**Spartina** Introductions and Consequences in Salt Marshes

ARRIVE, SURVIVE, THRIVE, AND SOMETIMES HYBRIDIZE*  

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Maritime Spartina species define and maintain the shoreline along broad expanses of temperate coasts where they are native. The large Spartina species grow lower on the tidal plane than other vascular plants; tall, stiff stems reduce waves and currents to precipitate sediments from turbid estuarine waters. With the right conditions, roots grow upward through harvested sediments to elevate the marsh. This engineering can alter the physical, hydrological, and ecological environments of salt marshes and estuaries. Where native, Spartinas are uniformly valued, mostly for defining and solidifying the shore. The potential to terrestrialize the shore was the rationale of many of the scores of Spartina introductions. In a time of rising sea levels, these plants are valued as a barrier to the sea in native areas and in China and Europe where they have been cultivated. In contrast, in North America, Australia, Tasmania, and New Zealand, nonnative Spartinas are seen as a bane both to ecology and to human uses of salt marshes and estuaries. Four of the seven large-scale invasions involved interspecific hybrids between introduced and native Spartinas, or intraspecific hybridization between formerly allopatric populations. Rapid evolution driven by selection of genotypes particularly adapted for invasive behavior could be the cause of observed high spread rates of hybrid cordgrass. The study of Spartina introductions is a rich mixture of social and basic sciences, with interaction of human values, ecology, and evolution.

*Spartina* species, cordgrasses, are powerful ecosystem engineers and grow over a great range of elevations in the intertidal zone (see chap. 16 in this volume). Their tall, stiff stems reduce wave energy and cause sediments carried in estuarine waters to precipitate (see chap. 2); the plants then grow into these sediments with the result of marsh elevation. The motivation for many early Spartina introductions was to stabilize shorelines and terrestrialize intertidal lands. Storm and tidal defenses in

*“Arrive, Survive, and Thrive” as a rubric for species introduction and invasion was coined by Kevin Rice, Richard Mack, and Spencer Barrett.*
a time of rising sea levels are more recent values for these plants on the low coasts of Europe and China, as well as where the maritime *Spartina* species are native. In other places, such as North America, Australia, Tasmania, and New Zealand, the potent ecosystem engineering of nonnative and hybrid *Spartinas* is seen as a bane both to ecology and to human uses of salt marshes and estuaries.

Many of the scores of *Spartina* introductions for which we have records have been purposeful, and a few have come about as inadvertent hitchhikers on other human activities. Most introductions failed, some spread little, and a few have spread widely by dint of the ability of the seed of these plants to float on the tide. Seed-laden inflorescences can disperse great distances within rafts of wrack, which form in the fall when the aboveground parts of the plant senesce. The four most extensively introduced species are the maritime species *S. alterniflora*, *S. patens*, *S. densiflora*, and the allopolyploid of recent origin, *S. anglica*.

Growing near docks, cordgrasses were an abundant and convenient source of cushioning for ballast. The oldest known introduction, *S. densiflora*, from South America to the Gulf of Cadiz, Spain, in the sixteenth century (Castillo et al. 2000), may well have been ballast packing. The first records of this practice are from seventeenth-century England (Ranwell 1967). On the East Coast of North America, bales of *S. patens* and *S. alterniflora* were packed as cushions among heavy items in the holds of ships (Civille et al. 2005). However, the large numbers of voyages from the Atlantic to the Pacific from the sixteenth century onward resulted in no known introductions of *Spartina*. All of the Pacific introductions came with the twentieth century, and none are known to have resulted from ballast.

The first recorded introductions of *S. alterniflora* were to France (1803) and England (1816) from North America. In both countries, the invasions led to stands of the plant that were used by people. For example, early in the nineteenth century, residents used *S. alterniflora* to thatch roofs on the Itchen River, England (Marchant 1967). These invasions initially thrived then receded. Patches of dieback are not unusual for *S. alterniflora* (Mendelsssohn and McKee 1988) and *S. anglica* (Goodman, Braybrooks, and Lambert 1959). *S. alterniflora* apparently did not spread much beyond its introduction sites in Brittany and the southwest of France (Baumel et al. 2003), and it is now extremely rare in the United Kingdom (Gray, Marshall, and Raybauld 1991). In both countries, early ranges of *S. alterniflora* overlapped with *S. maritima* in multiple places, giving great potential for hybridization. Marchant (1967) speculates that these *S. alterniflora* introductions were from ships’ ballast from America. While it is possible that the European introductions were inadvertent, it is also reasonable that European visitors to North America purposefully carried the plant home. *S. alterniflora* is a much taller and more robust plant than the European *S. maritima*, and the American species had obviously greater potential to produce fodder and fiber. It is also reasonable to assume that people who used the plant would encourage its growth and spread.

The contrast between salt marshes along the Atlantic Coast of North America, the center of diversity for *Spartina*, and those where cordgrasses have been introduced illustrates the influences of these plants. In Atlantic North American estuaries, there are no invasive cordgrasses, and the natives are distinctly valuable in maintaining the shoreline habitat (Warren et al. 2002). Only at the fringes of the range of the genus—in Europe, the South Atlantic, and the Pacific—do native and invading *Spartinas* coexist. In estuaries of the Pacific, Australia, Europe, and China, nonnative *Spartinas* bring large changes (see chap. 16 in this volume). Human introductions of *Spartinas* have led to hybrids, some of which spread rapidly and are powerful ecological engineers. Four of the seven largest invasions are by hybrids between introduced and native Spartinas (*S. anglica* in Europe, China, and Puget Sound, Washington; and *S. alterniflora* × *S. foliosa* in San Francisco Bay, California) and another (*S. alterniflora* to
China) was by intraspecific hybrids selected for vigor and fertility. The other two large-scale invasions are *S. alterniflora* in Willapa Bay, Washington, which is not hybridized, and *S. densiflora* in Humboldt Bay, California, which could bear a remnant of hybridization with *S. alterniflora* (Baumel et al. 2002).

*Spartina* is a small genus of halophytic species in the Chloridoideae, a monophyletic lineage of the Poaceae (Hsiao et al. 1999). Most species are native to the maritime, north temperate Atlantic, New World (Mobberley 1956; Baumel et al. 2002). *S. alterniflora* is native to the Atlantic shore of South America, and *S. densiflora* is native to both the Atlantic and Pacific of South America. Before *S. anglica*, only one species was native to Western Europe (*S. maritima*); *S. anglica* is an allopolyploid hybrid species that arose in the nineteenth century, in Europe, shortly after one of its parents, *S. alterniflora*, was introduced there from the New World. *S. maritima* was the European, male parental species (Ferris, King, and Gray 1997). North America is home to most species. Many maritime salt marshes of the Atlantic and Gulf coasts of North America are dominated by *S. alterniflora*, the smooth cordgrass, which ranges from Canada through the Gulf of Mexico and along the Atlantic coast of South America. The second-most widespread and abundant North American species is *S. patens*, the salt hay grass, which ranges from Canada through the Gulf and into Mexico and into the Caribbean. Pacific maritime estuaries have only two natives, *S. foliosa* in California from San Francisco Bay south through Baja California, and *S. densiflora* in the Pacific of Chile and the Atlantic of South America. The Argentine *S. longispica* is inferred to be a hybrid of the native *S. densiflora* and *S. alterniflora* there (Orensanz et al. 2002). While no evidence exists that such species as *S. alterniflora* and *S. densiflora* are hybridized, they are hexaploids. Research will possibly reveal evidence of hybridization in their history, such as that hinted at in *S. densiflora* in Humboldt Bay, California (Baumel et al. 2002). In this review, we focus on *Spartina* species that have been introduced beyond their native ranges.

**SPARTINAS ARE ECOSYSTEM ENGINEERS**

*Spartinas* can be particularly influential to other species especially when they affect marsh elevation of the marsh. In one well-studied marsh in New England, the accumulation and loss of mineral sediment and organic matter have maintained equilibrium of the marsh surface with sea level for four thousand years (Redfield 1972). Modification and regulation of the environment that is mediated biologically and large relative to abiotic influences is termed ecological or ecosystem engineering (Jones, Lawton, and Shachak 1994, 1997). Although ecological engineering by organisms is neither a simple nor a single phenomenon (Reichman and Seabloom 2002), wide-ranging discussion over the past decade has verified ecological engineering as widely important in nature; the concept comprises a multifaceted set of notions with evolutionary, ecosystem, and community implications as well as shorter-termed autecological ones (Bruno 2000).

*Spartina* plants are the head engineers in temperate marshes where they occur, just as are mangroves in the tropics. *Spartinas* epitomize organisms with powerful reciprocal influences between biotic and physical environmental features and have been called “foundation species” (Pennings and Bertness 2001). The ecosystem engineering prowess of *Spartinas* comes from their erect, stiff stems, which create drag, dissipate hydrodynamic forces, and reduce wave height and current velocity (see fig. 1.1). Stiffer stems are more costly metabolically than more flexible stems and can be seen as an adaptation to harvest sediment, which increases plant fitness (Bouma et al. 2005). Sediments that are delivered to marshes by the tides, storms, rainfall, and riverine input (Allen and Pye 1992; Neumeier and Ciavola 2004) are trapped within the *Spartina* canopy. Roots grow up through the harvested sediment, elevating the marsh. With these influences, cordgrasses can affect the ecology of the marsh
well above and below where they grow on the tidal plane.

With the appropriate conditions, the sediment harvesting of *S. alterniflora* can maintain broad, flat monospecific salt marsh platforms close to the mean high tide. In a South Carolina estuary, primary productivity of *S. alterniflora* was greatest toward the lower tidal elevation tolerance of *Spartina*, at a depth between 40 and 60 centimeters below mean high tide (see fig. 1.2). This was where most sediment was trapped and salinity lowest. Hypoxia limited productivity at depths below maximum productivity, while hypersaline pore water owing to evaporation limited growth at higher elevations; stunted, short-form *S. alterniflora* grew at these higher elevations. This processes created a potentially hump-shaped function of primary productivity with position along the intertidal gradient (Morris et al. 2002). It is these relationships that allow *S. alterniflora* marshes to maintain equilibrium with sea-level changes over short and very long time scales.

The coast of the Mississippi Delta was built on sediments deposited by the river and elevated in this manner by *S. alterniflora* as sea levels rose during the Holocene (Redfern 1983). Decreasing sediment supply has led to loss of coast areas in the delta (Stockstad 2005). In the Netherlands, a declining sediment budget could affect many aspects of salt marshes and *S. anglica* dynamics in the future (Riese 2005). In San Francisco Bay, a deficit of sediment will hamper restoration of the massive South Bay Salt Ponds. Sediment supply in the south arm of the estuary is less than 1 million cubic yards (MCY) per year, while the restoration project will require well over 100 MCY (Siegel and Bachland 2002). In New Zealand, both introduced *S. alterniflora* and *S. anglica* accreted so much sediment as to negatively affect mangroves and salt marshes (Lee and Partridge 1983). In Ireland (Hammand and Cooper 2002), the United Kingdom (Goss-Custard and Moser 1988), Tasmania (Kriwoken and Hedge 2000), and San Francisco Bay (Stralberg et al. 2005).
nonnative *Spartina* and hybrids cover the soft sediments and exclude the invertebrate food of shorebirds.

**RATIONALES, HISTORIES, AND EVOLVING VALUES IN SPARTINA INTRODUCTIONS**

And that old man asked me to think of United States Marines in a Godforsaken swamp. “Their trucks and tanks and howitzers are wallowing,” he complained, “sinking in stinking miasma and ooze.” He raised a finger and winked at me. But suppose, young man, that one Marine had with him a tiny capsule containing a seed of ice-nine, a new way for the atoms of water to stack and lock, to freeze. If that Marine threw that Seed into the nearest puddle.

Kurt Vonnegut, *Cat’s Cradle*

Many *Spartina* introductions were the product of high, if vague, hopes to solidify soft mud and increase the economic value of salt marshes. The “most obvious economic application of *Spartina* is to use it for the reclamation and stabilization of muddy foreshores. There is no plant in the world better fitted for this particular purpose” (Oliver 1925, 84). Though muted, early concerns about *Spartina* introductions anticipated those of today: overly optimistic scenarios, adverse effects on other economic uses of estuaries and salt marshes (e.g., oyster culture and navigation), limited agricultural value of reclaimed salt marshes, decreased recreational and aesthetic value of beaches invaded by the plant, and threats to the ecology and wild life of salt marshes (Ranwell 1967). “Whether the result will in the end be beneficial or to the...
contrary will depend greatly on local conditions. In any case it will be a change worth watching and studying” (Stapf 1908, 34). Herbicide applications to introduced Spartina were under way in the United Kingdom by the mid–twentieth century (Ranwell and Downing 1960).

EUROPE

Today in Iberian and Mediterranean regions, S. maritima gives desired protection against erosion during storms; unlike the more robust species and hybrids forming the bulk of this review, the small, diffusely growing S. maritima does not accrete sediment during calm periods (Neumeier and Ciavola 2004). The distribution of S. maritima may have been influenced by humans; it “has been known for a long time (since 1629), and is beyond doubt truly indigenous to Europe” (Stapf 1908, 33). At the same time, this species is found along the west coast of Africa and in South Africa (Mobberley 1956). It is possible that S. maritima is a Southern Hemisphere (“tropical”) species long ago introduced to Europe by early shipping (Marchant 1967, fig. 3). A report of Spartina pollen in early Holocene sediments of South Africa (Meadows and Baxter 2001) raises the possibility of fragmented S. maritima populations strung along the Atlantic coasts of southern Europe and Africa. Such a distribution would mirror the disjunctive populations of S. alterniflora that range along the South American Atlantic coast.

S. patens, first detected in Europe in 1849, was thought until recently to be native there (Mobberley 1956). It has long been widespread and harvested for hay and fodder on the Atlantic and the Mediterranean coasts of Europe as well as in its native range (Ainouche, Baunel, and Salmon 2004). Reports of the invasive S. patens in Spain (Javier et al. 2005) do not mention any desirable features of the species, such as protection against erosion. Forming dense monocultures, it is now seen as a threat to native high marsh vegetation in natural areas of the Mediterranean and Iberian coasts (Castillo et al. 2005).

S. densiflora, a native of Chile and Argentina, is believed to have been introduced, either accidentally or purposefully, in the sixteenth century to the southwestern corner of Spain on the Atlantic. In the Gulf of Cadiz, S. densiflora has spread to eight estuaries and a number of shoreline habitats including dunes, high marsh, salt pans, and intertidal flats. A North African invasive population is presumably derived from the Spanish introduction (Castillo et al. 2005).

S. anglica is presumed to have invaded France by floating without human aid across the English Channel. It was first detected in France in 1906, at Baie des Veys, Normandy (Baunel, Ainouche, and Levasseur 2001). The invasion proceeded during the remainder of the twentieth century from Normandy southward through Brittany mainly without human intervention. S. anglica now occupies nearly all suitable habitats along this shore of France. The prodigious abilities to accrete sediment of S. anglica can greatly change intertidal elevations and ecology where it has invaded in France (Guénégou et al. 1991).

The Netherlands and Germany were invaded by S. anglica during the 1920s (Gray et al. 1991). It grew lower than the native vegetation and trapped volumes of sediment there. The influence of S. anglica is now greatest in areas with most available sediment, and its influence decreases to the north where colder winters hinder the plant (Bakker et al. 2002). In the southeastern Netherlands, S. anglica was important for holding sediments and building elevated land that is now being restored with native vegetation (de Jonge and de Jong 2002). S. anglica spread to Ireland in the 1930s and is now seen as a bane to natural areas and conservation. The intentions are to eradicate it from Ireland, and only a shortage of funds has prevented attainment of this goal (Hammond and Cooper 2002). The twentieth century saw a shift from agriculture to sea defenses as the major human value of salt marshes in both the Netherlands and the United Kingdom.

Rising sea levels and increasing storm strength maintain the value of S. anglica in parts of Europe as a protection from coastal
flooding (Bouma et al. 2005). Productivity of *S. anglica* in the United Kingdom could increase with rising temperatures and higher atmospheric CO$_2$ concentrations, but other factors, such as competition with other marsh species, complicate this picture (Gray and Mogg 2001). In the Netherlands, human influences on salt marshes have long rivaled, if not exceeded, those of weather, geology, and hydrology. In the late twentieth century, terrestrialization of the shore has vied for limited fine sediments with ecologically and economically valuable intertidal mud flats—a phenomenon called “the Wadden Sea squeeze” (Delafontaine, Flemming, and Mai 2000). The sediments from large rivers that would feed the marshes of shallow coastal areas are now shunted offshore down deep shipping channels into the North Sea (Riese 2005).

Sediment loss via shipping channels is also a threat to coastal marshes of Louisiana in North America (Redfern 1983). The dredged, deep-water passage of the Mississippi River carries sediments offshore into the Gulf of Mexico. Six hundred square kilometers of coastal Louisiana salt marsh have washed into the sea in the last decade, and the loss is greater during hurricanes (Stockstad 2005). Were these sediments to be delivered over the fresh- and saltwater marshes of Louisiana, as before dredging of the Mississippi channels, the rate of coastal loss would be much less (Committee on the Restoration and Protection of Coastal Louisiana 2006). Vast monospecific stands of *S. alterniflora* define this coast, and the prodigious sediment-holding and -elevating capacities of this plant would contribute substantially to the maintenance of the land there.

Protection from the sea is the value of *S. anglica* in the southeastern United Kingdom, where the Earth’s crust is subsiding while sea level rises. However, multiple values of restoration, conservation, mariculture, and sea defense combine—and even come into conflict—in salt marsh issues in the United Kingdom. For example, the removal of *S. anglica* in marsh restoration and conservation has led to lawsuits based on allegations that liberated sediment harmed nearby oyster culturing (Kirby 1994). Complications for managing *S. anglica* in European Union countries arise from needs to meld traditional with modern uses of the shoreline differently among regions (Pethick 2002). Moreover, the human values of salt marshes are evolving rapidly. “Until the last decade, salt marsh has often been conceived as coastal wasteland with minimal economic value, which has led to considerable loss through land reclamation for use as agriculture, caravan sites, industrial developments and marinas.” (King and Lester 1995, 181). In recent years, sea defenses that include *S. anglica* have risen to the highest levels among these multiple values of salt marshes (King and Lester 1995), but this can conflict with conservation. In parts of the United Kingdom, dense monospecific swards of *S. anglica* replaced mud flats and excluded native invertebrates and the shorebirds that feed on them (Goss-Custard and Moser 1988; Frid, Chandrasekara, and Davey 1999). Subsidence of the southeastern UK coast means a sediment deficit in the long run, and even *S. anglica* can afford little protection to rising sea levels under these conditions.

**NEW ZEALAND**

Early in the twentieth century, there was unabashed enthusiasm for the potential of nonnative *Spartina* in New Zealand. “For thousands of years tidal salt mud flats the world over have made entrances to harbours unsightly and treacherous and have remained as vast areas of waste flats. . . . In the past they have provided an almost unconquerable challenge to man. . . . Now such mud can be conquered, and . . . reclaimed to form useful and stable farmlands. This plant which has such an important role is . . . *Spartina townsendii*” (Harbord 1949, 507). By 1950, the slow growth of introductions of *S. anglica* and *S. × townsendii* on the North Island of New Zealand shifted attention to *S. alterniflora*, albeit with a soft counterpoint of caution. “Extensive areas of tidal flats round New Zealand’s coastline, usually difficult and
costly to develop, have become the subject of renewed interest with the introduction of the maritime grass *Spartina alterniflora*, which will enable many farmers to capitalize on these naturally fertile soils.... However, farmers are warned that the adverse influences may not always be readily apparent” (Blick 1965, 275). In the subsequent decade or so, attitudes reversed from conquering to preserving salt marshes. “In some places the problems caused by its spread are virtually insurmountable. With renewed appreciation of estuarine wetlands in their natural states, planting of any species of *Spartina* around the coast of New Zealand should not be allowed to take place. Suitable control and eradication measures need to be developed where *Spartina* is already present” (Partridge et al. 1987, 567). During the last sixteen years, new herbicides and new methods of application have eradicated all meadows and patches of *S. anglica* on the South Island (Miller 2004).

AUSTRALIA AND TASMANIA

The motivations for introduction of *S. anglica* into Australia were vague and mostly the product of little more than curiosity among European colonists about what might grow there. Unlike the United Kingdom, the Netherlands, and New Zealand, where farmland from marshland was a focused objective, Australia had no general engineering or agricultural problems to be solved by the plant (Boston 1981). The successful plantings were clustered in southwestern Australia, where the last recorded planting was made in 1962.

In Tasmania, the objective for *S. anglica* was clear: “to stabilize the mudflats so that they would eventually be above high water level and become relatively useful land...[and]...force stream flow into the central part of the river, creating a scouring effect and keeping the main channel free of mud” (Wells 1995, 12). Plantings of *S. anglica* were done from 1930 until 1968. Values changed and the negative results of the plant came into focus: reduction of areas of soft sediments where shorebirds forage, harm to native animal communities, large unwanted changes to the appearance of the shore and beaches, and lack of access to the water across the *S. anglica* sward, which had been an open sward, was also seen as a threat to the Tasmanian oyster industry (Hedge and Kriwoken 2000). During the early 1990s, *S. anglica* was seen as undesirable and was removed with herbicides and other means in both Australia and Tasmania (Wells 1995). In recent years in Tasmania, opinion has shifted to retaining *S. anglica* as a habitat and food source for native species that have lost habitat to land clearing and industrial activity (M. Sheehan, personal communication)

CHINA

Shorelines in China have been densely occupied for thousands of years, and shoreline dynamics have long been affected as much by human activities as by geology, weather, and hydrology (Li et al. 1991). In the last half of the twentieth century, several species of *Spartina* were introduced. While future coastal sediment loads will decrease with new dams (Chen et al. 2005), recent decades have seen staggeringly large volumes of sediment discharged from the vast, densely populated watersheds of the Yangtze, Yellow, and Pearl rivers. From two to three square kilometers of new intertidal lands appeared on these sediments annually (Han et al. 2000). Some botanically inclined authors have praised introduced *Spartinas* in China. *S. anglica*, introduced in 1963, was planted in about a hundred locations over 2,700 kilometers of coastline and spread to 33,000 hectares by the 1980s. Accreting sediment at high intertidal levels, *S. anglica* was touted as protecting dikes from erosion during typhoons and contributing to the creation of new pastureland (as part and parcel of polderizing: diking, freshwater flooding, and drainage). *Spartina* was harvested for green manure, animal fodder, fish food, and cellulose for paper and rope (Chung, Zhuo, and Xu 1983, 1993). The taller *S. alterniflora* was planted widely in China in 1975 and grew lower on the tidal gradient than *S. anglica*. It accreted sediment at a prodigious rate in a
band two hundred kilometers long and ninety kilometers wide by 1997 (Chung et al. 2004; Zhang et al. 2004). Brief accounts of concern that S. alterniflora displaces native marsh species have been published recently (Zhang et al. 2004; Xie et al. 2001; An et al. 2004). At least some view nonnative Spartina to be distinctly undesirable in China (Ding et al. 2008).

A different perspective comes from the literature of physical geography, where Spartina comprises no more than the most minor of footnotes. Coastal areas of China are extremely vulnerable to sea level rise (Han et al. 2000). Agriculture by diking has been practiced on the shores of the Pearl River Delta since the Han Dynasty, beginning around 200 BCE. Age-old human effects on the shoreline accelerated with industrial development when China opened to the outside world. Dikes have always been the main means of reclamation of intertidal lands, and building of dikes does not need Spartina. Dikes line almost the entire Pearl River Delta, and any appearance of a tidal flat is immediately diked, drained, and flushed of salts. Wetlands, mangroves, and tidal flats have been completely eliminated. The entire region is on very low, muddy, subsiding ground that is vulnerable to freshwater floods from inland and typhoon flooding from the sea.

SAN FRANCISCO BAY, CALIFORNIA
The salt marshes of San Francisco Bay are a casualty of 150 years of “reclamation,” in which the vast majority of intertidal and supertidal habitat, both brackish and salty, were diked and drained for agriculture, urban development, and industry (Williams and Faber 2001). The remaining 125 square kilometers, 5 percent of those found by Euro-Americans in this huge Pacific Coast estuary, are the foundation of conservation efforts with shorebirds of the Pacific flyway and of three federally endangered species (a mammal, a bird, and a plant). These tenuous salt marshes, and brackish and freshwater wetlands upstream, form a narrow buffer for wildlife and ecosystem services between San Francisco Bay and surrounding human population and agriculture.

Introduced Spartina played virtually no role until 1975, when the U.S. Army Corps of Engineers planted S. alterniflora, which hybridized with the native S. foliosa soon afterward (Faber 2000).

Ironically, native S. foliosa was a poster child for the destruction of salt marshes. “This species is useful in reclaiming salt marshes, and in several places about San Francisco Bay it has modified the coast line and increased the acreage of many farms. The town of Reclamation received its name from the fact that in that vicinity many acres of land have been reclaimed chiefly by the use of this grass” (Merrill 1902, 6). Actually, Reclamation was not a town but rather a “locality” with few inhabitants on San Pablo Bay, upstream on the Sacramento River from San Francisco Bay (Durham 1998). A post office was established at Reclamation in 1891 and discontinued in 1903 (Salley 1977). S. foliosa is a modest ecosystem engineer, small, diffusely growing, and shallow rooted. It is but a minor league sediment trapper compared to S. anglica, S. alterniflora, and the massive S. alterniflora × S. foliosa hybrids now spreading through San Francisco Bay. Reclamation, California, originally salt- and freshwater marshes and now extensive hay and oat fields, was formed by diking, dredging, and draining the wetlands. While S. foliosa probably made little contribution to the reclamation, it is playing a role in restoration of a small fraction of the shore. Conservation interests opened 340 hectares to the sea during the 1990s, and S. foliosa will grow to form a band at the lowest tidal elevation on at least part of erstwhile Reclamation, California (Marcus 2000).

INVASIVE SPARTINAS ON THE PACIFIC COAST OF NORTH AMERICA
Perhaps the first Pacific introduction was S. densiflora to Humboldt Bay, California, speculated to have been introduced there as early as the 1850s from Chile (Spicher and Josselyn 1985; Kittleson and Boyd 1997) and identified in 1984 (Faber 2000). In 1999, it was found in 329 hectares and 94 percent of the salt marshes...
of Humboldt Bay (Pickart 2001). *S. densiflora* was dominant over a wide tidal range, from low *Salicornia virginica* marsh to the species-rich high marsh (Eicher 1987). It is the object of control by herbicides and cutting, as it threatens two rare plant species classified as endangered under State of California and federal regulations, Menzies’ wallflower, *Erysimum menziesii*, and the beach *Layia*, *Layia carnosa* (Pickart 2005). *S. densiflora* from Humboldt Bay was planted at least twice in San Francisco Bay in the 1970s and 1980s (Faber 2000) and had spread from Marin County to about five hectares at three sites by 1999 (Ayres et al. 2004). In 2002, a few plants of unknown origin were found in Gray’s Harbor, Washington (Murphy 2004); and in 2005, it was discovered in Vancouver, Canada (G. Williams, personal communication).

The first known Pacific introduction of *S. alterniflora* is to Willapa Bay, Washington, an estuary forty-four kilometers long and twenty kilometers wide just north of the Columbia River. The plant probably arrived as a hitchhiker in live oyster shipments rather than from shipping ballast (Civille et al. 2005). The first Euro-American settlements on Willapa Bay exploited native oysters and began export to San Francisco in the 1850s. The oyster industry grew rapidly, but by the 1880s, native oysters were in decline owing to overexploitation in Willapa Bay. For a few years, Atlantic oysters, *Crassostrea virginica*, were imported from populations cultivated in San Francisco Bay. If California cordgrass, *S. foliosa*, was introduced in these shipments, it was never detected and has become extinct in Willapa Bay. In 1893, eighty barrels of Atlantic oysters were imported to Willapa Bay directly from Atlantic marshes on the new transcontinental railroad. The origins of the oysters were from areas in New York Harbor and Long Island, where native *S. alterniflora* flourished. Upon arrival at Willapa Bay, after the nine- to thirteen-day rail journey, the contents of the barrels were spread widely in the intertidal. More than three hundred railcars of eighty to one hundred barrels each of oysters were imported to Willapa Bay from New York between 1893 and 1919. Cordgrass seed and plants could easily have been placed into the barrels with the oysters. Most likely, the introduction was inadvertent. We know of no economic value for cordgrasses at that time and place, and the abundant discussion in the press during the early twentieth century about introductions from the Atlantic to the Pacific Coast of oysters and other species with commercial potential lacks any mention of *Spartina*. Whether the large colonies of smooth cordgrass that appeared in several places in Willapa Bay a few decades later were introduced and spread inadvertently or had some intentional component is not known. Oystermen, who were the biggest users of the bay in the early twentieth century, viewed the plant as undesirable (Sayce 1988).

The earliest written record is an anecdotal account that implies but does not say that *S. alterniflora* was in the bay in 1911 (Sheffer 1945). The earliest photographs of it show large plants in several widely spaced areas in Willapa Bay (Civille et al. 2005). A Sheffer photograph of 1940 (Civille et al. 2005), the earliest known of smooth cordgrass in Willapa Bay, shows a plant or group of plants about 42 meters in diameter, covering nearly 1,385 square meters. Aerial photographs from 1945 show similarly large plants at seven widely separated sites on the bay, some twenty kilometers apart from one another. Present-day growth rates of *S. alterniflora* in Willapa Bay suggest that the plants in the photos were about fifty years old. This implies that *S. alterniflora* had dispersed, or was spread by humans, widely in Willapa Bay and thrived very soon after the earliest oyster trains dumped oysters there from the Atlantic, in 1893 (see fig. 1.3).

Maritime *Spartina* seed disperses long distances quickly without human help by floating on tides and currents. There is no evidence that maritime *Spartina* has a seed bank, and all recruitment comes from seeds less than a year old. Floating seed was responsible for virtually the entire invasion of Willapa Bay, and rhizome fragments have made virtually no contribution to the spread of *S. alterniflora* there (Civille et al. 2005).
New areas have consistently been invaded at densities so low that young individual plants grew separated by meters of open intertidal mud. These isolated recruits grew rhizomatosely into isolated circular plants, each composed of a single genet. The lack of other emergent plants on the open mud makes new colonies of cordgrass obvious on aerial photographs, reminiscent of bacterial colonies growing on agar. Over several decades, isolated plants grew rhizomatosely into continuous meadows of *S. alterniflora*. These meadows completely cover the intertidal mud (Davis, Taylor, Civille, et al. 2004).

Isolated plants comprised a very large fraction of *S. alterniflora* in Willapa Bay through the twentieth century and contributed little to the spread of the invasion because they set very little seed (Davis, Taylor, Civille, et al. 2004).

The meadows produced most of the seed and were responsible for driving the invasion. The seed set of meadow plants was nearly tenfold that of isolated plants, 20 percent compared to 2 percent of florets set seed, respectively. While 92 percent of meadow plants produced at least some seed, only 37 percent of isolated plants produced any seed at all. The lower reproductive rate of isolated plants than of those in meadows was an Allee effect. Because the lowest densities of isolated recruits had high survival, grew rhizomatosely, and did set some seed, the Allee effect was weak (Taylor et al. 2004). *S. alterniflora* is self-incompatible, outbreeding, and therefore requires pollen from another plant in order to set seed (Daehler 1998). The cause of the Allee effect was sparse pollen among the isolated plants. Only in the much older meadows was the density of the

The coverage of *S. alterniflora* in Willapa Bay grew at a remarkably constant 12 percent or so annually over the fifty-five-year history of aerial photographs. In 2000, nearly a hundred years after the invasion began, the invader covered about 1,670 hectares, or 27 percent of the 6,000 hectares of the intertidal habitat of Willapa Bay. Without the Allee effect, the invasion would have covered virtually the entire bay long ago (Taylor et al. 2004).

Other small infestations of *S. alterniflora* appeared in Washington, Oregon, and northern California during the twentieth century. Duck hunters introduced *S. alterniflora* to Dike Island in Padilla Bay, Puget Sound, Washington, between 1940 and 1946 (Riggs and Bulthuis 1994). The seed was provided by a nursery in Wisconsin, but there is no record of the maritime area from which the nursery obtained the seed. The Padilla Bay introduction had spread to cover about 1.4 hectares by 1979 and about 4.9 hectares by 1991. Flowering stems were first seen in October 1992. Some of this seed was viable, and seedlings had appeared around Dike Island by the late 1990s. Control efforts are greatly reducing *S. alterniflora* and *S. anglica* in Padilla Bay (Riggs 2005). In the 1990s, several small infestations were discovered: in Grays Harbor, Washington, twenty-five kilometers to the north of Willapa Bay; in Conner Creek farther north; and in the Copalis River yet farther to the north (Murphy 2004). These presumably arose from seed that floated northward in *S. alterniflora* wrack on currents from Willapa Bay, without human help. The environmental community in Washington is aware of several other small infestations of *S. alterniflora* in Puget Sound (Riggs 2005; Murphy 2004), and we infer that the lack of reporting indicates that these either have been eradicated or are not spreading.

In Oregon, *S. alterniflora* from Georgia on the Atlantic Coast of North America was purposefully planted in the 1970s, in the Siuslaw River at the entry to Coos Bay, Oregon (Frenkel and Boss 1988). The patch had grown to cover about two hectares by 1994, when it was sprayed with herbicides and dug up. With no visible growth, it was declared to be eradicated in 1997. In 2005, five culms of *S. alterniflora* were found on the same site, and another patch of this species was discovered downstream in Coos Bay, presumably brought there as rhizome material in dredge spoils from the first site (Howard et al. 2007). This indicates potential for local dispersal by rhizomes. In Humboldt Bay of northern California, a single large patch of *S. alterniflora* was presumably eradicated by the efforts of the California Department of Fish and Game during the 1980s or early 1990s (Cohen and Carlton 1995).

The Pacific Coast of North America had two known introductions of *S. anglica*, both recent. That in Puget Sound was planted in 1961, perhaps with seed from England (Hacker et al. 2001). During the intervening forty years or so, the infestation spread to more than seventy sites over a roughly linear course of about 160 kilometers to affect 3,300 hectares and to cover solidly nearly 400 hectares. The San Francisco population of *S. anglica* was detected in the 1980s and by 2004 had grown to only twenty-four individuals covering 360 square meters. The largest plant was eight meters in diameter, and what was inferred to be the oldest plant was six meters in diameter (Ayres et al. 2004).

In August 2003, *S. anglica* was discovered in southwest British Columbia, Canada, in the Fraser River estuary, the largest estuary on the Pacific Coast of Canada (Williams et al. 2004). Seeds presumably originated from the *S. anglica* populations in Puget Sound, which extend as far north as Orcas Island, about twelve miles south of the Fraser River mouth. By October, mapping had been completed, and manual removal began. Surveys in November discovered another invaded site in Boundary Bay. In 2004, a multiagency committee was established to conduct removal, begin outreach and education of naturalists, and enlist volunteer support.

Invasions in North American Salt Marshes

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S. patens, salt marsh hay, has been introduced to the Pacific Coast of North America, as well as to Europe and China (described earlier). It was first known in Oregon as three small patches in a 1939 aerial photograph of Cox Island in the Siuslaw River. Fifty years later, it had grown to ninety large monospecific patches (Frenkel and Boss 1988). In San Francisco Bay, two plants of S. patens were found in 1970 at the mouth of Suisun Bay near the town of Benicia, in the Southampton marsh (Ayres et al. 2004).

SPARTINA HYBRIDIZATION

In 1974, the U.S. Army Corps of Engineers conducted test plantings of S. foliosa and Salicornia virginica on unconfined dredge spoils deposited along Coyote Hills Slough (also known as New Alameda Creek) near Fremont, California (37°33’58.62” N by 122°07’44.52” W) as part of a larger study to quantify and ameliorate the impact of dredging and dredged material disposal in San Francisco Bay (U.S. Army Corps of Engineers 1976). The immediate goal of these plantings was to determine the feasibility of using native marsh species to create a salt marsh on dredge spoils confined in a former salt pond (pond 3) adjacent to New Coyote Hills Slough, while the eventual goal was to evaluate whether this approach had potential utility as a means to both dispose of dredge spoil and create new salt marsh. After determining that native species were able to establish from sown and tidally borne seed, the Corps of Engineers inexplicably planted S. alterniflora in pond 3 from seed it had obtained from an environmental consulting firm in Maryland (Faber 2000). According to personal communication in 2005 between Jun Bando of the University of California, Davis, and L. Hunter-Cario, the firm’s nursery manager, the S. alterniflora seed came from marshes in Maine and Virginia in the 1970s. A genetic survey of plants growing along Coyote Hills Slough in 1994 found equal numbers of S. alterniflora and hybrids between S. alterniflora and S. foliosa, and a single S. foliosa (out of forty-five specimens) (Ayres et al. 1999).

In 1978, the Corps of Engineers planned to use both native and exotic smooth Spartina to control shoreline erosion at Alameda Island, fifteen miles to the north of pond 3 (U.S. Army Corps of Engineers 1978). When this population was genetically surveyed in 1998, only hybrid and smooth cordgrass was found; the native species was absent (Ayres et al. 1999). Similarly, the native species was absent from an introduced population at San Bruno marsh that contained equal numbers of hybrid and S. alterniflora plants in 1994.

In recent surveys, hybrid cordgrass is spreading rapidly in the San Francisco estuary, while the native and nonnative parents are now becoming rarer (Ayres, Baye, and Strong 2003; Sloop 2005). The hybrid swarm hinders access to shorelines, blocks flood control channels, overgrows intertidal foraging areas of shorebirds, and without control could lead to the extinction of the native S. foliosa in San Francisco Bay by means of competition and pollen swapping (Ayres et al. 2003). The potential spread of these hybrids southward through the range of S. foliosa, in southern California and Baja California, carries the risk of global extinction of S. foliosa (Ayres et al. 2003). A large control program is trying to eradicate hybrid cordgrass from San Francisco Bay (www.spartina.org).

Hybridizations resulting from human introductions loom large in Spartina biogeography and in the huge influence that nonnative cordgrasses have had in salt marshes around the world. The history and incidence of Spartina hybridizations are incompletely known. For example, the S. densiflora in Humboldt Bay, California, has genetic features that suggest introgression from S. alterniflora (Baumel et al. 2002). S. × townsendii is a sterile F1 homoploid hybrid species that formed in Southampton Water in southeastern England in the nineteenth century (Gray et al. 1991). The parental species were S. alterniflora, introduced from America, and S. maritima, presumably native to Europe. The first notice of these homoploid hybrids noted was in Southampton Water, England, in 1870. It was given the name S. × townsendii (Marchant 1967).
while other hybridizations of these parental species occurred in France and are named S. neyrautii (Ainouche et al. 2003). Only in Southampton Water did subsequent chromosomal doubling occur. It gave rise to the fertile, dodecaploid, allotetraploid species, S. anglica, around 1890 (Gray et al. 1991).

*S. anglica* was spread and dispersed on its own to salt marshes throughout Britain (Raybould et al. 1991), France (Gray et al. 1991), and beyond. The introduced *S. alterniflora* is now extremely narrowly restricted in Britain, at Southampton Water at the hybridization site (Gray et al. 2001). *S. alterniflora* maintains small, vigorous populations at the three sites in France to which it was introduced in the early twentieth century (Baumel et al. 2002). The lack of spread could be due to pollen scarcity as *S. alterniflora* is largely self-incompatible (Davis, Taylor, Civille, et al. 2004; Davis, Taylor, Lambrinos, et al. 2004).

*S. × townsendii* is rare today. It was not fully discriminated from *S. anglica* until the 1960s, after many years of exportation from Poole Harbor. The *Spartina* nursery at Arne had both forms in the sward in the 1950s. *S. × townsendii* grew together with *S. anglica* in the south and southeast of England and on the Isle of Wight (Goodman et al. 1969, fig. 3). While little information exists on export to most places except New Zealand, sterile *S. × townsendii* would have been outcompeted by fertile *S. anglica* in mixed swards. East Anglia marshes had both forms through the 1930s and 1940s (Gray et al. 1991).

In a world survey, Ranwell (1967) grouped *S. × townsendii* with *S. anglica* under the rubric *S. townsendii* sensu lato (s.l.) and noted that by 1870, one or both of these hybrids had been spread about the United Kingdom. While seed of the allotetraploid *S. anglica* disperses on the tide, the sterile diploid sets no seed and could be spread only by humans or, rarely, by means of floating vegetative fragments that might break loose from an eroding bank. Globally, both were spread widely and covered more than twenty-eight thousand hectares around the world when Ranwell (1967) recorded twenty-two successful introductions and twenty-two failures. Specifically, for 1967, Europe saw thirteen success and no failures; Australia and New Zealand, eight successes and three failures; and Puget Sound, one success, no failures. The rest were apparent failures: India and Asia, seven; South Africa, two; the Red Sea, one; the Mediterranean, one; the western Atlantic, five; Greenland, one; British Columbia, one; and Hawaii, one (Ranwell 1967, fig. 1). The higher success rate in Europe was matched by wider spread there (in maximum estimated hectares in 1967): the United Kingdom, 12,000; France, 8,000; Netherlands, 5,800; Germany, 800; Denmark, 500; Ireland, 400; Tasmania and New Zealand, each 40; Australia, 20; and Puget Sound, less than 1.

The second known hybridization of *S. alterniflora* with a native species occurred in San Francisco Bay after introduction of this Atlantic native in 1976 by the U.S. Army Corps of Engineers (Faber 2000). Most introductions of *S. alterniflora* to the Pacific were beyond the ranges of native *Spartina* species and posed no possibility of hybridization. The northern limit of the only native north temperate species in the Pacific, *S. foliosa*, California cordgrass, is Drake’s Estero, forty kilometers north of San Francisco Bay. Introductions north of San Francisco Bay, to Washington, Oregon, and northern California, were into regions with no native *Spartina*. California cordgrass, *S. foliosa*, was the native parent species of these hybrids. Although not known at the time, many of the hybrids were purposefully spread during the 1980s from the earliest site of hybridization, which was in pond 3, adjacent to Coyote Hills Slough (New Alameda Creek) at the southeastern end of San Francisco Bay. Seed floating on the tide spread the hybrids to many other marshes over eastern and western shores of the sixty kilometers of shoreline in the southern arm of the bay. A few hybrid colonies established in salt marshes of Marin County, on the north side of the Golden Gate. In the earliest published record of this invasion (Callaway and Josselyn 1992), cordgrasses assumed to be
S. alterniflora, but probably hybrids, were found to be competitively superior to, and to have a wider tidal range than, the native S. foliosa.

Hybrids were detected in the mid-1990s when plants were found that contained genetic material unique to each parent (Daehler and Strong 1997). The highly diverse nuclear and cytoplasmic composition together with chromosome numbers equal to or close to the parents’ suggested that these plants comprised a swarm of backcrossing hybrids rather than an allopolyploidization, as per S. anglica (Ayres et al. 1999; Anttila et al. 2000). Much of the shoreline and most creeks flowing into the southern arm of San Francisco Bay were invaded by hybrid cordgrass by 2004 (see fig. 1.4).

Native California cordgrass, S. foliosa, is shorter, with shallower roots, and grows less densely than vigorous hybrid genotypes (Daehler and Strong 1997). The vigorous subset of hybrid genotypes is transgressive; it grew larger and produced more inflorescences, pollen, and seed than either parent species (Ayres et al. 1999, 2003). Transgressively vigorous hybrids are now found at the two leading edges of the hybrid invasion. One leading edge is in the native marshes.
of dense *S. foliosa* growing above mean sea level. In native marshes, hybrids spread by vegetative competitive displacement of the native species and by swamping native stigmas with pollen, which leads to hybrid seed. Where large hybrids are growing, most *S. foliosa* flowers set hybrid seed. The other leading edge of the invasion is below mean sea level on the vast, open, intertidal mud flats of the bay. While very few recruits of native California cordgrass appeared in open areas in the San Francisco estuary in recent years (Sloop 2005), the hybrid swarm increased tremendously in numbers and coverage in both native marshes and previously open mudflats. Both vegetative expansion and multiple episodes of seedling recruitment contribute to the invasion by hybrids.

The area of San Francisco Bay covered by hybrids in 1975 was about two hectares. By 1990, about 650 circular plants expanding vegetatively were noted on aerial photos, and we estimated this to amount to five hectares. In 1993, the number of such hybrids had increased to one thousand, many had coalesced to form meadows, and we estimated the cover to be nearly ten hectares. In 2001, cover of hybrids was 190 hectares. While exponential growth in cover gives a semilog straight line, the semilog plot of the data for hybrid cover from these years gives a convex line. This indicates that the rate of spread of hybrid cordgrass has increased. The transgressive traits caused by hybridization undoubtedly contributed greatly to the very high rate of spread in San Francisco Bay.

In China, intraspecific hybridization of multiple *S. alterniflora* populations may have created genotypes with a propensity to spread rapidly. Seeds and cutting of *Spartina alterniflora* from Morehead City, North Carolina, Altamaha Estuary, Georgia, and Tampa Bay, Florida, were sent to C. H. Chung at Nanjing University in China in 1979 (Chung et al. 2004). They were grown in the Botanical Garden their first year, and their growth was carefully monitored. There were striking differences among the populations in phenotypic characters; for example, the maximum height of Georgia plants was almost three meters, while the largest Florida plants were half that height (An et al. 2004). Differences were also found in isozyme banding patterns, indicating genetic as well as phenotypic variation among the populations. In 1981, rooted cuttings from the nursery population were planted into a 1,300-square-meter field site at Luouyuan Bay. Ecotypic differences persisted in the field plantation. In 1985, a nursery was established in a village paddy near Chengmengkou using mixed seed collected from the Luouyuan Bay field site. Plants and/or seeds (references don’t say which) from the nursery were outplanted into three field sites for experimental monitoring.

The allopatric *S. alterniflora* provenances cultured together in China could have readily hybridized. They were mixed within a small 1,300-square-meter plot. The potentially hybrid seed was sown into a common paddy, and a mixture of genotypes was selected, with preference for Georgia provenances, in the first large field trials. Adding to this genetic farrago, at some point 0.5 kilogram of seeds from North Carolina was introduced, and one source claims that it was this source that led to most of the salt marshes in coastal China (An et al. 2004). It is not unlikely that hybrids and the most vigorous progeny were spread widely. Intraspecific hybridization could well have played a role in the rapid spread of *S. alterniflora* through Chinese marshes.

The high planting densities in the Chinese planting could have overcome Allee effects (Davis, Taylor, Civille, et al. 2004; Davis, Taylor, Lambrinos, et al. 2004). It is also possible that the rapid spread is a product of evolution of self-compatibility, which occurred in the hybrids of *S. foliosa × S. alterniflora* in San Francisco Bay (Sloop 2005). No interspecific hybridization is known for Chinese *S. alterniflora*, but it is possible that the intraspecific hybridization of the three North American provenances produced self-compatible genotypes.

**Acknowledgments.** We thank Daniel Goldstein of the University of California, Davis, library for help with the history of Reclamation, California; Tjeerd
Bouma and Alan Gray for advice about S. anglica on the coast of the Netherlands and the United Kingdom, respectively; Kevin Rice, Richard Mack, and Spencer Barrett for coining "Arrive, Survive, and Thrive"; and three anonymous reviewers for helpful suggestions on the manuscript. T. B. C. Shaw provided inspiration.

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