major role in structuring this ecosystem, rather than local-scale species interactions (Menge et al., in press).

Nonetheless, even in the face of substantial variation in mussel recruitment among sites, the sea star *Pisaster ochraceus* is consistently able to exclude mussels from the low zone (Paine, 1974; Menge et al., 1994; Robles et al., 1995). Predation can also dampen the effects of variable prey recruitment on community successsion and final prey abundance, as long as prey recruitment rates do not swamp consumption rates. This variable dampening effect was clearly illustrated for subordinate predatory whelks on both barnacles and mussels during community succession in mussel bed patches originating in different years (Berlow, 1997). In a larger analysis of the effects of total predation among many sites, Menge and Menge (2013) likewise found that despite high variation in predation rates among sites, the late-successional (final) effects of predators on prey abundance were fairly consistent, except where predation rates were very low, perhaps reflecting low predator recruitment rates. The rate of predation (by sea stars and whelks) and its total effect across different stages of succession can increase as phytoplankton abundance and prey recruitment rates increase (Menge and Menge, 2013). These differences in subsidies, and the associated variation in community dynamics, generate substantial differences in community structure among sites (Fig. 7.3; Menge et al., 1997; Connolly and Roughgarden, 1998).

Importantly though, high inputs at the base of the food web, although correlated with the abundance of predators (Figs. 7.3, 7.4), do not necessarily translate into increased predator populations through food chain mechanisms in the
Figure 7.3  Regional variation in rocky intertidal ecosystems on the west coast of North America. Capes represent areas under the influence of a major oceanographic cell, typically a region that has characteristic nearshore circulation features that influence nutrient availability and transport of propagules (error bars = 1 SE of site level averages). Each cape includes data from three to four sites surveyed over 3 to 4 years (cover and density are from annual surveys of 0.25 m² quadrats (n = 10–30), recruitment data are annual averages of monthly estimates (n = 3–5), and nutrients and chlorophyll a (chl-a) data are annual averages of water samples collected monthly during spring and summer months (n = 3)). Capes are arranged geographically from north to south: Cape Mendocino sites are located in northern California while the remaining sites are in central and southern Oregon. Macrophytes include macroalgae and surfgrasses; here, broken down into crustose forms (crusts), kelps and other Phaeophyceae (browns), Chlorophyta (greens), Rhodophyta (reds), and surfgrasses. Greens and other browns are too scarce to be visualized. Sessile invertebrates include mussels, barnacles, anemones, sponges, bryozoans, tunicates, hydroids, and tube-dwelling polychaetes. Grazers include mobile invertebrates that are primarily herbivorous. Figures based on data presented in Menge et al. (in press).
intertidal, with the exception of predators with closed (local) populations (consistent with predictions of simple demographic models) (Wieters et al., 2008). Instead, in direct contradiction of a food chain mechanism, mussel and barnacle abundances are positively correlated with the abundance of predators on the west coast of North America (Fig. 7.4d). In contrast, in a synthetic study of barnacles and mussels and their predators on the west coasts of North and South America, Wieters et al. (2008) found that predatory whelks with crawl-away juveniles do track the subsidies (recruitment rates) of their (demographically open) prey, but are not correlated with their abundances. In their analysis, abundance of sea stars and muricid gastropod predators with open populations did not track prey recruitment rates (at a local scale), as expected for open populations (Wieters et al., 2008), although on the northwest coasts of North America and the South Island of New Zealand, predator consumption rates track prey recruitment (Menge and Menge, 2013). This may lead to differential reproductive output back into the regional, pelagic larval pool among sites (Wieters et al., 2008). Empirical evidence of this phenomenon is scarce for rocky intertidal organisms. However, per capita reproductive output of *Pisaster* does respond to regional variation in prey recruitment, as predicted. In Oregon, where prey recruitment is relatively high, per capita reproductive output of *Pisaster* was on average higher (Sanford and Menge, 2007) than in northern California (Wood, 2008), where prey recruitment is much lower (Fig. 7.3; Connolly et al., 2001; Broitman et al., 2008).

The inherently open population dynamics in the phytoplankton, sessile suspension-feeding invertebrates, predators sub-web, and the cross-ecosystem spatial subsidies of phytoplankton and prey from pelagic ecosystems do not conform to simple, food chain model assumptions (Oksanen et al., 1981; Menge, 2000; also, see Chapter 1). Thus, it is not terribly surprising that the predicted relationships among trophic levels are not observed when examined across sites that vary substantially in phytoplankton availability (proxied by chlorophyll a concentration (chl-a)) (Fig. 7.4). In this sub-web, phytoplankton and predator abundances should be positively correlated among sites, while neither should be correlated with the abundance of suspension feeders. Instead, among sites we observe: (1) a strong positive correlation between the abundances of predators and herbivores (Fig. 7.4d); (2) a weaker (and non-linear) positive relationship between herbivores and chl-a (Fig. 7.4g) and (3) no correlation between chl-a and predators (Fig. 7.4f). Initially though, intertidal researchers framed these spatial gradients in phytoplankton abundance and prey recruitment (e.g., Fig. 7.3) as “bottom-up” factors. High variation in phytoplankton among sites was conceptualized as a gradient in productivity that co-varied with larval recruitment rates, possibly due to pelagic ecosystem food chain effects (Menge et al., 1997). Thus the effects of variation in prey recruitment on predation rates were viewed as the interaction of bottom-up and top-down processes (Menge et al.,
Figure 7.4 Correlations among trophic levels and space occupiers in rocky intertidal communities. Geographical regions and number of surveys are as in Fig. 7.3. Data are annual averages for each site (error bars = 1 SE of annual averages). Correlations
1997; Menge, 2000). However, Menge (2000) also recognized the limitations of simple food chain models due, in part, to the prevalence of omnivory in most rocky intertidal food webs.

Emerging meta-ecosystem theory (Loreau et al., 2003; Leroux and Loreau, 2008) seems to hold more promise for modeling the dynamics of (local scale) communities that are so inextricably dependent on the exchange of life history stages, as well as energetic and nutrient subsidies from adjacent ecosystems (Fig. 7.2). These subsidies are often driven by regional rather than local-scale processes (Loreau et al., 2003; Menge et al., unpublished data). The scale(s) of demographic processes for animals with pelagic larval stages is a function of the interaction of larval behavior and duration with oceanographic transport (Kinlan and Gaines, 2003; Shanks, 2009; Morgan and Fisher, 2010). Models explicitly incorporating spatial subsidies and cross-scale interactions, such as meta-ecosystem models, may more accurately represent the dynamics shaping the structure of this rocky intertidal sub-web. Additionally, it may be critically important to include horizontal interactions (i.e., competition and facilitation) with the second major sub-web in this ecosystem, as we discuss below.

**Sub-web #2: effects of consumers and pelagic subsidies on benthic macrophytes**

Benthic macroalgae and surfgrasses form the base of the second main sub-web, and are the other major space-occupying organisms, besides sessile invertebrates, in this ecosystem; they also interact with adjacent ecosystems in terms of nutrient subsidies, larval dispersal, and predators (Fig. 7.2). Larger kelps, rockweeds, and surfgrasses form algal canopies which are important refuge habitats for many taxa, especially in the high intertidal zones where the potential for

(except e) are grouped within the two major sub-webs of rocky intertidal communities in accordance with expected relationships if simple food chain dynamics influence the relative abundance of trophic levels. In the macrophyte–grazer–predator sub-web, if top-down effects are strong enough to influence the base of the food chain then:

(a) predator and macrophyte abundances should be indirectly and positively related;
(b) grazer and macrophyte abundances should be unrelated (however, if predators are not effective, then grazer and macrophyte abundances should be positively related); and
(c) predator and grazer abundances should not be related. Similarly, in the phytoplankton–sessile invertebrate–predator sub-web: (f) predator and phytoplankton abundances should be indirectly and positively related; (g) sessile invertebrate and phytoplankton abundances should be unrelated (however, if predators are not effective, then sessile invertebrate and phytoplankton abundances should be positively related); and (d) predator and sessile invertebrate abundances should not be related. Sessile organisms compete for limited space, thus (e) sessile invertebrates and macrophytes should be negatively correlated. Figures based on data presented in Menge et al., (in press).
desiccation and thermal stress is high (e.g., Bertness et al., 1999; Burnaford, 2004; Moulton and Hacker, 2011). Urchins, chitons, limpets, and other gastropods, as well as a suite of meso-grazers (e.g., isopods, gammarid amphipods, small gastropods) feed directly on benthic macroalgae, the smaller epiphytic algae that colonize them, and the microalgae, algal spores, and cyanobacteria that form thin films on otherwise unoccupied rock surfaces. Urchins, chitons, and limpets (especially the larger Patellogastropoda, Fissurelidae, and Siphonariidae) can have strong negative effects on the abundance and diversity of intertidal macroalgae (e.g., Paine and Vadas, 1969; Duggins and Dethier, 1985; Duran and Castilla, 1989; Nielsen, 2003). Smaller limpets, if abundant, have strong effects on early successional stages, but can be swamped if macrophyte growth rates are high (e.g., Dethier and Duggins, 1984; Freidenburg et al., 2007), as their ability to feed on the upright portions of larger, attached algae is limited.

Surfgrasses (*Phyllospadix* spp.) only occur in the North Pacific (Short et al., 2007). *Phyllospadix scouleri* is a dominant, late-succession species (Turner, 1983; Moulton and Hacker, 2011). It is relatively invulnerable to direct herbivory due to a combination of chemical and structural traits, but some specialized limpets feed on the leaves (Fishlyn and Phillips, 1980). Surfgrasses are vulnerable, however, to seed predation by small crustaceans (Holbrook et al., 2000). Low intertidal zone meadows of surfgrass are an important, and sometimes dominant, seascape element that provides habitat for dozens of species of macroinvertebrates (Moulton and Hacker, 2011) and nearshore fishes (Galst and Anderson, 2008).

In the macrophyte-based sub-web, there are fewer allochthonous inputs of organic matter than in the sessile, suspension feeder sub-web. Drift algae from adjacent subtidal or intertidal rocky habitat is the most common subsidy to this sub-web. In South Africa, drift of subtidal kelps supports limpets that live at such high densities they occupy most of the substratum, pre-empting other organisms (Bustamante et al., 1995). Once these limpets exceed 5 cm in length, they escape their primary predators, the oystercatcher *Haematopus moquini* and the giant clingfish *Choriscochismus dentex* (Bustamante et al., 1995). When limpets are denied access to drift kelp, they starve to death. This subsidy probably not only intensifies herbivory on other algae within the foraging range of the limpets, but also increases competition for space between limpets and algae. This exemplifies the strong influence cross-ecosystem subsidies can have on simple food chains, but subsidy effects of this magnitude are not commonly observed in this sub-web. Most invertebrate herbivores rely on attached benthic micro- and macroalgae, including, importantly, algal gametophytes and sporelings (Duggins and Dethier, 1985; Paine, 1992). Survivorship of kelp spores can be facilitated by other organisms such as the dense, calcified algal turfs that are resistant to grazers (Milligan, 1998; Menge et al., unpublished data).

As noted previously, intertidal macrophytes are largely supported by exogenous nutrient inputs. In some instances, nutrients recycled within intertidal
habitats can augment nutrient supply (Aquilino et al., 2009). Where seabirds are abundant guano may contribute to the nutrient budget, but this is also an exogenous source and its effects can be variable (e.g., Bosman and Hockey, 1986; Wootton, 1991; Kolb et al., 2010). Variation in macroalgal standing crop due to differences in nutrient loading is often apparent only at the lowest levels of herbivory, at the small spatial scales of experimental plots (Nielsen, 2001; Guerry et al., 2009). Where nutrients are plentiful, such as in upwelling regions, they may only be limiting high on the shore, in areas where flow rates are low, or during periods of reduced availability (e.g., El Niño years) (Wootton et al., 1996; Nielsen, 2003; Bracken and Nielsen, 2004). However, experimental manipulations of nutrients may not be sufficient in duration or magnitude to elicit a response (Nielsen, 2003; Kraufvelin et al., 2006). In contrast, and despite evidence that herbivory is generally high in intertidal ecosystems (Poore et al., 2012), algal abundances are often elevated where regional nutrient loading is naturally higher, including near centers of localized coastal upwelling (Fig. 7.3 (Capes Blanco and Mendocino), Bosman et al., 1987; Broitman et al., 2001; Nielsen and Navarrete, 2004; Bustamante et al., 1995; Menge et al., in press), although light availability may also be important (Kavanaugh et al., 2009). At larger spatial scales, correlations among multiple sites in western North America reveal that (new) nutrients are positively related to macrophyte abundance, but the relationship is stronger for macroalgae alone (details as in Fig. 7.4, data not shown), consistent with data from the west coast of South America (Nielsen and Navarrete, 2004; but see Bustamante et al., 1995 for contrasting results in South Africa).

In food chain models with two trophic levels (i.e., no predators), algal standing crop is predicted to remain unchanged in the face of increasing nutrients, but herbivore abundances should increase with nutrients (Oksanen et al., 1981). In small-scale experiments, this outcome has not been observed (Nielsen, 2001; Guerry et al., 2009). Larger herbivores probably forage over scales greater than the typical experimental replicate (usually < 1 m²) and may not aggregate to feed in high productivity plots. However, chitons and limpets foraging in areas with increased availability of microalgae are often larger and more fecund (Dethier and Duggins, 1984; Bosman et al., 1987), as are intertidal urchins near regions of coastal upwelling where nutrients and drift kelp from subtidal ecosystems are abundant (Lester et al., 2007). Local populations with enhanced reproductive output may make a disproportionate contribution to a regional larval pool. But, population responses to localized nutrient enhancement at small spatial scales would not be expected for the most common herbivores enumerated and manipulated in intertidal ecosystems (i.e., urchins and molluscs) due to their open populations at this scale. Interestingly, the few experiments where increased nutrients did increase herbivore abundances involved species with closed populations. Small herbivorous arthropod or “mesograzers” with short
generation times (or brooders) – such as gammarid amphipods, isopods, chironomids, and the snail \textit{Littorina saxatilis} – all show positive responses to experimentally increased nutrient levels (Wootton et al., 1996; Worm et al., 2000). However, consistent with the results above for larger herbivores, observational data from multiple rocky shore sites in western North America show no correlations between either herbivore or predator abundances and nutrient availability or macrophyte cover (Fig. 7.4b and c).

Although there is scant evidence of food chain-mediated nutrient effects on benthic herbivores, predators such as crabs and birds can have strong top-down impacts on intertidal herbivores (Lubchenco, 1978; Ellis et al., 2007). In addition to direct effects, they can alter the behavior of their prey through risk cues, indirectly enhancing predator effects on lower trophic levels (Trussell et al., 2004). On northeastern rocky shores of North America, the subtidal crab \textit{Cancer borealis} forages in the intertidal zone during high tides on two other predators (the green crab \textit{Carcinus maenus} and the whelk \textit{Nucella lapillus}) in addition to the herbivore \textit{Littorina littorea}. However, large-scale experiments where gulls were scared away from 50 m stretches of shore (by researchers during low tides) demonstrated that gulls initiate a trophic cascade by reducing the abundance of foraging crabs (Ellis et al., 2007). In separate experiments, Trussell et al. (2004) demonstrated that the green crab can have both trait- and density-mediated indirect effects on the algae in this ecosystem. Thus, gulls have the potential to initiate a trophic cascade through five trophic levels (Ellis et al., 2007).

\textbf{Synthesis of the two rocky intertidal zone sub-webs: a meta-ecosystem perspective}

Until this point we have focused on the separate effects of the two sub-webs without considering how they interact or the potential for horizontal interactions (competition and facilitation). A central dogma of rocky intertidal ecology is that mussels are competitive dominants that exclude macroalgae and other low zone organisms in the absence of predators (Paine, 1966; 1974). Yet observations across many sites suggest that the base of one or the other sub-webs (sessile invertebrates or macrophytes) typically dominates low zone seascapes (Menge, 1992; Menge et al., 1997; Broitman et al., 2001). Recent research suggests that these differences appear to be driven by meta-ecosystem dynamics mediated through regional oceanographic influences on nutrient subsidies and plankton transport (including larvae and phytoplankton) (Menge and Menge, 2013; Menge et al., in press). Macrophytes dominate where nutrient loading rates are high but phytoplankton levels are low (coinciding with narrow continental shelves) (Fig. 7.2). Here, alongshore and offshore currents carry abundant phytoplankton blooms, generated by nutrient-rich and well-lit upwelled water, away from these upwelling centers. The inevitable time lag between the initial phytoplankton “seeding” of newly upwelled waters and a phytoplankton population growth response (Dugdale et al., 1990) effectively decouples locations of
high phytoplankton and high benthic algal production (Broitman and Kinlan, 2006). High mussel and barnacle growth and recruitment rates often co-occur with high phytoplankton concentrations on wider continental shelves, or where upwelled waters are detained or entrained (e.g., mesoscale oceanographic gyres, headland–lee complexes, etc.). Furthermore, evidence from field experiments and observations indicate growth rates of intertidal kelps can be light-limited in regions where phytoplankton flourish (or accumulate), pre-empting light before it reaches the benthos (Kavanaugh et al., 2009). Sessile invertebrates should be strong competitors for space in these locations. Interestingly though, recent field experiments (across multiple sites and years on the west coast of North America) provide a different perspective (Hacker et al., unpublished data). The effect (interaction strength) of sessile invertebrates on low zone macrophytes is consistently very small or zero, while macrophytes can have substantial negative effects on sessile invertebrates, except where phytoplankton abundance is very high. Thus, meta-ecosystem dynamics driven by oceanographic regimes appear to also influence the horizontal interactions (in this case, competition for space) that help shape the structure of rocky intertidal communities.

The use of the conceptual terms “top-down” and “bottom-up” to refer to nutrient availability and trophic cascades, respectively, as originally conceived by Hunter and Price (1992) was not explicitly or implicitly intended to encompass the kinds of demographic and spatial complexities that typify rocky intertidal ecosystems. However, the broader conceptualization of bottom-up and top-down processes (and their interaction) that ensued encouraged rocky intertidal ecologists to re-examine their assumptions about the primacy of top-down processes. The exchange of energy, nutrients, and propagules between pelagic and rocky intertidal ecosystems, exploitation of prey by terrestrial and pelagic consumers, and virtually complete spatial segregation of the “brown web” and its associated role in nutrient recycling to other marine ecosystems have a substantial influence on the way bottom-up (e.g., nutrients and light) and top-down processes are manifested at the meta-ecosystem scale and thus determine the structure of rocky intertidal communities. This more mature appreciation for the complexity and cross-ecosystem connectivity of rocky intertidal systems, along with the increasing prevalence of conducting research in larger interdisciplinary teams, provides an excellent foundation for investigating the influence of these factors (including meta-ecosystem models that explicitly incorporate them) on top-down and bottom-up process.

**Bottom-up and top-down interactions in salt marsh systems**

**Introduction to salt marsh systems**

Coastal salt marshes are regularly inundated by tidal flooding. Marshes harbor plant communities that show zonation depending on the elevational gradient. Characteristic plant species growing in these environments have to cope with
salt stress, and waterlogged and anoxic soil conditions. Their nutrient supply depends on the substrate – peat, sand, clay, or pebbles – and input from marine sources. In addition to abiotic conditions, top-down forces, in the form of invertebrate (e.g., snails, crabs, grasshoppers, and stem-borer and sucking insects) and vertebrate (e.g., wild guinea pigs, geese, hares, and cattle) herbivores and predators (e.g., blue crabs), can have a large effect on plants. The relative importance of bottom-up and top-down forces varies within salt marsh communities; for example, in temperate European salt marshes, predators have not been identified as important actors (Kuijper and Bakker, 2005). In addition, once plants have died and transformed into detritus, detritivores play an important role in this system. We will discuss the conditions that determine the importance of these abiotic and biotic (bottom-up and top-down) factors in shaping the community composition of salt marshes.

Atlantic salt marshes
Here, we consider salt marshes at either side of the Atlantic Ocean, which have been studied in great detail over the last 50 years. In terms of structure, they differ in vertical accretion – namely, plant parts, dead organic material, and plant litter in northwestern (North America) and southwestern (South America) marshes compared to silt and sand in northeastern (Europe) marshes. Overall, northwestern and northeastern Atlantic salt marshes have been intensively modified for centuries by different human activities (i.e., livestock grazing, hay cutting, and agriculture), while southwestern Atlantic marshes have remained more pristine.

Northeastern (Europe) Atlantic salt marshes (as well as western Atlantic salt marshes) mainly include the interaction between plants, sediment/nutrients, and (in)vertebrates. The lack of naturally occurring large herbivores on salt marshes in Europe implies that the effects of large herbivores are restricted to livestock grazing. In fact, livestock grazing has been the most common land use of European salt marshes in the last millennia (Bakker et al., 2005a; Davy et al., 2009).

Northwestern (North America) and southwestern (South America) Atlantic salt marshes
Northwestern (North America) and southwestern (South America) Atlantic marshes naturally occur on relatively sheltered soft-bottom intertidal areas. In most northwestern Atlantic marshes the vertical accretion (between 0.9 and 17.8 mm/year) mainly depends on the organic contribution of decaying plant litter and roots (Turner et al., 2002). In addition, these marshes exhibit natural drainage systems with meandering creeks and levees. However, during the 20th century, many northwestern Atlantic marshes were artificially ditched to
control mosquito populations, which dramatically altered drainage, and consequently affected plant communities (Bromberg Gedan et al., 2009b). Main plant species in the southwestern Atlantic include *Spartina alterniflora*, which dominates the low marsh, and *Spartina densiflora* and *Sarcocornia perennis* (usually acting as a pioneer species) that typically occur at higher elevations. In the northwestern Atlantic, *S. alterniflora* (often described as a foundation species; i.e., Bruno, 2000) also dominates the low marsh, *Spartina patens* dominates the seaward edge of the high marsh, *Phragmites australis*, *Juncus gerardii*, and *Juncus roemerianus* are more abundant at higher elevations, and *Distichlis spicata* can be found throughout the high marsh following a fugitive strategy (Pennings and Bertness, 2001; Pennings et al., 2005; Isacch et al., 2006). The relative abundance of these species also varies with environmental conditions. *Spartina alterniflora*, *S. perennis*, and *D. spicata* are more abundant in higher salinity sites, while the remaining species prefer lower salinities (Pennings et al., 2005; Isacch et al., 2006). Thus, the abiotic context plays a key role in determining small- and large-scale patterns of plant species dominance.

**Northeastern (Europe) Atlantic marshes**

Northeastern (Europe) Atlantic marshes emerge along the coast with sufficient elevation, shelter against energy by streaming and wave action, and enough supply of suspended sediment and seeds or plant parts. On such intertidal flats, the first plant species such as *Salicornia* spp. or *Spartina anglica* can establish. During succession, the marshes become older and higher by vertical accretion, developing into suitable habitat for late-successional species, such as the tall grass *Elytrigia atherica* on the high marsh and shrub *Atriplex portulacoides* on the low marsh (Olff et al., 1997). Thus, in these marshes, sedimentation strongly determines zonation and successional patterns.

In Europe, two types of salt marshes can be distinguished based on their development: back-barrier and foreland salt marshes. Back-barrier marshes establish in the lee of a sand barrier. They show a natural drainage system with meandering creeks and levees with higher elevation than the adjacent depressions. They have a relatively thin layer of clay (up to 0.5 m). In contrast, foreland marshes develop without the shelter of a sandy barrier. They have a thick layer of clay, which can amount to several meters. These salt marshes either have an extensive natural creek system, or are located within man-made sedimentation fields with a drainage system of ditches and are grazed by livestock or left fallow after previous grazing (Bakker et al., 2005a). These marshes are minerogenic, as their vertical accretion mainly depends on the input from tidal flooding. In the case of back-barrier marshes, the elevation gradient runs from the upper marsh at the foot of a dune; in foreland marshes, the elevation gradient runs from the foot of the seawall along the foreland coast to the intertidal flats. This elevational gradient influences the rate of sedimentation, which is the main driver
of plant succession. Sedimentation rates differ largely between back-barrier and foreland marshes due to wave activity, which is artificially reduced on foreland marshes to enhance sedimentation. The rate of sediment input on northeastern Atlantic salt marshes varies from $<5$ mm/year on sandy back-barrier marshes to up to 20 mm/year on marshes with sedimentation fields (Bakker et al., 2005a). As a result of these differences in development, successional trajectories markedly differ between these two types of salt marshes. Whereas high and low marshes feature their own successional pathway on back-barrier marshes (Leendertse et al., 1997), the low marsh transforms into high marsh on foreland marshes (De Leeuw et al., 1993). In the high marsh on back-barrier marshes and on foreland marshes, the tall grass *Elytrigia atherica* will ultimately dominate the vegetation, and its occurrence and dominance are positively related to elevation and accretion rate (Suchrow et al., 2012).

**Spatial variation in salt marshes**

Elevation determines the duration and frequency of flooding, and thus is the best predictor of species distribution along the elevational gradient (Fig. 7.1). Among the physical stressors that covary with elevation, salinity and redox potential (mediated by sediment type) have been shown to greatly influence plant productivity and zonation (Hacker and Bertness, 1995a). Additionally, salt marshes around the world are nutrient limited, and N additions increase plant production (e.g., Kiehl et al., 1997; Van Wijnen and Bakker, 1999; Silliman and Zieman, 2001; Alberti et al., 2010b) and arthropod numbers (Vince et al., 1981; Levine et al., 1998), as well as regulating both competitive hierarchies and zonation patterns (i.e., subordinate plants like *S. alterniflora* become dominant after nutrient additions and move their upper zonation limit upwards; Emery et al., 2001).

Experimental studies also revealed that both invertebrates and vertebrates can exert strong control on salt marsh plant production and zonation (geese: Esselink et al., 1997; crabs: Bortolus and Iribarne, 1999; geese and hares: Kuijper and Bakker, 2005; snails: Silliman et al., 2005; grasshoppers: Bertness et al., 2008; small aboveground rodents: Bromberg Gedan et al., 2009a; belowground rodents: Kuijper and Bakker, 2012). Moreover, human activities in European and North American salt marshes have removed a significant amount of plant production through livestock grazing and hay cutting (Bakker et al., 1993; Bos et al., 2005; Bromberg Gedan et al., 2009b).

*Elevation (and its effects on oxygen availability and salinity)*

The importance of trophic interactions is expected to decrease as environmental stress increases (usually toward lower elevations) because higher trophic levels are more sensitive to stressful conditions (Menge and Sutherland, 1987). Given
that salt marshes usually exhibit marked environmental differences across elevation and thus tidal duration and frequency, it is assumed that the relative importance of top-down and bottom-up factors would vary with elevation. This prediction is supported by results from field experiments. For example, the abundance of different crab predators (*Callinectes sapidus*: Silliman and Bertness, 2002; *Panopeus herbstii*: Silliman et al., 2004) increases with decreasing elevation in many salt marshes located between Georgia and Delaware, USA. These crabs strongly control grazer snails (*Littoraria irrorata*), which in turn control *S. alterniflora* biomass, and thus, crabs indirectly release otherwise herbivore-controlled plants (Silliman et al., 2004), particularly at low elevations (Silliman and Bertness, 2002). Even more, the loss of top predators (most often crabs and fishes in these salt marsh systems) due to human activities has been hypothesized to be a fundamental cause of massive die-offs of *S. alterniflora* in northwestern Atlantic salt marshes, because herbivore populations grow wildly due to relaxed predation (Altieri et al., 2012).

In addition, experiments conducted in a southwestern Atlantic salt marsh manipulating nutrients and crab herbivores revealed that results are strongly variable across elevations (Alberti et al., 2010b). At the lowest reaches of the marsh, the relative importance of crab (*Neohelice granulata*) herbivory is highest and, jointly with nutrients, controls plant biomass. At intermediate elevations, the relative importance of crab herbivory and nutrients is greatly reduced and hypersalinity turns into the major driver of plant performance (Alberti et al., 2010b). At the highest reaches of the marsh, physical stressors (salinity, anoxia, and flooding frequency) are greatly reduced, leading to increased species diversity (see next section), and, as in the opposite end of the tidal gradient, both herbivory (by the wild guinea pigs, *Cavia aperea*) and nutrients interact to determine plant biomass, diversity, and overall species assemblage (Alberti et al., 2011). This is analogous to the results described above for the northwestern Atlantic where herbivorous crabs exert a strong control on the low marsh, while snails can reduce plant biomass on the high marsh. Studies from European back-barrier marshes illustrated that intermediate-sized, vertebrate herbivores (geese and hares) have pronounced effects on the successional pathway of plant species at low marsh elevation, whereas their effects were less pronounced on the high marsh (Kuijper and Bakker, 2005).

Besides affecting trophic interactions, elevation generally affects the relative importance of physical stress. More and longer flooding often creates saline, but also waterlogged conditions, with lower oxygen levels in the soil resulting in reduced redox potentials and leading to increased production of aerenchymatous roots (air-filled channels that allow transfer of gases between the shoot and the root) to cope with these anoxic conditions (Burdick and Mendelsohn, 1987). Oxygen limitation diminishes the production of salt marsh plants such as *Spartina* (Linthurst and Seneca, 1981; Castillo et al., 2000), but crab burrowing
can ameliorate this stressful scenario by oxygenating the sediment (*Uca pugnax*: Bertness, 1985; *Neohelice granulata*: Daleo et al., 2007). Indeed, the positive effect of crab burrowing on plant production is then translated to higher trophic levels, benefiting rodents (*Akodon azarae* and *Oligoryzomys flavescens*: Canepuccia et al., 2008) and stem-borer moths (*Haimbachia* sp.: Canepuccia et al., 2010a). Similarly, bioturbation by a small crustacean (*Orchestia gammarellus*) on northern European Atlantic marshes has recently been hypothesized to be important for the establishment of anoxia-intolerant plant species such as *Elytrigia atherica* (Schrama et al., 2012). Finally, a rush, *Juncus gerardii*, in New England salt marshes has been shown to increase species diversity through its ability to increase oxygen conditions and decrease salinity for neighboring plants, which serve as the base of the food chain for insects and their predators (Hacker and Bertness, 1995b; 1996; Hacker and Gaines, 1997). Thus, facilitator species, particularly in the salt marsh, represent a clear interaction of bottom-up and top-down forces that has important implications for community and ecosystem processes.

Effects of elevation and sediment redox potential have been distinguished from each other in a United Kingdom salt marsh. Anoxic conditions occurred at lower elevation, with redox potential generally increasing with elevation, resulting in oxic sediments at higher elevation. However, sediment oxygenation at any given elevation was variable, particularly at intermediate levels in the tidal range. This imperfect correlation between elevation and sediment redox allowed quantification of their independent effects on species distributions (Davy et al., 2011). Some species were affected by both elevation and redox potential (*Elytrigia atherica*), while other species were more affected by redox potential than by elevation (*Suaeda maritima*, *Atriplex portulacoides*).

Among many other abiotic factors that regulate marsh functioning, salinity is probably one of the most intensively studied in salt marshes (Odum, 1988). High salinities inhibit nitrogen uptake by plant roots and can impose serious restrictions on plant vigor and growth, masking the otherwise positive effects of increased nutrient availability (Linthurst and Seneca, 1981; Hacker and Bertness, 1995a). The impact of salinity does not only affect plants; it can also affect habitat use, and densities and numbers of herbivores. For example, in many southwestern Atlantic salt marshes, salinity increases during dry years, preventing wild guinea pigs (*Cavia aperea*, a terrestrial herbivore) from using the marsh due to reduced plant quality (Canepuccia et al., 2010b). In addition, estuarine salinity gradients influence plant assemblages in the northwestern Atlantic. Only a few species can tolerate the most saline extreme of the gradient, whereas they are outcompeted by other plant species at locations with lower salinity (Odum, 1988; Crain et al., 2004). Moreover, at the lower end of the salt gradient, the impact of herbivorous rodents on plant biomass (Taylor and Grace, 1995) and diversity (Bromberg Gedan et al., 2009a) is more pronounced. Along the elevational gradient of a northeastern Atlantic salt marsh, Brent geese (*Branta
bernicla) forage on the relatively saline, low marsh, whereas Barnacle geese (Branta leucopsis) mainly forage on the higher, less saline marsh. This difference was confirmed by experimental addition of salt water to the high marsh. Brent geese have a bigger salt gland than Barnacle geese (Stahl et al., 2002), which enables them to forage in different portions of the marsh.

However, the negative effect of salinity on plant vigor can also act synergistically with herbivory, imposing severe and persistent reductions in salt marsh plant cover and biomass. For example, drought-induced increases in salinity in northwestern Atlantic marshes caused plant decay and formation of snail fronts that propagated through healthy marsh, leading to massive die-offs (Silliman et al., 2005). These results led to a refinement of the community organization models originally proposed by Menge and Sutherland (1987; i.e., the importance of negative biotic interactions decreases as physical stress increases), predicting that, in these scenarios, plant cover would rapidly decrease as physical stress increases (Silliman et al., 2013). Collectively this evidence reveals that physical stress can negatively affect plants while negatively or positively affecting their consumers, depending on the system.

Sediment type
Sediment type can modify the aforementioned gradients driven by elevation. Salt marshes throughout the world develop on very different substrates including cobble/pebble, sand, peat, and silt/clay (peat: Bertness et al., 2009; clay: Van Wijnen and Bakker, 1999; clay – various substrate types: Daleo and Iribarne, 2009). As well as other environmental factors, sediment type can play a key role in marsh functioning, determining the relative importance of top-down and bottom-up interactions. For example, massive die-offs of S. alterniflora marshes have been occurring in Cape Cod (Massachusetts, USA), driven by elevated herbivorous crab densities (Altieri et al., 2012). However, this extremely negative effect of crabs on salt marsh plants depends on sediment type. Crabs recruit and burrow in peat but not in sandy marshes, so substrate type thus determines the potential for occurrence of this key grazer and its control of the marsh die-off (Bertness et al., 2009).

A similar influence of sediment type on plant–animal interactions occurs in southwestern Atlantic salt marshes. These salt marshes occur across a gradient of silt/clay-dominated to cobble/pebble-dominated sediments, which closely parallel a gradient of increasing oxygen availability in the sediment. On marshes with larger grain size, oxygen limitation is less common and, consequently, the relative importance of the positive effect of crab burrows on plant production is outweighed by the negative effects of crab herbivory (Daleo and Iribarne, 2009). Sediment type therefore regulates plant productivity and, consequently, the relative strength of positive and negative impacts of grazers on plants and the overall net effect of top-down and bottom-up control.
Salt marshes often exhibit gradients in nutrient availability (particularly N) that are correlated with plant density and biomass (Valiela et al., 1978; Alberti et al., 2010b), and can even lead to distinctive growth forms such as the short and tall forms of *S. alterniflora* (Valiela et al., 1978). Additionally, salt marshes are threatened by increasing N inputs due to human activities (sewage discharge, runoff from agricultural fields, and atmospheric deposition; Adam, 2002). Persistent ecosystem scale N enrichment can have severe consequences for salt marshes given that the globally observed increase in aboveground production (e.g., Van Wijnen and Bakker, 1999; Silliman and Zieman, 2001) occurs jointly with a reduction in belowground biomass that leads to marsh loss by creek-bank collapse (Deegan et al., 2012). Many experimental studies that jointly manipulated nutrients and herbivores have found that both factors regulate plant biomass and/or diversity (Silliman and Zieman, 2001; Bertness et al., 2008; Alberti et al., 2010b; 2011; Kuijper and Bakker, 2012). Nutrient additions increase overall plant production, while the effects of herbivores range from moderate to high enough to consume all the extra plant biomass produced under nutrient-enriched scenarios. In particular, the consumption of extra plant biomass promoted by nutrient additions (e.g., Bertness et al., 2008) likely occurs due to increased herbivore densities in fertilized plots. The varying impact of herbivores depends on their densities (Abraham et al., 2005), the presence of their predators (Silliman and Bertness, 2002), and the abiotic context (Bromberg Gedan et al., 2009a).

However, rather than acting in isolation, nutrients interact with herbivores in marshes (as in other systems); the relative importance of these forces in regulating plant production is likely context-dependent. As salt marshes often occur in very dynamic habitats (e.g., exposed to tidal wave action and extreme weather events), the alternation of bottom-up and top-down factors dominating trophic interactions might be a common feature of these unique systems. Whereas herbivores might play an important role in influencing plant species composition, their effects could be overruled when extreme events change the abiotic conditions and reset the successional clock to earlier stages (Kuijper and Bakker, 2012).

Short-term succession across environmental gradients in salt marshes
Natural disturbance by floating plant debris (wrack), sediment deposition, herbivores, fire, and ice can all play an essential role in marsh functioning by creating unvegetated areas and eliciting short-term secondary succession (Pennings and Bertness, 2001). For example, goose herbivory in the Canadian Arctic can be intense enough to create unvegetated areas that can remain unchanged for years due to changes in edaphic conditions (Abraham et al., 2005). Recovery is usually
driven by sexual or asexual colonization of bare patches and can be modulated by herbivores and bioturbators regulating sediment dynamics. Indeed, as salinity is reduced from salt to freshwater marshes, plant species diversity increases (Odum, 1988), as well as the importance of herbivory during secondary succession in northwestern Atlantic marshes (mostly initiated by wrack deposition), and thus, full recovery after disturbance takes longer if herbivores are present (Bromberg Gedan et al., 2009a). Similarly, recovery in southwestern Atlantic salt marshes occurs very slowly due to the impact of herbivores at different intertidal heights (Alberti et al., 2008; 2010a; Daleo et al., 2011; 2014). In contrast, sediment dynamics seem to play a greater role in regulating succession in northeastern Atlantic marshes, even mediating the impact of herbivores. It is suggested for northeastern Atlantic marshes that herbivory and bioturbation by the ragworm *Nereis diversicolor* may account for a loss of salt marsh vegetation from the pioneer zone by foraging and burial of seeds and seedlings. It is also possible that abiotic conditions such as mobility of the top layer during winter periods may cause removal of seeds (Wolters et al., 2005). Experiments in the field and in mesocosms revealed that the establishment of small *S. anglica* plants in the pioneer zone is inhibited by the lugworm *Arenicola marina* because of low sediment stability induced by the lugworms. In turn, *Arenicola* establishment in *Spartina*-dominated patches is limited by high silt content and compactness and dense rooting of the sediment by *Spartina* (Van Wesenbeeck et al., 2007), illustrating the potential for negative interactions to determine community composition. Similarly, Greylag geese (*Anser anser*) feed on aboveground biomass of grasses and dicotyledons, as well as on rhizomes and winterbuds of *S. anglica* and tubers of *Scirpus maritimus*. Exploitation of juvenile plants of *Spartina* by geese prevented new establishment on bare soil. After removal of tuber biomass by geese, recovery took 2 years in an exclosure experiment. Without exclosures, bare soil remained (Esselink et al., 1997). Overall, these examples suggest that herbivores alone, through modulation of sediment dynamics, generally retard secondary succession after disturbance. This highlights the importance of top-down forces and their potential interaction with bottom-up processes in short-term succession of salt marsh ecosystems.

**Long-term succession: a case study from European back-barrier salt marshes**

*Changes in abiotic conditions and biotic interactions during salt marsh succession*

An inherent problem of studying succession is the time required to study an entire successional sequence. Space for time substitutions provide a useful tool to deal with the problem of lack of successional studies over many decades. The back-barrier salt marsh of the Dutch island of Schiermonnikoog represents a rare, clear chronosequence. The establishment of vegetation in different parts
of the salt marsh can be derived from aerial photographs (Olff et al., 1997). The chronosequence including very young marsh (from 0 years onwards) to older marsh (up to 100 years) allows an inference of succession of soil, vegetation, vertebrate, and invertebrate animals in the same ecosystem and the opportunity to look at the relative importance of bottom-up and top-down forces during succession.

Along this chronosequence, the cover of bare soil decreases, whereas the depth of deposited sediment increases with age of the salt marsh (Fig. 7.5). Deposited sediment contributes to surface elevation change, and it also contains N. The N pool of the rooting zone of 50 cm is positively correlated with the thickness of the clay layer on back-barrier marshes (Olff et al., 1997). As N mineralization is positively related to the N pool (Bakker et al., 2005b), plant production increases and vegetation grows taller with an increase in clay layer thickness. Hence, the chronosequence represents a productivity gradient.

Early in succession, external input from marine sources such as macroalgae plays an important role (Fig. 7.6a). In this early stage, large numbers of the dipteran *Fucellia maritima* occur under decaying algae, as well as microbivores and their predators (Schrama et al., 2012). This stage thus harbors a food web dominated by detritivores (i.e., a brown food web) and a low plant standing biomass. Stable isotope analyses revealed that marine-derived N is not only found in the various layers of the food web, but also in the pioneer plants at this stage (Schrama et al., 2013a). Nutrient flows from the marine ecosystem to the terrestrial ecosystem thus drive early successional communities in the salt marsh from the bottom-up.
Figure 7.6  Schematic representation of the changes in the dominant plant and animal species along the chronosequence of the barrier island of Schiermonnikoog, The Netherlands. Gray arrows depict dominant top-down and bottom-up drivers that maintain the status quo in each of the four different states. Thick open arrows represent the bottom-up or top-down drivers that force the system from one stage to the next.

**Effects of plants on intermediate-sized vertebrate herbivores (bottom-up control)**
Intermediate successional stages are characterized by a strong increase in above-ground standing plant biomass. This is accompanied by a strong increase in the biomass of small (invertebrates) and intermediate-sized herbivores (e.g., geese and hares; Fig. 7.6b). Along the productivity gradient, densities of herbivores, such as migratory Arctic-breeding geese (e.g., Brent geese (*Branta bernicla*...
bernicla), Barnacle geese (*Branta leucopsis*), sedentary European brown hares (*Lepus europaeanus*), and European rabbits (*Oryctolagus cuniculus*), initially increase to an optimum at intermediate productivity, but decline at sites with high productivity (Van de Koppel et al., 1996; Bakker et al., 2009). According to the exploitation ecosystem hypothesis (EEH), at sites with low productivity, plant biomass is too low to support herbivore populations, and plant growth will be regulated by bottom-up effects such as nutrient availability (Oksanen and Oksanen, 2000). With increasing productivity, a shift from bottom-up to top-down effects is expected to occur. Top-down regulation of plant biomass occurs at sites of intermediate levels of productivity, with herbivore populations regulated by top-down processes (namely, carnivores) at high productivity (Oksanen and Oksanen, 2000). However, in the absence of carnivores, bottom-up effects play an important role even at highly productive sites. Forage quality declines at sites of high biomass and tall canopy (Van Der Wal et al., 2000a), featuring a decreasing leaf:stem ratio. As a result, herbivore density at high biomass sites can decrease even in the absence of carnivores in these systems because intake rate and foraging efficiency of geese level off or decline with plant biomass above a certain threshold (Van Der Wal et al., 1998; Bos et al., 2004; Van Der Graaf et al., 2006) and hare foraging conditions are negatively affected by increasing biomass (Kuijper et al., 2008; Kuijper and Bakker, 2008). This bottom-up control of herbivore density at highly productive sites is referred to as the “quality threshold hypothesis” (Van De Koppel et al., 1996; Olff et al., 1997). This hypothesis states that without top predators, plant quality can exert strong bottom-up effects that regulate herbivore density at highly productive successional stages.

There is good evidence that the aforementioned patterns of herbivore density are related to succession and in this way linked to dietary quality and foraging conditions for intermediate-sized herbivores. Geese numbers were estimated at young, intermediate, and older parts of the salt marsh on Schiermonnikoog between 1971 and 1997. In the late 1970s, Brent goose numbers were high in the old marsh. However, geese numbers declined significantly in the following 20 years (Van Der Wal et al., 2000b). This decrease was not related to a decrease in size of the area, as the surface area increased over the years as a result of ongoing vegetation succession. Geese numbers increased in the intermediate-aged salt marsh, followed by a slight but significant decrease toward 1997. In the young salt marsh, geese numbers only increased. Furthermore, the development of new young marsh led to an eastward movement of geese on this salt marsh (Van Der Wal et al., 2000b). Hence, the reduction of the community with preferred food plants in the western parts was compensated for by an increase in this community in newly developed eastern parts of the salt marsh. We observed that ongoing plant succession pushed the geese eastward and geese had to follow the changing vegetation. Thus, vegetation succession evicted spring staging geese (Van Der Wal et al., 2000b). Similarly, the increasing abundance of the
unpalatable, tall plants during salt marsh succession reduces the grazing intensity of non-migratory hares (Kuijper et al., 2008; Kuijper and Bakker, 2008). As a result, hare numbers also decrease with increasing salt marsh age (Van De Koppel et al., 1996) and bottom-up factors control the vegetation at the older, productive successional stages (Bakker et al., 2005a).

While the biomass of herbivores decreases toward late succession, biomass of detritivores increases (Fig. 7.6c). This coincides with a stable biomass of live plants toward late-successional stages, and a continuous increase in dead biomass. The crustacean macropod detritivore beach hopper *Orchestia gammarellus* becomes dominant in the final stages of succession (Schrama et al., 2012). It creates oxic conditions by digging (“bioturbating”) in the upper layer of the sediment. This increases net N mineralization and promotes dominance of the tall grass sea couch, *Elytrigia atherica*. The spreading of this tall grass during salt marsh succession is a phenomenon of natural succession on back-barrier marshes (Veeneklaas et al., 2013).

**Effects of intermediate-sized herbivores on plants (top-down control)**

Are intermediate-sized herbivores only a victim of plant succession? The effects of intermediate-sized herbivores on vegetation were tested in long-term field experiments. At four sites along the chronosequence on the island of Schiermonnikoog, exclosures were established. After 7 years, top-down effects of herbivores on the vegetation were most pronounced in the low salt marsh. Plant species of later successional stages increased in cover inside full exclosures, especially at the youngest, least productive marshes. These experiments revealed that herbivory retarded the establishment and spread of late-successional species (i.e., *Atriplex portulacoides* and *Elytrigia atherica*) on the low salt marsh. Hares are estimated to retard vegetation succession for at least 20–25 years (Van Der Wal et al., 2000a; Kuijper and Bakker, 2005). The open vegetation in the young, least productive marshes offers the opportunity for establishment of late-successional species, as long as selective grazing by herbivores is absent. Once late-successional species have established, they will spread more rapidly in the absence of herbivores, indicating that establishment is actually the limiting factor in this invasion, but that herbivory can retard further spread (Kuijper et al., 2004). In the absence of herbivores, late-successional species can directly invade, during the “window of opportunity” in young marshes, and will dominate the vegetation at an earlier stage. Hence, the top-down effects of the herbivores combined with the bottom-up effects of the vegetation can retard vegetation succession in these salt marsh systems for several decades (Kuijper and Bakker, 2005) until herbivores themselves are evicted by vegetation succession.

Importantly, *Elytrigia atherica* is not always the final successional stage. Sites far away from the intertidal flats receive little or no sediment. Hence, they are building a sedimentation deficit due to continuous sea-level rise, and hence get
wetter. The result is that *Elytrigia* stands decline and become replaced by the native *Phragmites australis* (Veeneklaas et al., 2013). This implies that successional pathways to climax communities are governed by bottom-up and top-down control at young successional stages, but that in some cases, bottom-up control may play a dominant role in determining the final successional stage. It appears that herbivorous snails in eastern Atlantic marshes take a similar top-down position to geese and hares in northwestern Atlantic salt marshes (Silliman et al., 2005).

**Effects of large herbivores on plants and smaller herbivores (top-down control)**

Natural large herbivores are nowadays lacking in European salt marshes. However, these natural grasslands likely were important foraging sites for extinct large grazers such as aurochs (*Bos taurus*, 17th century) and Tarpan (*Equus ferus*, 18th century), which once occurred throughout Eurasia (Hall, 2008). Northwestern European salt marshes have often experienced millennia of livestock grazing (Bakker et al., 2005a; Davy et al., 2009), which can be seen as a substitute for the processes induced once by natural large herbivores. Grazing by large herbivores causes soil compaction by trampling, with subsequent increased bulk density, increased water content, reduced redox potential, and hence reduced rates of net N mineralization on grazed sites compared to ungrazed sites (Fig. 7.6d). This coincides with a strong decline in the abundance of *Orchestia gammarellus* and a resulting decrease in bioturbation. Such differences were found on clay marsh with fine-grained sediment, and not at the foot of dunes with sandy coarse-grained sediment, and thus depend on the type of sediment. This suggests that grazing by large herbivores affects the ecosystem more by habitat destruction (i.e., trampling) than by removing biomass and hence competition for light (Schrama et al., 2013b).

Livestock grazing in the final stage of succession in the chronosequence can set back the successional clock toward earlier stages in the vegetation (Bos et al., 2002; Schrama et al., 2013b). Such plant communities pave the way for intermediate-sized herbivores that would otherwise have been evicted by vegetation succession. Geese were found to depend on the facilitation by livestock (Bos et al., 2005), and hares also profit from the better foraging conditions created by livestock on older salt marshes (Kuijper et al., 2008). High densities of livestock, hares, geese, and herbivorous invertebrates turn the brown food web back to a green food web (Schrama et al., 2012). It seems that both top-down and bottom-up factors simultaneously control plant species composition when grazing by large herbivores occurs on old, productive back-barrier salt marshes.

**Summary of salt marsh systems**

Nutrients, physical stressors, plant communities, and herbivore pressure vary within and between marshes largely because of changes in the elevational gradient. Rather than acting in isolation, these factors interact in many different ways
and their balance is strongly spatially and temporally context-dependent. For example, while nutrients generally have positive short-term impacts on plant production, they might also promote herbivore densities and grazing pressure, as well as marsh erosion in the long term. Analogously, physical stress usually has negative impacts on plant biomass (e.g., inhibiting nutrient uptake), and it can also promote or deter herbivory, depending on whether herbivores are affected by that stressor. Both nutrients and herbivores influence plant communities, but in addition, changes in plant communities over time influence herbivores, determining the relative importance of bottom-up or top-down forces. Overall changes in a natural salt marsh succession reveal a transition from a brown food web in the earliest stages, to a green food web during intermediate successional stages, followed again by a brown food web at the oldest, most productive stages of salt marsh succession (Schrama et al., 2012). Along this successional gradient, there are clear shifts in bottom-up and top-down processes that co-occur with changes in food web configuration. Plant and animal communities in very early and late-successional stages are mainly regulated by bottom-up processes. The availability of nutrients, either from marine sources or from oxygenated sediment, as well as the local abiotic conditions, largely determine plant and animal species composition. In both cases, the food web is largely dominated by brown web trophic groups (Schrama et al., 2012). However, in intermediate stages of succession, trophic groups of the green web (e.g., intermediate-sized herbivores, such as geese and hares) reach their highest biomass. Here, they have the biggest impact on the vegetation, thus top-down processes are playing an important role in shaping plant community composition. In late-successional stages, plant–plant interactions play an important role, when the geese and hares can no longer cope with the high plant production, and the tall grass *Elytrigia atherica* outcompetes low-statured plant species. Importantly, the introduction of livestock in the final stage of succession can set back the successional clock toward earlier stages in plant and animal communities. These results show how the balance between top-down and bottom-up forces varies across environmental gradients, highlighting the strong spatial and temporal context-dependency of these interactions.

**Overall summary of rocky intertidal and salt marsh systems**

The two coastal interface ecosystems we have focused on in this chapter share many characteristics. First and foremost, both experience the rhythm of the tides, which sets the scene for most of the abiotic conditions and biotic factors that influence these ecosystems. In these systems, community structure and the relative importance of top-down and bottom-up factors result from differences in oceanographic and climatological conditions, geographical location, substrate type, and local and regional species’ pools.

A striking difference between rocky shore and salt marsh ecosystems is the opposed orientation of their major vertical stress gradients: abiotic stress on
rocky shores is strongly linked to the duration and conditions of atmospheric exposure during low tides, whereas stressful conditions on the salt marsh arise from the duration of inundation by seawater (Fig. 7.1). Rocky shores generally become less physiologically stressful for macrophytes and sessile invertebrates lower on the shore, where periods of inundation are longer, whereas abiotic stress for salt marsh plants generally decreases with increasing salt marsh elevation. For rocky shore macrophytes, winds and insolation result in desiccation, and thermal and light stresses are greater higher on the shore, where nutrients are also less readily available. In contrast, the soils of salt marshes are highly heterogeneous with respect to salinity, nutrients, and redox potential, and these factors, absent from rocky shores, are important determinants for plant community composition in salt marshes. However, mobile marine consumers in both ecosystems are negatively influenced by atmospheric conditions at higher elevations, and both rocky intertidal and salt marsh communities are vulnerable to terrestrial consumers. On rocky shores, these are primarily birds, whereas mammals and birds are common on salt marshes.

Further, one of the most fundamental differences between salt marsh and rocky shore ecosystems is the difference in substrates, noted above. Detritus does not accumulate in rocky intertidal ecosystems and contribute to the formation of soil; instead, it is largely exported to adjacent beaches (Fig. 7.2) and other benthic marine ecosystems. As a result, there is limited opportunity for consumers to influence nutrient recycling or ecosystem nutrient supply rates. Rather, exchange or inputs of nutrients and energy with adjacent ecosystems are both common and more influential. In contrast, salt marsh plants and animals can influence nutrient dynamics and sediment properties through uptake and sequestration of nutrients in plant biomass, bioturbation and excreta (e.g., pseudofeces of mussels at the edge of the marsh), and the brown food web. Top-down and bottom-up processes differ markedly between these systems. Trophic interactions on rocky shores can be strong, but also vary as a function of environmental stress and oceanographically mediated subsidies of energy, materials, and propagules from adjacent ecosystems. Some of these processes mediate bottom-up effects (e.g., oceanographic processes that affect nutrient supply or light availability), but many are spatially structured subsidies transported among ecosystems by ocean currents. Adjacent pelagic ecosystems serve as “nurseries” that also provide avenues of dispersal for larvae. Additionally, the marine macro- and microalgae that are the dominant primary producers on rocky shores have lower C:N ratios and thus higher forage quality than the vascular plants that dominate salt marshes. Although this makes rocky shore autotrophs more palatable and nutritious, these macrophytes often go uneaten, and in some places, especially where nutrients and light are plentiful, they can dominate the shore. Mobile rocky shore herbivores seem to have the greatest impact early in succession before macrophytes grow large, escaping
vulnerability. Suspension-feeding invertebrates do not make much of a dent in nearshore phytoplankton concentrations, yet phytoplankton abundance fuels the growth and fecundity of suspension feeders, and of their invertebrate predators. Thus, energy from cross-ecosystem subsidies plays a major role in supporting rocky shore consumer populations.

In comparison, the greatest impacts of herbivores in salt marshes occur at intermediate stages of succession in European salt marshes (Kuijper and Bakker, 2005), and during early and intermediate stages of succession in South American salt marshes (Alberti et al., 2008; 2010a; Daleo et al., 2014). Top-down forces in salt marshes often play a relatively small role in structuring communities. However, this strongly depends on the geographical range. On the vast low-lying western Atlantic marshes, herbivore top-down control can play a major role; consumer assemblages in these areas are often dominated by marine grazers (for example, snails and crabs), or a mix of terrestrial and aquatic grazers (such as aphids, stem-borer moths, nutrias, wild guinea pigs, and other rodents). In the extensive lower marshes, plants can be completely devoured by consumer fronts of snails, which overwhelm the vascular plants. Low-lying salt marshes in South America are also top-down controlled by invertebrate grazers (e.g., crabs). In contrast, in northeastern Atlantic marshes (Europe), which are dominated by high marsh, grazers are mostly terrestrial vertebrates, such as hares and geese. Grazing by these vertebrates, especially in early successional stages, can have a profound effect on vegetation development. In later stages of salt marsh development, only grazing by large vertebrate herbivores (livestock) can have a similar impact. In general, top-down control by carnivores is rare in salt marshes.

Ecosystems of the land–sea margin are characterized by their strong connectivity with adjacent pelagic, estuarine, shoreline, and terrestrial ecosystems (Menge et al., 1997; in press; Polis et al., 1997 (and references therein); Menge, 2000; Valiela et al., 2002; Dugan et al., 2003; Silliman and Bertness, 2004; Schrama et al., 2012; 2013a; Menge and Menge, 2013). Empirical studies in rocky shore and salt marsh (and other) land–sea margin ecosystems have made important contributions to our increasing appreciation of the interplay between bottom-up and top-down processes, and how they structure communities and influence ecosystem functioning. In addition, these systems highlight the importance of spatial and temporal scales (see Chapter 11) in determining the interaction of bottom-up and top-down processes at the land–sea boundary.

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