

Control and consequences of *Spartina* spp. invasions with focus upon San Francisco Bay

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Abstract Maritime *Spartina* spp. are powerful ecosystem engineers that accrete sediment, define shorelines, create habitat, and generate prodigious primary productivity both where they are native and where they have been introduced. Invasive *Spartina* spp. can compete vigorously with native species, diminish biota, change hydrology, and confound human uses of estuaries. Herbicides have been effective in controlling several *Spartina* spp. invasions. One of the most recent successes is a 15-year campaign that has virtually eliminated *S. alterniflora* from the large, century-old invasion in Willapa Bay, WA, USA. Hybridization between native and introduced *Spartina* spp. has created new species and hybrid swarms. In San Francisco Bay, CA, USA (SF Bay) a complicated situation continues to play out from the purposeful introduction of *S. alterniflora*, which hybridized with native California cordgrass, *S. foliosa*. The hybrids spread rapidly and led to a long list of environmental problems, which led to an herbicide program that was successful in greatly diminishing the hybrid and saving the open mud habitat of migratory shorebirds. However, it was belatedly realized that the non-

migratory, endangered Ridgeway's rail uses the tall, dense hybrid *Spartina* as a surrogate for habitat that was lost during the twentieth century to urbanization and agricultural transformation of marshes around SF Bay. This realization has made difficult the simultaneous management of hybrid *Spartina*, wildlife conservation, and marsh restoration in San Francisco Bay. Restoration of native vegetation could satisfy the multiple goals of preserving open mud and conserving Ridgeway's rail.

Keywords *Spartina* · San Francisco Bay · Shorebirds · Ridgeway's rail · Conservation · Herbicide

Introduction

The hybrid swarm of native *Spartina foliosa* x *S. alterniflora*, introduced from the Atlantic, posed such an ecological threat to the intertidal San Francisco Bay that a large scale herbicide campaign was conducted against it during the first years of the new millennium. The campaign was a success in its primary objective of saving open mud for foraging of shore birds. However the success brought an unexpected threat to the endangered Ridgeway rail, which was found to thrive in stands of the tall, dense hybrid plants. Simultaneously managing hybrid *Spartina* and Ridgeway rails present substantial challenges to conservation of the intertidal habitats in San Francisco Bay.

Guest editors: Alan Gray and Malika Ainouche/Invasive *Spartina*.

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A small genus

Spartina comprises 13 original species known to have existed before the Columbian Exchange (Strong and Ayres 2013). New species and swarms have arisen from hybridization between native and human introductions of *Spartina* for perhaps the last 500 years. All but two of the original species are native to the Western Hemisphere. The exceptions are *S. maritima* native to Europe and South Africa and *S. arundinacea* native to a few remote islands of the south Atlantic and Indian oceans. *Spartina* species are temperate zone specialists that are usually overgrown by mangroves at low latitudes. *Spartina alterniflora* and *S. patens* have the greatest native ranges. The long-standing belief that *S. alterniflora* is native to South America has been challenged (Bortolus et al. in press); if the challenge is valid, then the native range of this species is from Newfoundland to the subtropical mangrove shorelines of North America. *S. patens* is a high marsh specialist that ranges from Newfoundland to Uruguay, with interruption by mangroves at low latitudes. *S. alterniflora* is tall, dense, and lives from the middle to low intertidal zone. *Spartina patens* lives in the high intertidal, and *S. cynosuroides* is a giant plant that grows in oligohaline reaches of estuaries from the mid-Atlantic of North America through Texas. *Spartina bakeri* and *S. spartinae* grow from high salt marsh into upland areas. The former occurs from South Carolina to Texas, and the latter occurs only on the Gulf coast. Native *S. densiflora* grows in the Atlantic of Brazil into the Pacific in Chile from mid intertidal into high salt marsh habitats. *Spartina foliosa* is an intertidal specialist that ranges from San Francisco Bay to Central Baja California, Mexico. *Spartina ciliata* and *S. argentinensis* grow on coastal dunes in Argentina. *Spartina pectinata* and *S. gracilis* are the only two species with continental distributions far from the sea. The former is a specialist of freshwater marshes with vast monospecific stands from central to northeastern North America, and the latter lives on inland salt pans and saline lakeshores of northwestern continental North America.

Ecosystem engineers

Powerful influences upon habitat and other species have earned the marine *S. alterniflora*, *S. densiflora*, *S.*

foliosa, *S. maritima* and the new allopolyploid *S. anglica*, a central place in the ecology of salt marshes and in human affairs of shorelines of mid latitudes. *Spartina* species participate in vigorous reciprocal interactions between the biotic and physical environment and have been called “foundation species” (Pennings and Bertness 2001). Their stiff tall stems reduce wave energy and current speed, and roots grow upward into the sediments precipitated from waters calmed by their presence (Morris et al. 2002). The consequence is stabilization and elevation of the marsh to match sea level. The equilibrium between loss to erosion and gain of organic detritus and mineral sediment due to *Spartina*’s ecological engineering has been shown to maintain shorelines for thousands of years (Redfield 1972).

Wrack deposition from *S. densiflora* has been monitored in invasive populations in Humboldt Bay, CA (Kittelson and Boyd 1997) and Spain (Castillo et al. 2008). Bare patches that were created by tidal deposition of *S. densiflora* wrack were colonized by lateral expansion of *S. densiflora* in Humboldt Bay—lateral spread of plants adjacent to or within bare patches increased 15-fold compared to those plants surrounded by *S. densiflora*. By changing wrack dynamics, and associated decomposition rates, light interception, thermal amplitude, and environmental heterogeneity (Facelli and Pickett 1991) invasive plants can act as ecosystem engineers. A positive feedback loop arises when litter from an invasive species creates a colonization niche for that species (Farrer and Goldberg 2009; Kaproth et al. 2013) as seems to be the case for *S. densiflora* in Humboldt Bay and perhaps elsewhere.

Spartina invasions

Where maritime *Spartina* species are native, they are uniformly valued for providing habitat to wildlife, for defining and preserving a constant shoreline, and as a base to ecologically and economically valuable food webs. Where they have become invasive, *Spartina* species are usually viewed as a bane usually owing to the habitat transformations and threats to other animals and plants that these plants cause (Strong and Ayres 2009, 2013).

Just as is the case for species introductions in general (Zenni and Nunez 2013), most *Spartina*

introductions have failed. *Spartina anglica* is a hybrid species between *S. alterniflora* and *S. maritima* that arose in the nineteenth century in England. English populations of the new species were widely spread by humans (Gray et al. 1991); 22 out of 44 of the known introduction attempts in the first half of the twentieth century failed (Ranwell 1967). *Spartina anglica* also became extinct in the Falkland Islands after surviving for some time there (Orensanz et al. 2002) and failed to spread after introduction to San Francisco Bay (Hogle 2011, p. 11). China, which has no native *Spartina*, imported *S. anglica* in 1963. With planting, this species spread to more than 36,000 ha by 1985. After propagation efforts ceased, it declined to cover less than 50 ha by 2007 (Chung 1990; An et al. 2007). *Spartina cynosuroides* and *S. patens* were introduced in 1979, but neither spread and both are either extinct or extremely rare now. *S. alterniflora* was introduced to China in 1979, spread widely, and now occupies a very large fraction of estuarine habitats in China (Zuo et al. 2012). Perhaps the most notable failure is the dearth of *Spartina* species invasions within the native ranges of nine *Spartina* species on the east coasts of North America and South America (Strong and Ayres 2013).

Most of the scores of recorded *Spartina* introductions have been purposeful. A few have persisted without much spread, and others have spread widely. Marine *Spartina* spreads by seed that floats on the tide. *S. alterniflora*, *S. patens*, *S. densiflora*, and *S. anglica* have been most widely introduced and are the most consequential invaders. The first known introduction was *S. densiflora* from South America to the Gulf of Cadiz, Spain early in European exploration of the New World (Castillo et al. 2000). The first interspecific *Spartina* hybridization likely occurred there between *S. densiflora* and *S. maritima* which produced several hundred sterile hybrids in three estuaries by 2008 (Castillo et al. 2010). All of the known introductions to Pacific shores occurred in the twentieth century.

Early invasions: sources, vehicles, and propagules

The Columbian exchange across the Atlantic was but a prelude to the accelerating global exchange of species among all parts of the world that has occurred in the five centuries since 1492 (Crosby 1986). Inadvertent introduction by shipping was the most common vector of marine species introductions in general. *Spartina*

species were useful as ballast packing material. Perhaps from as early as the beginning of the sixteenth century, when Portuguese explorers first visited southern latitudes high enough for *S. alterniflora* and *S. densiflora*, these plants have been ferried around the world in the holds of sailing ships. Some was probably cast ashore without purpose from ships sailing from Atlantic America to other destinations. Similarly plausible is that *Spartina* was among the many species of New World plants brought home to Europe for cultivation in the centuries after Columbus' discovery. Transportation of some cordgrass in a manner that increased chances of surviving the voyage would have followed from the knowledge that *Spartina* is nutritious fodder and the fibrous leaves are fine thatching material. Another possibility is that it was feral New World *Spartina* species thriving around the docks in Europe that was discovered and then propagated for animal feed and thatch there (Strong and Ayres 2009).

Invasions derive from propagules that must arrive, survive, and then thrive in their new home. Most propagules introduced to new areas fail to make it through this sequence. *Spartina* species are not dense enough for ballast, but are well suited as packing material that probably would have been composed of both kinds of potential propagules, plant fragments and seeds. More seeds would have been in *Spartina* packing made up in late summer and early winter. Probably, many more *Spartina* introductions happened than are known. On the other hand, hundreds if not thousands of sailing voyages passed from shores with native *Spartina* to other parts of the world in the century or so between the first detection (from South America to Iberia) and next detections (of *S. alterniflora* from North America to France in 1803 and to England in 1816). This raises the possibility that transportation, survival, or disposal of cordgrass was not very frequent. One intriguing possibility is that *Spartina* packing material was too valuable to throw away (Strong and Ayres 2013).

Another vehicle

The next major introduction was of *S. alterniflora* to Willapa Bay WA at the end of the nineteenth century (Civille et al. 2005). Evidence suggests that the plant came across the continent via the new transcontinental railroad in barrels of live oysters, iced, and wet, from New York Harbor and the Chesapeake Bay. More than

300 carloads, each holding upwards of 100 barrels of live oyster seed and adults, were imported from New York Harbor and Long Island Sound to Willapa Bay, WA between 1893 and the second decade of the twentieth century. Conditions in the barrels were as salubrious for *S. alterniflora* as for oysters, among which this plant grows. The seven distant areas of Willapa Bay, some 20 km from others, to which oystermen distributed the oysters taken from the trains were where the earliest populations of *S. alterniflora* grew.

Spread by seed after introduction

While *Spartina* can be cloned readily from fragments of roots attached to a shoot, fragments are by far the least successful *Spartina* propagules in nature. Fragments of shoots and roots routinely break off in chunks of mud as the plants are eroded from channel banks and marsh foreshores. However, the mud is denser than seawater, and most of these fragments sink in situ, remain submerged, and die. While the odd live rhizome can be washed out from its muddy base and float away, there is little if any evidence that *Spartina* species routinely spreads by plant fragments.

On the other hand, abundant evidence exists that *Spartina* invasions spread rapidly by floating seeds (Strong and Ayres 2009). Seed bearing wrack was probably how *S. anglica* spread similarly widely among English estuaries after its hybrid origin there. It floated to or was carried to the Netherlands and Ireland then probably spread by floating seed within both of these countries. *Spartina densiflora* spread by seed around the coastline of the Atlantic and Mediterranean coasts of Portugal and Spain after its introduction in the sixteenth century. It also spread widely by floating seed after its introduction to Humboldt Bay, CA early in the twentieth century. *S. alterniflora* has spread by floating seed within the areas to which it has been introduced: Willapa Bay, WA, San Francisco Bay, CA, New Zealand, and South Africa. Floating seed has played a role in dispersal of *S. alterniflora* to more than 19 degrees of latitude—from 39°N near North Korea to 20°N near Viet Nam—since its introduction to China in 1979; China is the only place known where *Spartina* invades and threatens mangroves (Zhang et al. 2012). The hybrid swarm of *S. foliosa* × *S. alterniflora* spread rapidly and widely by seed floating around San Francisco Bay.

Introductions accelerate

At the dawn of the twentieth century the new hybrid *S. anglica* crossed the English Channel, probably by seed, to Baie des Veys then spread southward, along the coast of Brittany from the colonization site in Normandy after its detection in 1906 (Ainouche et al. 2012). *Spartina anglica* was introduced to New Zealand, the Australian mainland, and Tasmania early in the twentieth century, and Puget Sound, WA a few decades later (Saarela 2012); *S. alterniflora* was introduced to New Zealand about this time. During the last half of the twentieth century four species of *Spartina* were introduced to San Francisco Bay as part and parcel of salt marsh rehabilitation as this habitat segued from a trash dump to the waterfront view of expensive real estate. In China, after the failures of *S. anglica*, *S. cynosuroides*, and *S. patens*, *S. alterniflora* was imported in 1980 (Zuo et al. 2012). Since its introduction, *S. alterniflora* has been spread to a large number of estuaries in China. The most recent known introduction is of *S. alterniflora* to South Africa (Adams et al. 2012).

Spartina alterniflora is the most influential cordgrass in both native areas and where it has been introduced. The United States Army Corps of Engineers introduced it to San Francisco Bay in 1973 (Ayres et al. 1999). They planted seed from the Atlantic coast at one site in New Alameda Creek near the city of Hayward. Some evidence suggests that this *S. alterniflora* seed came from marshes in Maine and Virginia in the 1970 s (Strong and Ayres 2009, p. 15). The plants that grew from this seed hybridized with native *S. foliosa* (California cordgrass) to form a hybrid swarm that backcrossed to both parental species as well as among themselves. Seed of the hybrids floated to other sites, and hybrids were disseminated in mitigation and marsh restoration projects to multiple parts of the Bay during the following two decades. The hybrid nature of these plants was discovered in 1997 (Daehler and Strong 1997). The hybrids grow densely above and below the tidal elevation of native *S. foliosa* with potential to negatively influence habitat, flood control, and human uses of the shore. Hybrids that grow down the intertidal plane to cover intertidal mud are a particular threat to the foraging habitat of migratory shorebirds. The effect of hybrids upon other species ranges from unknown, to neutral, to negative, to positive. In the distinctive case

of the native, non-migratory, Ridgeway's rail, the effect of non-native *Spartina* is positive. Predation rates on Ridgeway's rail are high, and the tall dense plants provide cover from predators at high tide (Overton et al. 2014).

Control

The most common motivation for introducing *Spartina* was to stabilize mud and prevent erosion on the shores of estuaries. Following introduction—whether intentional, incidental, or of unknown cause—opinion about *Spartina* has almost always become negative as this plant changed the physical and biological nature of its new home. In the majority of cases, invading *Spartina* came to be seen as a threat to conservation of native species, fishing, mariculture, navigation, access to the shore, and to the aesthetic value of the estuarine landscape (Strong and Ayres 2009).

Herbicides

The first use of herbicides to control *Spartina* was in the 1950s in the United Kingdom, where *S. anglica* had become a bane. The attitude in New Zealand switched from enthusiasm for the plants to desire to extirpate them over three decades from the 1950s to 1980s. With vague rationalizations of possible value, *S. anglica* was introduced to Australia during the first half of the twentieth century. Introductions ceased by 1962, and concerted control with herbicides has been practiced in recent decades (Cutajar et al. 2012). The most recent large invasion stems from the purposeful introduction of *S. alterniflora* in China, where the consequences are beginning to be assessed (Strong and Ayres 2013).

Willapa Bay

One of the largest invasions was *S. alterniflora* to Willapa Bay, WA. After almost a century of spread, two decades of effort has virtually eliminated the plant from this huge estuary. The cover of invasive *S. alterniflora* grew to ca. 27,000 ha of intertidal and supratidal habitat during the twentieth century. This invader was seen to threaten the wildlife of the Willapa Bay National Wildlife refuge, migratory shore birds, and a valuable century-old oyster industry,

as well as navigation, intertidal habitat, and the aesthetics of the landscape. In 2008, the herbicide glyphosate, which had been used with disappointing results for almost a decade, was replaced with another herbicide, imazapyr, which quickly gave favorable results (Patten 2002). By 2011, only a few hectares total of scattered plants remained, and total extirpation was anticipated. The control effort had cost ca. \$30 million from the beginning of the program until 2011 (Strong and Ayres 2013).

San Francisco Bay

Hybrid *Spartina* is only the latest in more than a century of rapid environmental change brought to San Francisco Bay by European colonization (Booker 2013). The plentiful native shellfish of the shoreline of the Bay, where both native *S. foliosa* and invasive *Spartina* grow now, long contributed substantially to the nutrition of the dense Native American population. These shellfish were consumed in great volumes by the expanding immigrant population of San Francisco in the second half of the nineteenth century. Native San Francisco Bay oysters, *Ostreola conchaphila*, were a food so valuable as to lead writer Mark Twain to report that a 1865 theft of oysters ranked in criminal severity with “massacre, rape, and firebombing churches” (Booker 2013, p. 133). As the Bay's native oysters were depleted, other oyster species were imported from as far away as Willapa Bay in the north and Mexico to the south. The transcontinental railroad brought the first carload of Atlantic oysters to the Bay in 1869, and by the beginning of the twentieth century the most valuable fishery in California was Atlantic oysters, *Crassostrea virginica*, raised in San Francisco Bay from spat brought annually across the continent. Atlantic oysters do not naturally reproduce in the cold water of northern California. Production boomed until the beginning of the twentieth century, when it began a fluctuating decline as massive siltation from hydraulic gold mining, agricultural water diversion upstream from the Sacramento and San Joaquin Rivers, and sewage and industrial pollution of the Bay degraded oyster habitat and growing conditions (Conte 1995). Demand for oysters also decreased, perhaps owing to fear of oyster-borne pathogens such as typhoid in untreated sewage of the day (Booker 2013). The oyster industry virtually died in San Francisco Bay just before WWII, but it has continued

in other California estuaries to the north. The greatest environmental mystery of SF Bay is why the nearly 50 years of oyster importations from the Atlantic did not incidentally introduce *S. alterniflora*, as importation of Atlantic oysters did in Willapa Bay WA.

Salt marshes of California were greatly reduced during the twentieth century. The San Francisco estuary was diked, polderized, and filled-in so that only a small fraction of the nineteenth century extent of saltmarshes remained (MacDonald 1977). Agriculture, cities, and refuse dumps covered what was previously intertidal shoreline. Cities and industrial activities such as salt evaporation ponds, chemical plants, gunpowder manufacture, railroads, petroleum refineries, and garbage collection dumped their waste into the Bay. After WWII, real estate development became the valued use of land around and in the Bay. A 1959 plan, which failed, proposed to create industrial properties by damming and filling in 325 square miles of the Bay's 487 remaining square miles of remaining tidal wetlands. By this time, environmental consciousness had grown to cause fierce industry-versus-environment conflicts (Booker 2013). Among the most iconic battles played out when Mobil Oil, diversifying its holdings, planned to build 4700 homes on the 1214 ha of Blair Island, near Redwood City, which was the largest extant salt marsh on the west side of the south Bay. The plan was defeated at the ballot box after a famous environmental campaign. When Japanese developers resurrected the plan a few years later, environmentalists again defeated it. Blair Island and its salt marshes became part of the Don Edwards San Francisco Bay National Wildlife refuge after The Peninsula Open Space Trust purchased it for \$15 million in 1997 (Rogers 2015).

Several *Spartina* species were introduced to San Francisco Bay, but *S. alterniflora*, introduced in the 1970s by the US Corps of Engineers for hazy reasons, created the greatest problems (Strong and Ayres 2013). *Spartina alterniflora*, a robust plant, grows higher and lower on the intertidal plane of SF Bay than the short-statured, native, *S. foliosa*. The introduced *S. alterniflora* crossed with *S. foliosa* in SF Bay to produce a backcrossing hybrid swarm. Some hybrid genotypes were extremely vigorous, overgrowing the native species, and able to self-pollinate as well as showering native stigmas with hybrid pollen; native plants then set hybrid seed (Ayres et al. 2008). These super vigorous hybrids, through enhanced tolerance to

inundation and salinity (Lee et al., this volume) grew even higher and lower than the *S. alterniflora* parent and invaded the high intertidal and supratidal as well as extending their range out onto the mudflats below the native *S. foliosa*.

By the end of the 1990s, expert opinion focused upon the threat of hybrid *Spartina* to multiple environmental and biological elements of San Francisco Bay (Anonymous 2003).

These threats included:

1. Genetic assimilation and the potential for extinction of *S. foliosa* (Ayres et al. 2003).
2. Loss of tidal flats and foraging areas for migratory shore birds (Strahlberg et al. 2010).
3. Invasion of formerly-diked Bay lands and thwarting of their rehabilitation (Ayres and Strong 2010).
4. Destruction of tidal sloughs and channels, which are rich with wildlife (Anonymous 2003).
5. Diminution and reduction in quality of habitat of many plant and animal species, including several endangered species.
6. Interference with the dynamics of beaches.
7. Increased need and expense for dredging, flood control, and mosquito control.
8. Production of vegetative wrack and below ground biomass with substantial direct and indirect effects upon biota (Grosholz et al. 2009).

In San Francisco Bay, the value of native *Spartina foliosa*, the organisms that it fosters, and its role in structuring shoreline have made the control of invasive *Spartina* and its hybrids much more difficult than in Willapa Bay, New Zealand, and other places that lack native species of *Spartina*. Herbicide treatment needed to avoid the native and focus upon the hybrid swarm and *S. alterniflora*. The Invasive *Spartina* Project (ISP, www.spartina.org) was begun in 2003 to control these non-native plants. Large expanses of hybrid cordgrass, identified by correlations between morphology and molecular systematics that discriminate hybrids from the parental species, were sprayed with glyphosate, and more recently hybrids were sprayed with imazapyr. The extent of non-native cordgrass was reduced from ca 325 to 13 ha by the ISP (Kerr 2014). A primary conservation objective of protecting open mud, especially for foraging by migratory shorebirds, was a success.

By 2008 expert opinion had focused upon another problem, which, ironically, had been made more

severe by reduction of hybrid *Spartina*. While hybrid *Spartina* is an ecological bane in multiple ways, it is a boon to the non-migratory, endangered Ridgeway's rail. Indications of a positive effect of the hybrid upon this bird emerged after almost 5 years of control of hybrid *Spartina*, when decreases in Ridgeway's rail were detected. Multiple year censusing is necessary to detect trends in rail numbers. Population estimates are made mainly by interpreting both the presence and expected-but-absent calls of the birds, which requires great skill complemented by sophisticated statistical interpretation of the data (Liu et al. 2012).

The early nineteenth century range of Ridgeway's rail extended over 800 km, from Humboldt Bay in the north to Morro Bay in the south. It became extinct everywhere but SF Bay and the upstream estuaries of the Sacramento River. Market hunting took a huge toll. It was sold in restaurants of San Francisco (Kennerly 1859), and "thousands" were killed in a single day in 1859 (Wilbur and Tomlinson 1976). Prohibitions on hunting in 1913 allowed numbers to increase, and the bird persisted at several sites around SF Bay during the early twentieth century (Grinnell and Miller 1994).

Mercury pollution (Schwarzbach et al. 2006; Ackerman et al. 2012) and predators (Overton et al. 2014) further reduced numbers. Only between 4200 and 6000 individuals remained in the 1970s, and the bird was listed as an endangered species. Rapid decreases, to as few as 700, in the 1980s are attributed to predation by the introduced red fox (Evens et al. 2010).

The spread of hybrid *Spartina* coincided with, and could have contributed to, a brief period of increase in Ridgeway's rail (Overton et al. 2014). In the early 1990s numbers increased to between 1000 and 1200, which could have been a result of control of red fox (Evens et al. 2010). As many as 1300 birds were estimated for the period of 1992–1998, and numbers grew to almost 1500 birds between 2005 and 2008. The growth in numbers of Ridgeway's rail after 2000 correlated with the spread of hybrid *Spartina* in San Francisco Bay. The taller stature and denser culms of hybrid *Spartina* afford better protection during the highest tides than native *Spartina*. It is during these king tides that the birds suffer greatest mortality, when nests drown and predators kill birds that have been flooded out of shorter vegetation (Overton et al. 2014).

The increases were short lived, however. The ISP reduced hybrid *Spartina* to about 4 % of its 2005 extent. One estimate of change in the Ridgeway's rail population during this period is a decline to about 50 % of their numbers from 2005–2007 to 2008. Numbers remained fairly stable from 2009 to 2011 (Liu et al. 2012).

Modeling suggests that multiple factors were at work in these dynamics. While the greatest decreases in rail numbers occurred in South SF Bay, where the reductions of hybrid *Spartina* were greatest, numbers varied through time independently of hybrid *Spartina* at other sites. Higher rail densities occur in more saline conditions, which might provide better prey for the bird, and salinity varies with annual rainfall. Larger marshes, with lowest ratio of perimeter to area, support higher densities. Connections between marshes that allow dispersal and metapopulation dynamics probably lead to higher densities. The modeling suggests that young marshes support much lower densities of Ridgeway's rail than do older marshes (Liu et al. 2012). The optimistic side of this scenario is that Ridgeway's rail populations could, albeit slowly, rebuild themselves. A substantial fraction of the ISP efforts are now dedicated to revegetation with California cordgrass and other native plants such as the shrubby perennial gumplant, *Grindelia stricta*. The optimistic scenario is that sloughs and channels, where the rails feed and hide, will develop and be colonized by the invertebrate food species of the rails as revegetation proceeds. Experimental elevation of tiny islands planted with native vegetation has produced encouraging results. These elevated islands could provide protection from predators at very high tides (Overton et al. 2015).

Coda

The difficulties of controlling hybrid *Spartina* while preserving Ridgeway's rail in San Francisco Bay illustrates the contradictions of contemporary conservation,

In California, restoration projects to pull out nonnative spartina grass on beaches were called into question when the endangered clapper rail was found to nest there. Controlling nature can be risky (Marris and Aplet 2014).

An additional, equally ironic, facet to this situation is that the largest, densest intertidal plants, *Spartina* hybrids, could afford some protection for developed shoreline from the highest tides. Tall *Spartina* attenuates waves and could lessen the erosion and flooding of the rising tides. However, the full potential of *Spartina* spp. to protect the shore can only be realized when the plant is able to grow up the tidal gradient as the average sea level increases, and such growth depends upon open space for *Spartina* spp. colonization in high intertidal and supratidal zones. Roads, levies, and other human-built structures prevent upward marsh growth into those border areas most in need of protection from sea level rise. A second requirement is an abundance of sediments to build the upward marsh growth. While SF Bay has only a limited supratidal area for upward *Spartina* growth, and sediments are not abundant there, a barrier of tall plants near shore could buffer the effects of the highest tides, at least for a few decades. This scenario would entail active management to prevent hybrid plants from reinvading habitats valued for their absence, such as low-lying open mudflats for shorebird foraging, and perhaps encouraging the upward migration of hybrid-dominated marsh. However, even the most robust *Spartina* hybrids will likely not survive the projected 1–1.4 m sea level rise forecast for SF Bay by 2100 (Cayan et al. 2009).

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