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INVASIVE SPARTINA

A review of 15 years of *Spartina* management in the San Francisco Estuary

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Abstract Regional, ecosystem-level conservation projects with significant vegetation management components require planning, coordination, and responsive management strategies to minimize negative impacts and maximize ecological benefits over time. The California State Coastal Conservancy's Invasive *Spartina* Project (ISP) offers an example of a complex, ecosystem-scale weed eradication effort guided by regional conservation goals. We review the management framework developed by the ISP, describe decision thresholds used for site-specific management transitions over the project's 15 years, and present strategies being used to address major challenges to project completion. These strategies include developing genetics and weed mapping approaches to aid with identification of hybrids between the introduced *Spartina alterniflora* and the native *Spartina foliosa.* The ISP also developed a tidal marsh restoration project to enhance habitat for an endangered bird, the California Ridgway's rail (*Rallus obsoletus obsoletus*), that uses tall, dense forms of hybrid *Spartina* as high tide refugia and nesting substrate. By 2014, the ISP had installed over 300,000 native plants and recorded a greater than 96 % estuary-wide reduction in hybrid *Spartina* (from 323 ha to 12 net ha) despite treatment restrictions imposed at 11 sites since 2011 to protect the rail. Approximately 80 % of the remaining hybrid *Spartina* occurs in areas currently restricted from treatment, delaying project completion. The successes and setbacks of the ISP illustrate the complexities of achieving ecosystem-level conservation goals dependent on large-scale vegetation management.

Keywords Hybridization · *Spartina* · San Francisco Estuary · Management · Invasive plants · Restoration · Mapping

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Introduction

The impacts of invasive species on native ecosystems are well-documented (Vitousek 1990) with a wide body of literature devoted to control techniques at the site level. Successful control of biological invasions in the context of regional conservation efforts at the ecosystem level requires a rational framework for setting management objectives and can often require complex implementation strategies (Hobbs and Humphries 1995; Zavaleta et al. 2001). Yet few publications provide guidance on a pragmatic approach to invasive weed management once the scope expands beyond a small, experimental scale (Kettenring and Adams 2011). In this paper, we present the example of the San Francisco Estuary Invasive *Spartina* Project (ISP) to document management steps taken throughout the course of a landscape-scale invasive weed removal project. The project provides a good practical example of potential complexities due to its long history, its location in a highly urbanized estuary, its management of a hybridized weed, and its interaction with endangered species. The ISP has been operating for over 15 years with the goal of eradicating the highly invasive *Spartina alterniflora* × *foliosa* (hereinafter referred to as hybrid *Spartina*).

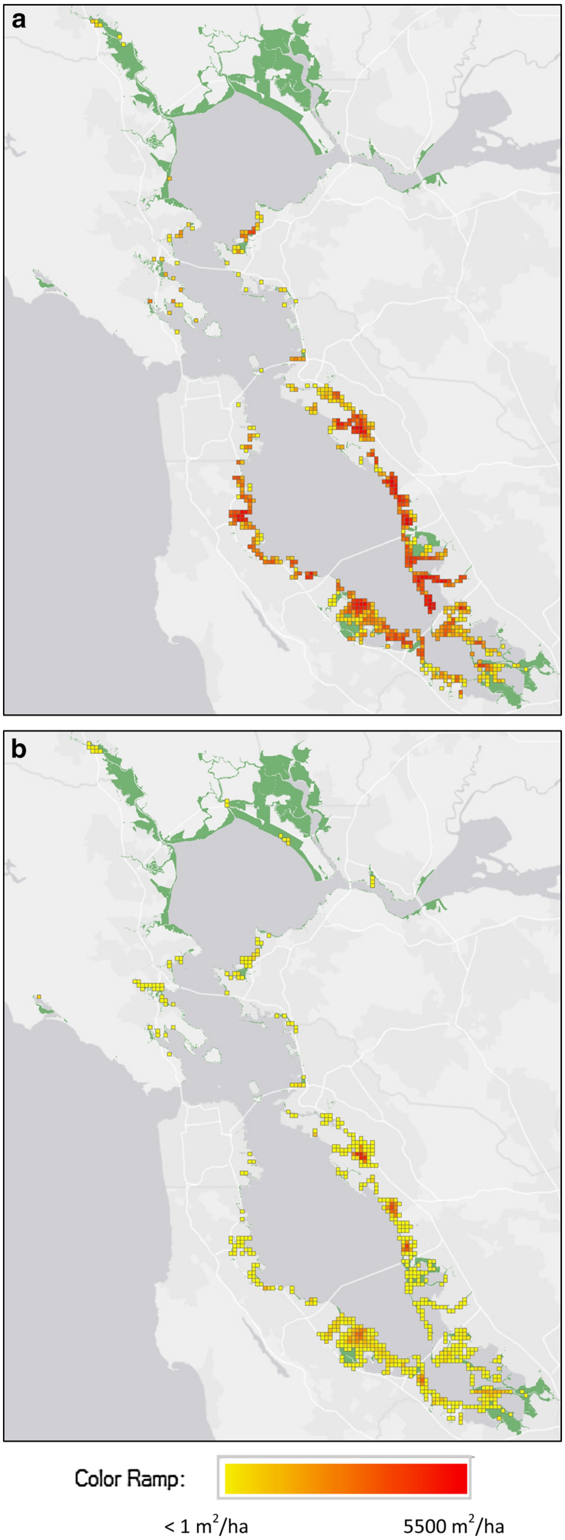
The San Francisco Estuary (hereinafter referred to as Estuary) is the largest estuary on the Pacific coast of the United States and provides key habitat for a broad range of flora and fauna including endemic tidal marsh species (Baye et al. 1999; Jones and Perlmutter 2012). The Estuary is also one of the most invaded aquatic systems in the world (Cohen and Carlton 1998). One of the worst invaders has been *S. alterniflora* (Atlantic smooth cordgrass), an autogenic ecosystem engineer that was introduced by the U.S. Army Corps of Engineers in 1970s for dredge spoils stabilization and erosion control (Williams and Faber 2001). There have been numerous introductions of *Spartina* around the globe that have proven invasive (Ainouche et al. 2009; Strong and Ayres 2009), including *S. alterniflora* plantings in China that have spread to thousands of hectares, and for which treatment is currently in the experimental phase (Qiu 2013).

Spartina alterniflora is a rhizomatous perennial grass that grows at elevations between mean low water and mean high water (Callaway and Josselyn 1992), which is the same tidal zone inhabited by Pacific coast native *Spartina foliosa* (Pacific cordgrass) (Baye et al. 1999). By the 1980s, *S. alterniflora* had expanded beyond its original planting sites in the Estuary (Ayres et al. 2003; Callaway and Josselyn 1992), and fertile hybrids between *S. alterniflora* and native *S. foliosa* were found soon thereafter (Daehler and Strong 1997). Backcrossing and introgression formed a self-fertile, fecund hybrid swarm (Sloop et al. 2009). Hybrid *Spartina* grows more rapidly and over a wider ecological range (e.g., at both lower and higher tidal elevations) than native *S. foliosa*; in intertidal areas near the original introduction site, hybrid *Spartina* quickly became the dominant vegetation type (Ayres et al. 2004a).

The spread of hybrid *Spartina* was most rapid on mudflats, vital foraging habitat for resident and migratory shorebirds along the Pacific Flyway, and in the numerous restoration projects converting former salt evaporator ponds and agricultural land back to tidal marsh (Ayres et al. 2003; Stralberg et al. 2004). Restoration sites were shielded from wave energy by partial levees and graded to elevations designed to promote vegetation establishment, making them particularly vulnerable to invasion (Ayres et al. 2003), presumably because of their optimal physical characteristics and low biotic resistance (Dethier and Hacker 2005). In areas near the original *S. alterniflora* introduction sites, the presence of hybrid *Spartina* altered restoration trajectories by hindering channelization and precluding the establishment of the diverse species composition typical of native marshes, even 20 years after tidal breaching (Boyer and Thornton 2012). If the hybrid *Spartina* threat can be removed to allow these marshes to develop along their intended restoration trajectories, they can provide much-needed support to tidal marsh biota that have been seriously impacted by the loss and degradation of the historic wetlands around the Estuary (Goals Project 2015).

In recognition of the potential for invasive *Spartina* to preclude the achievement of restoration goals (Goals Project 1999), the California State Coastal Conservancy (Conservancy), in partnership with the United States Fish and Wildlife Service (USFWS), established the San Francisco Estuary Invasive *Spartina* Project (ISP) in 2000. This regional vegetation management program and its potential impacts were evaluated in a Programmatic Environmental Impact Statement/Environmental Impact Report (PEIS/EIR), adopted by the Conservancy in 2003 (State Coastal Conservancy 2003). Treatment began in 2005, reducing hybrid *Spartina* from 323 to 12 net hectares by 2014 (Fig. 1a, b), and active revegetation efforts have installed over 300,000 native plants since 2011.

Here we present the experience of the ISP through the lens of a generalized strategic framework (Fig. 2) that may capture many of the decisions faced by conservation projects centered on vegetation



◀**Fig. 1** **a** Density map of *Spartina alterniflora* × *foliosa* cover in 2006 (**a**) and 2014 (**b**) within the San Francisco Estuary, California, USA. Hybrid *Spartina* locations have been converted to 500 m × 500 m grid cells for display at an Estuary-wide scale. Highest density areas in 2014 occur within those sites where treatment has not been permitted since 2011. Surveyed *Spartina* habitat is displayed as a green background layer. Data provided by the California Coastal Conservancy's San Francisco Estuary Invasive *Spartina* Project

management. We developed a retrospective flowchart to illustrate the progression of the ISP from its initiation based on regional goals to the development of a vegetation management plan, adaptation of weed mapping and treatment methods as infestation densities changed, active revegetation, and feedback loops of project review. Deciding whether and when to proceed with weed eradication efforts has been covered by others (Rejmánek and Pitcairn 2002; Simberloff 2003). The framework posits that vegetation management in this restoration context requires that a project identify target weed populations, determine if eradication is feasible, identify and address impacts to sensitive species, and identify effective weed treatment strategies. Once implementation begins, the project should adapt and refine monitoring and treatment methods into an effective eradication strategy, conduct active revegetation if necessary and where appropriate, and regularly evaluate progress towards meeting project goals through continuous feedback loops.

Other complex conservation projects have had to reconcile two of the most challenging aspects for the ISP: hybridity and the presence of sensitive species that benefit from the target plant. Hybridity confuses the biological species concept and makes it more difficult to define and detect the target plant (Allendorf et al. 2001). Examples include cryptic common reed (*Phragmites* sp.) (Saltonstall 2002), cattail (*Typha* sp.) (Larkin et al. 2012) and salt cedar (*Tamarix* sp.) (Gaskin and Schaal 2002). While invasive vegetation is normally associated with its negative impacts, it may also provide shelter or food for sensitive native wildlife (Schlaepfer et al. 2011). Examples include the Pacific chorus frog (*Pseudacris regilla*) using introduced reed canary grass (*Phalaris arundinacea*) (Holzer and Lawler 2015), and the endangered

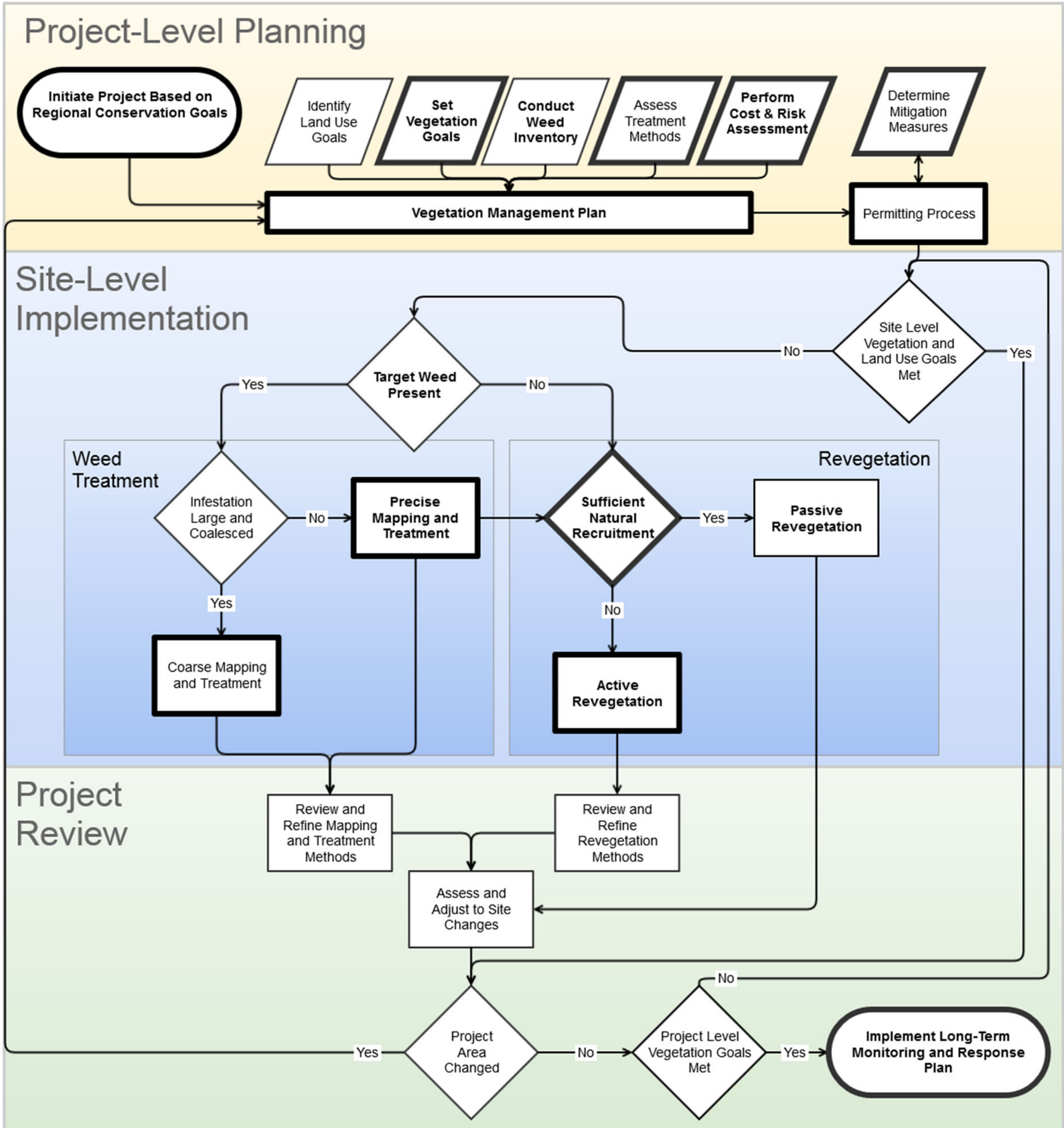


Fig. 2 Flowchart diagramming the generalized strategic framework of the ISP. *Bold borders* highlight process and decision steps impacted by sensitive species concerns (see Sensitive Species Box). *Bold text* indicates hybridity concerns (see Hybridity Box)

southwestern willow flycatcher (*Empidonax traillii extimus*) relying on invasive salt cedar (*Tamarix* sp.); in the latter case, the target invasive was declared critical habitat due to the widespread infestation and loss of appropriate native riparian vegetation, such as willows (*Salix* sp.) (Sogge et al. 2008). Both hybridity and sensitive species will be explored further in greater detail below.

Box 1: Sensitive Species

If sensitive species are present within a project area, they can be affected by unintended ecological impacts either during the treatment of a weed (DiTomaso 1997) or as secondary effects after weed removal (Zavaleta et al. 2001). These impacts should be assessed early in project planning, since they may influence the permitting process and increase the cost and length of the project, or may render the project infeasible. Without adequate anticipation of non-target impacts from the outset, project proponents risk falling short of their conservation goals.

The ISP PEIS/EIR identified 47 sensitive species of plants and animals that could occur within the waters and adjacent lands of the San Francisco Estuary (State Coastal Conservancy 2003). Of these 47 species, 19 were determined to be at sufficient risk of direct, indirect, or cumulative adverse impacts to warrant site-specific evaluation and potential mitigation. The ISP worked with USFWS and other stakeholders to develop appropriate mitigation measures that were incorporated into the Mitigation Monitoring and Reporting Program for the project in order to minimize or eliminate short term impacts (State Coastal Conservancy 2003). Hybrid *Spartina* removal was expected to have long term benefits for many of the special status species that were evaluated, including the endangered salt marsh harvest mouse (*Reithrodontomys raviventris*) that uses perennial pickleweed (*Sarcocornia pacifica*) for both habitat and as a food source. Pickleweed is an important component of the mid-elevation marsh that benefitted from *Spartina* removal, greatly increasing at many sites where the marsh elevation was appropriate (Elrod et al. 2013).

However, one species, the California Ridgway's rail (*Rallus obsoletus obsoletus*, hereinafter RIRA), has presented a more difficult planning and implementation issue. RIRA use tall, dense forms of hybrid *Spartina* for cover from predators and for nesting. In areas where hybrid *Spartina* colonized mudflats and new restoration marshes, RIRA habitat was created where previously none had existed (Casazza et al. 2016).

RIRA prospered in marshes that had become near-monocultures of invasive *Spartina*. Following hybrid *Spartina* removal by ISP partners, these sites generally contained abundant pickleweed, but lacked the structural complexity provided by other native vegetation, such as *Grindelia stricta* and native *Spartina foliosa* that had been excluded by invasive *Spartina*. Extant marshes that became dominated by the invader lost biodiversity (Elrod et al. 2013), but supported elevated RIRA numbers due to the additional cover provided by the tall hybrid cordgrass across all tidal elevations (Casazza et al. 2016).This is not to say that native marshes are incapable of supporting a high density of RIRA. Much of the Estuary still contains an intact *S. foliosa* component as well as other native marsh vegetation that can support thriving RIRA populations, despite only a minimal or non-existent hybrid *Spartina* presence (Liu et al. 2012).

The RIRA population declined significantly in 2008, both in the South Bay where the greatest proportion of *Spartina* had been removed and in areas that had never been impacted by invasive *Spartina* or its removal (Liu et al. 2012). In response to concerns about the overall population declines of RIRA, the Endangered Species Recovery branch of USFWS restricted treatment of invasive *Spartina* at 11 sites in 2012, and established a threshold of RIRA population increase (over a 2010 baseline) that they deemed necessary to re-initiate consultation. Successful treatment continued throughout the rest of the Estuary, and as of 2014 these 11 sites contain about 80% of the remaining hybrid *Spartina* (Rohmer et al. 2016). Removal of hybrid *Spartina* from these marshes would likely result in reduced RIRA numbers, since there are no adjacent marshes that possess the habitat characteristics required for successful RIRA emigration at the scale necessary to accommodate all displaced birds.

Since natural recruitment and establishment of tall native vegetation did not occur rapidly enough to enhance RIRA breeding and survivorship and generate the population increases required by the permitting agency to resume full treatment, the ISP initiated a large-scale active revegetation program. The Conservancy has worked with additional partners (United States Geological Survey, Save the Bay, Don Edwards National Wildlife Refuge) and consultants to develop other key measures directed towards RIRA conservation, including creation of small, high-tide refuge islands, removal of avian predator perches in marshes, trapping mammalian predators, deploying floating islands in treatment areas (Overton et al. 2015), and supporting ecotone restoration efforts by partner organizations. The RIRA population around the Estuary has been relatively stable since 2008 (Liu et al. 2012).

Box 2: Hybridity

Anthropogenic hybridization is becoming increasingly common and is causing extinctions of many taxa (Allendorf et al. 2001; Rhymer and Simberloff 1996). Hybridity between native and non-native plants presents a conservation conundrum, as it complicates the detection and identification of the plant to be targeted for removal. Molecular techniques can be an aid, but can also be expensive and have their own limitations (Allendorf et al. 2001).

The desire to eradicate hybrid *Spartina* was in part motivated by concerns over the potential for the extinction of native *S. foliosa* by hybridization (Ayres et al. 2004b). For conservation purposes, *Spartina alterniflora* × *foliosa* is a "Type 5" hybridization (Allendorf et al. 2001): despite widespread introgression there are healthy extant *S. foliosa* populations, and efforts are focused on maintaining and expanding the remaining native populations. The ISP uses multi-locus genetic markers to help distinguish native *Spartina* from hybrid individuals targeted for treatment. Treatment decisions are not based on a potential link between degree of invasiveness and degree of introgression; in fact, no clear consensus exists regarding such a relationship (but see Feinstein 2012; Strong and Ayres 2009).

One of the more difficult decisions for managers is how stringent to be in attempting to prevent or limit the introgression of introduced genes into the native genome. That is, how "pure" does a native population need to be in order to warrant conservation, or to declare a project like the ISP complete? Standards that are too loose threaten to erode the genetic integrity of native populations, while overly stringent standards may result in removing evolutionarily-important natural polymorphism from the natives (Allendorf et al. 2001). Given the near-impossibility of preventing all introgression with native populations, realistic goals need to be set with regard to how much introgression can be tolerated without compromising the native gene pool or putting native ecosystems at risk of recurring invasions.

The cut-off values in the genetic assignment tests used by the ISP to declare a sample as hybrid, native, or uncertain were arrived at empirically and work well in this system, but they should not be considered broadly applicable. The threshold for the amount of admixture that is tolerable will vary in different situations (Allendorf et al. 2001), so managers should approach this question carefully. The ISP found it beneficial to hire specialists to ensure proper tests are being performed to detect hybrid individuals, reliable results are being delivered, and staff and stakeholders understand the applications and limitations of the data.

Project-level planning

Restoration of native habitats via removal of exotic weeds is an important tool in land management (Randall 1996), but without sufficient planning, successful eradication can have unintended consequences on ecosystem dynamics (Zavaleta et al. 2001). The decision to target specific weeds for control or eradication should be made based on their actual and potential interference with regional conservation goals. Management of invasive species should only be undertaken if leaving the weed unchecked will result in more damage than controlling it (Tu and Meyers-Rice 2011). Therefore, when planning a weed management project, it is important to have a clear understanding of site-specific habitat goals and the likely consequences of weed removal.

Propagules from outside of the project area can reinfest treated areas, even from distant, remote infestations in the case of aquatic plants. If reintroduction of the invasive from the surrounding landscape is reasonably likely, full eradication is not a realistic goal unless other entities also work to eradicate the invasive and prevent its reintroduction. Eradication is often a misnomer applied to the general control of an invasive species, although few projects ever reach that end goal, with adequate funding being a common roadblock (Panetta 2009). However, even if full eradication of a species from all areas where it was introduced (intentionally or not) is not possible, local or regional eradication may be an appropriate conservation goal if the risk of reinvasion is negligible. Finally, the period of seed viability for the target species may dictate the feasibility of pursuing eradication or simply implementing a control program. Some noxious weed seeds remain viable for decades, longer than rigorous mapping and treatment efforts can reasonably be expected to continue (DiTomaso et al. 2013).

The vegetation management goals of the ISP stemmed from the vision presented in the San Francisco Baylands Ecosystem Habitat Goals Report (Goals Project 1999), which identified targets to improve habitats for many kinds of plants and animals within the tidelands of the Estuary. Over the past 160 years, 79 % of tidal marsh in the Estuary has been lost due to reclamation policies that promoted draining intertidal habitat for agriculture, commercial salt production, urban development, and industry (Goals Project 1999; Nichols et al. 1986). Since the 1970s, federal and state restoration efforts in the Estuary have sought to reverse the loss of marsh ecosystems, with the largest acreage acquisitions coming in the form of the purchase and tidal breaching of salt evaporator ponds (Williams and Orr 2002), with the ultimate goal of more than doubling the tidal marsh footprint in the Estuary to 40,500 hectares (100,000 acres) (Goals Project 1999). The recent Goals update (Goals Project 2015) recommends accelerating this restoration in anticipation of predicted sea-level rise and other aspects of climate change. To date the largest investment towards this goal was made in 2003 with the $100 million purchase of 6110 hectares to initiate the South Bay Salt Pond Restoration Project (SBSP) (http://www.southbayrestoration.org/).

Eradication of invasive *Spartina* was singled out as a conservation priority because hybrid *Spartina* marshes are not functionally equivalent to native marshes. Hybrid *Spartina* grows denser, taller, and with thicker rhizome mats than the native (Callaway and Josselyn 1992), and once established, hybrids may change wetland hydrology, resulting in altered marsh geomorphology, reduced flood control capacity and increased mosquito breeding zones. Invaded marshes are less complex than native marshes and contain little zonation, truncated channels, and altered chemistries (reviewed in Strong and Ayres 2009). As a result, heavily invaded marshes contain an altered biota with changes in benthic invertebrate guilds, modified food webs, and reduced species diversity (Levin et al. 2006; Neira et al. 2006). Hybrid *Spartina* also displaces endemic flora and threatens the local extinction of native *S. foliosa* through either direct competition or genetic introgression (Ayres et al. 2004b). Restoration projects such as SBSP, which were in close proximity to large infestations of hybrid *Spartina*, were colonized to varying degrees. Their marsh development trajectory was likely to be altered once these infestations established and expanded (Ayres and Strong 2010).

The ISP's primary goal at the outset was to arrest and reverse the spread of non-native cordgrass in the Estuary to preserve and restore the ecological integrity of the intertidal habitats and estuarine ecosystem (State Coastal Conservancy 2003). The ISP works in the tidelands of nine counties with numerous partners, landowners, non-governmental advocacy groups, and contractors for treatment of invasive *Spartina*, monitoring of endangered species in the project area, and revegetation. The PEIS/EIR developed at the start of the project laid the foundation for permitting most of this work; Conservancy and ISP managers coordinate the acquisition of all other required permits, including the USFWS section 7 Biological Opinion for work in endangered species habitat. The active involvement of prominent, long-time residents of the community through various environmental advocacy groups helps facilitate the ISP's presence by endorsing the legitimacy of the intentions behind the eradication.

Vegetation management plan

The development of an effective vegetation management plan requires a fundamental knowledge of the biology of the target invasive and an understanding of the ecological components of the system (Fig. 2, top section). These factors, along with data on the extent of the infestation, will influence the choice of invasive plant management strategy: eradication, containment, control or mitigation (Wittenberg and Cock 2001). If eradication is the chosen strategy, potential habitat within a likely propagule dispersal distance can be used to determine appropriate project boundaries. Vegetation goals must be established on a site-specific basis to guide plans for weed treatment and assess potential revegetation activities. These goals will likely be based on a combination of historic conditions at the site, conditions at a reference site, and the intended restoration outcome for the site (Tu and Meyers-Rice 2011; Wittenberg and Cock 2001).

Cost-effective treatment methods should be chosen based on their effectiveness on the target species while minimizing direct and indirect impacts on non-target species and the abiotic environment (Rinella et al. 2009). The life cycle of the plant influences the timing of treatment and the choice of treatment methods. The duration of seed viability will inform how long inventories should continue for an eradication project, and influences the potential timeline to project completion. If the project area includes sensitive species (see Sensitive Species Box), restrictions as to when and how treatment can be implemented effect the selection of the optimal method (e.g., avoiding breeding season or a particularly sensitive life stage). Pilot studies may help to fine-tune the plan before full implementation. Direct removal of the invasive weed may not necessarily be the best method for restoring the desired native community. A combination of techniques may provide a better approach to realizing habitat goals, such as shifts in cultural practices in the case of rangeland management (Firn et al. 2010).

The Conservancy and USFWS identified eradication as a realistic goal for the ISP for several reasons. The chance of reinvasion was considered small since the known extent of the hybrid *Spartina* invasion was confined to this Estuary. The seed viability is short, on the order of a year (Epanchin-Niell and Hastings 2010; Xiao et al. 2009), and an effective herbicide (imazapyr) was already being used on a similar *Spartina* invasion in Washington State (Patten 2003). In addition, the target plant is so invasive and has such damaging impacts that neither a containment nor a control program would have satisfied regional conservation goals.

The ISP considered various treatment alternatives during preparation of the PEIS/EIR. However, many of these methods were never implemented due to concerns over damage to sensitive resources or high cost. For example, treatment methods that involved excavation, maceration, or breaking *Spartina* rhizomes would likely alter marsh topology. Because of this issue, along with the expense and low efficacy of this method (Natural Heritage Trust and Tasmania Department of Primary Industries Water and Environment 2002), the ISP did not implement these forms of treatment. Tarping (covering with heavy duty landscape fabric) was implemented for small-scale treatment (infestations of a single clone or small stand) at sites with low wave energy, but this approach would have been expensive and would likely have long-term destructive impacts if implemented on a larger scale (Hammond and Cooper 2002). Tarping is not selective to the target vegetation and is difficult to remove by hand once it has been buried by sediment accretion.

At the start of the project, glyphosate was the only herbicide approved for use on monocots in California estuaries (Kerr 2011). While this treatment method ranked well in its cost effectiveness when compared with excavation or tarping and was the least impactful to the tidal marsh and mudflats, its efficacy was highly variable, likely due to the tendency of glyphosate to adsorb strongly to sediment or salt deposited on the leaves of *Spartina*. Herbicide bound to depositional material is precluded from uptake and translocation throughout the target plant.

A second herbicide, imazapyr, was approved for use in estuarine systems in California in 2005, the first year of estuary-wide treatment by ISP partners. Imazapyr does not adsorb to soil particles like glyphosate, requires less dry time to enter the plants before the next tidal inundation, and breaks down faster in water (Leson and Associates 2005). In addition, it can be applied at low volume by helicopter, which allows for more efficient treatment conducted earlier in the season than would have been possible using time-consuming ground-based methods.

Site-level implementation

Once a vegetation management plan has been developed and permitting is complete, the project enters the implementation phase (Fig. 2, middle section). An initial inventory should be conducted to determine the presence or absence of the target weed at suitable habitats within the project area. This can be accomplished through field surveys, such as inventory mapping or plot surveys (Barnett et al. 2007; Rew et al. 2006), or remote sensing methods, such as manual or automated imagery classification, capitalizing on increasingly available aerial imagery sources (López-Granados 2011; Xie et al. 2008). If the target weed is found, this triggers the need to delineate a site and map weed distribution and abundance at a scale appropriate to inform treatment efforts. If no weeds are found during initial monitoring, future monitoring frequency should be based on likely invasion potential at a site (Tu and Meyers-Rice 2011).

The spatial distribution and abundance of target weeds within the site will largely determine the optimal weed mapping and treatment strategy (Fig. 2, weed treatment section). Plants can be distributed as distinct, isolated patches or large, coalesced infestations, or a mixture of both. Large, coalesced infestations can be near-monocultures over substantial areas, while isolates may be identified as distinct individual plants, new seedlings, or small patches of multiple individuals. Treatment methods should be optimized to the level of infestation, with increasing spatial resolution of weed control as density and aggregation of weed patches decrease (Christensen et al. 2009). Similarly, mapping data should be collected at a resolution appropriate to the scale of treatment to be performed (Gerhards 2013; Rew and Cousens 2001). Mapping and treatment approaches may differ within a site. For example, outliers along the leading edge of a coalesced infestation may be mapped as distinct isolates, as the optimal approach to weed mapping and treatment of these may differ from that for the central infestation.

Initial inventory during the ISP project planning stage focused primarily on coarse mapping and population size estimation in locations where hybrid *Spartina* was known to be present. Once project implementation began, the ISP began using aerial imagery and on-the-ground investigation to identify and accurately delineate potential habitat for the target invasive throughout the known extent of the invasion. Potential habitat boundaries are now refined annually during inventory mapping as changes are noted, expanding as levees are breached for tidal marsh restoration. Defining large, sprawling areas with multiple marshes as a single site proved to be problematic for the ISP. Portions were sometimes overlooked during a busy treatment season, especially if they were not contiguous to the primary site. Splitting large sites into subsections, such as discrete smaller marshes, has better facilitated treatment planning and the tracking of population change over time at a scale useful for management purposes.

The ISP focuses its annual hybrid *Spartina* inventory on sites where the target was detected within the last 3 years, and surveys all other potential habitat in the Estuary at least every 2–3 years. The frequency of monitoring throughout the portions of the Estuary where hybrid *Spartina* has never been detected is based on two factors: (1) difficulty of monitoring, which is a function of travel, labor or specialized equipment costs such as airboat, and (2) susceptibility of the area to invasion, which is a function of distance from and size of any nearby populations of invasive *Spartina*, as well as where prevailing currents and wind are likely to disperse propagules. Highly susceptible areas include mudflats and formerly diked marshes recently restored to tidal action that have low biotic resistance to invasion, and are near large existing populations of hybrid *Spartina* (Sloop et al. 2009, 2011; Thornton et al. 2013). Areas far from any of the original introductions appear to have lower invasion pressure and are surveyed less frequently. Because propagules can disperse throughout the open tidal system of the Estuary, all potential habitat must be monitored periodically until full regional eradication is achieved.

We reviewed mapping and treatment methods employed at all ISP sites in 2006, 2010, and 2014 and found a quantifiable threshold where site-level strategies transitioned from coarse to precise (Table 1). In general, the ISP classified large, coalesced infestations as containing hybrid *Spartina* populations at densities of 500 m^2/ha or greater, within sites covering eight or more hectares, with perimeter-to-area ratios less than 1:10. Populations with lower densities, those located in smaller sites, or in sites with higher perimeter-to-area ratios, were generally categorized as isolates and more precise methods were used for mapping and treatment. However, not all sites fit this general trend, especially when proximity to residential development, land manager concerns, or logistical constraints necessitate the use of a sub-optimal approach relative to the infestation size.

The 500 m^2/ha density threshold is based on "treatment area", a concept developed by the ISP in 2008 to better estimate the treatment effort required within a site. The treatment area within the mapped feature (point, line or polygon) will be covered by herbicide during an efficient application. This approach differs from net area, an estimate of the area covered by *Spartina* ignoring spaces between stems and leaves. Site-level summaries of treatment area data allow crew leaders to determine the amount of herbicide mix to prepare, and how much to transport when deploying personnel to traverse the marsh. This increases efficiency and reduces worker fatigue, thereby enhancing safety while working in the marsh. When hybrid *Spartina* is dense, treatment cover can be near 100 %, but net area and treatment area can be significantly lower within scattered patches that have been reduced by treatment or are new colonizers.

Coarse methods

Site-specific weed management using coarse-scale mapping and treatment approaches can be the most cost-effective and efficient when dealing with large,

Table 1 Site-level weed mapping methods and the conditions under which they were used by the San Francisco Estuary Invasive *Spartina* Project, California, USA

	Site and Infestation Type	Treatment Type	Mapping Method	When Used
Coarse Strategy	Large, coalesced populations with greater than 500 m^2/ha treatment area, in greater than 9 ha sites with low perimeter-to-area ratios (<1:10)	Broadcast Treatment	Aerial Imagery Analysis	Target can be distinguished via remote sensing methods
			Grids	Quick summary of level of infestation and distribution across the landscape is desired, and neither the exact location of target plants nor differentiation from non-target plants within the grid area is necessary.
			Field-Based Infested Area Mapping	Site can be accessed (by ground or helicopter) to allow coarse GPS mapping of infested areas using large polygons, or by digitizing over background layers.
Precise Strategy	Densities less than 500 m^2/ha *or* Small (<9 ha) sites *or* Sites with high (>1:10) perimeter-to-area ratios	Spot Treatment	Long Distance Offsets (Points)	Patches can be seen only at a distance (cannot be reached efficiently). Identification may be questionable.
			Points	Small and/or isolated patches
			Lines	Linear patches
			Polygons	Exact border of the patch is important for informing treatment, or precise tracking of patch expansion over time is desired

coalesced weed infestations (Rew and Cousens 2001; Rew and Pokorny 2006; Van Wychen et al. 2002). Coarse mapping results in a rough estimation of weed density in a given area, but may not allow for the detection of isolates within the mapped area (Shaw 2005). Mapping methods may include field sampling techniques to estimate cover within a large area, cursory field mapping of large, obvious patches, visual estimation of cover within predetermined mapping units, or coarse-scale geospatial imagery analysis. The resulting maps are useful for planning the implementation of coarse treatment methods, which may include broadcast herbicide delivery systems, cultural control techniques such as mowing or tilling, or release of biological control agents. Coarse mapping and treatment methods may have high initiation costs, such as the acquisition of aerial imagery or use of specialized equipment, but are normally less labor-intensive and thus more cost-effective than precise methods when used over large areas containing relatively dense infestations (Barroso et al. 2004).

The ISP has mapped hybrid *Spartina* using three different coarse mapping methods (Table 1). Aerial imagery interpretation used early in the project was abandoned when standing dead vegetation obscured the ability to detect live vegetation growing beneath it. Estimation of weed cover within spatially-defined grids is highly efficient and cost-effective, but does not provide the spatial resolution required to inform efficient treatment unless weed densities are high and no native *Spartina* exists to confuse identification of the target weed. The ISP seldom attempts to distinguish hybrid from native *Spartina* during coarse mapping work due to the spatial overlap between the plants and the presence of interspersed immature hybrid clones that cannot be differentiated without DNA testing. There is also the risk that untreated native *Spartina* can be pollenated by adjacent hybrid and produce hybrid seed. While helicopter-based mapping was found to be efficient and cost-effective for mapping dense infestations in large, remote sites, applying this technique to the mapping of isolates in sites with low weed densities yielded poor detectability when compared with ground surveys.

The optimal treatment methods used to control large, dense infestations also tend to be coarse, and in the case of the ISP, virtually all coarse treatment relied on helicopter broadcast during the first 5 years of the project. This aerial herbicide delivery system was efficient at reducing hybrid *Spartina* at the most heavily infested sites, and applications could be conducted in just a few days over hundreds of acres with little disturbance to the tidal marsh wildlife. Turning the boom sprayer pump off when flying over a gap in the target vegetation or a high-value stand of native plants important to wildlife afforded a degree of precision to this otherwise coarse application technique.

Although highly time-efficient, one of the main drawbacks to broadcast treatment is cost, both in terms of equipment deployment and wasteful over-application of herbicide to areas that do not contain a sufficient density of the target plant. The ISP found that as patches became smaller, the variability in efficacy from broadcast treatment increased. This increase may have been due to the need to turn the boom sprayer on and off frequently, producing finer particles that can drift off target enough to miss smaller clones, or because the pilot failed to identify an isolated target stand.

Precise methods

Precise mapping methods are used to inform thorough, efficient spot treatment of individual weed patches (Fig. 2, Weed Treatment section). Methods can include field mapping of individual point, line, or polygon features that are managed in a GIS (Rew and Pokorny 2006; Van Wychen et al. 2002) or fine-scale geospatial imagery analysis with the ability to detect individual target plants (López-Granados 2011). Precise mapping is more labor-intensive and time-consuming than coarse mapping, so the transition to this level of effort should be made once the benefits justify the costs (Rew and Cousens 2001). For example, once a project has reduced site-level infestations below the large and coalesced level described above, this reduction triggers the need to transition to more precise map-based site-specific weed control strategies (Gerhards 2013). The project-specific threshold for this transition will likely occur when coarse methods are no longer producing results adequate to inform efficient treatment. In the case of the ISP, successful reduction of hybrid *Spartina* in response to control efforts required transitioning to precise mapping and treatment methods in much of the project area, with an associated increase in staff necessary to handle the additional workload (Fig. 3a–f).

ISP staff map hybrid *Spartina* in the field using GPS-enabled GIS mapping software to collect point, line, and polygon features. The field software platform ArcPad (ESRI, Redlands CA) allows project staff to view, navigate to, and query the attributes of current and past years' data and genetic results in the field. This information facilitates mapping and hybrid treatment decisions, and can help ensure thorough detection and treatment of isolates.

Precise treatment methods allow for targeted spot treatment of individuals and small patches of plants. Precise herbicide delivery systems allow the applicator to direct a nozzle towards specific target plants, while avoiding damage to adjacent desired plants, or potentially wasting overspray on open ground. The ISP uses three high-volume, ground-based platforms (airboat, amphibious vehicle, and truck) for precise treatment after infestations are reduced by coarse methods, or at sites with moderate infestations at the initiation of treatment efforts. These platforms can also be used to transport personnel to remote locations to treat smaller infestations and to resupply applicators. Amphibious vehicles were useful for accessing infestations on the marsh plain, and were helpful on the mudflats due to their low ground pressure. However, airboats have provided the greatest level of utility for the ISP. They are capable of travelling long distances to remote marshes, such as islands or sites with no upland access point, and are essential for treating plants on the open mud of new restoration marshes. For full plant exposure, the application must be performed at low tide when an outboard boat motor cannot operate.

In general, as the precision of treatment increases, efficiency is reduced, which increases labor costs and the time to complete treatment. The most precise

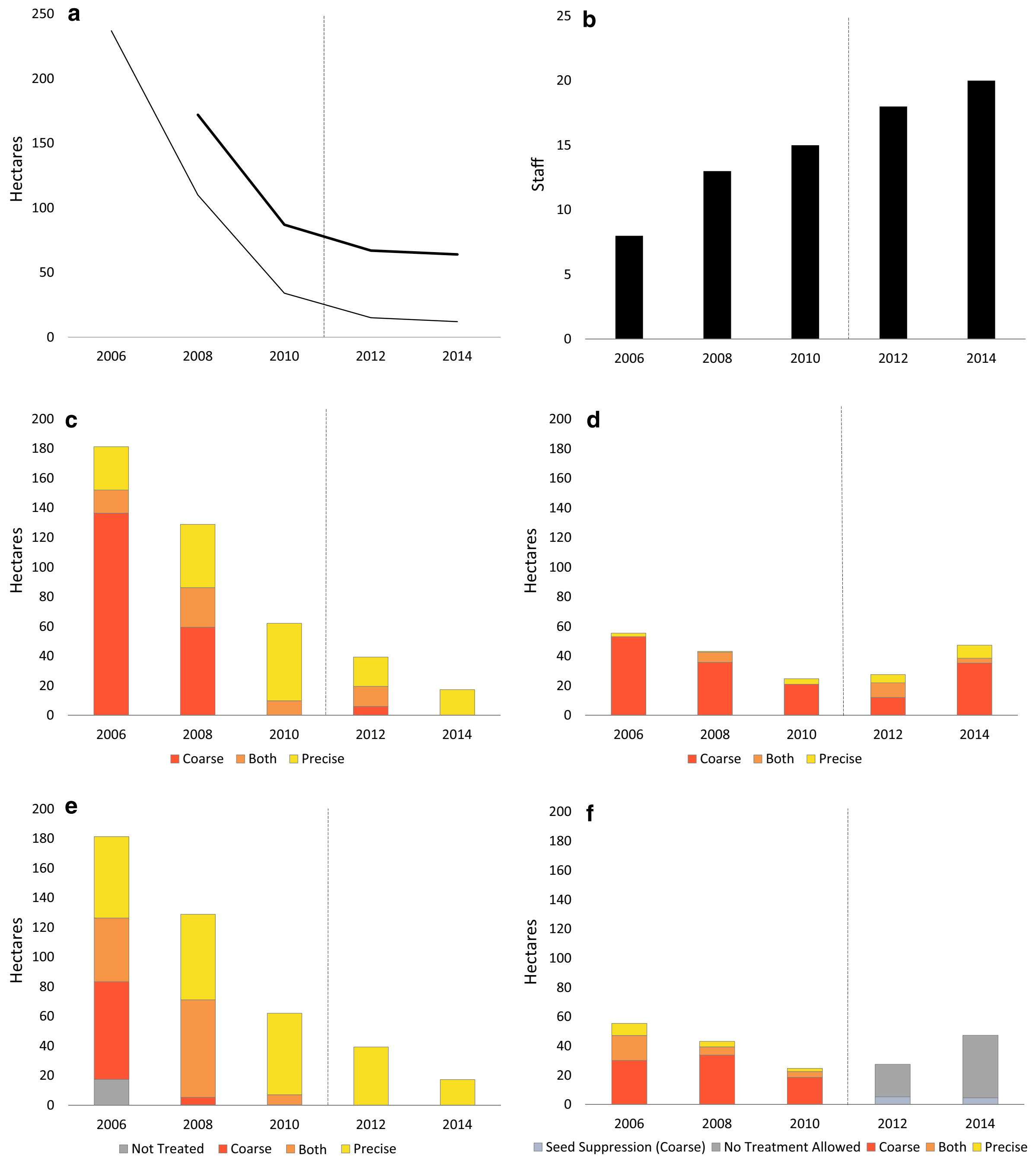


Fig. 3 *Dotted line* in all figures indicates initiation of treatment restrictions in 2011; **a** Size of *Spartina alterniflora* × *foliosa* infestation within the San Francisco Estuary, 2006 to present, as measured in net hectares (*thin line*) and treatment hectares (*thick line*); **b** Number of field staff required for ISP weed mapping and treatment survey efforts; **c** and **d** Site-level mapping methods used by the ISP by treatment area within (**c**) sites where treatment has been permitted 2006-present, and (**d**) sites where treatment has been restricted 2011-present; **e** and **f** Site-level treatment methods used by ISP by treatment area within (**e**) sites where treatment has been permitted 2006-present, and **f** sites where treatment has been restricted 2011-present

delivery systems tend to carry the lowest capacity, so the time to refill in the field must also be factored into the budget. Low pressure backpack or handheld sprayers are the most common, high-precision method; but in extreme cases, tank pressure can be taken out of the equation entirely by swiping or painting the herbicide directly onto to the target plants to remove the possibility of particulate drift. The ISP uses this precision method at one site where the presence of an endangered annual plant (*Chloropyron molle* ssp. *molle*) justifies the substantial increase in time and labor.

Recommendations from the original herbicide manufacturer (BASF) were that imazapyr needed only 1 h of dry time on the plants before subsequent tidal inundation, but it has been the experience of the ISP that at least 4 h over the majority of the height of the plant was a more realistic threshold, with additional time being preferred. However, as a natural resource management entity, and considering all the variability in the hybrid swarm, the ISP did not have the capacity to study this rigorously.

Additional detection tools

Additional tools and increased field efforts can be used to help ensure the detection and treatment of all target weeds. Potential tools include advanced mapping technologies, tissue sampling for molecular or other lab identification techniques, or the use of dogs for detecting unique volatile compounds (Goodwin et al. 2010). The cost and level of effort required to employ such tools is unlikely to be justified if the treatment efforts have not yet progressed past the coarse mapping and treatment stage (Rew and Cousens 2001).

The ability to detect hybrid *Spartina* in the field is largely determined by the phenology of the plants, the vantage point of the surveyor (walking, boating, helicopter, etc.), proper training, and the technical skill of the person in distinguishing hybrid from native *Spartina*. Differentiation of hybrid *Spartina* is based on multiple morphological traits and cannot consistently be determined based on any one trait (Feinstein 2012). Where identification of target weeds is difficult due to hybridity with native *S. foliosa* or other issues, the ISP frequently employs additional detection tools, almost exclusively in low-density sites with precise mapping and treatment strategies.

The ISP employs various mapping technologies to help ensure thorough detection to inform treatment. GPS-enabled data collection software displays past years' inventories and patch-specific treatment data, records the surveyor's tracklines, and displays project-specific background layers customized to help ensure full coverage of the marsh. Background layers include aerial imagery, digitized marsh channels, detailed habitat boundaries for the target invasive, and "tracking polygons." Tracking polygons are a color-coded grid system developed in a GIS to divide individual sites into navigable sections used to allocate work during mapping and treatment, adding a spatial dimension through which to communicate logistics in a tidal environment lacking in prominent landmarks. A recent innovation enables mobile two-way web synchronization of collected data in the field, allowing staff to view the team's progress, ensuring more complete treatment coverage of previously-mapped patches of invasive *Spartina* at a site while enhancing efficiency.

Genetic testing

When the precise mapping and treatment stage is reached at a site, the need to reliably distinguish individual hybrids from native *Spartina* becomes more pressing. Identification can usually be made in the field using morphological characters, but in some cases (less than 1.5 % of mapped features in 2014), identification requires additional data provided by genetic markers. There are multiple scenarios in which genetic sampling may be warranted. First, a plant may be at an early phenological stage where identification is difficult or impossible. Second, typical differences may be obscured by marsh topology or microhabitat. Third, at sites approaching local eradication, where the management strategy hinges on the presence or absence of a single hybrid plant, a sample may be desired to confirm a field identification. Fourth, a suspected hybrid will be sampled when an extra degree of confidence is needed before informing the landowner. Finally, samples are taken at sites where hybrid reduction has not proceeded as quickly as expected, possibly due to the misidentification of one or more hybrid morphs as native.

The ISP analyzes multi-locus microsatellite genotypes from 15 loci using the Bayesian assignment test STRUCTURE (Pritchard et al. 2000) to estimate the proportion of each sample's genetic ancestry that associates with a *S. foliosa* genetic "cluster" or a non-native cluster, as described in Ort & Thornton (this issue). For management purposes, a sample that groups with the native cluster with an estimated proportion of ancestry in the range 0.9–1.0 is regarded as *S. foliosa*. Samples within the range 0–0.8 are regarded as non-native *Spartina*, and samples in the range 0.8–0.9 are considered "uncertain" and require additional scrutiny before a treatment decision is made. The ancestry cutoff points are somewhat arbitrary, but are founded in an attempt to balance being stringent enough to guard against the introgression of *S. alterniflora* genes into *S. foliosa* while trying to accommodate and conserve natural polymorphism in native populations (see Hybridity Box).

Estimating the proportion of admixture precisely is difficult with a limited number of microsatellite markers, and since we have few known parental *S. alterniflora* samples in the dataset, we do not represent that we have performed a study of admixture. The ISP therefore does not attempt to distinguish between *S. alterniflora* and its hybrids, since the management goal is the same for both: eradication. Since the relationship between invasiveness and genotype is unknown, and the ISP samples proportionally few plants overall, specific genotypes are not targeted for treatment. Instead, a probabilistic approach is taken in assigning a sample as native or non-native based on the estimates of the proportion of *S. foliosa* ancestry.

Treatment monitoring and additional survey rounds

By 2009, as invasive *Spartina* densities decreased and remaining plants became more difficult to locate and identify, the ISP further adapted its vegetation management strategy by developing approaches to improve the precision, accuracy, and thoroughness of treatment. The necessity of thorough detection and treatment was highlighted in a study by Patten and Milne (2009) (personal communication) which found that unsupervised applicators in Willapa Bay, Washington, USA, detected and treated only 63 % of the target *Spartina* plants, even without the complications of a native cordgrass and highly-fertile hybrid swarm found in the San Francisco Estuary. Their average efficacy from the imazapyr application was 75 %, resulting in a disappointing 47 % reduction each year. This study helped the ISP to justify instituting treatment monitoring and hiring seasonal biologists to accompany crews in the field for every treatment event.

Using ArcPad, staff members navigate back to the previously-mapped targets, leading the applicators through the marsh and updating each feature as it is treated. This supervision improves *S. foliosa* preservation through biologist identification of hybrid targets, reduces disturbance, makes the treatment crews more efficient within the narrow tidal windows, and enhances efficacy by ensuring thorough herbicide coverage of each target. ISP treatment survey monitoring allows for an additional opportunity for trained biologists and experienced applicators to identify patches that were not detected during inventory mapping, and provides the strict supervision by USFWS-certified biologists required when in sensitive RIRA habitat.

In 2013, ISP piloted a second round (R2) of inventory and treatment at a subset of sites that were approaching eradication. Typically, target plants are mapped and treated from June to September during the height of the growing season, with R2 in October or November to help overcome some of the inherent challenges to thorough detection. This additional round can capture hybrids that had not matured to the point of detectability among native *Spartina*, plants of small stature (seedlings or stunted regrowth from previous treatment), or plants that did not possess any above-ground biomass during the first round (both late-emerging plants as well as those that experienced either herbivory or sub-lethal herbicide applications). The reduction in hybrid *Spartina* persisting into the following year has proved worth the investment in additional labor. There have been more detections during R2 surveys than expected, leading to an increasing number of zero detection sites the following year.

Reinvasion potential and revegetation strategy

When determining a site-specific revegetation strategy, the potential for reinvasion and the likelihood of passive restoration should be assessed to determine whether active revegetation is necessary to meet conservation goals (Fig. 2, Revegetation section). The target invasive must be reduced to such a degree that spot treatment efforts can continue and plantings will not be outcompeted or otherwise compromised by the remaining weeds through soil modifications (Reinhart and Callaway 2006), or pollen swamping in the case of hybrids.

In addition to weed removal, establishment of desirable vegetation is a crucial success metric for most weed eradication projects (Zavaleta et al. 2001). Among other benefits, the presence of dominant native plant species has been shown to increase natural barriers to colonization and expansion of undesirable species (Kettenring and Adams 2011). This activity may involve establishing an interim state that is expected to transition over time into the vegetation community envisioned by the project goals. If weed impacts are minimal or abundant sources of native propagules are nearby, desired vegetation may rebound from passive recruitment. However, if a habitat is highly fragmented or weed impacts are major, there may be too little native seed rain in proximity to the site(s) to provide for sufficient recruitment for self-sustaining native plant establishment at a timescale appropriate to achieve restoration goals. If dealing with a hybrid species, it may be necessary to use genetic tools or to monitor the site over several seasons in order to verify that new recruits are native.

The ISP has two different thresholds regarding reinvasion and initiation of revegetation. For *G. stricta*, the standard is simply having the target invasive reduced to a limited distribution within the immediate planting area and an annual treatment plan that involves spot applications (no broadcast methods). For reintroduction of the native *S. foliosa*, the standard is much higher, necessitated by the risk of hybridization with the invader, which could perpetuate the infestation. In the case of *S. foliosa*, the infestation site must be approaching local eradication, with an active annual treatment program to ensure that new detections are eliminated early in their phenology so as not to produce viable propagules. An exclusion zone around the planting areas must be free of hybrid *Spartina* to mitigate the risk of pollen swamping or encroachment by the invader.

Since the Estuary is a mosaic of habitat types, including mudflats, young restoration marshes, and historic marshes, site-level vegetation goals are determined by both site age and geographic location. Following removal of hybrid *Spartina*, sites that had minimal hybrid presence generally restore naturally through passive recruitment (Fig. 4a–d). However, at sites near the invasion epicenter, recovery of some components of the native ecosystem has been slower. During the onset of the invasion, this area contained many young restoration projects with expansive unvegetated habitat at suitable elevations for invasive hybrid colonization and establishment. Once dense hybrid *Spartina* meadows were established, colonization by native vegetation was precluded. Following hybrid *Spartina* removal, mudflat and pickleweed plain habitats returned, but *S. foliosa* and *G. stricta* have been slower to colonize, presumably due to limited propagule presence in close proximity or insufficient dispersal into the site.

In 2011, the ISP began implementing an active revegetation program to improve the habitat at formerly invaded marshes. The five-year program was designed to enhance habitat for RIRA in areas affected by the invasion and subsequent removal of hybrid *Spartina* (see Sensitive Species Box). While mudflat and pickleweed are a component of RIRA habitat, marshes must also support plants that provide vertical structure needed for nesting and high tide refuge, such as *G. stricta* and *S. foliosa*. To date, the ISP has installed over 300,000 plants at 40 revegetation sites (Hammond 2016). For each site, the ISP has developed a plan designed to rapidly establish dense, strategically-located patches of vegetation with specific ecological benefits to rails. Because of the unique elevations, soil types, and site histories of restoration sites, a pilot approach to planting was developed and each marsh analyzed on a site-specific basis.

The scope of this project has provided a unique opportunity to study factors that limit desired plant establishment in tidal marshes. The reintroduction of *S. foliosa* has been a particularly complex component of the ISP's restoration effort. Additional challenges to restoring native cordgrass were discovered, including intense grazing pressure by herbivores, limited sources of suitable local donor population material, limited restoration literature for *S. foliosa*, and the continued presence of hybrid *Spartina* in the Estuary. In order to address these challenges, the ISP developed academic partnerships and implemented replicated planting designs of multiple restoration techniques. Twelve different planting designs were developed to investigate the influence of a wide range of biotic and

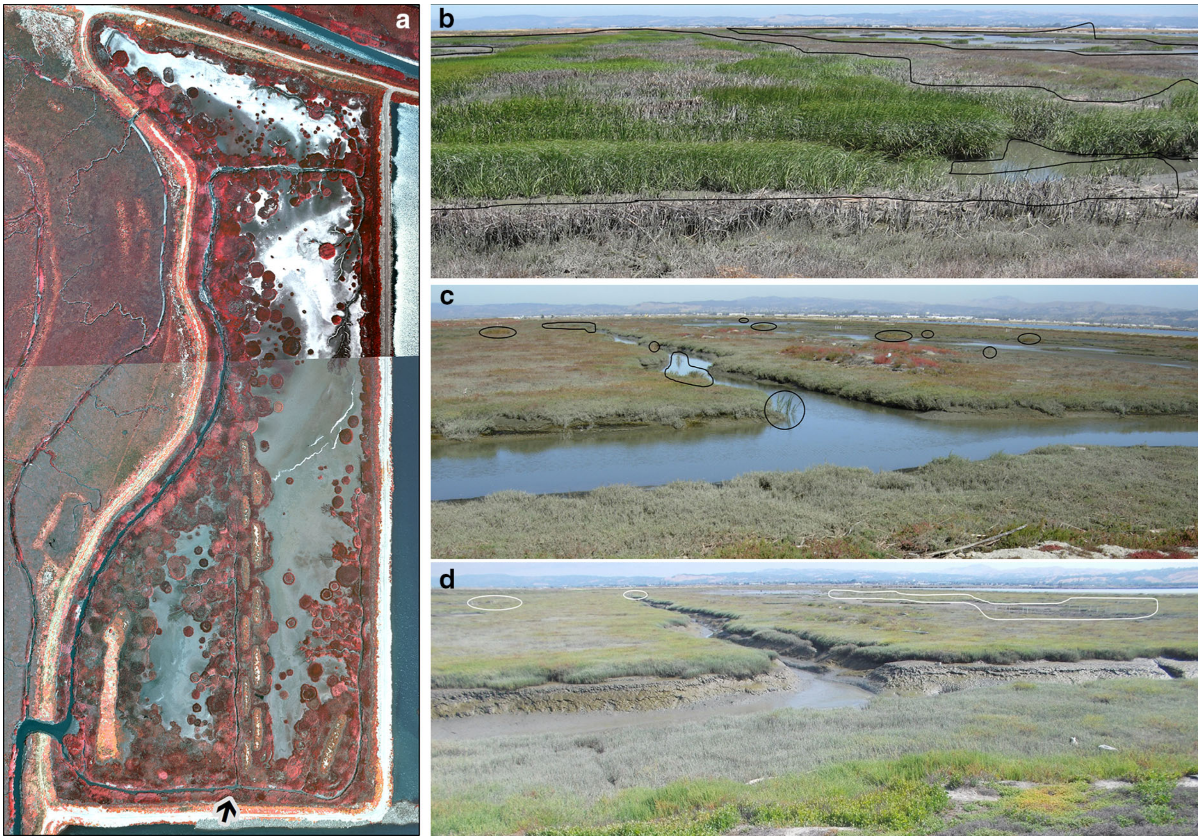


Fig. 4 Photo series from Cargill Marsh, a restoration site that was invaded by hybrid *Spartina* after breaching in 1998. Color infrared aerial photos in 2005 **a** indicated that hybrid *Spartina* covered 9 ha of the 21 ha site; individual hybrid *Spartina* clones are visible as round patches of vegetation. *Arrow* in figure **a** indicates location of time-series photos (**b–d**). In 2006 (**b**), hybrid *Spartina* (*outlined in black*) filled channels and dominated the site. By 2010 (**c**), hybrid *Spartina* was reduced to sparse patches. In 2014 (**d**), less than 1 m^2 of hybrid *Spartina* remained at this site, none of which is visible in this photo. ISP is actively planting native *S. foliosa* and *Grindelia stricta* (*outlined in white*) among the perennial pickleweed (*Sarcocornia pacifica*) that revegetated passively and now dominates the site

abiotic factors. Research topics included the practical methods of preventing plant herbivory, the influence of sediment characteristics on growth and survival of plantings, the influence of donor source material and planting method on survivorship, and the interaction of planting elevation with site and habitat type (Thornton 2016). As a result of the ISP's planting efforts, native cordgrass is now well established and spreading in several areas where previously passive recruitment was minimal.

Project review

The ISP has used regular review and self-evaluation to ensure that it stays effective, efficient and relevant. Figure 2 illustrates project review feedback loops built into all aspects of the ISP, from the initial development of the vegetation management plan, to the site-level implementation of weed treatment and revegetation, through the attainment of the project's vegetation goals. Methods were regularly reviewed and refined as the project progressed from the early work at a coarse scale through to the selection of precision tools intended to carry the ISP through to completion. To meet new challenges as they arose, the ISP has added technical experts to the project team and formed technical advisory committees to derive new solutions from outside experts and stakeholders working collaboratively.

The ISP's centralized framework has been essential to facilitating effective regional coordination, standardizing the technical aspects of implementation, and realizing efficiencies in permit acquisition and project administration. Long-term staff retention has proven especially valuable, and expertise in multiple disciplines—weed control, GIS, genetic analysis, plant ecology, avian ecology, restoration, and management—has led to innovative responses to complex challenges as they arose. Integration of genetic results and patch-level mapping and treatment data into a GIS have become a critical part of the decision-making process. Refinements in GPS field mapping software and real-time data sharing continue to drive improvements in detection and treatment. These technological innovations required a substantial upfront investment but provided the ISP with a solid return in the form of increased efficiencies. The ISP is currently researching new sophisticated tools, especially in the area of genetic testing and the use of Unmanned Aerial Vehicles (UAVs) for remote sensing.

Since the project's inception in 2000, the region's hybrid *Spartina* infestation and the methods used to treat it have changed substantially. Prior to regionally-coordinated treatment, much of the hybrid *Spartina* was comprised of dense monocultures. Mapping these populations via aerial photo interpretation was relatively simple, and annual field mapping of smaller populations was completed by just a few individuals. Once an effective herbicide was available, dense monocultures were efficiently diminished by coarse treatment through aerial broadcast spraying. Reduction of hybrid *Spartina* cover was rapid and dramatic (Fig. 3a).

The reductions of dense meadows down to sparse patches necessitated much more precise mapping and treatment efforts (Fig. 3c–f), and required a new staffing paradigm with increases in project costs (Fig. 3b). As treatment progressed, native marsh vegetation and mudflat habitat began to recover, and there were fewer examples of heavily invaded marshes to illustrate the urgency of hybrid *Spartina* control. It became more difficult to engage new land managers, regulatory agencies, and funding entities, since they had not personally witnessed extensive, hybrid *Spartina*-dominated marshes and mudflats and their dramatic recovery following treatment. Knowledge of these dilemmas reinforces the need for an active education and outreach component to invest in maintaining the political will to allow long-term projects to reach completion.

Project completion

Eradication implies that the target species has not been found for some specific period of time despite exhaustive surveys (Regan et al. 2006). The ISP has set a standard of 3 years of zero-detection of hybrid *Spartina* for the infestation at each site or complex to be declared eradicated. For projects where an assessment of the conservation goals has determined that passive recruitment will be sufficient for replacement of appropriate plants, the timeline to project completion will be driven by the removal of the target weed and exhaustion of the seed bank. When active revegetation is required, the full habitat value of plant installations or seeding may not be realized for some number of years beyond the end of weed treatment. These plantings may require additional assistance or maintenance in the initial years, but should become part of the self-sustaining natural system by the time of project completion.

The ISP strategy of targeting discernable hybrid individuals for treatment will likely allow the persistence of *S. alterniflora* alleles in undetected hybrids that exhibit no other phenotypically-identifiable hybrid traits. From an evolutionary perspective, the *S. alterniflora* alleles remaining in undetected hybrid individuals may introgress into the native *S. foliosa*, but long-term monitoring and treatment should continue to select against genetic combinations that produce new invasive phenotypes. Over time, this threat may be reduced as the *S. alterniflora* alleles become diluted in the remaining *Spartina* populations. For long-term management, it could be useful to quantify the degree of invasiveness to specific genotypes, but the ISP does not currently have the data to address this issue. Pilot work has been done in this area (Sloop et al. 2009) but it remains an open question. Additional markers should be employed in this investigation, perhaps using a genome-wide association study (GWAS), but the plants' hexaploidy complicates using this approach.

The San Francisco Estuary Invasive *Spartina* Project has achieved a 96 % reduction in the acreage of hybrid *Spartina* since 2005 through the use of integrated landscape-scale monitoring and treatment. Less than three net hectares of invasive *Spartina* remain in areas that are currently permitted for treatment. The California State Coastal Conservancy has demonstrated an unparalleled commitment to noxious weed eradication by providing primary funding for the ISP for over 15 years in an effort to preserve native wetlands and protect the investment in regional tidal restoration.

The ISP is developing a long-term monitoring and response strategy to commence upon the eradication of all discernable hybrids within the Estuary. This plan will likely include periodic monitoring and genetic testing of any suspect plants identified during inventory throughout the project area for a number of years to ensure no resurgence of invasive hybrids. The strategies developed by the ISP, and the innovations designed to implement them effectively, should enable full eradication of hybrid *Spartina* once treatment can resume at all infestation sites. The ISP is built on partnerships committed to clearly-defined goals, which allows for shared responsibilities for planning, implementation and acquisition of future funding. Feedback loops of regular assessment and adaptation are necessary to balance the complex issues of invasive species removal, sensitive species, hybridity issues, and revegetation efforts for this regional conservation project to succeed. The ISP is one example of non-native *Spartina* management among numerous worldwide efforts, and the issues of hybridity and endangered species are becoming more prevalent in natural resource management. Our goal in presenting this management framework and retrospective analysis of the ISP is that it will assist other groups in their planning and implementation of conservation projects with a focus on weed eradication and habitat restoration.

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