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Coastal Wetlands

An Integrated Ecosystem Approach

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CHAPTER 15

Ecosystem Structure of Tidal Saline Marshes

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1. INTRODUCTION

Saline marshes occur throughout the world as coastal features that often fringe shorelines and can dominate vegetated areas of estuarine environments. They vary from small and discrete marshes to broad and expansive areas and are typically located in sheltered, low-energy shoreline areas forming the interface between marine and terrestrial environments. Salt marshes are valuable ecosystems that are known to be highly productive, ranking with the most productive ecosystems of the world.

From a global perspective, tidal saline marshes are found in middle and high latitudes along shores throughout the world (Chapman, 1977). The largest concentrations of tidal marshes are found along the South Atlantic and Gulf coasts of North America followed by China (Greenberg et al., 2006). The physical features of tides, sediments, freshwater inputs, and shoreline geomorphology determine the development and extent of tidal saline wetlands, and their regional differences in productivity are likely related to the available solar energy (Mitsch and Gosselink, 2000). Tidal saline marshes are generally found in sedimentary environments and can be broadly classified into those that originate on reworked marine sediments and those that are formed at the margins of river deltas on riverine sediments. Tidal regimes vary from microtidal (<2 m) to macrotidal (>6 m) and can also be diurnal, semidiurnal, or mixed.

The impacts of human activities on coastal systems are not included in this chapter (but see Chapter 23), although we recognize that human activities and development have had

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substantial impacts, including salt marshes and associated estuaries (Baltz and Yáñez-Arancibia, 2009). Over several centuries, expanding human populations in the coastal zone and expanding fishing pressure on finite resources have led to altered estuarine and coastal ecosystems through a series of anthropogenic effects and can be characterized as the shifting baseline syndrome (Pauly, 1995). Fishing has generally been first and foremost, coming before pollution, habitat destruction, introductions of exotic species, and climatic change in the timing and degree of impact (Jackson et al., 2001). Historic alterations have significantly modified saltmarsh ecosystems to the point of dramatic functional impairment or outright marsh destruction (Bertness et al., 2002). To fully appreciate the current condition of saline marshes and foresee the direction of future changes, we need a better understanding of the history of interactions between nature and society in our coastal systems (Kates et al., 2001).

2. SALINE MARSH COMMUNITIES

In describing saltmarsh communities, we have attempted to not only cover the species that are best represented in the literature but also recognize that many important salt marsh species may not be included in our overview. Our coverage includes emergent vegetation and algae, up through fish, birds, and mammals.

2.1 Emergent Vegetation

Tidal saline marshes are defined as natural or seminatural halophytic emergent vegetation on alluvial sediments, with a connection to saline waterbodies (Beeftink, 1977). Typical hydrology involves periodic flooding of the marsh surface as water moves on and off the marsh, controlled by the local tidal regime. The emergent vegetation of tidal saline marshes changes in species composition depending on geographical location (Adam, 1990; Table 15.1). Salt marshes are generally replaced by mangrove swamps in coastal regions of the tropics and subtropics—between 25°N and 25°S latitude (Mitsch and Gosselink, 2000).

Within geographical locations, species composition varies along inundation gradients. A low (submergence) and a high (emergence) marsh zone are generally recognized. The marsh below mean high water is regularly flooded and has reduced soils for most of the time except along creek banks with good drainage (Armstrong et al., 1985). This zone is generally species poor and is dominated by species that are both salt and flood tolerant. The high marsh is found above mean high tide and is less frequently flooded and has oxidized soils that may briefly become reduced during flood events (Armstrong et al., 1985). In some areas, an intermediate middle marsh zone may be distinguished by different plant species composition. Salinity often decreases inland, but salinity inversions are relatively common, particularly when evapotranspiration exceeds precipitation (Mahall and Park, 1976; Callaway et al., 1990). In areas that are irregularly flooded, zonation may be absent or zonation may be related to distance from tidal creeks (Zedler et al., 1999; Costa et al., 2003). Flooding effects on biogeochemical cycling are described in detail in Chapter 16.

TABLE 15.1 Dominant Emergent Plant Species of Tidal Saline Marshes

Family	Species	Marsh Zone	Geographic Extent	Source
Amaranthaceae	*Salkomia virginica*	Low	Western North America	Pennings and Callaway (1992)
Amaranthaceae	*Sarcocornia quinqueflora*	Low	South Pacific	Thannheiser and Holland (1994)
Chenopodiaceae	*Arthrocnemum perenne*	Middle	Europe	Castellanos et al. (1994)
Chenopodiaceae	*Arthrocnemum subterminale*	Middle	Western North America	Pennings and Callaway (1992)
Chenopodiaceae	*Suaeda maritima*	Low	Japan	Adam (1990)
Cyperaceae	*Carex glareosa*	High	Arctic	Adam (1990)
Goodeniaceae	*Seleria radicans*	Middle	South Pacific	Thannheiser and Holland (1994)
Juncaceae	*Juncus kraussii*	High	South Pacific	Adam (1990)
Juncaceae	*Juncus roemerianus*	Middle to high	Eastern North America	Mitsch and Gosselink (2000)
Juncaginaceae	*Triglochin maritima*	Middle to low	Western Europe, Arctic, Asia	Bakker (1985) and Davy and Bishop (1991)
Plumbaginaceae	*Limonium vulgare*	Middle to Low	Europe and North Africa	Boorman (1967) and Bakker (1985)
Poaceae	*Distichlis scoparia*	High	South America	Cantero et al. (1998)
Poaceae	*Distichlis spicata*	Middle	Western North America, South America	Adam (1990) and Cantero et al. (1998)
Poaceae	*Festuca rubra*	High	Western Europe	Gray and Mogg (2001)
Poaceae	*Puccinellia maritima*	Middle to low	Western Europe	Gray and Mogg (2001)
Poaceae	*Puccinellia phryganodes*	Low	Arctic	Beaulieu and Allard (2003)
Poaceae	*Spartina alterniflora*	Low	Eastern North America	Mitsch and Gosselink (2000)
Poaceae	*Spartina anglica*	Low	Western Europe	Gray and Mogg (2001)
Poaceae	*Spartina densiflora*	Low	South America	Cantero et al. (1998)
Poaceae	*Spartina foliosa*	Low	Western North America	Adam (1990)
Poaceae	*Spartina maritima*	Low	Europe	Castellanos et al. (1994)
Poaceae	*Spartina patens*	High	Eastern North America	Mitsch and Gosselink (2000)
Poaceae	*Sporobolus virginicus*	High	Tropics	Adam (1990)
Poaceae	*Zoysia sinica*	High	Japan	Adam (1990)
Primulaceae	*Samolus repens*	Low	South Pacific	Thannheiser and Holland (1994)

The distribution of plant species in tidal saline marshes is determined by the physical, chemical, and biological environment. Physical and geochemical factors that affect the distribution of tidal saline marsh species include flooding, salinity, and the ratio of sodium to potassium, as well as the ratio of calcium to magnesium (Clarke and Hannon, 1970; Olff et al., 1988; Partridge and Wilson, 1989; Cantero et al., 1998; Alvarez Rogel et al., 2000; Huckle et al., 2000). Over a stress gradient, the distribution of a species is determined by physical constraints at higher stress levels and competition with other species at lower stress levels (Pennings and Callaway, 1992). Plant establishment where physical stress is high may decrease stress levels by increasing elevation, oxygenating the rhizosphere, or reducing soil salinity, thereby facilitating the establishment of higher marsh species (Bertness and Shumway, 1993; Castellanos et al., 1994; Figueroa et al., 2003). However, the relative effects of facilitation and competition are highly dependent on the stress tolerance of the local species (Pennings et al., 2003). Increasing nitrogen availability allows species to better compete and expand (van Wijnen and Bakker, 1999; Bertness and Pennings, 2000).

Sometimes parasitic plants can alter competitive outcomes. For example, in tidal saline marshes of the western United States, the parasitic saltmarsh dodder (*Cuscuta salina*) facilitates two relatively uncommon plant species, sea lavender (*Limonium californicum*) and sea heath (*Frankenia salina*), by selectively infecting and suppressing the competitive dominant glasswort (*Salicornia virginica*) (Pennings and Callaway, 1996). Interaction with animals also plays an important role. In many tidal saline marshes across the globe, invasive plant species have started to replace the historic/native vegetation due to introductions of nonnative plant and animal species, human alterations to the local hydrology, and increasing nutrient levels in estuarine waters (Thannheiser and Holland, 1994; Moyle, 1996; Castillo et al., 2000; Talley and Levin, 2001; Bertness et al., 2002; Valéry et al., 2004). In China, *Spartina alterniflora* (introduced in 1979) has spread over much of the coast and has proven to be competitive interacting with the native mangroves (Zhang et al., 2012).

2.2 Benthic Algae

Benthic algae occur on the sediments below and adjacent to the emergent vegetation of tidal saline marshes, as well as on the culms of the emergent vegetation (epiphytic algae). Diatoms are universally present (Sullivan and Currin, 2000). Extensive cyanobacterial populations develop during the summer in Europe (Birkemoe and Liengen, 2000; Quintana and Moreno-Amich, 2002), as well as northeast and southwest coasts of the United States (Blum, 1968; Zedler, 1982). Green and brown algae reach the largest population sizes during seasons in which emergent vegetation is not dominant (Brinkhuis, 1977; Houghton and Woodwell, 1980; Sullivan and Currin, 2000). Distinct benthic algal communities are associated with different emergent vegetation communities and are related to differences in elevation, soil temperature, soil moisture, interstitial ammonium concentration, and canopy height (Sullivan and Currin, 2000).

2.3 Nekton

Numerous factors and classifications have been proposed to characterize marsh habitat and the nekton that inhabit them. Marsh habitat (e.g., zonation) may drive structuring of nekton, and the collection of conditions has been referred to as the "marsh gradient" (Rountree and Able, 2007). From a species perspective, use of marshes may be driven by life history traits that include spawning, feeding, migration, and nursery (growth and refuge) functions, among others. Furthermore, marsh use within a species may vary. In South Carolina, resident and transient species entered during different phases of the tide (Bretsch and Allen, 2006). Species-specific differences in marsh use were also found to be size-dependent in a North Carolina marsh (Meyer and Posey, 2009).

The broadest division of marsh nekton might separate resident and transient species (Cowan et al., 2012). Transient species may be found in marshes (based on tide, season, or numerous other environmental variables) and include both fresh- and saltwater visitors, as well as diadromous forms such as salmonids, clupeids, and anquillids that are present or migratory for one or more life history stages (Baltz et al., 1993; Dionne et al., 1999). The resident and transient groups are still coarse, however, and subsequent classifications have been proposed. Peterson and Turner (1994), for example, suggest four categories based on marsh use: (1) residents on the marsh surface that generally remain at low tide in pools and puddles, (2) regular visitors at high tide that retreat to fringing vegetation along the marsh edge at low tide, (3) individuals of larger species that associate strongly with the marsh edge as juveniles and penetrate only a few meters into the marsh at high tide, and (4) other subtidal species that rarely penetrate far onto the flooded marsh but may be associated with tidal creeks. Although this may be regarded as a useful classification, others groupings may have value.

In Louisiana marshes, tidal amplitude (~30 cm) is at the low end of the microtidal range and it is easily dominated by winds making marsh flooding less predictable. Thus, interannual climatological variation influences flooding duration and frequency of saltmarsh habitats (Childers et al., 1990). In marshes with greater micro- and mesotidal ranges (>1 m), inundation is more predictable and some fishes may spend as much as one-third of their time in flooded smooth cordgrass (*Spartina alterniflora*) (Hettler, 1989). For species that use intertidal zones as nurseries, interannual variation in habitat availability may have a strong influence on recruitment, particularly in microtidal systems (Childers et al., 1990; Baltz et al., 1993, 1998). For example, climatic conditions affect marsh accessibility for juvenile shrimp and are related to interannual variation in shrimp landings (Childers et al., 1990).

Connolly (1999) reviewed study limitations that have hampered our understanding of the direct use of tidal saline marshes by nekton, primarily fishes, shrimps, and crabs, and suggested improvements to standardize sampling methods, overcome poor sampling designs, and improve assessment of flooding regimes and landscape structure. He also noted the uneven distribution of studies, largely limited to North America (90%), Europe (7%), and Australia (3%), although a disproportionate amount of the world's salt marshes occurs on these continents. Based on a review of 20 North American salt marshes along the Atlantic Ocean and Gulf of Mexico, 237 species of fish were detected (with the highest richness at a site being 86 species; Nordlie, 2003). Marine transients were the most represented group (>50%), whereas other groupings were much less represented, and interestingly, the proportion of marine transients was variable among sites, but did not change along a latitudinal gradient. Cattrijsse and Hampel (2006) reviewed intertidal marsh studies in Europe and contrasted floral, faunal, and physical patterns with North American coastal systems. In contrast to North American salt marshes, European salt marshes differ in having the lower limit of marsh vegetation defined by mean high water neap tides rather than mean tide level, vegetation typically dominated by sea purslane (*Halimione* spp.) rather than smooth cordgrass and a much higher stem density that inhibits nekton movement on the marsh surface. Laffaille et al. (2000) examined fish use of saltmarsh vegetation in the macrotidal system of Mont Saint-Michel Bay, France, which is accessible to fishes for only a few minutes or hours during high spring tides (5%—10% of tides). Due to this brief flood duration, no fishes are considered residents, but the annual pattern and three seasonal patterns of community structure are stable. Thirty-one fishes, netted in creeks as tides ebbed off of flooded marsh, included 7 marine stragglers, 13 estuarine-dependent marine species, 3 catadromous species, and 8 estuarine species. Most of the species can be characterized as euryhaline and eurythermal migrants.

In Australia, Connolly et al. (1997) examined fish use of flooded saline marsh in the high intertidal zone that is generally separated from open water by fringing mangroves. Compared with tidal creeks draining the same marsh flats, the number of species and individuals caught in the high intertidal zone was lower; however, the density of fishes on marsh flats (1 per 23 m^2) was higher than expected when creek numbers were parsed over drainage areas (1 per 134 m^2). Only the two most abundant species found in creeks were captured on high marsh flats, glass goby (*Gobiopterus semivestitus*) and smallmouth hardyhead (*Atherinosoma microstoma*).

2.4 Reptiles and Amphibians

Only a few species of snakes, turtles, and crocodilians can be considered common residents of tidal saline marshes (Neill, 1958; Greenberg et al., 2006). The saltmarsh snake (*Nerodia clarkii*, but comprised of three subspecies) is restricted to saline and brackish tidal wetlands along the Atlantic and Gulf coasts of North America. As a way to avoid predators, salt marsh snakes are nocturnal. The saltmarsh snake does not drink saline water and obtains water primarily from the food it eats (Pettus, 1958). Diamondback terrapin (*Malaclemys terrapin*) is the only North American turtle restricted to tidal saline marshes (Greenberg et al., 2006). Special glands in the turtle's eye region excrete excess sodium (Bentley et al., 1967). Juvenile and smaller male terrapins rely on the nearshore area where they forage on readily available prey such as clams, crabs, and small crustaceans. Interestingly, diamondback terrapins show high site fidelity, yet have less genetic structuring than might be expected because of historic mixing and stocking among populations (Hauswaldt and Glenn, 2005). A recent study determined an increase in contemporary gene flow into Chesapeake Bay populations (Converse et al., 2015). Another recent study in the Chesapeake Bay area highlighted vulnerability of species such as the Diamondback terrapin to potential loss of habitat and sea level rise (Woodland et al., 2017). A large number of amphibian and reptile species are occasional visitors to tidal saline marshes but are generally found in fresh to slightly brackish water (Greenberg et al., 2006).

2.5 Birds

Typically, saline marsh avifauna is dominated, at least numerically, by large numbers of Anseriformes (waterfowl), Ciconiiformes (long-legged wading birds), and Charadriiformes (shorebirds, gulls, and terns) (Goss-Custard et al., 1977; Custer and Osborn, 1978; Bildstein et al., 1982; Erwin, 1996). In addition, Passeriformes (songbirds) feed and breed in saline marshes (Brown and Atkinson, 1996; Dierschke and Bairlein, 2004). In many marshes, avian populations increase considerably seasonally, not only during migratory periods, when large numbers of waterfowl and shorebirds congregate to feed and rest, but also during the breeding season, when wading birds congregate at traditional coastal colonies to nest. The total number of breeding bird species whose habitat primarily consists of tidal marshes has been estimated to be between 11 and 21, with only 2 songbird species that are entirely restricted to tidal saline marsh in North America: the seaside sparrow (*Ammodramus maritimus*) and the saltmarsh sharp-tailed sparrow (*Ammodramus caudacutus*) (Greenberg et al., 2006). These species are adapted to nesting in cordgrass-dominated tidal marshes (Benoit and Askins, 1999). Several subspecies of birds restricted to tidal marshes have wider distributions (e.g., a subspecies of the slender-billed thornbill, *Acanthiza iredalei rosinae*) (Greenberg et al., 2006).

2.6 Mammals

The total number of mammalian species whose habitat primarily consists of tidal marshes has been estimated to range from 13 to 26, with rodents predominant (Greenberg et al., 2006). Of these, only the saltmarsh harvest mouse (*Reithrodontomys raviventris*) is restricted to coastal marshes. In addition to wild mammals, domestic or feral mammals (primarily cattle, sheep, and horses) graze in some tidal saline marshes (Bakker, 1985; Turner, 1987). Although saltmarsh mammals represent a relatively small portion of the potential species richness, they are notable for their ability to cause a dieback event through an “eat out” (Alber et al., 2008). “Eat out” events occur when overgrazing by mammals like the invasive nutria (*Myocastor coypus*; as well as by cattle, horses, and other mammals) destroy more vegetation than they consume (Mitsch and Gosselink, 2000), typically resulting in patches of bare mud. In some areas such as coastal Louisiana, the damaged marsh areas might not recover because of rising sea level and high marsh subsidence rates (Mitsch and Gosselink, 2007).

3. INTERACTIONS AMONG COMMUNITIES

3.1 Effects of Animals on Emergent Vegetation Distribution

Burrowing organisms such as fiddler crabs (*Uca* spp.) increase tidal saline marsh plant production through moderation of soil stresses; for example, they increase soil aeration, oxidation–reduction potential, and in situ decomposition of belowground plant debris (Bertness, 1985), although the increase in production may depend on the severity of the stresses (Nomann and Pennings, 1998). In return, the crabs benefit from the shade and the shelter that the increased plant cover provides (Bortolus et al., 2002).

Grazing by herbivorous waterfowl or cattle can significantly change the vegetation community in a tidal saline wetland (Ranwell, 1961; Bakker, 1985; Pehrsson, 1988). Grazing by breeding waterfowl in the Arctic can change the trajectory of plant succession by physically changing the environment. Moderate grazing preserves the dominance of grasses (Bazely and Jefferies, 1986), whereas heavy grazing can convert marsh to unvegetated mudflats (Handa et al., 2002). Intense grazing can also limit the distribution of plants along a maturation (time since plant establishment) gradient that is not related to elevation. Van der Wal et al. (2000) showed that the distribution of seaside arrowgrass (*Triglochin maritima*) in younger marshes is limited because of intense grazing by geese, hares, and rabbits. The distribution in more mature marshes is limited because of competition for light by taller species that are slower colonizers such as saltbush (*Atriplex portulacoides*). Field experiments indicate that the periwinkle (*Littoraria irrorata*) can overgraze otherwise healthy stands of smooth cordgrass and reduce them to bare mudflats when periwinkle predator density is low. Thus, periwinkle predators including blue crabs (*Callinectes sapidus*) and terrapins are capable of exerting top-down control of smooth cordgrass production (Silliman and Bertness, 2002). The density of grazers can be positively correlated with nitrogen availability (Bowdish and Stiling, 1998; Visser et al., 2006). The more stressful conditions in the low marsh may make plants at this elevation more palatable (Dormann et al., 2000) and grazing effects may be more pronounced in these more stressful environments (Kuijper and Bakker, 2005). Neighboring plant species may have both positive and negative effects on the level of grazing of a palatable species. Grazing on smooth cordgrass by an herbivorous crab (*Chasmagnathus granulata*) is more intense when the plant grows with alkali bulrush (*Scirpus maritimus*) than when it grows in monotypic cordgrass stands (Costa et al., 2003).

3.2 Emergent Vegetation as Animal Habitat

In some tidal saline marshes several species of wintering songbirds forage on the seeds of Limonium, Sueda, and Salicornia (Brown and Atkinson, 1996). In addition, bulrush and cordgrass seeds are eaten by waterfowl (Mendall, 1949; Hartman, 1963; Landers et al., 1976; Gordon et al., 1998). Birds feeding on small aquatic organisms along the marsh edge occur more frequently in areas that have more open water in the form of marsh creeks and ponds (Craig and Beal, 1992). Both rodents and birds nesting in tidal saline marshes use the available vegetation as nesting material (Shanholtzer, 1974). Nests are generally constructed from blades of grass. Similar to forest species, breeding birds in tidal marshes are often associated with larger marsh tracts (Craig and Beal, 1992). Although tidal saline marshes probably function in a variety of ways to enhance growth and survival of a particular nekton species, the relative importance of food versus refuge from predation is poorly understood (Boesch and Turner, 1984) and probably varies across species and life history stages. Both shallow water and vegetation in the marsh provide protection for small nekton from large predators, particularly from large piscivorous birds and fishes (Kneib, 1982a,b), and both provide a food-rich environment (Van Dolah, 1978; Gleason, 1986; Cyrus and Blaber, 1987; Gleason and Wellington, 1988). In experimental tests of predation as a factor determining the size-specific habitat difference between killifish (*Fundulus heteroclitus*) age classes, Kneib (1987) found that young killifish remained in high intertidal cordgrass habitat avoiding concentrations of larger piscivorous fishes in subtidal habitats, whereas habitat use by larger killifish is influenced by avian predators. Other field experiments indicate that predation pressure is lower and food availability is higher in vegetated than in unvegetated habitats (Rozas and Odum, 1988).

3.3 Nursery Function

Nurseries foster the growth and/or survival of early life history stages of fishes and macroinvertebrates (Beck et al., 2001). The particular environment used by a species may be characterized as nursery habitat if it can be shown that individuals are found at higher densities and experience enhanced survival and/or growth compared with nearby habitat types (Pearcy and Myers, 1974; Weinstein, 1979). It is difficult to separate the nursery function of flooded cordgrass marsh from that of adjacent habitat types. Baltz et al. (1993, 1998) examined the use of shallow open water and flooded smooth cordgrass as nursery habitat for a variety of resident and transient fishes in Louisiana estuaries. Small fishes and early life history stages of larger species often use shallow turbid water along the marsh edge at low tides and move onto flooded marsh at higher tides. Evidence suggests that the magnitude of fishery landings is correlated with the spatial extent of estuarine vegetation (Turner, 1977, 1992; Pauly and Ingles, 1988); therefore, extensive marsh loss in the northern Gulf of Mexico is a major concern for the sustainability of fisheries. Construction of dams and weirs in the upper Mississippi River Basin in the last century and downstream channelization have resulted in reduced sediment available for overland flow into the deltaic plain wetlands in Louisiana (Kesel, 1988), resulting in significant marsh degradation. However, the connection between fishery landings and marsh habitat loss in the northern Gulf of Mexico is not clear. Moreover, landings have increased for many species in spite of accumulating habitat alterations (Zimmerman et al., 1991). One hypothesis is that the marsh edge (i.e., the perimeter at the marsh—open water interface) is the essential habitat for many species and that the nursery function and value will not decline and result in reduced landings until the quantity of marsh edge perimeter begins to decline. During the process of marsh deterioration, the amount of marshedge initially increases as solid marsh is converted to broken marsh and then it declines as broken marsh is converted to open water (Chesney et al., 2000). A temporary increase in marshedge perimeter, which occurs in the broken marsh phase, may be masking the ultimate effect of habitat loss on landings (Browder et al., 1985, 1989). An alternative hypothesis is that the marshedge is not the essential habitat per se but serves as access to flooded marsh, which is essential. However, neither hypothesis may be appropriate for all species because a variety of species, whose microhabitat use patterns often differ, occur in high densities in marshedge and flooded cordgrass habitat types (Zimmerman and Minello, 1984; Rakocinski et al., 1992; Baltz et al., 1993; Minello et al., 1994). These alternative hypotheses are testable in experiments that examine growth and/or survival along the marsh edge by contrasting sites with and without access to flooded marsh.

3.4 Saline Marsh Food Webs

Saline marsh food webs are probably far more complex than we recognize. Certainly, the fishes and macroinvertebrates that form upper trophic levels add to this complexity, particularly if we take their large variation in size into account. Because many species of fish and macroinvertebrates continue to grow throughout their lives, they can individually function as multiple “species,” as their predator—prey relationships and habitat utilization patterns change with ontogeny (Livingston, 1988). The food webs are also complicated by interactions with subtidal ecosystem components. The traditional view of bottom-up control in saltmarsh food webs continues being supported in some work, yet it is clear that top-down effects play a larger role than previously thought (Sala et al., 2008).

3.4.1 Species Interactions

Kneib (1984) highlighted our lack of knowledge about the importance of complex species interactions in saline marsh communities that involve more than two trophic levels. Besides predation, there are many factors acting alone or in concert that may influence the distribution and abundance of invertebrates and their predators, primarily crustaceans, fishes, and birds. These include density-dependent processes, selective larval settlement or mortality, physical gradients that influence habitat selection, and both unpredictable and cyclical physical disturbances.

Pennings et al. (2001) compared the palatability of northern and southern populations of smooth cordgrass and saltmeadow cordgrass (*Spartina patens*) to a variety of grazing insects. In 28 of 32 trials, the insects showed significant preferences for the northern plants and supported the biogeographic hypothesis that lower latitude plants are better defended from herbivory. Whether the preferences are based on toughness, nutrient and mineral content, or secondary metabolites remains unclear and is likely to vary between plant-herbivore species pairs, although more recent experimental work (Ho and Pennings, 2013) also supports latitudinal trends. Somewhat counter to these findings, Marczak et al. (2011) demonstrated that latitudinal variation in plant quality (*Iva frutescens*) was less important than latitudinal variation in top consumers. Although climate may structure herbivores (e.g., through generation time), saltmarsh consumers still likely exert some top-down control. Although results from individual studies prove interesting, a large review (443 studies) of consumer control on vegetation found that saltmarsh herbivores often strongly suppress plant survival (He and Silliman, 2016).

Kneib (1991) explored the importance of indirect effects, particularly involving chains of predator—prey interactions, in soft-sediment communities. Indirect effects can influence primary producers, macrofauna, and meiofauna in marsh communities and are often implicated in counterintuitive outcomes of experiments intended to examine direct effects. Soft sediments reduce the feeding efficiency of predators on epibenthic meiofauna (Gregg and Fleeger, 1998). Large crustaceans are important predators in marshes. Grass shrimp have been well studied and are implicated as a connecting link between meiofaunal and nekton communities, especially as effective predators that focus their activities around the bases of smooth cordgrass stems (Gregg and Fleeger, 1998).

In an elegant field-caging experiment, Silliman and Zieman (2001) demonstrated that periwinkle (*Littoraria irrorata*) grazing could exert top-down control of smooth cordgrass annual net primary production. The periwinkle is an important grazer in marshes, but it is also an important prey of a large number of predators that forage on marshes, so its ability to control smooth cordgrass is questionable where it suffers normal predation. Sala et al. (2008) reported similar evidence of potential top-down control. When New England salt marshes became eutrophic, it was found that grazing increased such that dual control was likely structuring the community. In perhaps the most extreme investigation of top-down control, Nifong and Silliman (2013) manipulated the American alligator (*Alligator mississippiensis*) to demonstrate trophic cascades, behavioral changes on mesopredators, and indirect effects on grazing.

In addition to species interactions having to do with predation, other relationships are important for structure and function of salt marsh ecosystems. For example, Angelini et al. (2016) found that mussel mounds greatly enhanced cordgrass survival during drought conditions.

3.4.2 *Primary Producers*

Stable isotopes are useful for tracing the flow of primary production and nutrients through food webs (Fry, 2006). Stable isotopes of nitrogen, sulfur, and carbon, when used in combination, can greatly increase the power of the isotopic tracer approach in coastal food webs (Peterson et al., 1985) and help address questions about the role of cordgrass marshes in supporting marsh and estuarine consumers. Benthic microalgae and standing dead material may overshadow live cordgrass, macroalgae, and phytoplankton as sources of carbon (Sullivan and Moncreiff, 1990; Currin et al., 1995). Peterson et al. (1986) found that cordgrass detritus and phytoplankton were much more important than upland vegetation and sulfur-oxidizing bacteria as carbon sources for marsh macroconsumers. Killifish and mud snails relied more on cordgrass, while filter feeders typified by oysters and mussels relied on a combination of cordgrass and plankton. In addition to marsh and estuarine consumers, organic matter from marsh vegetation and estuarine plankton is exported to the offshore environment where it is consumed by marine organisms (Teal, 1962; Odum, 2000). Alber and Valiela (1994) provide evidence that microbial organic aggregates are more important in the nutrition of two marine mussels than particulate detritus or dissolved organic matter. Despite the longstanding support of cordgrass detritus as the base of the saltmarsh food web, Galván et al. (2008) used stable isotopes to suggest limited importance of cordgrass detritus in a New England salt marsh. Benthic algae and phytoplankton were found to be the dominant food source. In another study in southern California, cyanobacteria (microalgae) was found to play an important role in saltmarsh food webs and young salt marshes in particular (Currin et al., 2011). It is likely that the importance of primary producers may be more spatially and temporally variable than traditionally thought.

Nitrogen fixation by the community of epiphytes growing on standing dead stems contributes significantly to total nitrogen fixation in marshes where senescent plants are not flattened by ice (Currin and Paerl, 1998). The rate for natural salt marsh is 2.6 g N m^{-2} stem surface per year and is comparable with sediment rates and about half of rhizospheric nitrogen fixation. Rates are comparable to cyanobacterial mats 2–8 g N m^{-2} $year^{-1}$. While of little direct benefit to cordgrass, nitrogen fixation by epiphytes is important to animals that graze on them and to the nutrient cycle as a source of new biologically available nitrogen. Epiphytes are an important food resource for consumers (Currin et al., 1995). Diverse meiofaunal communities associated with algal epiphytes on smooth cordgrass stems are utilized by shrimp and fish (Rutledge and Fleeger, 1993; Gregg and Fleeger, 1998). Three saltmarsh macroinvertebrates, periwinkles (*Littoraria irrorata*), saltmarsh coffee bean snails (*Melampus bidentatus*), and talitrid amphipods (*Uhlorchestia spartinophila*), which feed by shredding dead and senescing smooth cordgrass leaves, also benefit from ingesting fungi; snails and amphipods also stimulate fungal growth (Graça et al., 2000). These grazing macroinvertebrates contribute to nutrient cycling and connect microbial decomposers to higher-order consumers such as blue crab and *Fundulus* species that prey on them (Graça et al., 2000).

3.4.3 *Indirect Interactions Among Species*

A general and realistic qualitative loop model (Levins, 1966; Puccia and Levins, 1991) of a simplified saltmarsh food web (Fig. 15.1A) was compiled based in part on the literature reviewed above to illustrate the importance of indirect interactions. The model includes 20 nodes and covers several trophic levels. In this graphical model, direct positive effects of one node on another are indicated by a link terminating in an arrowhead (→), and direct negative effects are indicated by a link terminating in a filled circle (•). A loop is a path of interactions through nodes (variables) that return to the node of origin without retracing itself through any node previously encountered. Model input is a community interaction matrix of direct interaction (i.e., −1, 0, or +1), and output (i.e., the adjoint matrix) is an evaluation of the net number of positive or negative feedback loops influencing each node of the community (Dambacher et al., 2002a,b). Loop models can predict the outcomes of one or more perturbations on a system providing that the community structure is stable (Bender et al., 1984; Dambacher et al., 2002a). A press perturbation (*sensu* Bender et al., 1984), which may be positive or negative, is a sustained alteration of species densities (or environmental variables), and if the press is maintained, the unperturbed species (or variables) reach a new equilibrium. In essence, the elements of an adjoint matrix are the algebraic summation of the number of positive or negative feedback loops that contribute to the direction of change of a given variable. We have simplified the model output to a graphical representation of a positive press on the variables (Fig. 15.1B).

While the analysis of many similar models is necessary to reveal general truths (Levins, 1966) about marsh food webs, we can gain some insights from a single model. Our greatly simplified model with only 20 nodes has several million feedback loops and supports Kneib's (1991) contention that indirect effects can influence primary producers, macrofauna, and meiofauna in marsh communities and are often implicated in counterintuitive outcomes of experiments intended to examine direct effects. As an illustration, we can revisit Silliman and Zieman's (2001) cage experiment in which nitrogen and periwinkles (gastropods) were manipulated. In our model, a positive press on nitrogen or periwinkles predicts an enhancement and reduction of *Spartina*, respectively (Fig. 15.1B). However, the experimental design also excluded major predators on periwinkles. In effect, the cage experiment can be interpreted as simultaneous perturbations of nitrogen, periwinkles, and their predators, most importantly blue crabs (Graça et al., 2000). A negative press on periwinkle predators, including blue crabs (−15,157 feedback loops) and raccoons (−13,493), greatly enhances the direct effect of augmenting periwinkles (−26,103) and offsets the enhancement due to nutrients (21,244). The overall effect on *Spartina* (−33,509) is strongly negative (Table 15.2). Moreover, the model indicates that virtually any positive or negative press, either alone or in concert, can strongly influence *Spartina* (Fig. 15.1B). The often-overlooked influence of indirect effects can be manifested by perturbations on all nodes in the model and should be more generally evaluated in nature before assuming bottom-up or top-down control of ecosystems.

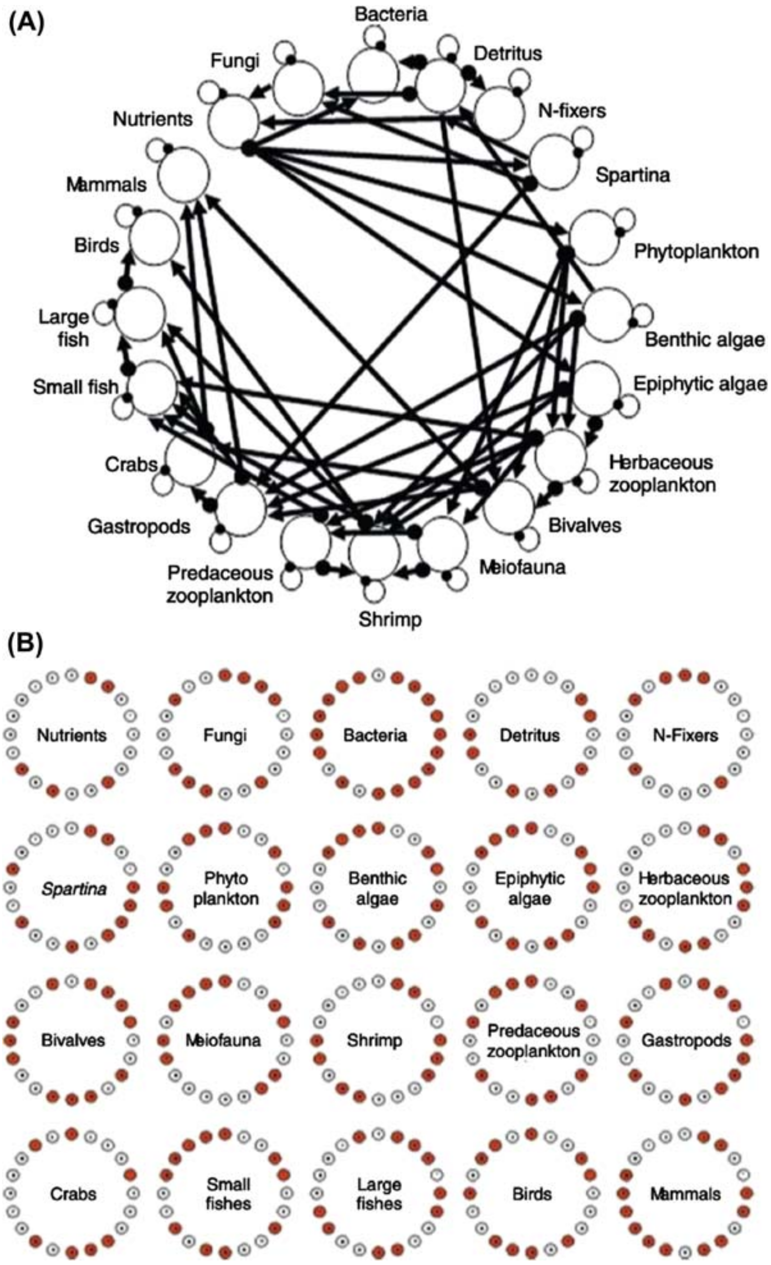

FIGURE 15.1 (A) A pictorial model of a *Spartina* marsh food web used to generate a qualitative loop analysis. Connections indicate positive (→) and negative (•) direct interactions between nodes and result in many positive and negative feedback loops that amount to indirect interactions. (B) A simplified graphical representation of a positive press on the named variables. Named variables occur inside a *circle* of 20 points, which correspond to the 20 *circles* in Fig. 15.1A. For example, in the first *circle*, nutrients are enhanced, which results in negative responses in the small red nodes (*circles*) corresponding to detritus, N-fixers, bivalves, predaceous zooplankton, and crabs. All other (white) nodes are enhanced. A negative press on a variable of interest can be seen by simply reversing the signs of all other elements.

TABLE 15.2 Individual Positive Presses on Nutrients and Gastropods and Negative Presses on Crabs and Mammals Result in a Mix of Responses by *Spartina*

	Nutrients (+)	Gastropods (+)	Crabs (−)	Mammals (−)	Summation
Nutrients	54,740	4856	10,556	−3832	66,320
Fungi	7559	−27,317	−17,796	−12,535	−50,089
Bacteria	41,055	3642	7917	−2874	49,740
Detritus	−13,685	−1214	−2639	958	−16,580
N-fixers	−13,685	−1214	−2639	958	−16,580
Spartina	21,244	−26,103	−15,157	−13,493	−33,509
Phytoplankton	28,852	29,074	14,415	−9424	62,917
Benthic algae	13,188	−20,000	−19,083	9023	−16,872
Epiphytic algae	13,188	−20,000	−19,083	9023	−16,872
Herbaceous zooplankton	4279	−11,900	−21,166	−2659	−31,446
Bivalves	−3452	−37,510	16,033	2562	−22,367
Meiofauna	25,061	25,192	1274	5689	57,216
Shrimp	11,336	−21,520	7296	−32,392	−35,280
Predaceous zooplankton	−3266	13,502	−15,321	14,620	9535
Gastropods	25,937	58,276	43,509	22,196	149,918
Crabs	−12,762	−12,786	−64,237	58,876	−30,909
Small fishes	21,270	21,310	−11,867	20,802	51,515
Large fishes	4254	4262	−38,052	39,839	10,303
Birds	15,590	−17,258	−30,756	7447	−24,977
Mammals	9723	7980	−4695	−94,759	−81,751

The summation of all four presses, two positive and two negative, results in an overall reduction of *Spartina*, and all other variables in the model are also influenced to some degree. This is an extract of the adjoint matrix and negative presses for crabs and mammals were generated by reversing the signs on all variables to reflect the effects of reducing crab and mammal abundances.

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