

California Clapper Rails in the San Francisco Estuary:

**Modeling habitat relationships at multiple scales
to inform habitat restoration and eradication of
non-native *Spartina***

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1.0 INTRODUCTION

Restoring native tidal marsh habitat that supports the endangered California clapper rail (*Rallus longirostris obsoletus*) and other special status species is a major goal for the Coastal Conservancy's San Francisco Estuary Invasive *Spartina* Project, the South Bay Salt Pond Restoration Project, and other regional restoration and management programs. However, planning is premised on assumptions about clapper rail habitat use that have not, in most cases, been quantified. In particular, the impacts on rail populations of both tidal marsh restoration and non-native *Spartina* spread and control have not been studied. Updated quantitative information about the California clapper rail's relationship with invasive *Spartina* and habitat use in general will facilitate the improvement of strategies for both invasive *Spartina* control and tidal marsh restoration design.

1.1 Background

The San Francisco Estuary has one native *Spartina* species, *S. foliosa*, found in lower elevations of tidal marshes. In the past quarter of a century, four non-native species, *S. alterniflora*, *S. densiflora*, *S. patens*, and *S. anglica*, have been introduced to the estuary. Since its introduction, *S. alterniflora* has hybridized with the native *S. foliosa*, creating *Spartina alterniflora* x *foliosa*. These first-generation hybrids back-crossed with parent species and with each other and created a "hybrid swarm." The hybrids have spread rapidly around the Estuary, particularly in Central and South San Francisco Bay. At some locations hybrids comprise up to 100% of the marsh vegetation. Restoration sites newly opened to tidal action in Central and South San Francisco Bay, particularly those adjacent to invaded sites, are at high risk for invasion by these hybrids. Some hybrid individuals are extremely tall and dense and are capable of growing at lower elevations than either parent species, significantly impacting marsh physical processes. Long-term *Spartina* hybrid invasion impacts would likely include loss of structural and biological diversity due to loss of native tidal marsh vegetation, channels, and unvegetated tidal mudflats (Collins 2002). Additionally, with the spread of hybrid genes in the bay, native *S. foliosa* faces localized extinction (Ayres et al. 2003; Ayres et al. 2004). In this report, we use the terms "invasive *Spartina*" and "*Spartina* hybrids" interchangeably, in both cases referring to *S. alterniflora* hybrids, the dominant form of invasive *Spartina* in the focal study area.

The endangered California clapper rail (*Rallus longirostris obsoletus*) is a tidal marsh-dependent bird whose distribution is restricted to the San Francisco Estuary. The native cordgrass, *S. foliosa*, has been shown to be a critical component of clapper rail habitat (Albertson and Evens 2000). Recent survey results indicate that the rail also occupies habitat dominated by the non-native *S. alterniflora* and hybrids (Evens et al. in prep). In fact, clapper rail surveys in 2005 and 2006 show that the most highly invaded areas in Central and South San Francisco Bay have some of the highest clapper rail densities in the region, in many cases surpassing densities found in undisturbed historic marshes that are considered high quality rail habitat (Spautz 2005; Spautz and McBroom 2006).

The hybrid *Spartina* invasion is assumed to negatively affect populations of other bird species utilizing the tidal areas of the bay. Tall stands of hybrid *Spartina* growing at lower elevations than native vegetation may create an ecological trap for nesting populations of the Alameda song sparrow (*Melospiza melodia pusillula*), a state species of special concern (Nordby et al., unpublished data). Because *Spartina* hybrids grow at lower elevations than *S. foliosa*, mudflats

have been converted to hybrid *Spartina* meadows eliminating habitat used by foraging shorebirds (Stralberg et al. 2004).

1.2 San Francisco Estuary Invasive *Spartina* Project

The Invasive *Spartina* Project (ISP) is a coordinated regional effort to eliminate introduced species of *Spartina* (cordgrass) from the San Francisco Bay Estuary. To achieve this goal, the ISP requires information on the population of endangered California clapper rail in the marshes affected by the non-native cordgrass invasion.

Initiated in 2000, the ISP has a number of programmatic components including monitoring, vegetation control, outreach, and permitting. For all sites where introduced *Spartina* has been identified site-specific *Spartina* control plans are in place that incorporate the latest *Spartina* monitoring data, *Spartina* biology research, and California clapper rail survey data. ISP staff has mapped the distribution of introduced *Spartina* species and quantified the net acreage of each of the four non-native species and their hybrids. The estimate of non-native *Spartina* in the estuary in 2005 was approximately 775 net acres (313 hectares (ha)); the majority of this area was *S. alterniflora* and hybrids.

The ISP developed a method to predict the short-term impacts on clapper rail carrying capacity of a range of invasive *Spartina* removal strategies, based on assumptions about treatment efficacy and habitat values before and after treatment (Non-native *Spartina* Control Impact Evaluation Matrix, “SCIEM”, Grijalva and Albertson 2005). For the sites with the highest predicted potential impacts to rail populations, the ISP developed a strategy to phase treatment across multiple years and implement a suite of mitigation recommendations, primarily involving enhancing vegetation by planting gumplant (*Grindelia stricta*; Baye 2005 in USFWS 2005).

In 2005, the ISP’s partners treated 70% of the infested marsh area, using manual, mechanical, and chemical techniques. In 2006, the treatment area was increased, and all known infestations were treated, with the exception of portions of Arrowhead Marsh, Cogswell Marsh and the San Bruno Marsh area, where phased treatment was implemented to minimize impacts to clapper rails.

1.3 Clapper Rail Habitat Requirements

Studies of California clapper rail habitat requirements have not evaluated sites highly invaded by non-native *Spartina*. This is primarily due to the fact that most of these studies were conducted (1993 and earlier) when non-native *Spartina* was in the early stages of invasion and was not found at more than a few sites. Site characteristics associated with larger clapper rail populations and/or higher density populations from these studies include:

1. **Site area-** Larger sites are more likely to have more rails; populations are the most dense in marshes > 100 ha (Collins et al. 1994; Albertson and Evens 2000).
2. **Location of site relative to bay mudflats-** Sites adjacent to the Bay, and at the mouths of rivers and major slough systems (e.g., Petaluma River and Napa River) are more likely to have higher rail densities than are sites further removed from the Bay (Collins et al. 1994; Albertson and Evens 2000).
3. **Channel density-** Sites with higher channel densities, particularly second and third order systems, are more likely to support rails. Sites with little to no channelization

are unlikely to support rails (Collins et al. 1994; Albertson and Evens 2000; Foin et al. 1997).

4. **High and low marsh-** Sites with a combination of low marsh (*Spartina foliosa*-dominated) and high marsh (with ample *Grindelia* lining the channels) are more likely to support higher numbers of rails per unit area than those lacking either of these marsh zones. Low marsh is critical for foraging and high marsh is critical for nesting and refuge from predators (Albertson 1995; Foin et al. 1997; Albertson and Evens 2000). Sites with extensive *S. foliosa* are considered prime habitat in the South Bay. In the North Bay, where low *S. foliosa* areas are less prevalent, rails tend to be associated with higher-elevation, highly-channelized marshes with *Scirpus maritimus* (synonym *Bolboschoenus maritimus*; Gill 1979; Foin et al. 1997; Albertson and Evens 2000).

Additional studies in South San Francisco Bay tidal marshes indicated the importance of related habitat characteristics for nest-site selection and within-site habitat selection:

1. **Channel density, particularly small channels-** Nests tend to be located in areas with more tidal channels, usually smaller/narrower channels (Keldsen 1997). Rail territories are also more likely to be located in areas with more tidal channels, particularly 2nd or 3rd order systems (Albertson 1995).
2. **Gumplant density-** Nests tend to be found in areas with more gumplant cover (Keldsen 1997).
3. **Pickleweed density-** Nests tend to be found in areas with less pickleweed (*Salicornia virginica*, syn. *Sarcocornia pacifica*) cover (Keldsen 1997).
4. **Mid-elevation vegetation-** Nests tend not to be found in areas with more extensive lower marsh vegetation (i.e., *Spartina*; Keldsen 1997). However, both pickleweed and *Spartina foliosa* are typically found around the nest and are used for nest materials and for nest canopies (e.g., concealment; Harvey 1980; Foerster et al. 1990).
5. **Areas with more vegetation-** Rails tend to avoid open areas, preferring areas with more vegetation cover (Albertson 1995).

Most of these previous studies concentrated on large, high-elevation mature marshes. Many of the smaller sites invaded by non-native *Spartina* were not surveyed for California clapper rails prior to 2005, and no attempt had been previously made to quantify the relationship between clapper rail population density and invasive *Spartina* cover. Many of the smaller highly-invaded sites were assumed by local rail ecologists to not support rails previously, and probably did not support rails prior to invasion (with the exception of a number of marshes within the EBRPD system). In addition, no previous studies of clapper rail habitat use have taken advantage of the array of GIS and remote sensing technologies available to generate habitat configuration and other landscape-level metrics. Previous studies have indicated the importance of habitat fragmentation, patch configuration, and type of surrounding land use to the distribution and abundance of other tidal-marsh breeding birds, and clapper rails would presumably be sensitive to some of these landscape-level habitat features at some scale (Spautz et al. 2006). Prior to this study, there had also never been an effort to characterize the *Spartina*-hybrid invaded marshes on a regional scale, by looking for correlations of invasive *Spartina* cover with other structural habitat parameters.

We hypothesized that the invasion of *Spartina* hybrids has created a unique new form of habitat in the San Francisco Estuary that is highly attractive to clapper rails because it combines high, dense structure for nesting with large areas of vegetated low marsh critical for concealed foraging. This habitat is unique because the *Spartina* hybrid zone is generally wider

than the typical *S. foliosa* zone found in mature historic marshes, encompassing a wider range in elevation relative to tidal height, and comprising a larger proportion of the overall marsh vegetation. Many *Spartina* hybrid clones, particularly those found at lower elevations, are also taller than the native *S. foliosa*, and are typically also denser, providing a potentially superior source of concealment from predators while foraging, and taller nesting substrate. The increase in vegetated low marsh is most pronounced in areas where *Spartina* hybrid clones have expanded significantly into mudflats on the edge of the bay. However, the strength of the choice of invaded habitat by clapper rails has not been previously quantified, and, perhaps even more importantly, the value of this new *Spartina* hybrid “super-habitat” for breeding and foraging has not been studied. We don’t know if *Spartina* hybrid marshes are population sources (producing young beyond the numbers needed to replace adults lost to mortality, thus providing extra individuals that emigrate to other sites to breed) or population sinks (producing fewer young than needed to replace adults lost to mortality). We don’t know if nests built in *Spartina* hybrids are more or less likely to be depredated or flooded by high tides than are nests in native vegetation, or whether predation of foraging adults is lower or higher in invaded than in non-invaded areas. There is evidence that benthic invertebrate density is lower in *Spartina* hybrid stands than in *S. foliosa*, probably due to reduced interstitial substrate (Brusati and Grosholz 2006), so the quality of foraging habitat for rails in terms of prey biomass per unit area may be lower. It is also possible that the overall food resource availability is higher in an invaded marsh because the available vegetated low marsh area is larger, even if the prey density is lower. In addition, there is evidence that the relative abundance and species composition of benthic invertebrates in invaded sites is site-specific, and may depend on relative location, age of invasion, and composition of adjacent habitats (Neira et al. 2005).

Because treatment of invasive *Spartina* is proceeding rapidly and eradication is expected to be complete within several years, we may never have the opportunity to study the effects of the invasion on clapper rail populations beyond the observed changes in abundance and distribution. We expect that removal of *Spartina* hybrids will cause localized decreases in clapper rail numbers, primarily at sites where densities are significantly higher than found in non-invaded habitat and at sites where all *Spartina* species will be eradicated for several consecutive years (ensuring that hybrid populations do not rebound). This loss is likely to be short-term at many sites, but at sites where critical habitat components are lacking, removal of *Spartina* hybrids may also result in permanent losses of clapper rail habitat. We do not make predictions here about the level of potential decreases in clapper rail populations due to *Spartina* hybrid removal, but we anticipate that the data we provide can be used to make more sophisticated predictions of those potential changes than have been previously possible.

1.4 Study Objectives

This study was initiated to better understand how clapper rail populations are distributed with relation to invasive *Spartina*, and to assess whether the apparently higher densities seen in invaded sites are statistically significant. We also wondered whether other characteristics of marshes, such as marsh size and channelization, affected the relationship between rail density and invasive *Spartina* cover.

The overall objectives of the California clapper rail studies reported here were to:

- Conduct surveys of clapper rails during the breeding season to quantify and track population sizes at specific treatment and non-treatment sites to aid in invasive *Spartina* control planning.
- Provide information to support development of strategies to minimize adverse affects of removal of invasive *Spartina* on California clapper rails while meeting treatment objectives.
- Provide information to improve regional habitat management and restoration strategies for the benefit of the clapper rail, and thereby contribute to the species' recovery.

To this end, we developed a suite of hypotheses about habitat use by clapper rail of non-native *Spartina*, and subsequent effects of *Spartina* control, including the following:

- Population densities tend to be higher in *Spartina* hybrid-invaded sites than would be expected in the absence of invasive *Spartina*. Many of these invaded sites do not seem to have the characteristics previously thought to be important to clapper rails.
- Rails require both low elevation marsh (for foraging) and high elevation marsh (for nesting and refuge during high tides), and sites with both are likely to have higher rail densities. This requirement would be expected to be important regardless of level of *Spartina* hybrid invasion. Invaded sites may provide vegetated low elevation areas for foraging in higher proportions than non-invaded sites, but probably have lower proportions of high elevation marsh.

To improve our understanding of the relationship between clapper rails and the *Spartina* hybrid invasion, we modeled clapper rail habitat relationships using a combination of clapper rail survey data collected at 44 sites in Central and South San Francisco Bay in 2005 (Figure 1; Table 1), and field and GIS-generated habitat data at multiple scales, including field-collected vegetation cover and structural data, 2005 invasive *Spartina* inventory spatial data, and other patch-level spatial data.

Habitat selection models such as the one we present in this paper cannot indicate direct causality (e.g., we cannot say more rails chose this site due to the presence of *Spartina* hybrids), which is possible only with carefully designed experimental studies. Models also do not provide an indication of relative habitat quality, because density is not always related completely to habitat quality (Van Horne 1983), and individuals may be attracted to habitat features that actually decrease survivorship (i.e., the habitat may function as an ecological trap; Kristan 2003; Battin 2004). Predation is thought to be one of the most important factors driving rail population sizes in the region, particularly in the South Bay, and predator control has resulted in localized major recoveries in populations (Albertson and Evens 2000; Harding et al. 2001). However, the relative importance of predation on rail populations is poorly understood in the estuary, and understanding how predation rates of adult rails and their nests are affected by the non-native *Spartina* invasion is beyond the scope of this study. Thus, the analyses presented here will give us a quantitative measure of the strength of the association between rail population sizes and spatial patterns of invasive *Spartina*, but they will not provide us with direct understanding of how invasive *Spartina* affects population dynamics.

2.0 METHODS

2.1 Study Sites

Study sites included in these analyses were a subset of the sites surveyed for California clapper rails during the 2005 breeding season in Central and South San Francisco Bay. In the East Bay, sites included marshes from Emeryville Crescent south to Mowry Slough; and on the west side of the Bay, included marsh fragments on the San Francisco Peninsula south to Palo Alto Baylands (Figure 1; Table 1). These sites were surveyed by ISP, PRBO Conservation Science, East Bay Regional Park District, USFWS, and Avocet Research Associates staff.

Forty-four sites were selected that represented, to the extent possible, the range of clapper rail densities, non-native *Spartina* invasion, channel configuration, overall site configuration (e.g., bordering a flood control channel vs. directly bordering the Bay), size, restoration status, and *Spartina* treatment status (Figure 1; Table 1). Due to the extent of the *Spartina* invasion in the region, there were very few marshes available to survey with little to no invasive *Spartina*, and most of these uninvaded (or only partly-invaded) sites were large, historic, and highly channelized marshes with an extensive high marsh plain. We included a number of small, seemingly marginal sites not previously known to support rails that were surveyed due to USFWS requirements prior to treatment of non-native *Spartina*.

2.2 Clapper Rail Breeding Season surveys

California clapper rail breeding season call count surveys were conducted between January 15 and April 15, 2005, using standardized survey protocols approved by the USFWS. Within each survey site, survey stations were established 200 meters (m) apart, primarily on peripheral footpaths, levees, and boardwalks, rather than within marsh vegetation, to minimize disturbance to habitat and for observer safety. The number of survey stations established at each site varied due to site area, configuration, and accessibility, but at most sites there were at least eight points. Sites were surveyed by a trained and permitted biologist during the two-hour period surrounding sunrise or sunset, three times during the season with at least seven days between visits. The observer stood at each point for 10 minutes, recording all rails detected visually or aurally. Pre-recorded clapper rail vocalizations were used at survey stations on the third visit to elicit response from rails if no rails were detected during the two previous passive surveys within 200 m of the survey station. For each bird or pair of birds detected, the observer recorded the number of birds, call type, distance, and angle on a pre-printed datasheet and plotted the approximate location on an aerial photo. Rails detected outside the 10-minute survey periods were recorded only when they were not otherwise recorded during the survey. At sites where rails had not previously been documented and were expected to be absent due to small size and absence of most required habitat elements, we used a modified protocol approved by the USFWS specifically for the ISP to pre-screen sites prior to invasive *Spartina* treatment. For these surveys we played pre-recorded vocalizations during each of three rounds to maximize the chances of detecting any rails that might be there. If rails were detected, vocalization tapes were immediately stopped and were not played again within 200 m of the estimated rail location. At most of these sites, there was only one survey conducted if rails were detected on the first survey. If no birds were de-

tected, three rounds were conducted. Otherwise the protocols used were identical to standard rail surveys.

The minimum and maximum number of rails breeding at each site was estimated on the basis of all surveys completed during the season. Usually these numbers were the maximum count for both minimum and maximum birds detected across three surveys. Locations of birds at higher density sites, especially where birds may have been detected from multiple points or by multiple observers, were triangulated by plotting rail locations in GIS (using ArcView 3.3) improving the estimate of numbers detected during each round. Using GIS, the area surveyed for clapper rails at each site was calculated as a 200 m buffer around each survey point that was then clipped to include only tidal marsh habitat within that circular area.

Estimates of rail numbers were entered into an Access database to be merged with habitat data.

2.3 Clapper Rail Habitat Measurements

Randomly-selected fifty- meter radius sampling plots were generated in ArcView 3.3 using AlaskaPak extension (National Park Service 2002). One to eleven sampling plots were selected for each site (mean 5.8 ± 2.94), based on site area, within the area surveyed for clapper rails (see Figure 6 for an example). The centerpoints of all random plots were separated by at least 30 m from other random plots and from clapper rail calling center plots. Calling center plots, which were not used for the analyses presented here, were based on clapper rail calling center locations and visual detections derived from clapper rail breeding season surveys.

All data were entered into an Access 2000 database and summarized by site.

2.3.1 Field-based Habitat Metrics

Sites were visited after the clapper rail breeding season had ended, between September 1 and November 31, to avoid disturbing breeding birds. Vegetation and habitat structure metrics were collected in the field focusing on the 50 m radius random plots and adjacent channels (Table 2). For each site, we calculated the mean values of all random point data for each site for analysis. We selected metrics that were previously shown to be important to rails (e.g., proportion of particular plant species; Collins et al. 1994; Albertson and Evens 2000), or to other tidal marsh bird species (e.g., vegetation structure; Spautz et al. 2006).

At each sampling plot, we measured the proportion of each plant species expressed as a proportion of all vegetation, and the proportion of unvegetated mudflat. At nine sub-sampling points (placed at the plot center and 10 m and 30 m from the center on four perpendicular transects radiating from the center, starting with a randomly-chosen angle) we measured the density of plant stems at 10 centimeter (cm) height intervals and the maximum vegetation height within a 1 m radius. We measured the distance to the nearest tidal channel, and characteristics of the 20 m portion of that channel closest to the sampling point, including channel width, proportion cover of each plant species on the channel edges (within 2 m on each side), and the proportion of the channel interior mudflat surface covered by *Spartina* hybrids or *S. foliosa* (Table 2).

2.3.2 GIS-based Landscape and Vegetation Metrics

GIS-based habitat metrics were calculated for the 50 m radius random sampling plots, larger radius plots surrounding the geographic centroid of the survey area, the surveyed area, or the entire marsh area, depending on the metric, using ArcView GIS 3.3 and ArcView 9.0 (Table 3; Figure 7). Metrics used were based, where possible, on existing digital data sources, in particular EcoAtlas (SFEI 1998) and PRBO sources (unpublished data; Spautz et al. 2006). We selected metrics that were previously shown to be important to rails in other parts of the estuary (e.g., distance to tidal mudflats; Collins et al. 1994), or to other tidal marsh species (e.g., marsh area and configuration, type of surrounding land use, and distance to uplands; Spautz et al. 2006), and/or were proposed to be important to rails but had previously not been quantified and tested in the Central and South Bay (e.g., degree of channelization, edge proximity, and type of surrounding land use; Albertson and Evens 2000).

In ArcView 3.3 and 9.0, we created polygons defining the extent of tidal marsh vegetation, using a visual interpretation of 2005 ISP aerial photography at 1:1000 where it existed, otherwise U.S. Geological Survey (USGS) 2003 Digital Orthophoto Quarter Quadrangles (DOQQs), excluding tidal channels greater than 10 m wide. Where non-native *Spartina* invasion created new marsh in the last 10 years, these polygons were significantly different than EcoAtlas (1998) marsh areas, and many smaller marshes were not present in EcoAtlas at all. In addition, at sites that were part of larger areas of contiguous marsh (Audubon, Dumbarton, Faber, Greco, Laumeister, Middle Bair, Mowry, Newark) we digitized the boundaries of the area surveyed, which was based on a 200 m buffer around survey points, and used these areas to calculate some of the site metrics. We converted these two sets of polygons to lines to create an edge shapefile, and categorized the edges as upland, internal levee, tidal channel, bay, or marsh. We also used the marsh polygons to clip tidal flat and other inter- and sub-tidal polygons in EcoAtlas (1998) to create a series of updated intertidal polygons representing unvegetated mudflats and subtidal areas.

We created 90% minimum convex polygons including all field sample points for each site, and calculated the site centroid (i.e., polygon center).

We calculated marsh area in several ways, in all cases using the marsh area polygons described above. We buffered the plot centroids by 100 m, 200 m, 500 m, 1000 m and 2000 m, and used these buffers to calculate the proportion marsh in the same way that we calculated the area and proportion of surrounding land use (see below). We also calculated the area of contiguous marsh separated by < 50m, < 100 m, and < 200 m, by buffering the marsh area polygons and joining overlapping area to determine which sites were clustered together, using X-Tools for ArcView 3.3.

We calculated distance-to-edge metrics for sampling points using the Alaska Pak extension for ArcView 3.x (National Park Service 2002); using edges derived from our updated tidal marsh polygons. We calculated the proportion of edge to marsh area using the linear edge length and the entire marsh area (i.e., we did not confine it to area surveyed for larger contiguous marshes).

To characterize adjacent upland habitats (natural, urban or agricultural) we used an existing composite land use layer for the San Francisco Bay region consisting of the most recent 1:24,000 land use GIS layers from the State Department of Water Resources (DWR 1993–1999) and 1:24,000 land use GIS layers from the USGS Mid-continent Ecological Science Center (1996; PRBO unpublished data; Spautz et al. 2006). Landscape composition metrics were calculated for each site centroid by creating circular buffers of different widths (100 m,

200 m, 500 m, 1000 m, and 2000 m) and clipping the land use polygons with these buffers to calculate the area of each land use category.

To quantify channels, we used existing ArcView shapefiles (PRBO unpublished data; USFWS unpublished data) where available. Where data were not available, we digitized channels using a visual interpretation of 2005 ISP aerial photography at 1:1000 where it existed or, if 2005 ISP aerial photography was not available for a site, we used USGS 2003 DOQQs. At several highly channelized large sites where digitizing every channel would be excessively labor-intensive (i.e., Greco North, Middle Bair, and Arrowhead) we digitized channels within the 50 m radius random sampling plots and calculated the mean channel density for these sub-sampled areas. For these sites, we used the mean density to calculate an estimate of the total channel length for the entire plot. To calculate channel density for other sites, we divided the total channel length by the total digitized marsh area. We counted the number of first, second, third and fourth (or greater) order channel systems, but at highly channelized sites we stopped counting at seven systems.

Non-native *Spartina* spatial data were generated using a combination of field-based and digital GIS methods as part of an annual effort by the ISP Monitoring Program to track the invasion and guide eradication efforts (Ayres et al. 2004). A hand-held GPS unit was used to document smaller infestations, and boundaries of larger infestations were digitized in ArcView 3.3 and 9.0 using high-resolution aerial photographs generated in the fall of 2005. The percent cover to the nearest 10 percent of *S. alterniflora* and hybrids was calculated for each polygon. Discrete dense circular clones were easiest to identify in aerial photographs and distinguish from *S. foliosa* or other plant species. In some areas with higher plant diversity, especially where shorter hybrid clones were interspersed with other species higher on the marsh plain than is typical for either *S. alterniflora* or *S. foliosa*, invasion extent and percent cover were more difficult to accurately digitize, and field-based data (including random sample point data collected for this project) were used as a visual aid.

We calculated the proportion of *Spartina* hybrids in each marsh using circles of radius 100 m, 200 m, 500 m, 1000 m, and 2000 m centered on the site centroid (see land use metrics) to clip the ISP shapefiles. We calculated the net area covered by *Spartina* as the sum of the area covered in each of the polygons of the ISP shapefile, and divided this by the total area of the plot. We repeated the process with only the ISP polygons classified as 70% or greater cover of invasive *Spartina*, i.e. the areas most likely to be made up of the taller, denser *Spartina* clones. We thought that clapper rails were more likely to respond differently to these denser clones than to sparser shorter forms. We also calculated the area of 50% or greater *Spartina* cover.

2.4 Statistical Analyses

All data were summarized and merged in Access 2000 and imported to Stata 8.0 (StatCorp 2003) for statistical analyses.

2.4.1 Exploratory Analyses

Dependant Variable

The mean of the final clapper rail minimum and maximum estimates was calculated for each site. This value was divided by the area surveyed to produce an estimate of density generally referred to in wildlife ecology as an abundance index, in terms of birds per hectare (Bart et

al. 2004; birds/ha). We will refer to this variable as rail density (Table 1). This variable was examined against the final selected *Spartina* hybrid variable to determine if a transformation (e.g., log or square) would improve the normality of the residuals.

Independent Variables

To select the appropriate subset of the independent variables for analysis, groups of local and landscape-level variables were initially tested for pair-wise correlations with rail density and the most significant variables retained and modeled separately. These groups of independent variables included the following:

- 1) **Hybrid *Spartina* variables:** The appropriate scale (entire survey area; mean of 50 m radius sampling points; or 100 m, 200 m, 500 m, 1000 m or 2000 m radius around the site centroid), location (marsh plain, channel edges, or channel bottom), density classes (all polygons, > 50% cover or > 70% cover) and transformation (untransformed, log transformed, squared) were chosen based on pair-wise correlations with rail density. The top seven variables were chosen based on the lowest p-values. The performance of these top variables was compared in the final multi-variable multi-scale regression and the best performing variable was used to rerun the analysis. The final hybrid *Spartina* variable was analyzed in relation to all other vegetation and habitat variables to provide a quantitative description of the characteristics of invaded sites, and to better understand the relationships among these site characteristics.
- 2) **Vegetation cover and structure variables:** The plant species cover (on the marsh plain and channel edge), and plant height structure variables were examined for correlation with the dependant variable, rail density. Variables with $p < 0.20$ were retained for further examination in the modeling process. If required, they were log-transformed to decrease the sensitivity of the results to a few extreme values.
- 3) **Habitat configuration and channel variables:** Edge distance, channel density, and other channel metrics were also examined using the above process and the most significant variables retained. If required, they were log-transformed to decrease the sensitivity of the results to a few extreme values.
- 4) **Marsh and surrounding land use area variables:** The appropriate scale of analysis (100 m to 2000 m radius) and land use types (marsh, urban, natural upland, bay mudflats, bay and channel mudflats, and all mudflats plus water) were selected using two steps. First, the most appropriate scale was chosen by running separate multi-variable linear regressions by spatial scale with the dependant variable, using all land use variables, and selecting the model with the highest r^2 value. Next, the correlation of each variable at this scale with the dependant variable was examined and variables with $p < 0.20$ were retained for further examination in the modeling process. This resulted in a subset of land use variables of a single scale.
- 5) **Summary habitat variables:** A principal components analysis was run with all local habitat and landscape variables. The value for each site was calculated for each of the first three components, producing a set of three composite variables (i.e. three principal components). The dependent variable was then regressed on these three variables. If any of these were significant they were considered for inclusion in the final multi-variable model.

2.4.2 Regression Analyses

- 1) **Vegetation cover and structure:** We first looked for the best-fitting linear model, regressing the vegetation cover and vegetation structure variables, including the best *Spartina* hybrid cover variable, on rail abundance. We started first with all variables that were retained in the initial screening process. Using a backwards-stepwise process, we removed the least significant variables from the model, one at a time, until the only variables retained were significant at $p < 0.2$. These variables were then examined for the lowest Mallows' Cp value using the "rsquare" command in Stata 8.0. Cp is a model statistic very similar to AIC, where a model's score is penalized for including excess variables that do not sufficiently improve the overall fit, or r^2 . Variables were removed if their inclusion did not improve the score. Using Mallows' Cp minimization, variables with p-values of up to 0.12 were retained, rather than using the traditional significance cutoff of $p < 0.05$. We then reran the model with the six alternative *Spartina* hybrid variables (determined in part 1 to be significant) to see which was the most significant when accounting for the variability due to the other variables.
- 2) **Habitat configuration and channels:** We repeated the backward-stepwise process with the habitat configuration and channel variables.
- 3) **Marsh and surrounding land use area:** We repeated the process with the land use variables.
- 4) **Multi-scale model:** The variables selected using the above process were combined in a multi-scale regression model, and the reverse-stepwise process was repeated.
- 5) **Interaction terms:** Each of the variables in the individual scale models was examined for interaction with *Spartina* hybrid cover, marsh area, and channel density, all variables we proposed could be potential sources of interaction in the dataset.
- 6) **Final model:** A final model was developed by combining the interaction terms with the multi-variable model, using Mallows' Cp to determine whether a given variable improved the model score, and removing it if it did not, as with the initial models.

3.0 RESULTS

3.1 Clapper rail survey data

Clapper rails were present at all but eight of the 44 study sites. At sites with rails, density ranged between 0.4 and 5.8 rails/ha (mean 0.80; Figure 3; Figure 8; Table 1). Most of the sites with high rail densities (> 1 bird/ha) had very high invasive *Spartina* cover ($> 50\%$ cover; $n = 7$), but two of the high density sites were thought not to be invaded (Faber and Laumeister marshes in Palo Alto; Table 1).

To improve normality of the residuals of this variable with the *Spartina* hybrid cover variable, it was log transformed. In all model results discussed, the rail density variable used was log-transformed, but in graphs it is displayed in the original scale.

3.2 Regression models

3.2.1 Invasive *Spartina* Data

Of the 44 sites selected, four had very low or no *Spartina* hybrid cover, eight had low cover ($< 5\%$), nine had moderate cover (5 – 30%), six had high cover (30 – 50%) and 17 had very high cover ($> 50\%$ cover; Figure 4; Table 1). This categorization of sites was similar using data derived from both methods of calculating invasive *Spartina* cover (random field sampling points vs. digitization of aerial photography augmented by field mapping; Appendix 1).

Of the 18 alternative *Spartina* hybrid variables examined for pair-wise correlation with log rail density, all were significant at the $p < 0.05$ level, except the proportion *Spartina* hybrid on channel edges ($p = 0.06$; Table 5). All scales and all transformed (squared) and untransformed *Spartina* hybrid variables examined were significant. The most significant variable was *Spartina* hybrid of at least 50% cover within 200 m, squared. Looking at the top seven variables, the most significant scales were 200 and 500 m using polygons of 50 – 70% *Spartina* hybrid only (Table 5). After examining all variables in multiscale models, we ultimately decided to use the 200 m 70% cover *Spartina* hybrid shapefile variable (generated by the ISP Monitoring Program; Figure 9). This performed the best and was also at the same scale (200 m) as the most significant land use variables. It was also the best performer with the channel density interaction variable (see below). We also retained the field-collected *Spartina* hybrid channel edge and channel bottom variables for analyses because we thought they were also potentially of high biological value.

Of the three *S. foliosa* variables examined, none were significant at $p < 0.05$, but all were retained for further examination because this variable was thought to be important at non-invaded sites. Eighteen sites had *S. foliosa* marsh plain cover, 17 had channel edge cover, and 12 had channel bottom cover. Emeryville, Faber, Laumeister, Greco, and Middle Bair were the only sites with $> 9.5\%$ *S. foliosa* cover.

The *Spartina* hybrid cover variable (within 200 m, $> 70\%$ cover; hereafter referred to simply as *Spartina* hybrid cover) was highly positively correlated with all other *Spartina* hybrid variables, as would be expected. It was also significantly positively correlated ($p < 0.05$) with cover of *Carpobrotus edulis* (iceplant), vegetation structure over 30 cm, maximum plant height

(Figure 5a.), amount of urban land use (particularly within 100 m and 200 m), bay mudflat area and all tidal mudflat area (Figure 5b.; Table 4). It was significantly negatively correlated ($p < 0.05$) with a larger number of variables: cover of *Cuscuta salina* (on the marsh plain) *Distichlis spicata* (on the marsh plain), *Frankenia salina* (on channel edge), *Grindelia stricta* (on channel edge), *Salicornia virginica* (on marsh plain and channel edge; Figure 5c.), *S. foliosa* (on channel edge and within channels), all high marsh plant species (on marsh plan and channel edge), vegetation structure under 30 cm, channel density (Figure 5d.), marsh area, and distance to water edge (Table 4). There were also several less statistically significant, but potentially ecologically important relationships ($p < 0.15$), including a positive relationship to wrack cover and upland to water edge ratio, and a negative relationship to the number of third-order channel systems and distance to upland (Table 4).

These correlations suggest that *Spartina* hybrids have a tendency to displace other plant species (or to grow where other plant species cannot tolerate the conditions), provide taller vegetation structure at higher strata, and create more tidal wrack. Sites included in the study with a higher level of invasion have less dense vegetation structure at lower strata (due to relatively lower cover of pickleweed or other dense, short-stature species), are less channelized, smaller, and closer to the bay front, and are in the more urbanized areas of the Central and South San Francisco Bay. Most of the invaded sites in this study were linear bayfront marshes, or along major sloughs or creeks, particularly near creek mouths. Many of these marshes grew out into mudflats from otherwise very narrow strips of marsh vegetation—most of which would previously have been too small or insufficiently channelized for clapper rails. Larger, historic and higher elevation marshes with complex channel systems have not become as highly invaded as the smaller, narrower marshes and restoration sites. This is probably due to a combination of high marsh plain elevation, high competition from existing high marsh plants, and lower proximity to non-native propagules. Strong and Ayres (2005) found that *Spartina* hybrids were less likely to invade the pickleweed zone within historic marshes. Most hybrid clones are confined to creek mouths and bayfront edges in historic marshes and these areas are a smaller proportion of the overall marsh area compared to the narrower bayfront marshes and narrow marsh strips that line creeks and flood control channels.

3.2.2 Vegetation Cover and Structure

A number of vegetation cover and structure variables were significantly correlated with rail density at $p < 0.2$. Those with positive correlations included percent cover of iceplant (*Carpobrotus edulis*) and wrack; vegetation structure between 40 – 50 cm, 50 – 60 cm, 60 – 100 cm, > 100 cm, and all summed over 30 cm; and maximum vegetation height. Variables with negative correlations included proportion *Limonium californica*, *Salicornia virginica*, and all high elevation plant species on the marsh plain and channel edges; and vegetation structure below 10 cm and 30 cm. Proportion cover of *Jaumea carnosa* on the channel banks was significant, but this relationship was driven strongly by a single outlying high value at Arrowhead Marsh. This observation was excessively influential. When the analysis was conducted on log-transformed *Jaumea* cover, the variable was not significant thus it was not further explored.

The final vegetation model included *S. foliosa* within channels, the number of stems between 50 and 60 cm, and the proportion of *Spartina* hybrid cover within 200 m, all positive ($r^2 = 0.285$; Table 6a).

3.2.3 Habitat Configuration and Channel Variables

A number of habitat configuration and channel variables were significantly correlated with rail density at $p < 0.2$. Variables with a positive correlation included the number of first order, second order and all channel systems, mean distance of sample points to upland, and mean distance to mudflats. The relationship with ratio of upland to water edge was negative. Variables that were not significantly correlated included proportion upland or water edge, width of channel, and channel density. The latter variable was nonetheless expected to be biologically significant and thus was explored further for interaction with *Spartina* hybrid cover (see below). Sites with high channel density values included historic marshes with complex channel systems (e.g. Arrowhead and Dumbarton marsh) and long, narrow sites with a central channel and little marsh habitat on either side (e.g. San Leandro Creek and San Lorenzo Creek). Distance to channel was also highly significant, but was driven by several highly invaded sites with very few channels and extremely large average distance to channel (> 200 m). If these sites were excluded the variable was not significant. In addition, log-transformed distance to channel was not significant, so the variable was not examined further.

The final habitat configuration/channel model included distance to mudflats and ratio of upland to water edge (both negative; $r^2 = 0.127$; Table 6b).

3.2.4 Land Use Variables

Of the land use variables examined, the 200 m scale variables were consistently the most highly correlated with rail density. Of the 200 m variables, rail density was positively correlated with the proportion of surrounding bay mudflats and all non-marsh intertidal area, and negatively correlated with the proportion of agriculture. The proportion of tidal and muted marsh, an index for marsh area, was not significant at any scale. However, when we examined only the sites with $< 10\%$ *Spartina* hybrid cover, there was a significant positive relationship between marsh area within 200 m and rail density. This would imply that there was an interaction between *Spartina* hybrid cover and marsh area, but the interaction was not significant (see below). The area of contiguous marsh separated by < 100 m or 200 m was also not significant, but there was indication that the contiguous area separated by < 50 m was very close to being statistically significant when examined with other variables in the final multi-scale model with interactions. The interaction of this variable with *Spartina* hybrid cover was similarly very close to being significant but was rejected based on the Mallows Cp score (see below).

The final land use model included only proportion of bay mudflats within 200 m, a positive relationship ($r^2 = 0.218$; Table 6c).

3.2.5 Summary Habitat Variables: PCA

The performance of the three factors or components in a regression model with log clapper rail density was poor compared to the individual variables examined. Each principal component was only marginally significant individually and the best model contained all three factors (Mallows Cp = 4.00); however r^2 was only 0.192, which was so low compared to the other models examined that it we did not explore these variables further.

3.2.6 Multiple Scale Regression Model

All variables retained in the individual models described above were included in a single multi-scale model. Removing those that were not significant left (+) stems between 50 and 60 cm, (-) ratio of upland to water edge and (+) proportion of mudflat in the surrounding 200 m ($r^2 = 0.383$; Table 7a). *Spartina* hybrid cover was not significant.

Interactions between all significant variables in the individual scale models, marsh area within 200 m (centroid-based), area of contiguous marsh, and channel density, were explored. The only interaction that was significant when controlling for the variability due to the other significant variables was channel density x *Spartina* hybrid cover. The interaction was explored both as a continuous variable (*Spartina* cover x channel density), and as a categorical variable, with channel density characterized as low (< 1.8 [100 m]/ha) or high (> 1.8 [100 m]/ha). The interaction between *Spartina* hybrid cover and channel density was slightly stronger when it was expressed as a continuous interaction but this was more difficult to visualize and represent graphically than a categorical interaction (Figures 10a and 10b). For the poorly channelized sites, the relationship between *Spartina* hybrid cover and rail density was significant and positive (slope or $\beta = 0.85 \pm 0.247$; $p = 0.003$; $r^2 = 0.384$). For the highly channelized sites the slope appears negative but was not significant ($p = 0.59$, $r^2 = 0.014$). The model fit, including all variables that were significant along with the interaction variables, was $r^2 = 0.458$ when including the continuous variable (Table 7b), and 0.452 when including the categorical variable (Table 7c).

4.0 DISCUSSION

California clapper rail densities in the study area were highly variable (0 to 5.8 birds/ha) and much of that variability can be explained by variation in *Spartina* hybrid cover. Variability was statistically significant only in poorly channelized sites; at sites with highly developed channels systems (historic larger marshes) variability of rail density was not associated with variability in hybrid *Spartina* cover. There was also a significant relationship between rail density and channel density, but only where hybrid *Spartina* percent cover was low (< 10%). Sites with high hybrid *Spartina* percent cover tended to have fewer channel systems and much lower channel density. Highly invaded sites also tended to have taller vegetation with more stems between 50 and 60 cm than native marshes, which was also a factor associated with higher rail densities.

Clapper rail density was not significantly associated with the marsh size and extent variables in our dataset, which was not expected, because in other studies marsh area was statistically significant (Collins et al. 1994). In our dataset, higher rail densities tended to be associated more with areas adjacent to tidal flats rather than with extensive historic high marsh plains. Rail density was also associated with a lower ratio of upland edge to water edge, where water edge was the sum of bay edge and channel edges. Interestingly, sites with higher *Spartina* hybrid cover tended to have a higher upland to water edge ratio (due both to being poorly channelized and their generally narrow configuration, with a long upland edge). This is one characteristic of invaded marshes that seems to be less favored by rails. Upland edges may be important to rails for refuge during high tides, but they are also a potential source of predators, and, in urban areas, of contaminants and other sources of disturbance (Spautz et al. 2006; Takekawa et al. 2006).

The finding that both high levels of channelization and high *Spartina* percent cover are important to rails, and that marshes usually have either one or the other, was discussed by Foin et al. (1997), in the context of comparing habitat affinities in the North vs. South Bay and making recommendations for habitat restoration priorities. In South San Francisco Bay, higher density clapper rail populations tended to be associated with *S. foliosa* cover. The light-footed clapper rail (*R. l. levipes*) in southern California also has a high affinity for *S. foliosa* (Foin and Brenchley-Jackson 1991; Zedler 1993). In the North Bay, where *S. foliosa* is less common, high channel density tended to be all the more important to rails (Foin et al. 1997).

With this understanding of the strong level of selection for habitat with *S. foliosa*, where it is present, it is not surprising that rails have a strong affinity for areas invaded by *Spartina* hybrids, especially where the extent of this vegetation is extremely high. The presence of *S. foliosa* probably signals the availability of prime food resources, and *Spartina* hybrids are highly likely to be interpreted by rails in the same manner. In most of the estuary, *S. foliosa* covers < 15% of the vegetated marsh area (PRBO unpublished data; data in Keldsen 1997), although in our study, *S. foliosa* cover in Faber and Laumeister marshes was higher (27% and 16% respectively) and early restoration sites are likely to also be higher. In our study, the percent cover of *Spartina* hybrids ranged from 1% to 96.6% (Appendix 1). The greater area and taller height associated with *Spartina* hybrids at most invaded sites (particularly where clones are growing at lower elevations) may actually result in the *Spartina* hybrids serving the function of a “super stimulus”, where an animal preferentially selects a novel habitat element with

higher levels of key characteristics than normally found in the environment. The federally endangered southwestern willow flycatcher similarly preferentially selects invasive saltcedar (*Tamarix* spp.) for nesting over the usually preferred willows in riparian habitats in the west (DeLoach et al. 2000), due to saltcedar's superior branching structure.

Although we now have evidence that clapper rails are selecting habitat with high levels of *Spartina* hybrid cover, and that their territories are typically more dense in these areas than in non-invaded sites, we don't really know how well these habitats meet the rails' requirements for food, shelter and nesting substrate, and whether the rail populations at these sites are stable. The assumption is that where bird densities are higher, they defend smaller territories because the habitat requirements are present in greater concentrations and the birds require a smaller area to fulfill their needs. We have not proven this for rails and *Spartina* hybrids in the estuary, but it is the most parsimonious explanation for the phenomenon of significantly higher densities. In marshes with a high percent cover of hybrid *Spartina*, the taller and denser *Spartina* stands probably offer (or present to the rails the probability of offering) increased refuge from predators while foraging in a larger area, and may actually reduce adult predation rates. Nests built in tall *Spartina* hybrid stands may be better hidden from predators than those built in *S. foliosa*, however, because *Spartina* hybrids can grow at lower elevations than rails expect, nests may actually be at greater risk of tidal flooding. Food resources for rails- typically benthic invertebrates- may be less dense in invaded areas (Brusati and Grosholz 2006), but the availability to rails may be greater than in non-invaded areas due to the greater area of vegetated low marsh (Figure 11). In the absence of more information about reproductive success and demographic rates (survivorship, emigration and immigration), we can only hypothesize that rail populations in *Spartina* hybrid-invaded marshes are experiencing atypical ecological processes, some of which may improve survivorship, and others that may reduce it.

In invaded areas, the ability for *Spartina* hybrids to colonize mudflats at lower elevations has implications for the entire ecosystem. *Spartina* hybrid stands growing on the bay edge and in the channels may offer improved concealment for foraging animals at low tides, while simultaneously reducing foraging resources with decreased invertebrate densities in the mud below. Additionally, sediments accrete around *Spartina* hybrid stands and raise the substrate elevation; at sites where the invasion has been established for many years, channels have started to exhibit signs of being filled in. If not controlled, this accretion could cause loss of tidal channels, and a decrease in the habitat value for rails. These potential structural and hydrological changes would have direct and indirect impacts on the entire marsh ecosystem, from invertebrates to plants, birds and mammals. On the outer bay edge, the invasion has caused losses of open mudflat required by foraging shorebirds at the elevations most critical to these species: the upper mudflat edge. If the invasion were to be allowed to continue, there could be a significant loss of mudflat habitat in the estuary at a time when regional large-scale salt pond conversion to tidal marsh is simultaneously reducing habitat for shorebirds (Stralberg et al. 2004). The hybrid *Spartina* invasion potentially affects the resident Alameda song sparrow less directly. Tall, robust *Spartina* hybrid stands provide habitat for the marsh wren, an aggressive competitor, thereby potentially reducing habitat quality for song sparrows (Nordby et al. unpublished data).

Many of the most highly invaded sites with the highest rail densities (including Bayfarm Island, Airport Channel, MLK Restoration, San Leandro Creek, Oro Loma, San Bruno Inner Harbor, Samtrans Peninsula) probably did not support clapper rail populations prior to the

invasion of *Spartina* hybrids, and with the exception of the restoration sites (MLK Restoration and Oro Loma, which are relatively large, wide, and highly channelized) do not have the characteristics typically associated with clapper rail habitat: extensive channelization and large marsh area. Most of these invaded sites are comprised of a very narrow strip of high marsh vegetation with extensive areas of hybrid *Spartina* at lower elevations, usually along the bay front, and a high upland edge to water edge ratio. When *Spartina* hybrids are removed, these sites will probably not have sufficient quantities of the other habitat elements required to support rail populations, i.e., tall vegetation, channelization or vegetated low marsh. This is likely to be the case in the short-term, for several years, while all *Spartina* species are controlled and the site is without vegetated high marsh as well as in the longer term after *S. foliosa* is allowed to re-establish. The area re-colonized by *S. foliosa* is likely to be smaller than the current area of hybrid *Spartina*, indicating that both the vegetated low marsh and total marsh area are likely to be smaller and similar to the pre-invasion marsh size.

5.0 CONCLUSIONS AND RECOMMENDATIONS

This study examined the relationship of *Spartina alterniflora* x *foliosa* hybrid cover to clapper rail population density. We documented a statistically significant positive relationship between the proportion of *Spartina* hybrid cover and rail density. We also confirmed the importance to rails of specific physical features, including channel density, the location of the marsh relative to bay mudflats, the proportion of adjacent mudflats, the ratio of upland edge to water edge, and tall vegetation structure. We found a significant statistical interaction between *Spartina* hybrid cover and channel density, indicating that rail densities were highest in areas with either high channel density or high *Spartina* hybrid cover. These characteristics tended to be mutually exclusive in the marshes we studied. Many of the invaded marshes with higher channel densities were composed of long narrow strips of vegetation on either side of a central channel (e.g., San Leandro Creek) rather than wide marsh plains with complex channel systems. Sites with a large proportion of *Spartina* hybrid cover had higher rail densities than would be expected given the other characteristics of a site. There were very high rail densities at a number of very small, poorly- or non-channelized sites that we would not expect to support rails if *Spartina* hybrids were absent and instead *S. foliosa* was present. Some of these sites were not previously known to support clapper rails at all (e.g., Bayfarm Island and Airport Channel).

The results presented here confirm those of previous studies, give us a deeper understanding of the habitat affinities of clapper rails, and allow us to make additional hypotheses about why rail densities are so high in marshes that are highly invaded by *Spartina* hybrids. In conjunction with the results of previous studies, we can predict which sites probably have significantly higher rail populations than they did before the non-native *Spartina* invasion. These results also allow us to make some general predictions about the types of sites that are most likely to have reductions in rail populations after *Spartina* hybrids are removed, both in the short- and long-term, based on their predicted habitat value when all *Spartina* species are absent, and after *S. foliosa* recolonizes the site, returning it to its pre-invasion condition. We can also use this information to make recommendations for habitat management, especially pertaining to invasive *Spartina* control, and habitat restoration in general.

5.1 Hypotheses Related to Clapper Rail Use of *Spartina* Hybrid Areas

We hypothesize that clapper rail densities tend to be higher in marshes invaded by *Spartina* hybrids than in otherwise similar marshes that are not invaded, due to the following:

- 1) Clapper rails use cues related to habitat structure, in particular vegetation height and density, to make decisions about habitat quality. Vegetation height and density are important characteristics of nesting substrate and for concealment from predators. *Spartina* hybrids tend to be taller than other vegetation in the portions of the estuary where rails are typically found (i.e. saline to slightly brackish), with the exception of alkali bulrush (*Scirpus maritimus*, syn. *Bolboschoenus maritimus*).
- 2) The combined characteristics of greater extent and taller structure make *Spartina* hybrid areas highly attractive to rails. This may represent an instance of a “super stimulus”,

where cues to habitat quality are much stronger than those typically found in the species' habitat, and result in preferential habitat selection (e.g., DeLoach 2000). If these *Spartina* hybrid-invaded areas do not function as well as the native habitat—for example, if predation is higher and nest success lower, these areas may function as an “ecological trap”.

5.2 Some Thoughts About Clapper Rail Use Pre- and Post-*Spartina* Invasion

We believe, based on historical data and our understanding of rail habitat affinities, that a number of sites in this study probably did not support rails prior to invasion of *Spartina alterniflora* and its hybrids, at least in the last 100-200 years since these areas were diked and/or filled for human use. These sites are: Bayfarm Island, Airport Channel, MLK Restoration, San Leandro Creek, North Marsh, Citation Marsh, Oro Loma Marsh, San Bruno Marsh, San Bruno Inner Harbor, and Samtrans Peninsula. Bunker marsh is not included in this list because, although it is still in the process of restoration, it has significant cover of species other than *Spartina* hybrids, and the total vegetation cover is comparable to that found at historic or fully-restored sites; we also don't know when *Spartina* hybrids first invaded the site and we don't know when clapper rails first arrived.

The list contains two different types of marshes: 1) restoration sites, and 2) narrow marsh strips that formed on the edge of levees, typically on the bay edge or along tidal channels. Sites in the first group, which includes North, Citation, Oro Loma, and MLK Restoration, are still young, are at relatively low elevations, and are less fully vegetated (56, 58, 33-47 and 55%, respectively) than the historic, highly channelized sites in the study (70-85%). *Spartina* hybrids are a major component (> 10%) of vegetation cover at MLK and Oro Loma West, and have probably made a significant contribution to the recent rapid sediment accretion. Prior to the invasion, clapper rails would probably not have found much habitat in these restoration sites. Sites in the second group, the narrow marsh strips, were probably very narrow strips of pickleweed with a scattering of *S. foliosa* along the edge prior to the invasion of *S. alterniflora* and hybrids. They probably lacked substantial areas of either low or high marsh and did not have complex tidal channel systems. They were not likely to be used for nesting, although they may have been used for foraging, particularly during the winter by young birds without territories, and if they were close to larger high quality marshes.

When hybrid *Spartina* is removed, rail populations are likely to decrease substantially at all sites in the list above, at least in the short term. The restoration sites are likely to become appropriate rail habitat after *S. foliosa* becomes re-established, and as marsh elevation increases. They were designed to have complex channel structure, and are likely to have extensive high marsh plains within several decades. However, the narrow linear sites will probably not regain habitat elements that clapper rails will find appropriate for nesting, even after *S. foliosa* re-colonizes.

The potential short-and long-term effects of invasive *Spartina* removal are more difficult to predict at sites with existing complex channel systems and significant areas of upper marsh. If clapper rail densities are higher than typically found in uninvaded marsh, there is likely to be a significant reduction in rail densities, at least for the short term.

5.3 Recommendations for Regional Tidal Marsh Restoration

We can also make some additional recommendations related to habitat restoration in the estuary:

- 1) Efforts should be made to enhance suitable clapper rail habitat in areas close to the sites that will be the most affected by *Spartina* removal. For the near term, enhancement of upper marsh areas may be the only practical option. However, long-term regional management plans should include creation of new tidal marsh areas with high channel complexity and healthy stands of *S. foliosa*, which will be accomplished to a large extent by the planned large-scale conversion of salt ponds to tidal marsh in the region. These efforts should not take place until invasive *Spartina* has been moved or sufficiently contained.
- 2) High quality California clapper rail habitat has the following components: complex channel systems, a low upland edge to water edge ratio, close proximity to bay mudflats, large areas of *S. foliosa*, and taller vegetation structure. Restoration sites should contain as many of these components as possible.
- 3) When any one of the above components is lacking, the other components increase in importance. Thus, sites that are unlikely to support vegetated low marsh (i.e., *S. foliosa*), but will support large areas of high marsh, are more likely to support clapper rails if they are highly channelized. Sites with low channel complexity are more likely to support clapper rails if they have extensive vegetated low marsh (i.e., *S. foliosa*).
- 4) The most valuable potential restoration sites are those closer to the bay edge. Those further upstream are less likely to be colonized by clapper rails, but the probability of colonization may increase if the area is managed for high *S. foliosa* cover or is highly channelized and fully tidal.
- 5) Where at all possible, restoration site plans should minimize the length of upland edges while maximizing the length of water edges (including channel and bay edges). This could be achieved by increasing the width of levee breaches, particularly those located at the bay front, or by completely removing levees.

5.4 Recommendations for Further Study

With eradication of invasive *Spartina* well underway, there are few opportunities for additional research to better understand the effects of the invasion on clapper rails. However, there are several sites, including the San Bruno Marsh complex, Arrowhead Marsh and Cogswell Marsh that have large rail populations where *Spartina* hybrid removal has been at least partly delayed as part of a regional treatment strategy. To the extent possible within these or other sites, we recommend the following additional studies:

- 1) Study the success of clapper rail nests at highly invaded sites to determine whether nests are placed in invasive *Spartina* preferentially, and if so, whether those nests are more or less likely to be lost to predation and/or tidal flooding than nests placed in other substrates. If nesting success is exceptionally low, this may indicate the presence of an ecological trap, and would probably indicate that immediate removal of all

Spartina hybrids would be in the best interest of the species, even at the sites that have caused the most concern for loss of rail habitat.

- 2) Continue to track clapper rail numbers throughout the *Spartina* treatment process and after eradication. If rail populations decrease more rapidly or more dramatically than anticipated as hybrid *Spartina* is eradicated, additional analyses should be completed to determine the relationship between habitat change (including factors other than hybrid *Spartina* removal) and decreases in rail numbers so that suitable mitigation can be rapidly implemented.
- 3) Determine the applicability and feasibility of replanting *S. foliosa* in areas where hybrid *Spartina* has been removed by reviewing existing studies and through experimental plantings.

6.0 ACKNOWLEDGEMENTS

Survey data were provided by Avocet Research Associates, East Bay Regional Park District, Olofson Environmental, Inc., PRBO Conservation Science, and U. S. Fish and Wildlife Service. Field biologist staff included P. Abbaspour, J. Albertson (and her staff at USFWS), J. Evens, M.A. Flett, L. Liu, R. Keck, A. Nelson, A. Robinson, R. Stallcup, E. Strauss, and D. Wimpfheimer, and the authors. K. Zaremba, A. Good, J. Good, T. McCandlish, and A. Nelson collected the invasive *Spartina* inventory data. N. Nur (PRBO) assisted with statistical analyses. D. Stralberg (PRBO) provided GIS data. Permission for site access was granted by East Bay Regional Park District, City of San Leandro, City of Palo Alto, and Don Edwards San Francisco Bay National Wildlife Refuge. Surveys were conducted under the authority of U.S. Fish and Wildlife Service permit TE118356-0 (issued to Olofson Environmental, Inc.) and a Memorandum of Understanding between Olofson Environmental, Inc. and California Department of Fish and Game. Funding sources included California Coastal Conservancy, California Resources Agency, CALFED Bay-Delta Program, California Wildlife Conservation Board, USFWS Section 6 grant to PRBO Conservation Science and Avocet Research Associates, East Bay Regional Park District, and U. S. Fish and Wildlife Service.

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8.0 FIGURES

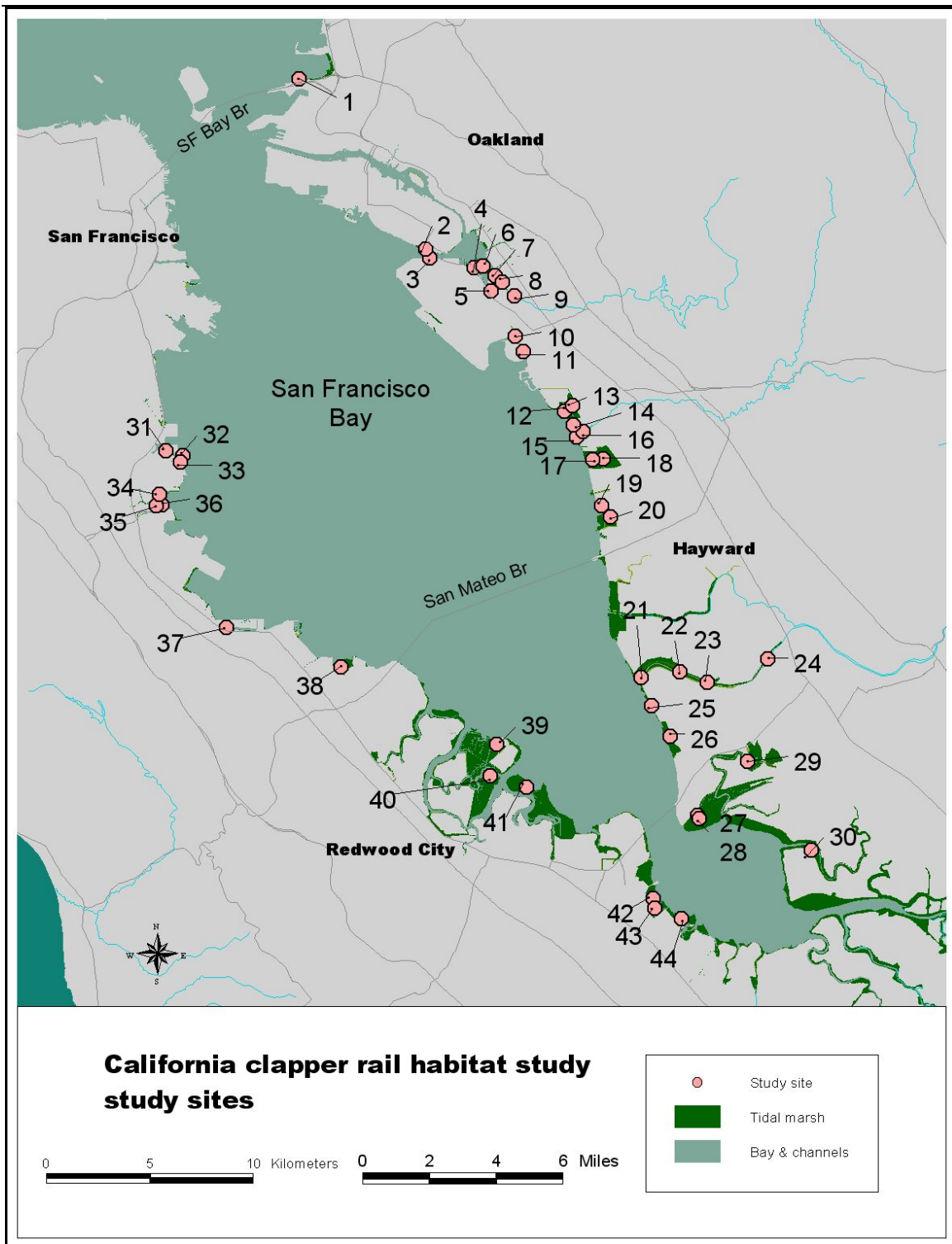


Figure 1. Study sites in San Francisco Bay.

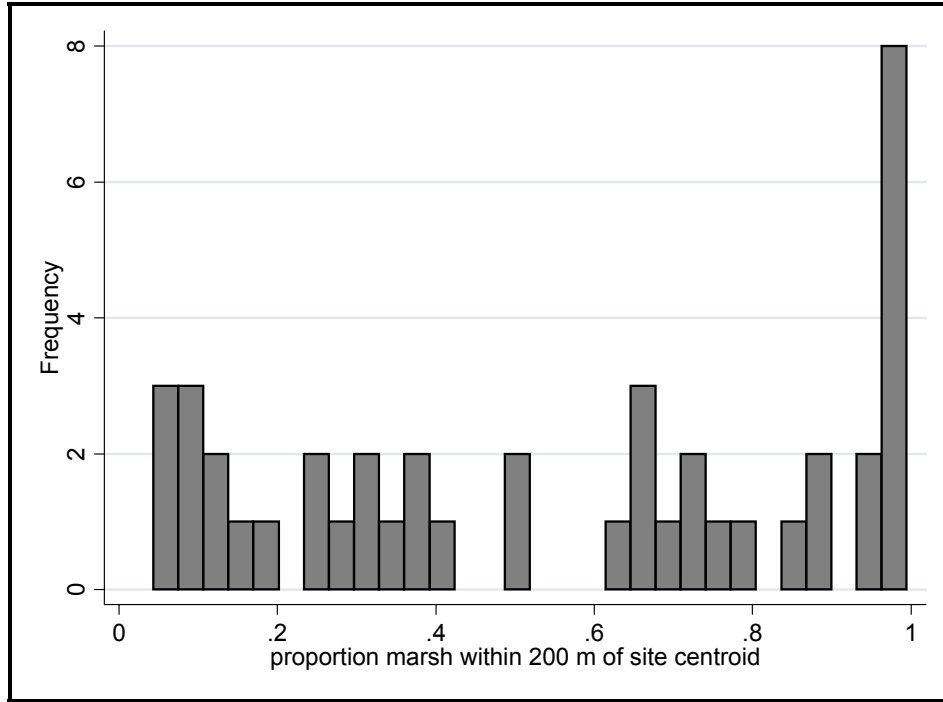


Figure 2. Distribution of sites by proportion of marsh within 200 m of site centroid.

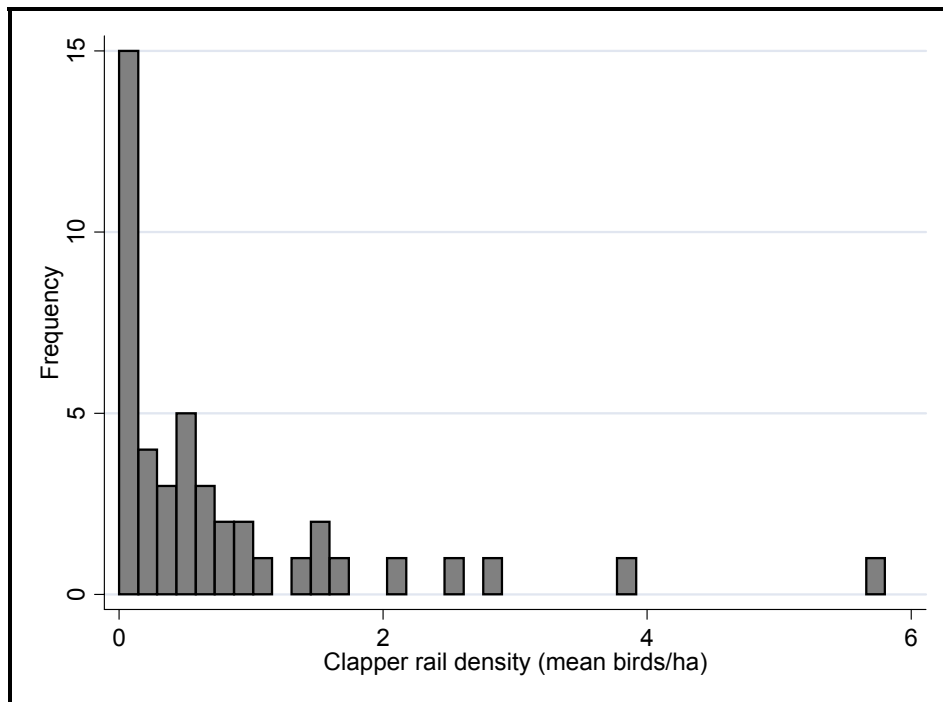


Figure 3. Distribution of sites by California clapper rail density.

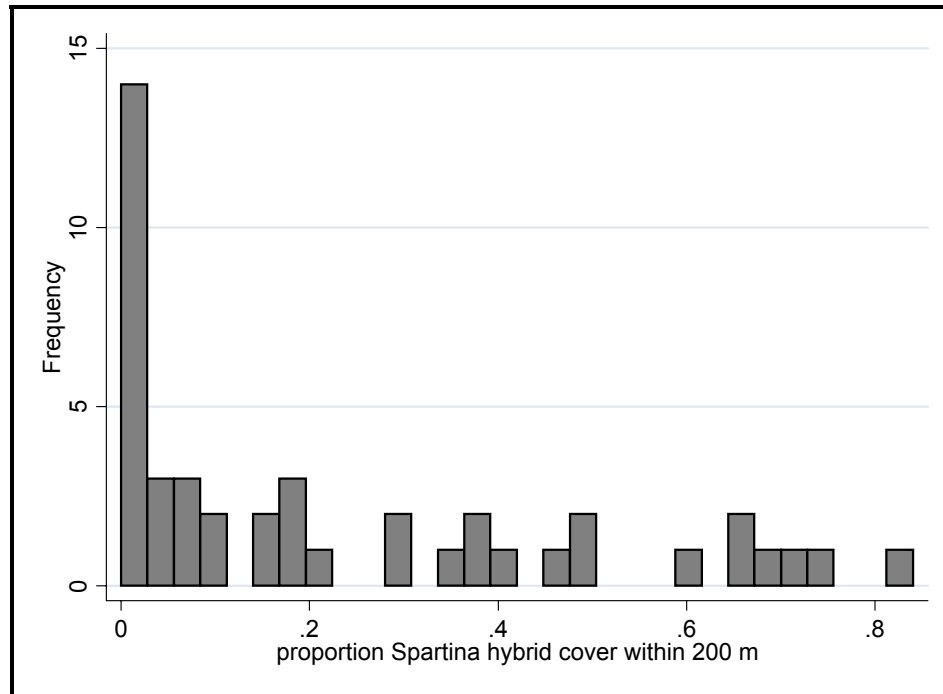


Figure 4. Distribution of proportion of high density (> 70% cover) *Spartina* hybrid cover within 200 m of site centroid.

Figure 5. Graphs of correlations of *Spartina* hybrid cover with select habitat variables.

Data points are shown for each of the sites in the study. Regression line and associated statistics are shown.

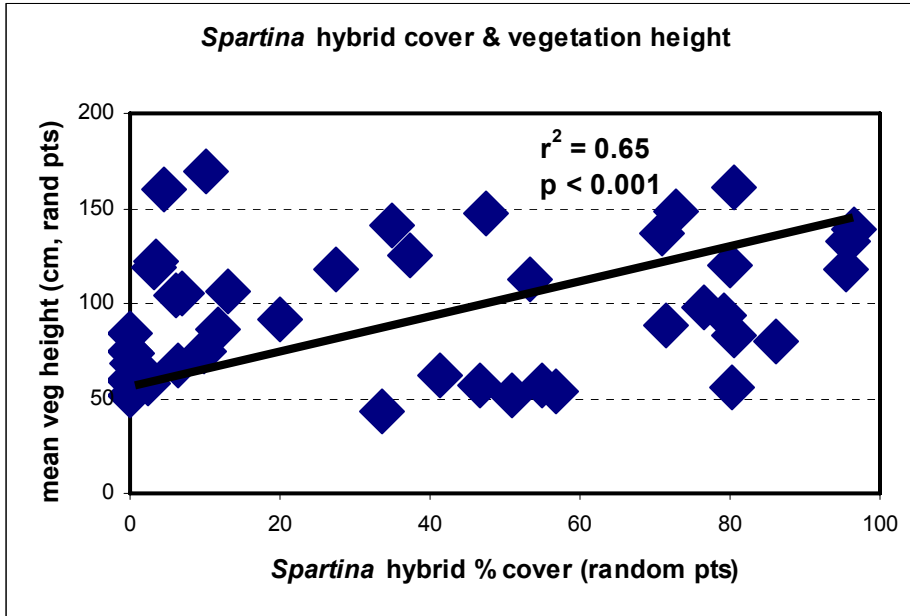


Figure 5a.

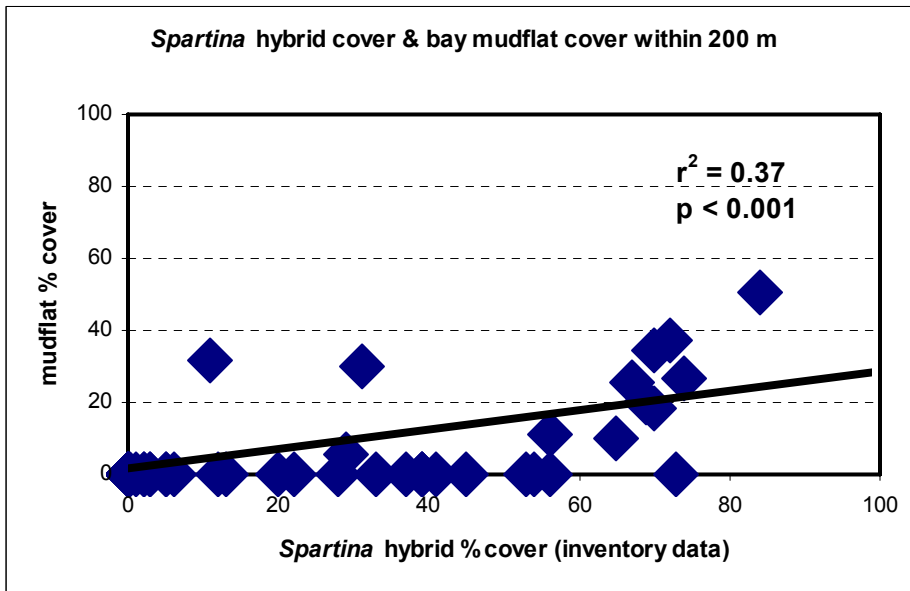


Figure 5b.

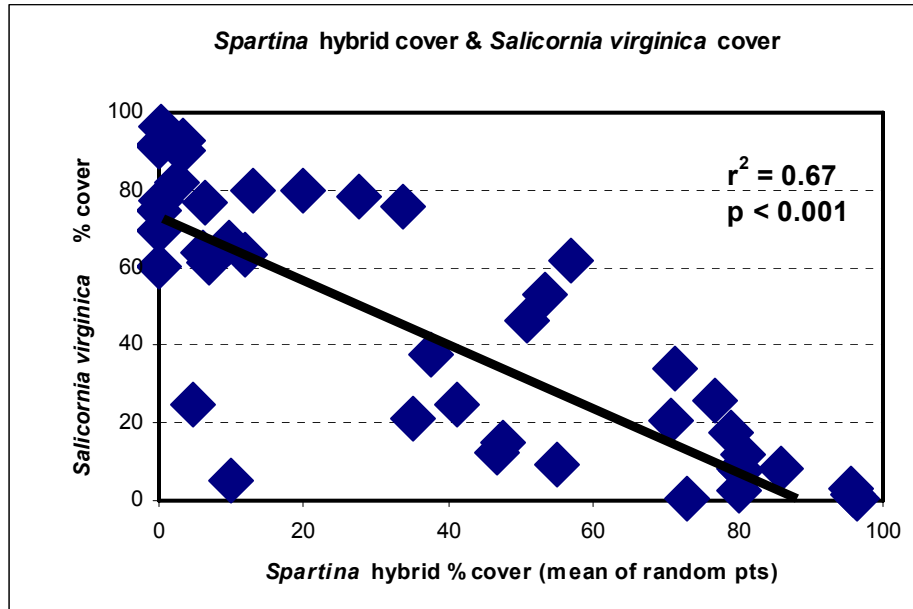


Figure 5c.

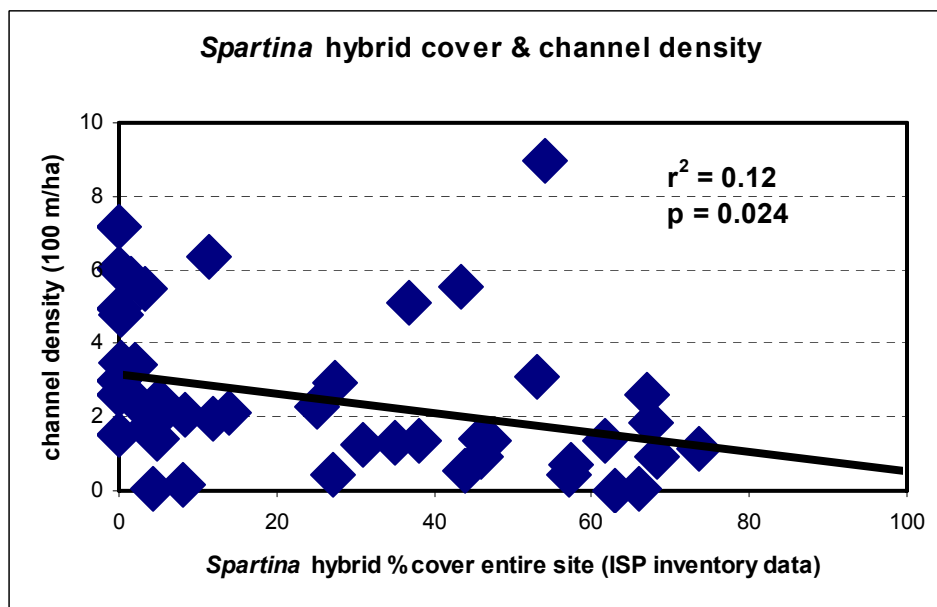


Figure 5d.

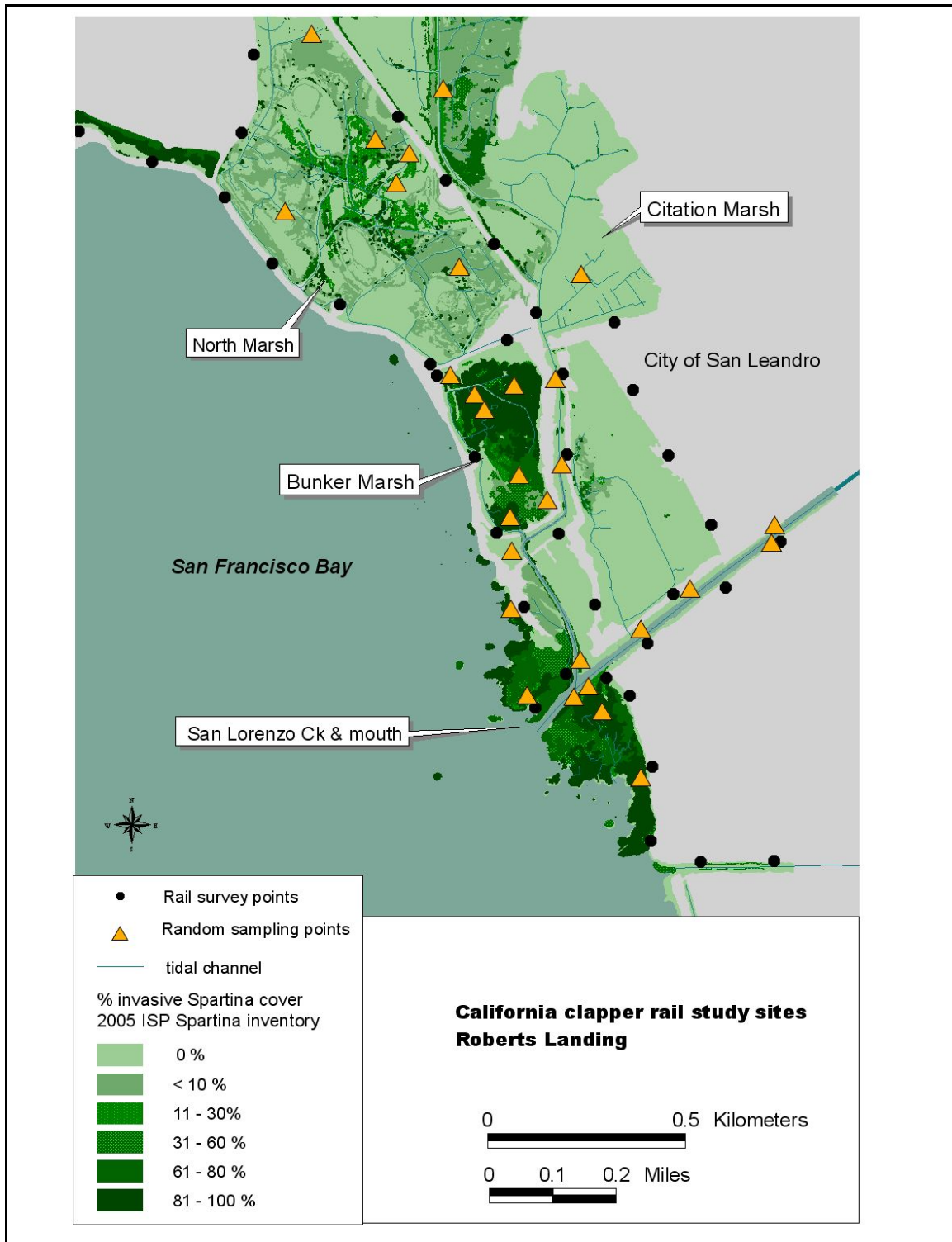


Figure 6. Example of distribution of rail survey points, random sampling points, and invasive *Spartina* cover at study sites at Roberts Landing, San Leandro (Table 1, sites 12 - 16).

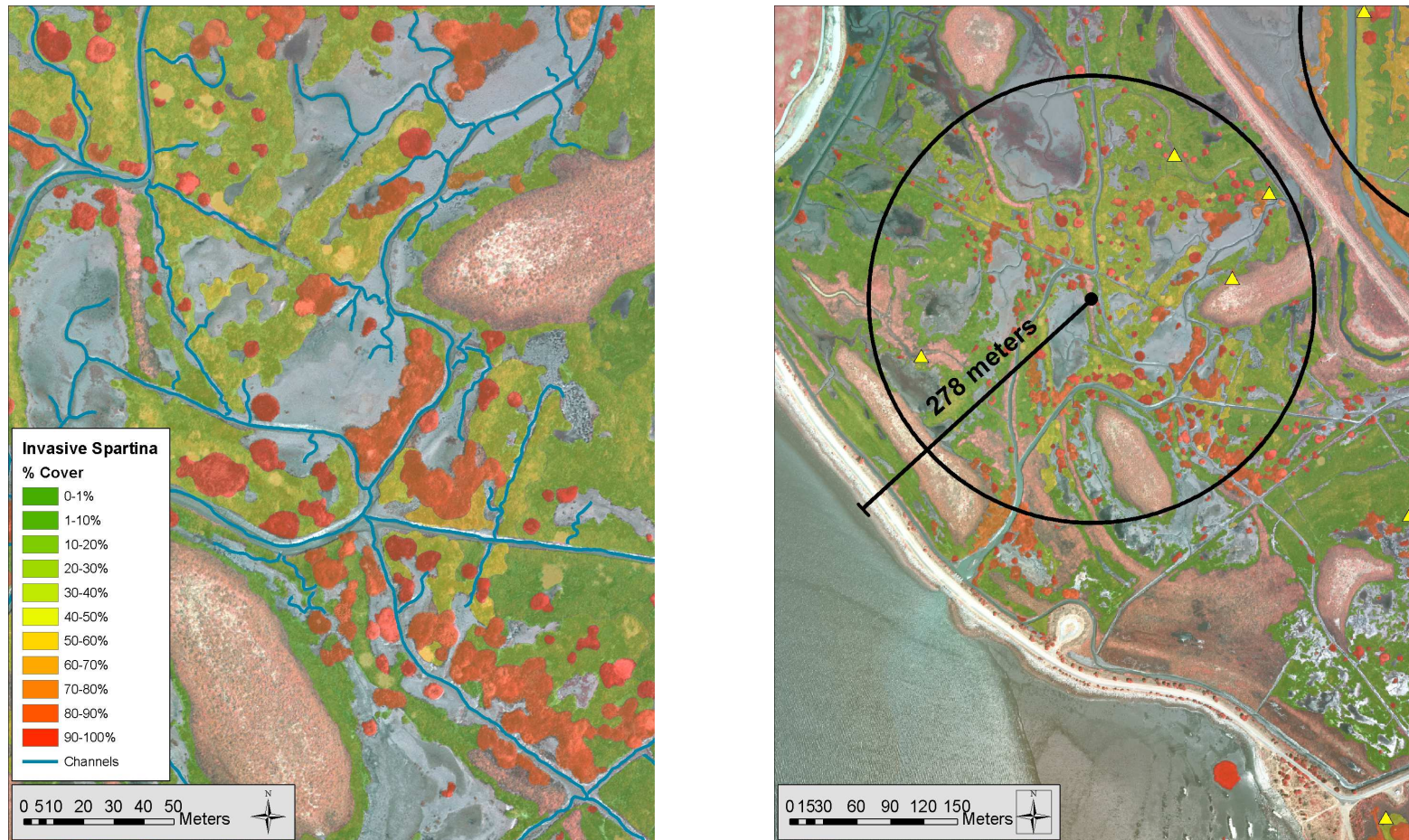


Figure 7. Example of GIS data calculated for North Marsh

Left: ISP invasive *Spartina* cover data and digitized channels. Right: 200 m radius circle centered on centerpoint of survey area, to calculate proportion of invasive *Spartina*, and distance from centerpoint to tidal mudflats (here 278 m). Random field sampling points are indicated by yellow triangles.

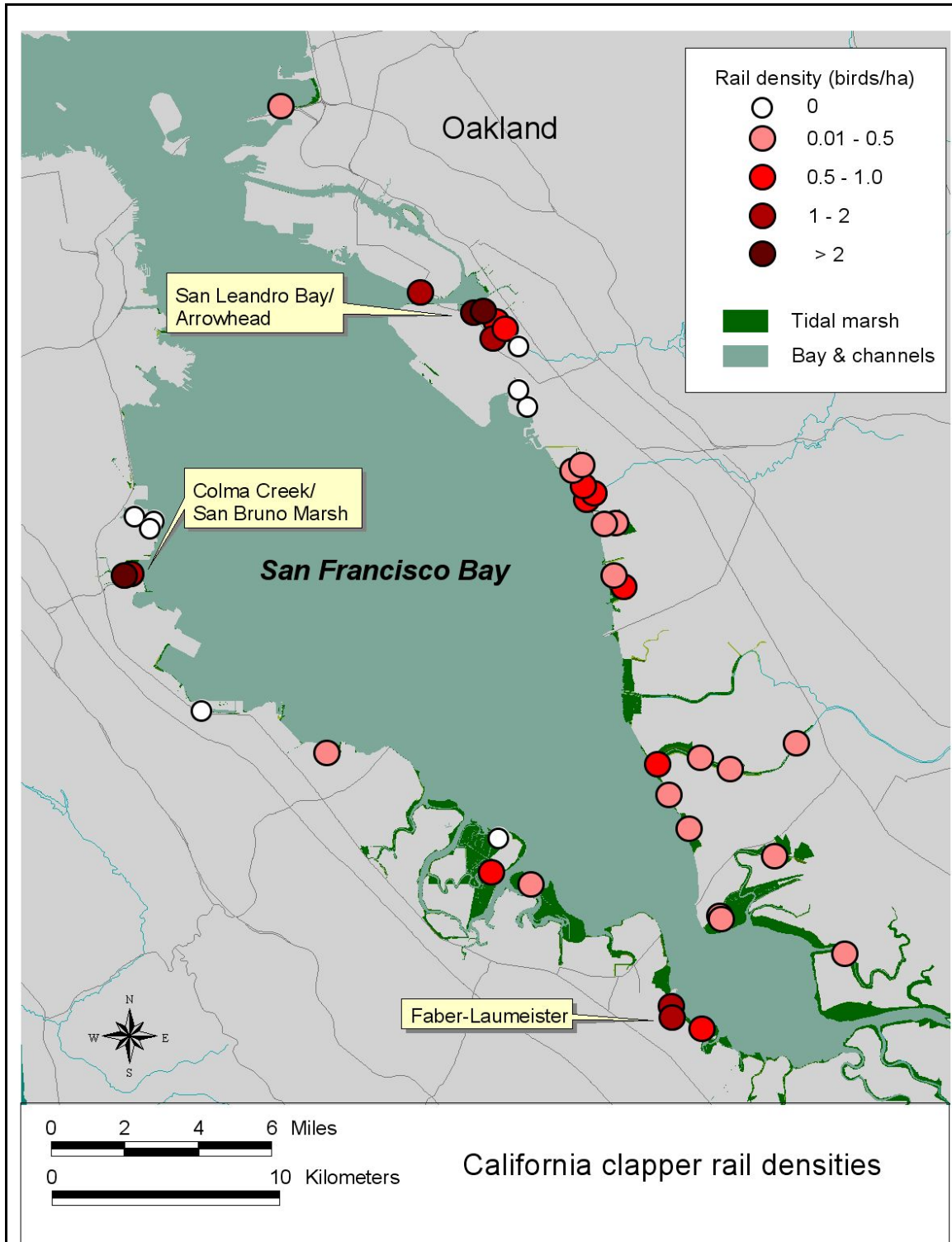


Figure 8. Map indicating study sites, color-coded by California clapper rail densities estimated in 2005 (n=44).

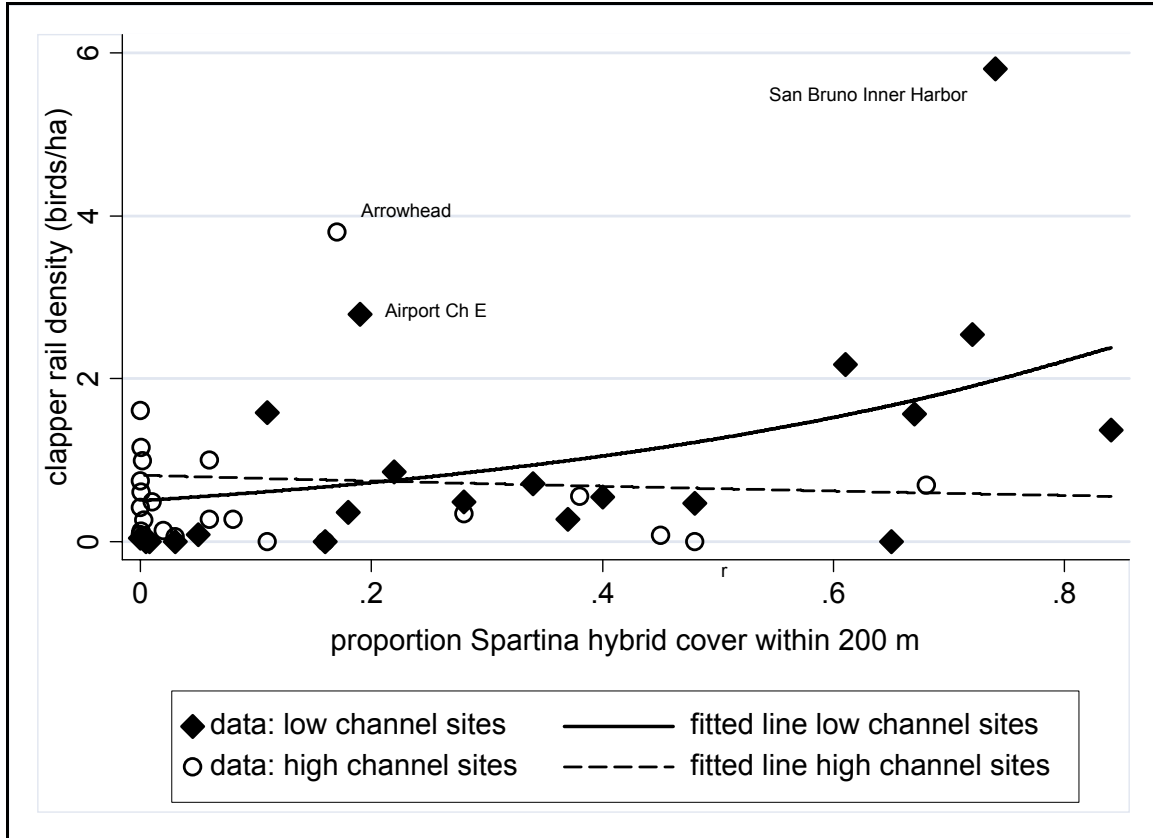


Figure 9. Relationship between proportion of *Spartina* hybrid cover within 200 m (> 70% cover only) and clapper rail abundance index: interaction with channel density.

Data points for the raw data are included for comparison; outlier sites are labeled. The line was fitted separately for highly channelized (dashed line) and poorly channelized sites (solid line) without other independent variables, using the log of rail density. The y-axis is the raw density; the exponent of the fitted values (based on a model with log rail density) was used to form the line, accounting for the slight curve. For the poorly channelized sites, the slope is significant: $\beta = 1.86 \pm 0.57$ ($p = 0.004$; $r^2 = 0.36$). For the highly channelized sites the slope appears negative but is not significant ($p = 0.55$, $r^2 = 0.02$). Channel density is calculated as $100 \times \text{channel length} / \text{marsh area (m/ha)}$.

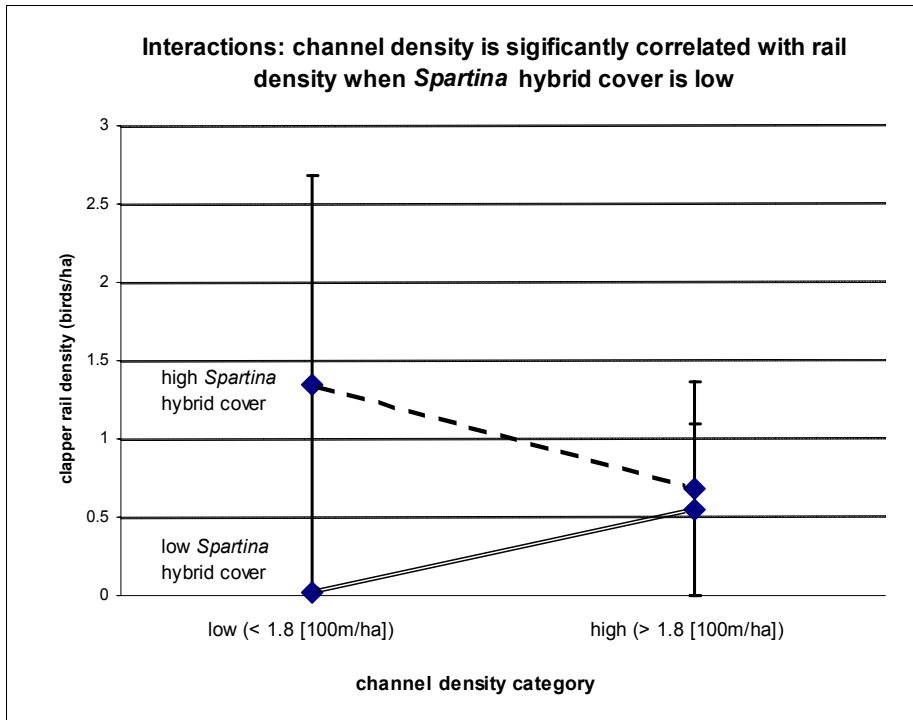


Figure 10a. Categorical interaction between *Spartina* cover and channel density.

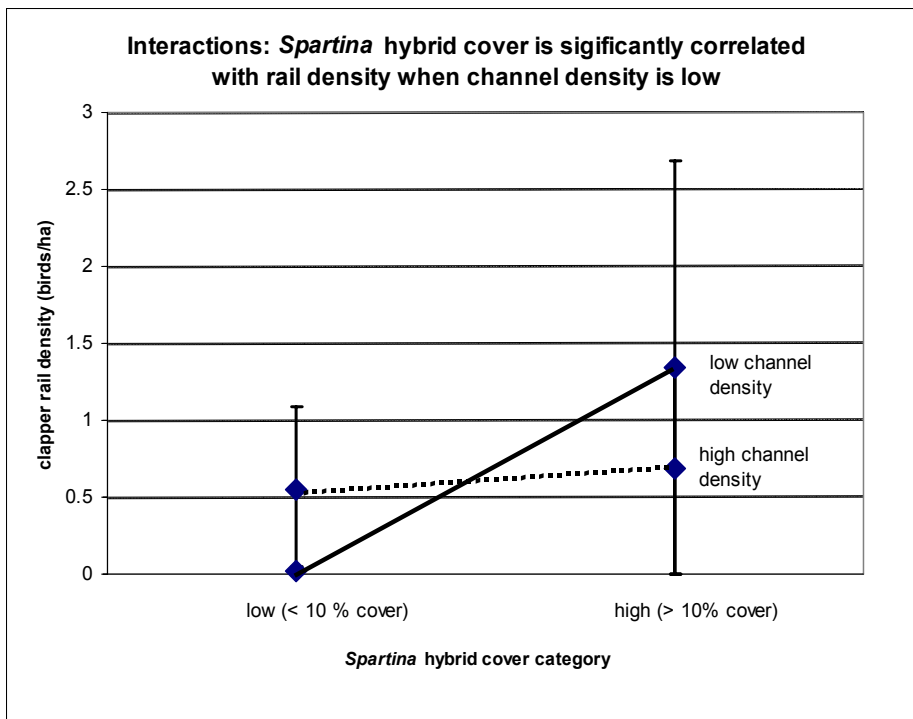


Figure 10b. Categorical interaction between *Spartina* cover and channel density.

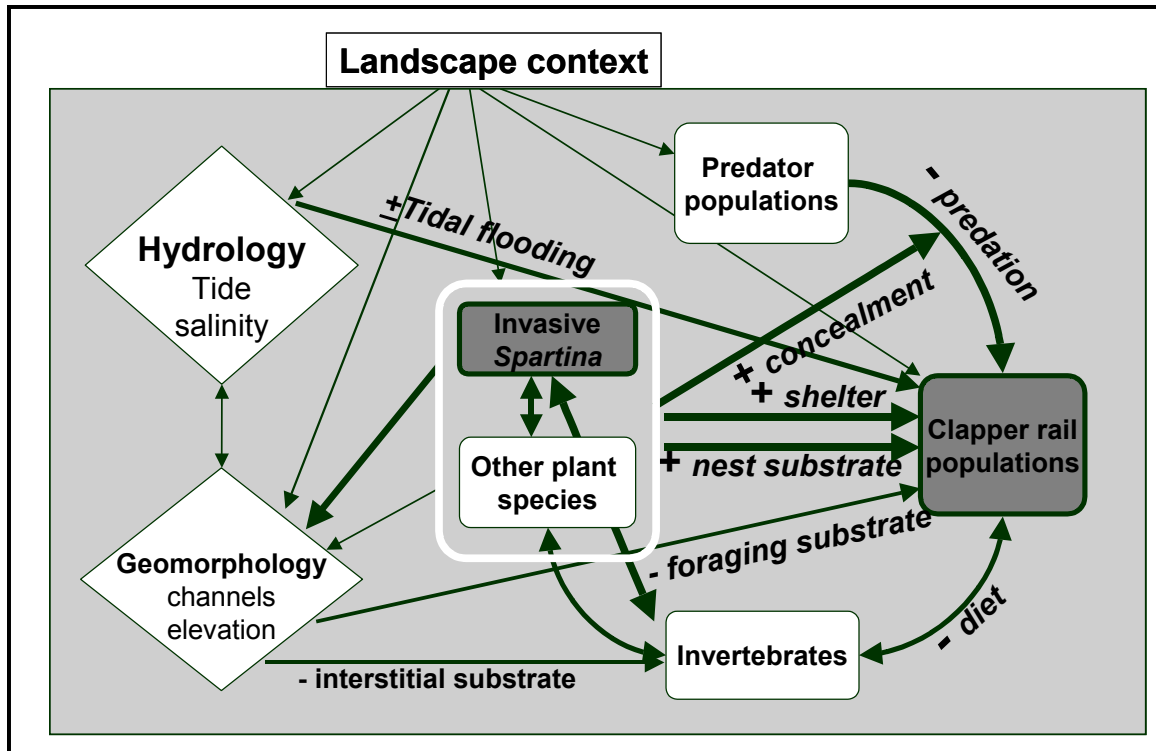


Figure 11. Conceptual model of the effects of non-native *Spartina* invasion on clapper rail ecology.

9.0 TABLES

Table 1. General characteristics of sites included in California clapper rail habitat analyses.

For site locations, see Figure 1. See Appendices for additional site-specific habitat metrics.

Map ref.	Site name	Site location / ownership	Area surveyed for rails (ha)	Number rails	Rail density, mean (birds/ha)	Rail density category ₂	<i>Spartina</i> hybrid invasion level ₃	Restoration status
1	Emeryville Crescent West	East Bay Regional Park District	14.6	2	0.14	low	low	natural
2	Elsie Roemer	Alameda/San Leandro Bay / EBRPD	7.1	10 – 12	1.56	high	very high	natural
3	Bayfarm Island ₁	Alameda/San Leandro Bay	2.8	4 – 8	2.17	high	high	natural
4	Airport Channel West ₁	Alameda/San Leandro Bay	1.4	4	2.79	high	very high	natural
5	Airport Channel East ₁	Alameda/San Leandro Bay	3.2	4 – 6	1.58	high	very high	natural
6	Arrowhead	Alameda/San Leandro Bay / EBRPD	16.8	64	3.80	high	very high	natural
7	MLK Restoration	Alameda/San Leandro Bay / EBRPD	14.0	12 – 16	1.00	moderate	High	restoration
8	San Leandro Ck North	Alameda/San Leandro Bay	2.7	1 – 2	0.55	moderate	High	natural
9	San Leandro Ck South	Alameda/San Leandro Bay	1.1	0	0.00	absent	very high	natural
10	Oyster Bay Regional Shoreline North ₁	East Bay Regional Park District (EBRPD)	2.4	0	0.00	absent	very high	natural

Map ref.	Site name	Site location / ownership	Area surveyed for rails (ha)	Number rails	Rail density, mean (birds/ha)	Rail density category ₂	<i>Spartina</i> hybrid invasion level ₃	Restoration status
11	Oyster Bay Regional Shoreline South ₁	East Bay Regional Park District	2.8	0	0.00	absent	moderate	natural
12	North Marsh	Roberts Landing, San Leandro	35.6	7 – 12	0.27	low	moderate	restoration
13	Citation Marsh	Roberts Landing, San Leandro	27.8	5 – 10	0.27	low	moderate	restoration
14	Bunker Marsh	Roberts Landing, San Leandro	13.4	8 – 11	0.71	moderate	very high	restoration
15	San Lorenzo Ck. Mouth	Roberts Landing, San Leandro	11.0	4 – 8	0.55	moderate	very high	natural
16	San Lorenzo Ck.	Roberts Landing, San Leandro	1.5	1 – 2	0.99	moderate	moderate	natural
17	Oro Loma West	East Bay Regional Park District	53.4	14 – 22	0.34	moderate	very high	restoration
18	Oro Loma East	East Bay Regional Park District	25.8	2	0.08	low	moderate	restoration
19	Cogswell A: Northwest	East Bay Regional Park District	14.1	0 ₄	0.07	low	high	restoration
20	Cogswell B: East	East Bay Regional Park District	39.8	27 – 28	0.69	moderate	very high	restoration
21	Alameda Flood Control Channel: mouth	Alameda Flood Control District	9.4	7 – 9	0.85	moderate	moderate	natural

Map ref.	Site name	Site location / ownership	Area surveyed for rails (ha)	Number rails	Rail density, mean (birds/ha)	Rail density category ₂	<i>Spartina</i> hybrid invasion level ₃	Restoration status
22	Alameda Flood Control Channel: lower	Alameda Flood Control District	53.9	23 – 27	0.46	moderate	very high	natural
23	Alameda Flood Control Channel: mid-reach	Alameda Flood Control District	24.3	6 – 7	0.27	low	moderate	natural
24	Alameda Flood Control Channel: upper reach	Alameda Flood Control District	13.9	0 – 1	0.04	low	moderate	natural
25	Ideal North	Don Edwards SF Bay NWR- East Bay	15.3	5 – 6	0.36	moderate	very high	restoration
26	Ideal South	Don Edwards SF Bay NWR- East Bay	51.4	2 – 6	0.08	low	low	restoration
27	Audubon Marsh	Don Edwards SF Bay NWR- East Bay	25.6	1 – 2	0.06	low	low	natural
28	Dumbarton Marsh	Don Edwards SF Bay NWR- East Bay	38.2	11 – 26	0.48	moderate	low	natural
29	Newark Slough	Don Edwards SF Bay NWR- East Bay	24.8	2 – 4	0.12	low	very low/absent	natural
30	Mowry Slough	Don Edwards SF Bay NWR- East Bay	33.5	8 – 20	0.42	moderate	low	natural
31	Oyster Pt Cove ₁	West San Francisco Bay	1.5	0	0.00	absent	high	natural
32	Oyster Pt Marina ₁	West San Francisco Bay	1.0	0 ₄	0.00	absent	high	natural

Map ref.	Site name	Site location / ownership	Area surveyed for rails (ha)	Number rails	Rail density, mean (birds/ha)	Rail density category ₂	<i>Spartina</i> hybrid invasion level ₃	Restoration status
33	Oyster Pt Park ₁	West San Francisco Bay	0.9	0	0.00	absent	very high	natural
34	San Bruno Marsh	Colma Creek/ San Bruno Marsh	9.8	22 – 28	2.54	high	very high	natural
35	San Bruno Inner Harbor	Colma Creek/ San Bruno Marsh	3.0	16 – 19	5.81	high	very high	natural
36	Samtrans Peninsula	Colma Creek/ San Bruno Marsh	4.8	6 – 7	1.37	high	very high	natural
37	Sanchez Marsh ₁	West San Francisco Bay	5.8	0	0.00	absent	low	natural
38	Seal Slough ₁	West San Francisco Bay	9.3	3 – 6	0.48	moderate	very high	natural
39	Outer Bair Island- B2 South	Don Edwards SF Bay NWR - West Bay	19.1	0 ₄	0.00	absent	moderate	restoration
40	Middle Bair Island	Don Edwards SF Bay NWR - West Bay	37.0	21 – 34	0.74	moderate	low	natural
41	Greco Island North	Don Edwards SF Bay NWR - West Bay	100.2	20 – 33	0.26	low	low	natural
42	Laumeister Marsh	Don Edwards SF Bay NWR - West Bay	13.9	10 – 22	1.15	high	very low/absent	natural
43	Faber Marsh	Don Edwards SF Bay NWR - West Bay	21.8	24 – 46	1.60	high	very low/absent	restoration
44	Palo Alto Baylands	City of Palo Alto	22.4	9 - 18	0.60	moderate	very low/absent	natural

¹ Surveys at these sites were conducted using a modified protocol approved by USFWS for ISP.

² Rail abundance index category. low: < 0.3 rails/ha; moderate: 0.3 to 1.0 rails/ha (regional mean approximately 0.7 to 0.8 rails/ha); high: > 1.0 rails/ha

³ *Spartina hybrid invasion category, based on field-measured mean proportion Spartina hybrid cover at random sample points: very low/absent: 0; low: < 5%; moderate: 5 to 30%, high: 30 to 50%; very high: > 50%*

⁴ No rails were detected at these sites in 2005, but rails were found to be present during 2006 surveys.

Table 2. Field-based habitat metrics analyzed for relationship with California clapper rail abundance.

The mean of the following random sampling point data was calculated for each site for analysis.

Metric	Methods
Plot vegetation cover	
Overall percent cover of each plant species.	Overall percent cover was estimated visually for each 50 m radius random sampling plot and expressed as a proportion of vegetated area.
Plot vegetation structure	
Vertical structure: number of stems hitting narrow dowel (Wiens pole)	At 9 points on randomly selected perpendicular transects within the 50 m radius plot, the number of stems hitting a 3/8" wooden dowel were recorded at 10 cm vertical intervals. These values were summed for each plot. Additional new variables were generated by summing these intervals (all < 30 cm and all > 30 cm)
Maximum height of vegetation	The maximum height of vegetation within a 1 m radius of each of the 9 height sampling points.
Plot channel characteristics	
Distance to closest channel	Measured in the field from center of sampling point when channels were within 50 m; otherwise measured in ArcView to closest digitized channel.
Channel width	At point of channel closest to centerpoint of plot, channel width, measured with a meter stick or estimated visually.
Proportion of channel bottom covered with <i>Spartina</i> hybrids or <i>S. foliosa</i>	Visual estimate of a 20 m segment of tidal channel closest to the plot centerpoint, expressed as proportion or entire channel area vegetated below the marsh plain level.
Proportion each plant species on channel bank	Visual estimate of the channel segment described above, proportion of vegetation within 2 m of channel edges.

Table 3. GIS-based metrics analyzed for relationship with California clapper rail abundance.

GIS metrics were based on entire marsh area, means of area around random sample points, or plot centroid, as indicated.

Metric	Source
Survey area	Tidal marsh habitat digitized using aerial photography (hereafter referred to as ISP marsh polygons; ISP 2005, USGS 2004) and EcoAtlas 2.0 (SFEI 1998) clipped to within 200 m of clapper rail survey stations for larger sites
Contiguous marsh area	Total area of tidal and muted marsh separated by < 50, < 100, and < 200 m of non-marsh habitat, using ISP marsh polygons and EcoAtlas 2.0 (SFEI 2000)
Proportion Invasive <i>Spartina</i>	
Proportion invasive <i>Spartina</i> within 100, 200, 500, 1000, 2000 m radius of plot centroid	Shapefiles generated by ISP's <i>Spartina</i> Inventory Project: combination of field-mapped using GPS and heads-up digitized in ArcView 3.3 and ArcView 9.0
Proportion high density invasive <i>Spartina</i> clones calculated separately using only polygons categorized as > 50% and > 70% cover	ISP shapefiles described above
Vegetation proportion	
Proportion vegetated marsh (entire marsh)	Calculated using Image Analysis in ArcView 3.3: image categorization with 10 bins, manually designated as vegetation or mud based on 5 – 10 sample areas; calculated range based on estimated accuracy of designation. At narrow marshes edging major channels, marsh area was digitized.
Proportion land use	
Proportion within 100 m, 200 m, 500 m, 1000 m, and 2000 m of plot centroid, of the following land use types:	Based on area surrounding centroid of random sampling plots. Centroids calculated with AlaskaPak extension in ArcView 3.3 (National Park Service 2002), buffered to the appropriate radius.
Proportion tidal marsh	ISP marsh polygons and EcoAtlas 2.0 (SFEI 1998)
Proportion mud flats: bay mudflats plus channel mudflats (channels > 30 m wide)	EcoAtlas polygons, modified by ISP to exclude all marsh area
Proportion all non-marsh intertidal: tidal flats plus shallow channels and bay	EcoAtlas polygons, modified by ISP to exclude marsh area
Proportion salt ponds	EcoAtlas 2.0 (SFEI 1998)

Metric	Source
Proportion urban	DWR (1993-1999); USGS (1996) ¹
Proportion natural upland	DWR (1993-1999); USGS (1996) ¹
Marsh edge characteristics:	
Length edge per unit area for entire marsh: calculated separately for bay, upland (including interior levees), major channels, ponds, pans and all edges.	ISP marsh polygons and EcoAtlas 2.0 (SFEI 1998)
Length water edge per unit area (bay + channels + 2 x major channels > 10 m wide)	ISP marsh polygons and EcoAtlas 2.0 (SFEI 1998)
Proportion high elevation / low elevation edges (upland edge / water edge)	ISP marsh polygons and EcoAtlas 2.0 (SFEI 1998)
Channel characteristics	
Channel density (length channel per marsh area)	Digitized lines using aerial photos (ISP, PRBO), divided by area digitized.
Number of channel systems: first, second, third and fourth order, and all systems	Visual inspection of aerial photography and digitized channels
Distance to marsh features and edges from sample plots	
Distance to upland edge	Edges clipped from ISP polygons and characterized visually. Distances calculated in ArcView 3.3 using AlaskaPak (National Park Service 2002)
Distance to water edge (Bay or large channel)	Edges clipped from ISP polygons and characterized visually. Distances calculated in ArcView 3.3 using AlaskaPak (National Park Service 2002)

¹Data compiled by PRBO.

Table 4. Correlation of *Spartina* hybrid cover with other habitat variables.

The *Spartina* hybrid cover variable used for these analyses was the proportion high-density (>70% cover) within 200 m of the site centroid, which was the same variable used to derive the clapper rail habitat use models. Where p-values are > 0.2, the relationship was deemed not significant (NS). The direction of the correlation is in parentheses.

Variable	r ²	p-value
<i>Atriplex triangularis</i> % cover		NS
<i>Baccharis pilularis</i> % cover		NS
<i>Bromus</i> spp. % cover		NS
<i>Carpobrotus edulis</i> % cover	0.36	(+) p = 0.02
<i>Cirsium</i> spp % cover		NS
<i>Cotula cornicopifolia</i> % cover		NS
<i>Cuscuta salina</i> % cover	0.34	(-) p = 0.03
<i>Distichlis spicata</i> % cover	0.36	(-) p = 0.02
<i>Foeniculum vulgare</i> % cover		NS
<i>Frankenia salina</i> % cover	0.21	(-) p = 0.16
<i>Grindelia stricta</i> % cover		NS
<i>Jaumea carnosa</i> % cover	0.28	(+) p = 0.06
<i>Lepidium latifolium</i> % cover		NS
<i>Limonium californica</i> % cover	0.24	(-) p = 0.12
<i>Mesembryanthemum crystallinum</i> % cover		NS
<i>Puccinellia</i> % cover		NS
<i>Salicornia europea</i> % cover		NS
<i>Salicornia virginica</i> % cover	0.54	(-) p < 0.001
<i>Salsola soda</i> % cover		NS
<i>Scirpus americanus</i> % cover		NS
<i>Scirpus maritimus</i> % cover	0.19	(-) p = 0.21
<i>Spartina densiflora</i> % cover		NS
<i>Spartina foliosa</i> % cover	0.22	(-) p = 0.14
<i>Triglochin maritima</i> % cover		NS
<i>Typha</i> % cover		NS
wrack % cover	0.27	(+) p = 0.07
all high marsh vegetation on channel % cover	0.63	(-) p < 0.001
all high marsh vegetation on marsh plain % cover	0.71	(-) p < 0.001

Variable	r ²	p-value
stems < 30 cm height	0.57	(-) p < 0.001
stems > 30 cm height	0.57	(+) p < 0.001
stems < 10 cm height	0.50	(-) p < 0.001
stems 10 - 20 cm height	0.55	(-) p < 0.001
stems 20 - 30 cm height	0.49	(-) p < 0.001
stems 30 - 40 cm height		NS
stems 40 - 50 cm height	0.28	(+) p = 0.068
stems 50 - 60 cm height	0.41	(+) p = 0.006
stems 60 - 100 cm height	0.63	(+) p < 0.001
stems > 100 cm height	0.58	(+) p < 0.001
maximum plant height	0.71	(+) p < 0.001
distance to nearest channel		NS
width closest channel		NS
<i>Spartina foliosa</i> within channel	0.30	(-) P = 0.05
<i>Spartina</i> hybrids within channel	0.48	(+) p < 0.001
channel cover <i>Atriplex triangularis</i>		NS
channel cover <i>Distichlis spicata</i>		NS
channel cover <i>Foeniculum vulgare</i>		NS
channel cover <i>Frankenia salina</i>	0.30	(-) p = 0.05
channel cover <i>Grindelia stricta</i>	0.46	(-) p = 0.002
channel cover <i>Jaumea carnosa</i>		NS
channel cover <i>Lepidium latifolium</i>		NS
channel cover <i>Salicornia virginica</i>	0.49	(-) p < 0.001
channel cover <i>Scirpus maritimus</i>		NS
channel cover <i>Spartina foliosa</i>	0.32	(-) P = 0.03
channel cover <i>Spartina</i> hybrids	0.72	(+) p < 0.001
channel cover wrack		NS
vegetated marsh % cover		NS
agriculture within 100, 200, 500, 1000 and 2000 m		NS
bay flat within 100 m	0.69	(+) p < 0.001
bay flat within 200 m	0.67	(+) p < 0.001
bay flat within 500 m	0.57	(+) p < 0.001
bay flat within 1000 m	0.40	(+) p = 0.007
bay flat within 2000 m	0.32	(+) p = 0.04

Variable	r ²	p-value
natural uplands within 100, 200, 500, 1000, 2000 m		NS
tidal marsh within 100 m	0.33	(-) p = 0.03
tidal marsh within 200 m	0.34	(-) p = 0.02
tidal marsh within 500 m	0.33	(-) p = 0.03
tidal marsh within 1000 m	0.35	(-) p = 0.02
salt pond within 100, 200, 500, 1000, 2000 m		NS
tidal flat within 50 m	0.38	(+) p = 0.01
tidal flat within 100 m	0.44	(+) p = 0.003
tidal flat within 200 m	0.40	(+) p = 0.007
tidal flat within 500 m	0.26	(+) p = 0.09
tidal flat within 1000 m		NS
tidal flat within 2000 m		NS
urban land use within 100 m	0.38	(+) p = 0.01
urban land use within 200 m	0.35	(+) p = 0.02
urban land use within 500 m	0.22	(+) p = 0.16
urban land use within 1000 m	0.24	(+) p = 0.12
urban land use within 2000 m	0.28	(+) p = 0.07
total edge density (m/ha)		NS
bay edge density (m/ha)		NS
water edge density (m/ha)		NS
upland edge density (m/ha)		NS
upland edge/ water edge ratio	0.23	(+) p = 0.13
channel density (m/ha)	0.36	(-) p = 0.02
first order channel systems		NS
second order channel systems		NS
third order channel systems	0.26	(-) p = 0.09
fourth order channel systems	0.24	(-) p = 0.12
mean distance to upland edge (of sample pts)	0.24	(-) p = 0.12
mean distance to water edge (of sample pts)	0.31	(-) p = 0.04

Table 5. Correlation of *Spartina* hybrid and *Spartina foliosa* variables with log clapper rail density.

Variable	Measurement type	r ²	p-value
<i>Spartina</i> hybrid % cover	mean of random points	0.36	p = 0.02
log (<i>Spartina</i> hybrid % cover)	mean of random points	0.18	NS
<i>Spartina</i> hybrids on channel edge	mean of random points	0.29	p = 0.06
<i>Spartina</i> hybrids within channels	mean of random points	0.39	p = 0.009
log (<i>Spartina</i> hybrids within channels)	mean of random points	0.28	p = 0.073
<i>Spartina foliosa</i> % cover	mean of random points		NS
log (<i>Spartina foliosa</i> % cover)	mean of random points		NS
<i>Spartina foliosa</i> on channel edge	mean of random points		NS
<i>Spartina foliosa</i> within channels	mean of random points		NS
all <i>Spartina</i> spp. % cover	mean of random points	0.40	p = 0.008
log (all <i>Spartina</i> spp. % cover)	mean of random points	0.36	p = 0.016
all <i>Spartina</i> spp. on channel edges	mean of random points	0.27	p = 0.073
all <i>Spartina</i> spp. within channels	mean of random points	0.42	p = 0.004
<i>Spartina</i> hybrid % cover within 100 m	proportion surrounding plot centroid	0.31	p = 0.04
<i>Spartina</i> hybrid % cover within 100 m, polys > 70% cover	proportion surrounding plot centroid	0.33	p = 0.03
<i>Spartina</i> hybrid % cover within 200 m	proportion surrounding plot centroid	0.37	p = 0.01
<i>Spartina</i> hybrid % cover within 200 m, polys > 50% cover	proportion surrounding plot centroid	0.40	p = 0.007
squared (<i>Spartina</i> hybrid % cover within 200 m, polys > 50% cover)	proportion surrounding plot centroid	0.42	p = 0.005
<i>Spartina</i> hybrid % cover within 200 m, polys > 70% cover	proportion surrounding plot centroid	0.38	p = 0.01
squared (<i>Spartina</i> hybrid % cover within 200 m, polys > 70% cover)	proportion surrounding plot centroid	0.41	p = 0.006
log (<i>Spartina</i> hybrid % cover within 200 m, polys > 70% cover)	proportion surrounding plot centroid	0.25	p = 0.0972
<i>Spartina</i> hybrid % cover within 500 m	proportion surrounding plot centroid	0.41	p = 0.006
<i>Spartina</i> hybrid % cover within 500 m, polys > 70% cover	proportion surrounding plot centroid	0.39	p = 0.008
<i>Spartina</i> hybrid % cover within 1000 m	proportion surrounding plot centroid	0.39	p = 0.009

9.0 Tables

Variable	Measurement type	r2	p-value
<i>Spartina</i> hybrid % cover within 1000 m, polys > 70% cover	proportion surrounding plot centroid	0.39	p = 0.008
<i>Spartina</i> hybrid % cover in survey area	proportion in survey area	0.32	p = 0.04
<i>Spartina</i> hybrid % cover in survey area, > 70% cover	proportion in survey area	0.28	p = 0.07

Table 6a. Regression coefficients and model statistics for local habitat regression model. Dependant variable: log clapper rail density.

$r^2 = 0.285$; adjusted $r^2 = 0.232$; Mallows' $C_p = 4.00$	$\beta \pm SE$	P	Partial r^2
<i>Spartina</i> hybrid cover within 200 m	0.437 \pm 0.194	0.030	0.090
Plant stem density 50-60 cm	0.309 \pm 0.150	0.046	0.076
<i>Spartina foliosa</i> within channels	0.017 \pm 8.90 e-3	0.051	0.072
Cover <i>Salicornia virginica</i>		NS	
Cover all <i>Spartina</i> spp.		NS	
All <i>Spartina</i> spp inside channels		NS	
Cover wrack		NS	
All high elev. plants: marsh plain		NS	
All high elev. plants: channel edges		NS	
Plant stem density > 30 cm		NS	
Plant stem density < 10 cm		NS	
Constant	- 0.313 \pm 0.74	< 0.001	
N	44		

Table 6b. Regression coefficients and model statistics for habitat configuration model. Dependant variable: log clapper rail density.

$r^2 = 0.127$; adjusted $r^2 = 0.084$; Mallows's $C_p = 4.00$	$\beta \pm SE$	P	Partial r^2
Ratio upland to water edge	- 0.220 \pm 0.117	0.068	
Distance to mudflats	- 5.76 e-4 \pm 0.2.84 e-4	0.049	
First order channel systems		NS	
Second order channel systems		NS	
All channel systems		NS	
Width channel		NS	
Constant	- 0.117 \pm 0.095	0.227	
N	44		

Table 6c. Regression coefficients and model statistics for surrounding land use model. Dependant variable: log clapper rail density.

$r^2 = 0.218$; adjusted $r^2 = 0.199$	$\beta \pm SE$	P	Partial r^2
Proportion tidal flats within 200 m	0.093 \pm 0.027	0.001	
Proportion mudflats and bay w/in 200 m		NS	
Proportion agriculture		NS	
Constant	- 0.157 \pm 0.050	0.003	
N	44		

Table 7a. Regression coefficients and model statistics for final multi-scale model. Dependant variable: log clapper rail density.

$r^2 = 0.383$; adjusted $r^2 = 0.337$; Mallow's $C_p = 4.68$	$\beta \pm SE$	P	Partial r^2
Plant stem density 50-60 cm	0.335 ± 0.143	0.021	0.090
Ratio upland to water edge	-0.274 ± 0.100	0.009	0.115
Proportion tidal flats within 200 m	0.077 ± 0.027	0.007	0.124
Constant	-0.106 ± 0.074	0.151	
N	44		

Table 7b. Regression coefficients and model statistics for final multi-scale model-including channel density x *Spartina* cover interaction term, continuous interaction. Dependant variable: log clapper rail density.

$r^2 = 0.458$; adjusted $r^2 = 0.387$; Mallow's $C_p = 6.00$	$\beta \pm SE$	P	Partial r^2
<i>Spartina</i> hybrid cover within 200 m	0.908 ± 0.244	0.001	0.197
<i>Plant stem density 50-60 cm</i>	0.320 ± 0.138	0.026	0.076
Ratio upland to water edge	-0.172 ± 0.109	0.122	0.035
Channel density	0.066 ± 0.028	0.024	0.079
Channel density * <i>Spartina</i> hybrid cover	-0.277 ± 0.099	0.008	0.111
Constant	-0.357 ± 0.125	0.007	
N	44		

Table 7c. Regression coefficients and model statistics for final multi-scale model including channel density x *Spartina* cover interaction term, categorical interaction. Dependant variable: log clapper rail density.

$r^2 = 0.452$; adjusted $r^2 = 0.349$	$\beta \pm SE$	P	Partial r^2
<i>Spartina</i> hybrid cover within 200 m	0.690+ 0.223	0.004	
<i>Plant stem density 50-60 cm</i>	0.364 \pm 0.141	0.014	0.132
Ratio upland to water edge	- 0.253 \pm 0.103	0.019	0.117
Channel density	0.162 \pm 0.118	0.180	
Categorical channel density * <i>Spartina</i> hybrid cover	- 0.861 \pm 0.368	0.025	0.193
Constant	- 0.242 \pm 0.118	0.047	
N	44		

10.0 APPENDICES

Appendix 1. *Spartina* cover at sites included in California clapper rail habitat analyses.

For site locations, see Figure 1.

Map ref	Site name	Vegetation % cover (mean of estimate) ₁	Mean % cover <i>Spartina</i> hybrids (field sample pts) ₂	<i>Spartina</i> hybrid % cover - high density area (> 70% cover, digitized) ₃	<i>Spartina</i> hybrid % cover - all densities (digitized) ₃	Mean % cover <i>Spartina densiflora</i> ₂	Mean % cover <i>Spartina foliosa</i> ₂	Mean % cover <i>Spartina</i> hybrids within channel ₂	Mean % cover <i>Spartina foliosa</i> within channel ₂
1	Emeryville Crescent West	70	0.3	2	2	0	9.5	0	14.6
2	Elsie Roemer	84	80.2	67	70	0	0	0	0
3	Bayfarm Island	88	70.0	61	67	0	0	30	0
4	Airport Channel West	80	80.5	19	31	0	0	94.2	0
5	Airport Channel East	80	80	11	37	0	0	50	0
6	Arrowhead	83	55.1	17	56	0	0	44.1	0
7	MLK Restoration	55	37.5	6	20	0	0	8.4	0
8	San Leandro Ck North	44	35	38	39	0	0	2	0
9	San Leandro Ck South	57	72.8	16	22	0	0	0	0
10	Oyster Bay Regional Shoreline North	90	95.5	65	65	0	0	40	0
11	Oyster Bay Regional Shoreline South	90	13.0	11	39	0	12	23.8	0
12	North Marsh	56	11.8	8	13	0	0.1	0.5	0
13	Citation Marsh	58	6.4	6	12	0	0.3	4.0	0.4
14	Bunker Marsh	81	50.8	34	45	0	0	55.2	0

Map ref	Site name	Vegetation % cover (mean of estimate) ₁	Mean % cover <i>Spartina</i> hybrids (field sample pts) ₂	<i>Spartina</i> hybrid % cover - high density area (> 70% cover, digitized) ₃	<i>Spartina</i> hybrid % cover - all densities (digitized) ₃	Mean % cover <i>Spartina densiflora</i> ₂	Mean % cover <i>Spartina foliosa</i> ₂	Mean % cover <i>Spartina</i> hybrids within channel ₂	Mean % cover <i>Spartina foliosa</i> within channel ₂
15	San Lorenzo Ck mouth	67	76.7	40	56	0	0	13.8	0
16	San Lorenzo Ck	32	9.8	0	0	0	3	0	0
17	Oro Loma West	33	79.1	28	28	0	2.3	1.8	0
18	Oro Loma East	47	6.0	5	6	0	0	0	0
19	Cogswell A: Northwest	86	33.7	45	54	0	0	18.6	0
20	Cogswell B: East	74	56.8	68	73	0	0	56.9	0
21	Alameda Flood Control Channel: mouth	80	20.0	22	39	0	0	0	0
22	Alameda Flood Control Channel: lower	81	71.4	48	53	0	0	55.2	0
23	Alameda Flood Control Channel: mid-reach	80	7.0	37	41	0	0	0.8	0
24	Alameda Flood Control Channel: upper reach	85	10.0	0	0	0	0	0	0
25	Ideal North	80	53.3	18	44	0	0	70.0	0
26	Ideal South	80	3.2	0	5	0	0	0.6	0
27	Audubon Marsh	63	0.2	3	3	0	0.4	0	0.2
28	Dumbarton Marsh	72	0.1	1	1	0	2.6	0	6.3
29	Newark Slough	84	0	0	0	0	2.4	0	0.1
30	Mowry Slough	40	3.4	0	0	0	4.6	0.2	2
31	Oyster Pt Cove	90	46.7	0	29	0	0	75.0	0

Map ref	Site name	Vegetation % cover (mean of estimate) ₁	Mean % cover <i>Spartina</i> hybrids (field sample pts) ₂	<i>Spartina</i> hybrid % cover - high density area (> 70% cover, digitized) ₃	<i>Spartina</i> hybrid % cover - all densities (digitized) ₃	Mean % cover <i>Spartina densiflora</i> ₂	Mean % cover <i>Spartina foliosa</i> ₂	Mean % cover <i>Spartina</i> hybrids within channel ₂	Mean % cover <i>Spartina foliosa</i> within channel ₂
32	Oyster Pt Marina	90	41.3	1	5	0	0	1.0	0
33	Oyster Pt Park	90	86.0	48	70	0	0	45.0	0
34	San Bruno Marsh	68	95.9	72	72	0	0	90.0	0
35	San Bruno Inner Harbor	76	96.5	74	74	0	0	65.0	0
36	Samtrans Peninsula	72	80.6	84	84	0	0	31.8	0
37	Sanchez Marsh	80	4.6	3	3	0.8	19.5	0	1.7
38	Seal Slough	80	70.8	28	69	0	1.0	70.5	2.0
39	Outer Bair Island-B2 South	82	27.5	16	33	0	0	7.8	0
40	Middle Bair Island	82	2.4	0	0	0	11.0	0	2.1
41	Greco Island North	77	2.0	0	2	0	9.5	2.0	5.4
42	Laumeister Marsh	83	0	0	0	0	14.2	0	16.0
43	Faber Marsh	73	0	0	0	0	16.7	0	27.0
44	Palo Alto Baylands	81	0	0	0	0	5.4	0	0.3

¹ Vegetation cover proportion quantified in ArcView GIS 3.3 using a combination of digital color categorization where multi-spectral imagery were available, heads-up digitization, and GIS-based visual estimates where multi-spectral imagery were not available (see Table 3).

² Mean of measurements at 2-16 randomly selected field sampling points (see Table 2).

³ *Spartina alterniflora* hybrid inventory (ISP Monitoring Program) cover GIS polygon shapefile data were calculated as percent cover of *Spartina alterniflora* hybrids per area of site, using a combination of field-collected data and digitized aerial imagery, with areas of like % cover grouped together (see Table 3).

Appendix 2. Vegetation cover and stem density at sites included in California clapper rail habitat analyses.

All variables are the mean of the measurements at 2-16 randomly selected field sampling points (see Table 2). For site locations, see Figure 1.

Map ref	Site name	Mean % cover Marsh gumplant (<i>Grindelia stricta</i>)	Mean % cover <i>Jaumea carnosa</i>	Mean % cover Pickleweed (<i>Salicornia virginica</i>)	Mean % cover all elevation plant species	Mean stem hits ≤ 30 cm	Mean stem hits > 30 cm	Mean maximum plant height (cm)
1	Emeryville Crescent West	1	5.5	77.57	100	7.4	0.74	68.3
2	Elsie Roemer	3.1	2.1	2.7	20	4.59	5.85	139.1
3	Bayfarm Island	8.5	1.37	15	44	2.2	7.3	140.9
4	Airport Channel West	2.25	7.25	7.83	26	4.2	5.0	118.2
5	Airport Channel East	3	6	8	23	2.7	6.4	136.7
6	Arrowhead	0.81	41.62	9.37	66	5.9	2.9	98.1
7	MLK Restoration	0.36	1.36	37.45	42	2.8	1.3	74.8
8	San Leandro Ck North	15.8	18	21	75	13.8	3.5	104.3
9	San Leandro Ck South	9.1	4.6	0.7	29	5.0	4.5	120.4
10	Oyster Bay Regional Shoreline North	1.75	0	3	10	1.7	5.6	161.1
11	Oyster Bay Regional Shoreline South	2.8	1.6	80	89	8.2	2.1	88.6
12	North Marsh	0	0.3	63.3	70	6.1	1.0	62.4
13	Citation Marsh	0.7	0	76.6	88	7.4	1.3	60.4
14	Bunker Marsh	5.7	2.2	46.2	57	5.3	3.6	106.0
15	San Lorenzo Ck mouth	0.6	1.3	25.8	33	5.1	2.7	86.6

Map ref	Site name	Mean % cover Marsh gumplant (<i>Grindelia stricta</i>)	Mean % cover <i>Jaumea carnosa</i>	Mean % cover Pickleweed (<i>Salicornia virginica</i>)	Mean % cover all elevation plant species	Mean stem hits ≤ 30 cm	Mean stem hits > 30 cm	Mean maximum plant height (cm)
16	San Lorenzo Ck	9.2	0.7	66.4	94	5.1	2.2	79.7
17	Oro Loma West	0	0	17.7	19	3.2	4.9	118.6
18	Oro Loma East	0.3	10.0	64.0	86	8.1	0.5	43.4
19	Cogswell A: North-west	0.2	0.3	75.7	77	5.6	1.2	67.6
20	Cogswell B: East	0	2.4	61.8	65	4.9	3.1	117.8
21	Alameda Flood Control Channel: mouth	0.5	1.0	80.0	85	9.7	0.6	62.2
22	Alameda Flood Control Channel: lower	0.6	0.4	34.0	38	3.0	3.2	125.1
23	Alameda Flood Control Channel: mid-reach	0	0.2	61.3	97	4.8	1.3	112.9
24	Alameda Flood Control Channel: upper reach	0.5	2.0	5.0	65	5.4	2.6	147.8
25	Ideal North	0.2	0.2	53.3	58	5.1	1.7	84.5
26	Ideal South	1.3	5.7	92.6	100	5.7	0.2	53.7
27	Audubon Marsh	1.8	1.4	96.2	100	9.8	0.6	51.3
28	Dumbarton Marsh	1.8	5.0	91.6	100	11.6	0.6	51.6
29	Newark Slough	12.9	8.9	69.6	100	13.5	1.3	55.8
30	Mowry Slough	1.6	5.0	90.3	100	9.2	1.0	58.0
31	Oyster Pt Cove	2.3	8.7	12.3	59	4.3	3.6	105.4
32	Oyster Pt Marina	0.6	10.0	25.0	61	4.6	2.7	91.9
33	Oyster Pt Park	0	1.0	8.3	13	2.2	5.1	169.5
34	San Bruno Marsh	0.1	0.6	1.5	5	1.6	3.6	148.4

Map ref	Site name	Mean % cover Marsh gumplant (<i>Grindelia stricta</i>)	Mean % cover <i>Jaumea carnosa</i>	Mean % cover Pickleweed (<i>Salicornia virginica</i>)	Mean % cover all elevation plant species	Mean stem hits ≤ 30 cm	Mean stem hits > 30 cm	Mean maximum plant height (cm)
35	San Bruno Inner Harbor	0.9	0	0.8	3	1.0	4.4	160.3
36	Samtrans Peninsula	1	0.1	11.6	20	2.4	3.8	132.8
37	Sanchez Marsh	6.5	25.3	24.7	81	8.1	0.3	56.7
38	Seal Slough	0.8	3.1	20.5	37	4.8	3.9	122.1
39	Outer Bair Island-B2 South	0	0.3	78.3	82	7.7	1.8	73.2
40	Middle Bair Island	0.4	4.8	82.1	100	7.4	0.3	57.0
41	Greco Island North	0.6	7.6	92.4	100	7.6	1.0	58.9
42	Laumeister Marsh	11.6	1.0	60.2	90	13.8	2.9	83.6
43	Faber Marsh	1.7	12.1	91.3	100	7.5	1.3	74.3
44	Palo Alto Baylands	2.1	8.7	74.7	94	11.4	4.4	94.2

Appendix 3. Channel and edge characteristics at sites included in California clapper rail habitat analyses.

For site locations, see Figure 1.

Map ref	Site name	Channel density (100 m/ha)	Number first order channel systems	Mean distance to channel (m)	Bay edge density (km/ha)	Water edge density (km/ha)	Upland edge density (km/ha)	Ratio upland edge to water edge
1	Emeryville Crescent West	2.48	4	8	10.6	35.3	17.2	0.49
2	Elsie Roemer	0.04	1	218	31.7	32.0	19.3	0.60
3	Bayfarm Island	0.00	0	6	61.7	61.7	56.7	0.92
4	Airport Channel West	1.43	0	267	106.1	229.8	144.7	0.83
5	Airport Channel East	0.46	1	630	8.8	79.4	37.6	0.81
6	Arrowhead	8.99	> 7	2	20.9	126.2	3.0	0.02
7	MLK Restoration	2.10	0	21	0	21.0	16.6	0.79
8	San Leandro Ck North	5.12	1	0.6	0	259.1	101.0	0.65
9	San Leandro Ck South	6.37	1	7	0	299.5	115.8	0.64
10	Oyster Bay Regional Shoreline North	0.70	1	6	0	100.2	60.9	1.14
11	Oyster Bay Regional Shoreline South	2.28	0	18	2.5	25.3	53.2	2.10
12	North Marsh	2.06	0	11	0	20.6	15.4	0.75
13	Citation Marsh	1.98	0	10	0	19.8	13.3	0.67
14	Bunker Marsh	1.37	0	24	0	28.0	25.7	1.23
15	San Lorenzo Ck mouth	1.38	2	31	19.2	45.7	9.7	0.25
16	San Lorenzo Ck	5.51	0	5	0	246.5	91.8	0.61

Map ref	Site name	Channel density (100 m/ha)	Number first order channel systems	Mean distance to channel (m)	Bay edge density (km/ha)	Water edge density (km/ha)	Upland edge density (km/ha)	Ratio upland edge to water edge
17	Oro Loma West	2.92	0	20	0.7	29.8	6.9	0.23
18	Oro Loma East	1.82	0	3	0	18.2	5.0	0.27
19	Cogswell A: North-west	3.12	0	14	4.1	35.4	12.4	0.35
20	Cogswell B: East	2.63	0	11	1.5	33.2	8.4	0.28
21	Alameda Flood Control Channel: mouth	1.34	1	22	3.5	40.7	10.2	0.35
22	Alameda Flood Control Channel: lower	0.93	0	17	0	39.0	12.2	0.51
23	Alameda Flood Control Channel: mid-reach	1.25	0	8	0	59.9	26.2	0.72
24	Alameda Flood Control Channel: upper reach	1.51	0	37	0	62.2	32.9	0.85
25	Ideal North	0.52	1	104	30.3	35.5	14.3	0.40
26	Ideal South	2.47	1	27	6.7	31.9	5.2	0.16
27	Audubon Marsh	3.45	0	31	0.1	42.3	7.3	0.19
28	Dumbarton Marsh	4.94	> 7	15	1.9	53.0	2.1	0.04
29	Newark Slough	3.47	0	25	0	116.8	21.9	0.24
30	Mowry Slough	4.80	1	22	0.4	60.8	5.9	0.11
31	Oyster Pt Cove	0.42	1	42	54.4	58.6	54.8	0.94
32	Oyster Pt Marina	0.14	0	214	117.7	117.7	106.5	0.90
33	Oyster Pt Park	5.53	1	22	33.6	86.4	122.5	1.42
34	San Bruno Marsh	1.16	3	174	19.1	61.9	18.2	0.38
35	San Bruno Inner Harbor	0.06	3	73	0	77.7	31.6	0.81
36	Samtrans Peninsula	0.91	0	124	21.6	36.7	25.9	0.78

Map ref	Site name	Channel density (100 m/ha)	Number first order channel systems	Mean distance to channel (m)	Bay edge density (km/ha)	Water edge density (km/ha)	Upland edge density (km/ha)	Ratio upland edge to water edge
37	Sanchez Marsh	1.42	0	27	0	37.6	23.0	0.89
38	Seal Slough	1.84	1	21	15.4	38.3	8.4	0.22
39	Outer Bair Island-B2 South	1.33	0	26	2.9	16.1	9.9	0.61
40	Middle Bair Island	2.98	0	16	0	45.7	3.8	0.10
41	Greco Island North	5.75	> 7	6	2.1	65.5	2.2	0.04
42	Laumeister Marsh	7.18	0	12	2.8	74.6	5.1	0.07
43	Faber Marsh	6.05	3	29	1.2	76.6	10.4	0.15
44	Palo Alto Baylands	2.60	0	39	4.9	36.2	4.2	0.13

Appendix 4. Mean edge metrics and surrounding land use at sites included in California clapper rail habitat analyses.

For site locations, see Figure 1.

Map ref	Site name	Mean distance to uplands (m)	Mean distance to tidal flats (m)	Percent marsh within 200 m	Percent tidal flat within 200 m	Percent natural uplands within 200 m	Percent salt ponds within 200 m	Percent urban within 200 m
1	Emeryville Crescent West	61.0	77.4	67.4	25.5	0	0	0.21
2	Elsie Roemer	27.7	27.4	24.9	39.9	0	0	0.41
3	Bayfarm Island	8.5	11	8.8	45.3	0	0	0.54
4	Airport Channel West	13.5	9	35.2	33.8	0	0	0.17
5	Airport Channel East	0	1	4.3	36.0	0	0	0.02
6	Arrowhead	285.3	40.0	69.6	40.7	0	0	0
7	MLK Restoration	48.9	112.0	66.3	11.9	0	0	0.16
8	San Leandro Ck North	6.5	3.5	8.3	10.2	0	0	0.52
9	San Leandro Ck South	5.2	5.0	5.4	3.5	0	0	0.43
10	Oyster Bay Regional Shoreline North	21.4	17.6	16.2	9.9	0	0	0.31
11	Oyster Bay Regional Shoreline South	9.4	85.6	13.0	5.3	0	0	0.42
12	North Marsh	38.7	344.2	99.5	2.5	0	0	0
13	Citation Marsh	66.9	719.3	79.6	0.0	0	0	0
14	Bunker Marsh	40.2	86.0	72.8	13.7	0	0	0
15	San Lorenzo Ck mouth	64.0	28.7	65.9	26.3	0	0	0
16	San Lorenzo Ck	10.8	6.0	36.4	8.2	0	0	0.33

Map ref	Site name	Mean distance to uplands (m)	Mean distance to tidal flats (m)	Percent marsh within 200 m	Percent tidal flat within 200 m	Percent natural uplands within 200 m	Percent salt ponds within 200 m	Percent urban within 200 m
17	Oro Loma West	85.3	296.3	99.5	6.2	0	0	0
18	Oro Loma East	55.6	781.0	99.5	0.0	0	0	0
19	Cogswell A: North-west	45.7	133.6	89.8	13.1	0	0	0
20	Cogswell B: East	57.0	173.6	86.9	4.5	0	0	0
21	Alameda Flood Control Channel: mouth	115.6	22.0	63.2	0.0	0	0.10	0
22	Alameda Flood Control Channel: lower	61.2	29.8	49.5	10.6	0	0.10	0
23	Alameda Flood Control Channel: mid-reach	29.7	20.8	50.1	7.6	0.06	0	0
24	Alameda Flood Control Channel: upper reach	0	38.0	17.7	6.9	0	0	0.58
25	Ideal North	31.0	45.3	31.1	35.8	0	0.33	0
26	Ideal South	90.6	167.6	75.4	4.8	0	0.19	0
27	Audubon Marsh	65.7	460.2	96.3	0.0	0	0	0
28	Dumbarton Marsh	126.3	372.7	97.6	0.7	0	0	0
29	Newark Slough	45.5	33.5	26.6	8.0	0.25	0.36	0
30	Mowry Slough	98.8	77.9	73.1	23.9	0	0.22	0
31	Oyster Pt Cove	15.8	11.8	9.6	34.1	0	0	0.41
32	Oyster Pt Marina	10.8	8.3	4.8	45.4	0	0	0.34
33	Oyster Pt Park	18.3	4.7	5.6	35.9	0	0	0.70
34	San Bruno Marsh	33.2	18.4	36.8	41.9	0	0	0.16
35	San Bruno Inner Harbor	25.2	11.2	24.2	22.3	0	0	0.52
36	Samtrans Peninsula	28.0	19.5	10.7	40.0	0	0	0.43

Map ref	Site name	Mean distance to uplands (m)	Mean distance to tidal flats (m)	Percent marsh within 200 m	Percent tidal flat within 200 m	Percent natural uplands within 200 m	Percent salt ponds within 200 m	Percent urban within 200 m
37	Sanchez Marsh	19.0	21.5	31.7	14.0	0	0	0.29
38	Seal Slough	83.0	88.6	39.3	14.4	0	0	0.18
39	Outer Bair Island-B2 South	77.2	147.2	97.0	4.7	0	0	0
40	Middle Bair Island	187.6	154.9	98.3	4.7	0	0	0
41	Greco Island North	63.2	211.2	99.5	4.3	0	0	0
42	Laumeister Marsh	84.6	212.9	96.1	5.0	0	0	0
43	Faber Marsh	77.1	135.0	97.9	4.4	0	0	0
44	Palo Alto Baylands	89.3	93.1	84.2	9.6	0	0	0
