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Permalink

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Journal

Biological Invasions, 16(9)

ISSN

1387-3547

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Publication Date

2014-09-01

DOI

10.1007/s10530-013-0634-5

Peer reviewed

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Biological Invasions

ISSN 1387-3547

Biol Invasions
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Tidal and seasonal effects on survival rates of the endangered California clapper rail: does invasive *Spartina* facilitate greater survival in a dynamic environment?

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Received: 13 February 2013 / Accepted: 25 December 2013
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Abstract Invasive species frequently degrade habitats, disturb ecosystem processes, and can increase the likelihood of extinction of imperiled populations. However, novel or enhanced functions provided by invading species may reduce the impact of processes that limit populations. It is important to recognize how invasive species benefit endangered species to determine overall effects on sensitive ecosystems. For example, since the 1990s, hybrid *Spartina* (*Spartina foliosa* × *alterniflora*) has expanded throughout South San Francisco Bay,

US, supplanting native vegetation and invading mudflats. The endangered California clapper rail (*Rallus longirostris obsoletus*) uses the tall, dense hybrid *Spartina* for cover and nesting, but the effects of hybrid *Spartina* on clapper rail survival was unknown. We estimated survival rates of 108 radio-marked California clapper rails in South San Francisco Bay from January 2007 to March 2010, a period of extensive hybrid *Spartina* eradication, with Kaplan–Meier product limit estimators. Clapper rail survival patterns were consistent with hybrid *Spartina* providing increased refuge cover from predators during tidal extremes which flood native vegetation, particularly during the winter when the vegetation senesces. Model averaged annual survival rates within hybrid *Spartina* dominated marshes before eradication ($\hat{S} = 0.466$) were greater than the same marshes posttreatment ($\hat{S} = 0.275$) and a marsh dominated by native vegetation ($\hat{S} = 0.272$). However, models with and without marsh treatment as explanatory factor for survival rates had nearly equivalent support in the observed data, lending ambiguity as to whether hybrid *Spartina* facilitated greater survival rates than native marshland. Conservation actions to aid in recovery of this endangered species should recognize the importance of available of high tide refugia, particularly in light of invasive species eradication programs and projections of future sea-level rise.

Electronic supplementary material The online version of this article (doi:10.1007/s10530-013-0634-5) contains supplementary material, which is available to authorized users.

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Keywords Invasive species · Demographic
bottleneck · Survival · Clapper rail · *Spartina* ·
Tides

Introduction

Invasive species eradication is often undertaken to restore ecosystem health or improve function. Invasive species directly and indirectly affect native populations and communities (Crooks 2002; Vitousek et al. 1997; Vitousek 1990). Direct effects include altered resource availability, chemical composition, and physical structure, and indirect effects include modification of food webs, species interactions, and disturbance regimes. In addition, invasions often coincide with habitat degradation or altered climate condition causing complex interactions with ecological communities (Didham et al. 2007; Marvier et al. 2004). However, effects of invasive species are not all negative, and the “native good, alien bad” philosophy has recently been questioned (Goodenough 2010). Mechanisms by which native species benefit from non-natives involve habitat modification, trophic subsidy, pollination, competitive release, predator release, and indirect effects resulting from predator-prey interactions or trophic cascades, potentially involving multiple invasive species (Bergstrom et al. 2009; Rodriguez 2006; White et al. 2006). In these situations, eradication may lead to insufficient “natural” habitat for native populations or the severing of biotic relationships that developed with invading species. Facilitation of native biota may also occur when the invasive species provides a limiting resource, functionally replaces a native species, or ameliorates depredation (Goodenough 2010, Rodriguez 2006). Facilitation by invasive species is increasingly recognized; for example, southwestern willow flycatcher (*Empidonax traillii eximius*) use tamarisk (*Tamarix* spp.) for nesting and migration stopover habitat where alternative habitat does not exist (Paxton et al. 2007). Facilitative interactions appear particularly important in stressful environments (Stachowicz 2001), and invasive species can ameliorate harsh environmental effects on other species, particularly when invasive species create novel habitats through ecosystem engineering (Rodriguez 2006; Watling et al. 2011).

Cordgrasses (*Spartina* spp.) are invasive ecosystem engineers that have invaded, hybridized (with related species), or created new invasive species through chromosome doubling (i.e. *Spartina anglica*), thereby invading saltmarshes in all continents (Ayres et al. 1999; Callaway and Josselyn 1992; Chambers et al. 1999; He

et al. 2011; Strong and Ayres 2013; Zedler and Kercher 2004). Smooth cordgrass (*Spartina alterniflora*) invaded San Francisco Bay through restoration activities in 1973 (Faber 2000). For over a decade, the plant went virtually unnoticed until it hybridized with the native Pacific cordgrass (*Spartina foliosa*). This hybrid, *Spartina foliosa* \times *alterniflora*, (hereafter hybrid *Spartina*) rapidly expanded throughout South San Francisco Bay (Ayres et al. 2004), and eventually reached northward to portions of San Pablo Bay. Native vegetation in San Francisco Bay saltmarsh conforms to strongly defined vegetation zones with *S. foliosa* at the lowest elevations, *Sarcocornia virginica* in the mid marsh, and a complex of high marsh vegetation including *Grindelia humilis*, *Distichilis spicata*, *Jaumea carnosa*, and *Frankenia grandifolia* in high or well-drained portions (Greenberg and Maldonado 2006; Hopkins and Parker 1984). Influx of freshwater in the northern reaches of San Francisco Bay allows various *Schoenoplectus* spp. and *Juncus* spp. to grow and creates qualitatively different vegetation conditions between the South and North Bays (C. Overton, personal observation). Hybrid *Spartina* grew in a similar manner to the tall-form of *S. alterniflora* on the Atlantic coast, which forms dense monotypic meadows in the low to mid marsh and is outcompeted by *Spartina patens* in the highest tidal reaches (Bertness 1991). However, hybrid *Spartina* grows both lower and higher on the marsh plain than either parent species. Compared to *S. foliosa*, hybrid *Spartina* is also taller, grows more densely, and leaves greater residual biomass during the winter, resulting in more sediment accretion (Callaway and Josselyn 1992; Daehler and Strong 1996; Rosso et al. 2006). Hybrid *Spartina* developed several traits not usually seen in either parent species including: self-compatibility, rapid vegetative expansion, higher seed set than *S. foliosa*, and an Allee effect of faster than exponential growth in established clones (Ayres et al. 2008; Daehler and Strong 1997; Sloop et al. 2009). These traits, along with hybrid *Spartina*'s preadaptation to conditions, autogamic reproduction, vegetative reproduction, and phenotypic plasticity, match characteristics of other highly invading species (Baker 1965; Richardson and Pyšek 2006). Fear of increased flood risk, irreversible changes to tidal marsh geomorphology, and altered habitat structure affecting many sensitive species prompted planning for a large-scale eradication effort using herbicide and manual removal treatments by 2003 (Strong and Ayres 2013).

The San Francisco Bay estuary also contains the last occupied habitat of the saltmarsh obligate California clapper rail (*Rallus longirostris obsoletus*; Takekawa et al. 2011); one of eight clapper rail subspecies in the United States and one of three Pacific Coast subspecies each of which are threatened or endangered (Eddleman and Conway 1998). Historically, the California clapper rail ranged among intertidal saltmarshes along the California coast from Morro Bay to Humboldt Bay. With the exception of periodic sightings along the outer coast, current populations only occupy the highly fragmented remnant and restored marshlands in San Francisco and Suisun Bays. California clapper rails typically breed and forage in mid and lower intertidal vegetation communities, including in hybrid *Spartina*. They vigorously defend small seasonal (2 ha) and annual (4 ha) home ranges but will forage and seek refuge during tidal inundation higher in marshes, within taller vegetation, and along levee faces where sufficient cover and channelization exists (Eddleman and Conway 1998; Garcia 1995; Rohmer 2010). However, when suitable refugia is not available, clapper rails will occupy any available substrate (e.g. floating objects) even if it does not provide any cover (Cogswell 1977). Habitat conversion to agriculture, salt production, and development was the primary reason for both population declines and endangerment during the last century (U.S. Fish and Wildlife Service 2010). Native, synanthropic, and non-native avian and mammalian species depredate California clapper rails. Non-native red fox (*Vulpes vulpes*) were the suggested cause of population declines during the 1980s and early 1990s (Foin et al. 1997; Harding et al. 2001). Contemporaneous research suggested low annual survival rates compared to other clapper rail subspecies (Albertson 1995). Predator management and tidal marsh restoration were credited with apparent population recovery from a few hundred individuals in the early 1990s to 1,040–1,264 by the late 1990s (Albertson and Evens 2000). However, expansion of hybrid *Spartina* also occurred during this period of clapper rail recovery which peaked in 2007.

Vegetation structure is often more important than species composition for vertebrates. This is especially true in saltmarsh where processes governing population dynamics (e.g., survival, reproduction and distribution) may be tidally driven. Lack of suitable escape cover during periods of tidal inundation may lead to

increased depredation (Dekker and Ydenberg 2004). Reproductive trade-offs between the risks of flooding and risks of predation exist for many species of tidal wetland birds including non-threatened populations of clapper rails (Burger 1985; Eddleman and Conway 1998; Frederick 1987; Frederick and Collopy 1989; Gaines et al. 2003; Meanley 1985; van de Pol et al. 2010). Both saltmarsh sharp-tailed (*Ammodramus caudacutus*) and seaside sparrows (*A. maritimus*) nest in taller than average vegetation which is important for success of seaside sparrow nests (Bayard and Elphick 2011; Gjerdrum et al. 2005). Tidal influences may extend beyond the nesting period as well. Louisiana clapper rails (*Rallus longirostris saturatus*) avoid the edges of marshes, particularly during the first few weeks after nesting (Rush et al. 2010). During tidal inundation of marshes, raptor hunting success increased and avian prey species modified their behavior and habitat selection (Dekker and Ydenberg 2004; Rosa et al. 2006; Whitfield 2003). California clapper rail space-use patterns show strong clustering during both high and low tide periods and low rates of emigration to escape high floodwaters (Casazza et al. 2008; USGS unpublished data). Plant structure may indirectly facilitate persistence through provision of cover and nesting substrate during periods of tidal inundation when alternative vegetation is not of sufficient height to enable use across tidal inundation periods. The greater height and stem density of hybrid *Spartina* than native vegetation in San Francisco Bay are consistent with increased provision of refuge cover for California clapper rails during periods of inundation.

Herbicide spraying to eradicate hybrid *Spartina* throughout San Francisco Bay began in 2005. Treatments included aerial, boat, vehicle, and backpack application of imazapyr (a non-selective, imidazolinone class, protein synthesis disruptor) to kill plants or conduct “chemical mow” treatments using reduced herbicide concentrations to prevent plant seed set and vegetative expansion (Invasive *Spartina* Project 2003). Despite the need for successive treatments to achieve complete removal, the effectiveness of the eradication program at removing *Spartina* in a single treatment was high (McBroom 2012). Prior to herbicide application, habitats used by radio-marked clapper rails in invaded marshes were taller than native marshes (USGS unpublished data). After two years of application, hybrid *Spartina* was shorter or absent

from locations while native vegetation regrew and maximum vegetation heights did not differ between treated and native vegetation marshes (USGS, unpublished data). Coincident with hybrid *Spartina* eradication, population monitoring of California clapper rails indicated large declines in abundance (Liu et al. 2009; McBroom 2012).

In this paper, we examined how habitat dynamics created by vegetation phenology and hybrid *Spartina* eradication efforts affected California clapper rail survival in relation to various levels of flooding. Two of the main factors influencing vegetation during our study were seasonal plant senescence during the winter and application of herbicide. We hypothesized that the amount of tidal refugia provided by vegetation would decrease through the winter and used repeated measurement of vegetation height at fixed locations to test this hypothesis. We also evaluated change in refuge cover before and after herbicide application using remotely sensed data depicting vegetation heights. Lastly, California clapper rail survival rates vary seasonally with the lowest survival rates during the winter (Albertson 1995). We hypothesized that tide levels and vegetation structure are responsible for this pattern. Therefore, we tested for effects of season of the year, tidal inundation, and hybrid *Spartina* on California clapper rail survival rates.

Methods

Study area and telemetry techniques

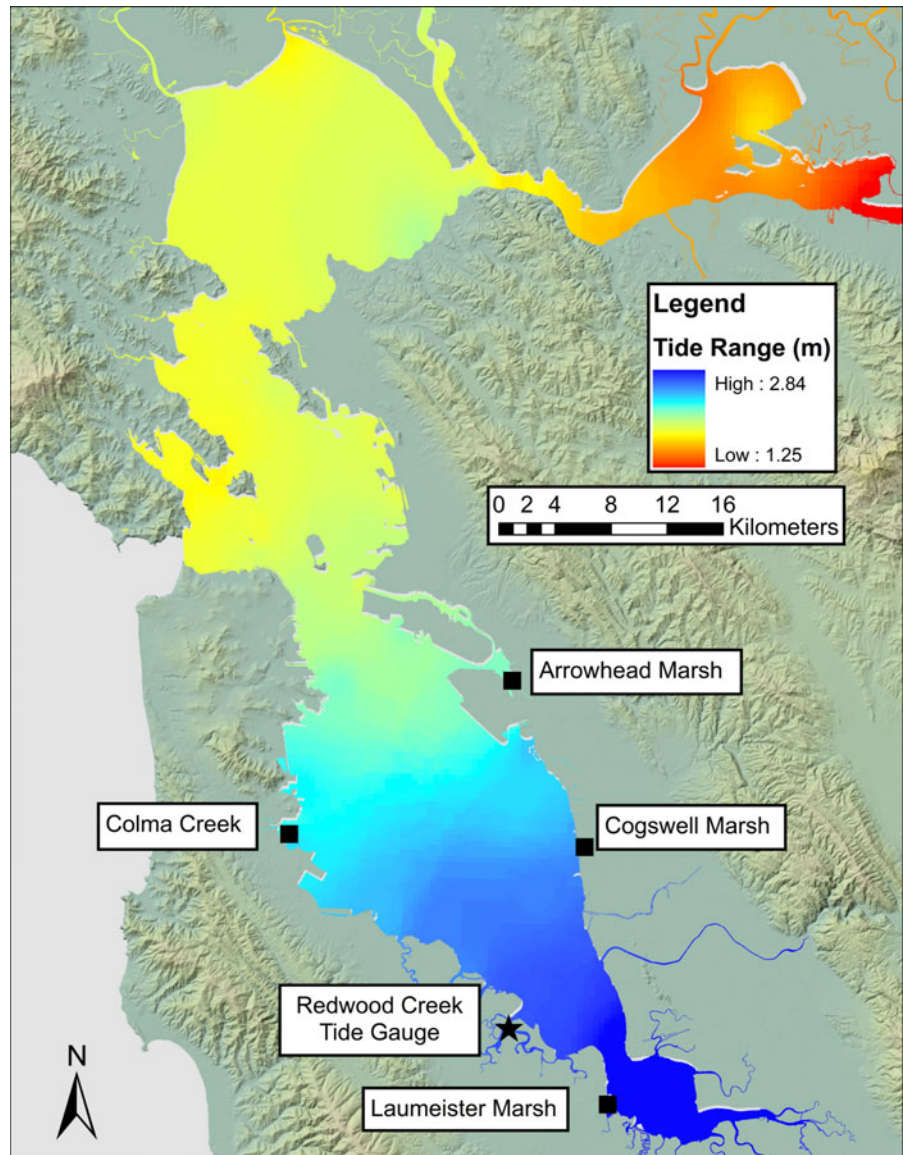
We captured and radio-marked California clapper rails with very-high-frequency (VHF) transmitters at four saltmarshes (Arrowhead [10 ha], Colma [25 ha], Cogswell [60 ha], Laumeister [36 ha]) in the southern reach of San Francisco Bay (Fig. 1) between 2007 and 2009. Arrowhead was created by sediment deposited after the Lake Chabot Dam failed in 1874. Cogswell was previously diked and used for salt production and restored to tidal marsh in 1980. Laumeister has been saltmarsh for over 110 years, making it one of the oldest remaining marshes in the South Bay. Colma has been highly modified since the 1950s. Historically, much of the current marsh was mudflat with limited vegetation that consisted mostly of *S. foliosa* and *S. virginica*. By the mid-1980s, hybrid *Spartina* had heavily invaded Colma and expanded throughout the

marsh into adjacent mudflats. Arrowhead Marsh was included in capture efforts beginning in the winter of 2008. Selection of marshes was limited by logistical and legal constraints. Populations of clapper rails needed to be sufficiently large to allow radio-marking without unduly risking viability of entire subpopulations. Additionally, hybrid *Spartina* eradication was being conducted at all known locations of invasion, and thus, randomized application of treatments was not possible. We contrasted estimates of survival between three treatment groups: marshes prior to hybrid *Spartina* eradication efforts (before); after efforts were initiated (after); and marshes with no hybrid *Spartina* to be treated (native marsh).

Capture and radio-marking occurred from December to March at all sites, and we employed two methods depending on the geomorphology of each marsh. We used drop-door traps modified with fishing line tripwires and placed in tidal channels to catch rails during lower tides at Cogswell and Laumeister marshes. At Colma and Arrowhead, we caught rails by hand and with dipnets during the highest tides of the tidal cycle. Clapper rails were fitted with 9.5 g backpack transmitters (Model A1120, Advanced Telemetry Systems, Asanti, MN, USA) attached using modified Dwyer harnesses (Dwyer 1972) made of TeflonTM ribbon (Bally Ribbon Mills, Bally, PA, USA). Rails were monitored intensively for the first two days after marking with repeated attempts at visually observing the bird to verify transmitter fit and acclimatization. We recaptured surviving birds and refitted them with new transmitters after 10–13 months (Table 1).

California clapper rails were relocated 1- to 10-times per week using handheld 3-element Yagi antennas from the perimeter of the marshes at distances 10–400 m from the bird. Transmitters included mortality switches designed to signal inactivity of more than 4 h in duration to enable rapid detection of mortalities. We identified proximate causes of clapper rail mortality based on the condition of remains and available ancillary evidence. Presence of plucked feather piles indicated raptor predation, while crushed bones and burying indicated mammalian predation. We sent samples with no obvious cause of mortality to the U.S. Geological Survey (USGS) National Wildlife Health Center (Madison, Wisconsin, USA) for necropsy. We discovered most carcasses within 2 days of mortality and were confident that scavenging did not bias the assignment of causes of mortality. When radios

Fig. 1 Survival rates of California clapper rails (*Rallus longirostris obsoletus*) were estimated during 2007–2010 from 108 radio-marked individuals at four tidal saltmarshes in South San Francisco Bay. Tide range varies throughout San Francisco Bay with greatest amplitude in the South Bay. Verified tide data used in analysis from NOAA Tide and Currents webpage was obtained at the Redwood Creek tide gauge (<http://tidesandcurrent.noaa.gov>; Accessed May 11, 2011)



failed, or emigrating individuals could not be relocated, ultimate fate could not be determined, and we right censored the individuals in the survival analysis (Kaplan and Meier 1958).

Analysis and covariates

We estimated the seasonal dynamics of intertidal vegetation structure in 2010 and 2011 at 50 random locations in Arrowhead marsh. We recorded maximum vegetation height within 1 m of each random point 4 times between September 2010 and April

2011. Each random point was marked with a Real-Time Kinematic (RTK) global-positioning system unit (Leica Geosystems, Norcross, GA) to record elevation (± 2 cm accuracy). We added vegetation height to ground elevation to identify the tallest cover with respect to tidal height. A Bayesian random slope and random intercept repeated-measures linear mixed regression model (LMM, WinBUGS version 1.4.3) was used to quantify senescence patterns and change in the provision of refuge cover across all points (Gelman and Hill 2006). The random intercept was included for each of the 50 sample locations with a

Table 1 Number of radio-marked California clapper rails (*Rallus longirostris obsoletus*) present in four South San Francisco Bay salt marshes during the capture season, November–March, and used to estimate survival rates, January 2007–March 2010

Marsh	2007	2008	2009	2010
Arrowhead		10*	14	10
Cogswell	11*	9*	13*	2
Colma	9*	16	14	9
Laumeister	10	16	5	1

Presence of hybrid *Spartina* prior to eradication efforts is indicated by an asterisk. Arrowhead Marsh was not included in capture efforts until the winter of 2008–2009. Capture in the winter of 2010 occurred only at Arrowhead and Colma Marshes for subsequent studies

random slope allowing the rate of vegetation senescence to vary according to initial vegetation height. This allowed estimation of a linear relationship between refuge cover height and time without violating the necessary assumption of uncorrelated and normally distributed error structure that would be present in heteroscedastic data (Jacqmin-Gadda et al. 2007).

We assessed vegetation change resulting from hybrid *Spartina* eradication efforts using LiDAR data collected before and after herbicide treatments.

representation of the refuge cover condition in marshes before treatments occurred. LiDAR data for 2004 were collected for the Federal Emergency Management Agency Flood Hazard Mapping Project or for the San Francisco Estuary Institute and USGS Center for Earth Resources Observation and Science. LiDAR data for 2010 were collected for the American Recovery and Reinvestment Act USGS San Francisco Coastal LiDAR Project. Surface elevation models were developed using ENVI software (Excelis Visual Information Solutions, Boulder, CO, USA). Elevation models were represented in 1-m square pixels using first return LiDAR data after mosaicking tiled datasets to the region of interest and filtering erroneous elevations. We used control points on unobstructed hard surfaces (e.g., roads, trails, flat building roofs) to verify vertical accuracy and consistency in estimated elevation for each LiDAR data set. Surface maps were then restricted to marsh boundaries plus a small buffer, approximately 5 m, representing both tidal flat foraging areas and potential upland-tidal marsh ecotone refuge areas. Tide conditions vary throughout San Francisco Bay, therefore all elevations were rescaled to represent local inundation patterns. Rescaling was done according to the formula:

$$\text{Refuge potential} = \frac{(\text{Surface elevation} - \text{Mean Sea Level})}{(\text{Mean Higher High Water} - \text{Mean Sea Level})}$$

We obtained LiDAR data through the Center for LiDAR Information Coordination and Knowledge website (<http://lidar.cr.usgs.gov>, Last Accessed March 24, 2012). Data on 2004 and 2010 habitat structure were available for each of our study marshes. The 2004 data were collected three years before the start of our radio-telemetry study when hybrid *Spartina* was near its maximum extent throughout San Francisco Bay (McBroom 2012). No major alterations to vegetation structure were evident in any of our study sites between the 2004 data acquisition and the start of our research, however hybrid *Spartina* continued to expand during this period. Therefore, the 2004 LiDAR data provides a

In the resulting scale, 0 represents mean sea level (MSL) and 1 represents mean higher high water (MHHW). The advantage to rescaling elevation was that vegetation composition in intertidal saltmarsh has strong zonation with different species tolerating different degrees of inundation that are best represented over large geographic scales using relative elevations as opposed to absolute elevation (Hinde 1954; Swanson et al. 2013).

We employed the Program MARK “Known Fate” subroutine (White and Burnham 1999), which uses the Kaplan–Meier product limit estimator, and a logit-link, to estimate weekly survival rates (Kaplan and Meier 1958). We developed a weekly encounter

history for each bird that indicated presence in the study area and incidence of death. Encounter histories were grouped by treatment type (before, after, and native marsh). Individuals alive through the pre-eradication period were right censored in the before treatment group at the start of the winter following the initial hybrid *Spartina* treatment and left censored in the after treatment group. One advantage of the Kaplan–Meier estimator lies in its ability to account for censored individuals using staggered entry (Pollock et al. 1989). We used time-varying indicator variables to assess seasonal differences in survival. Three ecologically relevant seasons were investigated; Breeding (March 15–July 14), Post-Breeding (July 15–November 14) and Winter (November 15–March 14). We chose the season names to represent the primary behavioral activities clapper rails exhibit during the periods. The period timeframe however represents the vegetation phenology occurring in the tidal marsh. The Breeding period occurs during spring green up and plant growth when plants are mostly below the maximum height attained in a year. The Post-Breeding period occurs when plants are at the maximum height and when flowering occurs. The Winter period is characterized by plant senescence and degradation by tides. We used time-varying continuous variables to estimate the effects of average and maximum weekly tide levels on survival. Individual covariates identifying capture site, sex, and time-varying indicator variables for year of study were included to test for potential confounding differences in survival. Random effects models can be used to account for temporal or spatial variation, but these effects were confounded with the primary effect and lacked sufficient levels to model their distributions properly (Burnham 2012). Our candidate model set included 10 models related to our three hypotheses, namely that survival of California clapper rails was related to tide height, season, and treatment status (before, after, or native marsh). The first two hypotheses relate to mechanisms by which hybrid *Spartina* may have facilitated greater survival in the California clapper rail; i.e., due to taller structure and more biomass remaining over the winter. The final hypothesis directly compares survival rates between treatment groups (before eradication, after eradication, and native marsh). An additional 19 models were evaluated that included potential confounding variation, such as survival differences between sites, years, or

sexes. A complete list of variables included and the 29 models considered are available online (Supplement 1).

We used Akaike Information Criterion (AICc) to determine the best-fitting models from those tested (Burnham and Anderson 1998). We contrasted group survival rates (before treatment versus after treatment versus native marsh) after accounting for environmental and temporal variation. We refer to “competing models” within 2 AIC units of the best performing model for clarity. Potential confounding spatial or temporal variation were evaluated independently (relative to null) of the competing models to provide robust model-averaged parameter estimates (Burnham and Anderson 1998). Site-level variation was highly confounded with treatment group and caused estimation and convergence failures when the two variables were included together in models. Therefore, we did not attempt to model site variation in conjunction with hybrid *Spartina* treatment group. Interpretation of our model results focused on model-averaged effect sizes (Burnham and Anderson 1998) and relative ranking of nested models (using AICc weights). We assessed effects of transmitter attachment on clapper rails through behavioral observation, changes in body condition, and comparison of survival rates between newly marked birds and birds that had shown resilience in carrying transmitters for a full year. Since age of individuals is not identifiable during the capture season, we could not assess this effect differentially between adults and hatch-year birds. We assumed that the resilience of individuals from the previous cohort year (previously marked birds) was the same as the following year (newly marked birds).

Captured rails were sexed based on morphology (Overton et al. 2009) or genetic analysis of blood samples (Zoogen DNA Services© Davis, CA). We obtained tide heights from a National Oceanic and Atmospheric Administration (NOAA) continuous tide monitoring station centrally located near Redwood Creek. Weekly MHHW and maximum higher high water (MaxHHW) were calculated from verified online data (NOAA website <http://tidesandcurrents.noaa.gov> accessed August 2nd, 2010). Local tide patterns constrain marsh vegetation, elevation, and geomorphology (Hinde 1954; Redfield 1972); therefore, a single relative tide height (e.g. Redwood Creek) was more appropriate to assess tidal effects across sites than tide heights at individual marshes.

The effect of high water on survival of rails was expected to be most pronounced during the winter when *Spartina* had senesced and been degraded by high tides. An interactive effect of tide height and season was therefore included in our statistical models. Herbicide application to eradicate hybrid *Spartina* occurred annually between August and October throughout the study. Methods of application included helicopter, vehicle-mounted, or backpack spraying using dyed herbicide to restrict application to hybrid *Spartina* only (Invasive *Spartina* Project 2003). This minimized effects of herbicide on native vegetation, which rapidly recolonized areas after hybrid *Spartina* removal (Hogle 2011). Laumeister was classified as the “native marsh” treatment because hybrid *Spartina* eradication was limited to a few isolated clones of <1 ha. Marshes in which hybrid *Spartina* initially occurred (“before”) were recategorized to the “after” treatment during the winter following the first application of herbicide treatments (Table 1). Efforts to finish eradication of hybrid *Spartina* were still ongoing at all sites at the end of our study, but significant reduction in hybrid *Spartina* cover and biomass occurred in the first year following initial treatments (Hogle 2011, McBroom 2012). Prior to herbicide application invaded marshes had significantly taller vegetation than the native marsh. Following herbicide treatment, hybrid *Spartina* decreased in height while native vegetation, particularly *Sarcocornia virginica*, regrew (Hogle 2011). After two years of herbicide application, the maximum vegetation heights were not different between invaded and native marshes (USGS unpublished data).

Results

We rejected the null hypothesis that availability of refuge habitat remained consistent throughout the winter. The maximum elevation of vegetation at Arrowhead Marsh declined by 4.3 cm in every bimonthly sampling period (95 % credible interval = -6.2 to -2.3 , $n = 200$) resulting in an average total decline of 34.4 cm from September 2010 to April 2011. However, this decline was not uniform across the marsh since plants that represented the tallest vegetation and greatest refuge cover declined more rapidly than shorter and lower elevation plants (i.e. random slope and intercept effects were correlated,

Fig. 2). The proportion of vegetation providing adequate refugia for rails during winter tides remained consistent between September and November, and then declined rapidly in February and April (Fig. 3).

Longer term habitat dynamics resulting from hybrid *Spartina* eradication efforts, as indicated by LiDAR derived digital elevation models, showed decreased availability of high tide refuge cover relative to conditions prior to eradication. LiDAR maps consistently estimated elevation of static surfaces (e.g. roads) between 2004 and 2010 with ranges from -7 cm to $+8$ cm for all marshes. This was lower than the 12 cm vertical root mean squared error (RMSE_z) standard which was the maximum error for individual data sets assessed using ground control points and an Airborne Global Positioning System base station (Dewberry 2011a, b; Foxgrover and Jaffe 2005). Thus, LiDAR change within the marshes between 2004 and 2010 indicated change in plant structure following hybrid *Spartina* eradication efforts, rather than inconsistent elevation estimates. Surface elevations and the proportion of habitat above mean higher water declined for all three marshes

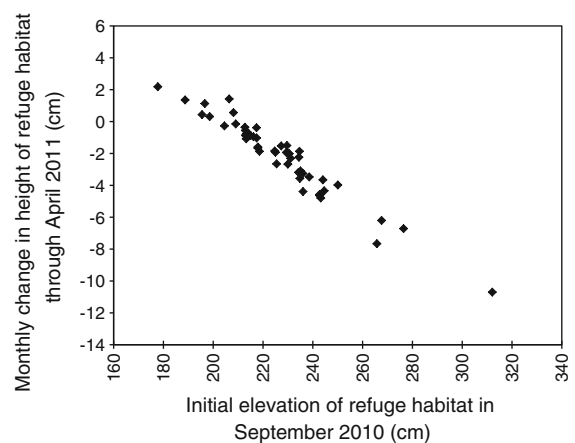


Fig. 2 Average monthly change in vegetation elevation (Height above Mean Lower Low Water [MLLW]) at 50 locations in Arrowhead Marsh, Oakland, CA between September 2010 and April 2011. Points represent predicted random slopes for each sample location. The surface elevation of Arrowhead Marsh averages 162 cm in elevation. Mean High Water (MHW) during the winter was 200 cm, Mean Higher High Water (MHHW) was 220 cm, and Maximum Observed Tide Level (MaxHHW) was 240 cm. Plants higher in the tidal prism declined in total height more rapidly than plants lower in the prism; indicating progressive limitation in intertidal refuge cover throughout the winter

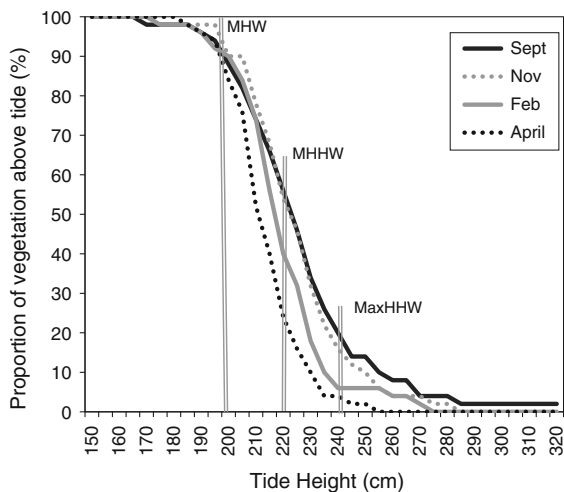


Fig. 3 Arrowhead Marsh refuge elevation (marsh elevation plus vegetation height) as proportion of available habitat showing senescence pattern and progressive loss of refuge habitat from September 2010 through April 2011 ($n = 50$). Observed mean high water (MHW), mean higher high water (MHHW), and Maximum observed tide (MaxHHW) indicated by vertical bars

where hybrid *Spartina* eradication occurred (Fig. 4, Table 2). At Laumeister Marsh, where hybrid *Spartina* did not occur, surface elevations and proportion of habitat above MHHW increased very little between 2004 and 2010 (Fig. 4, Table 2). Our results indicate a marked decline in refuge cover available for clapper rails in marshes following hybrid *Spartina* eradication efforts, despite recolonization by native vegetation (McBroom 2012; USGS unpublished data).

We captured and radio-marked 108 California clapper rails (males = 49; females = 59) in four marshes (Table 1) and estimated survival over 166 weeks. Most clapper rails died due to predation. Raptors depredated 30 individual clapper rails and mammals depredated 27. Two individuals died of diseases identified by the USGS National Wildlife Health Center. One individual died of trauma unrelated to predation. Many of the remaining 48 birds were suspected to have died due to predation for which specific agents could not be determined. We found no evidence that transmitters lowered initial survival rates following capture, changed physiology, or prevented breeding. Transmitter and capture effects should be identifiable through lower survival soon after marking, but over the same time period, newly marked birds had no detectable difference in survival than individuals marked the previous year (95 % Confidence

Limits [CL]: -7.0% to $+7.8\%$). Both males and females nested, including several pairs where both adults were radio-marked. Mass of individual clapper rails recaptured one year following marking on average dropped less than 1 % from initial marking ($n = 24$; range -8.2% to $+12.2\%$). Data were not available for an independent validation of survival rates and assessment of transmitter effects, but the data available indicate that capture and marking had little effect on survival and marking did not affect body condition or reproductive potential.

Four competing models contained variables accounting for seasonal differences in survival rates, MaxHHW, and differences in rates due to hybrid *Spartina* treatment (Table 3). Potential confounding spatial or temporal variation were evaluated independently (relative to null) with the four top-ranked models from the candidate model set to provide robust model-averaged parameter estimates (Burnham and Anderson 1998). Site-level variation was highly confounded with treatment group and caused estimation and convergence failures when the two variables were included together in models. Therefore, we did not attempt to model site variation in conjunction with hybrid *Spartina* treatment group. Covariates accounting for survival variation according to site, sex, or annual differences in survival rates all received little support from the data. The model-averaged survival rate was 0.978 (95 % CL: 0.960–0.988) per week across all marshes, treatments, and years. These estimates yielded average annual survival rates across all marshes of 0.315 (95 % CL: 0.120–0.541). Parameter estimates for all competing models are provided in the supplementary material (Supplement 1).

Our best-supported model contained effects on survival relating to all three of our primary hypotheses; season, tide level, and hybrid *Spartina* eradication treatments. Models containing each effect individually outperformed the null hypothesis; therefore, we rejected all three related null hypotheses. Seasonally varying survival was present in all competing models and was the most important effect in our models based on relative likelihood values for models containing that effect. Model-averaged weekly survival probability was lower in the winter season (November 15–March 14; 0.963; 95 % CL: 0.934–0.979), with breeding (March 15–July 14) and post-breeding season (July 15–November 14) survival rates approximately equal (0.985; 95 % CL:

Fig. 4 Proportion of habitat above tidal ranges at Arrowhead Marsh (a), Cogswell Marsh (b), Colma Marsh (c), and Laumeister Marsh (d) in South San Francisco Bay in 2004 (dotted line) prior to hybrid *Spartina* eradication and in 2010 after eradication efforts (solid line). The x-axes are standardized to represent local tidal ranges (Mean Sea Level—MSL; Mean Higher High Water—MHHW) rather than absolute elevations because tide range varies throughout San Francisco Bay

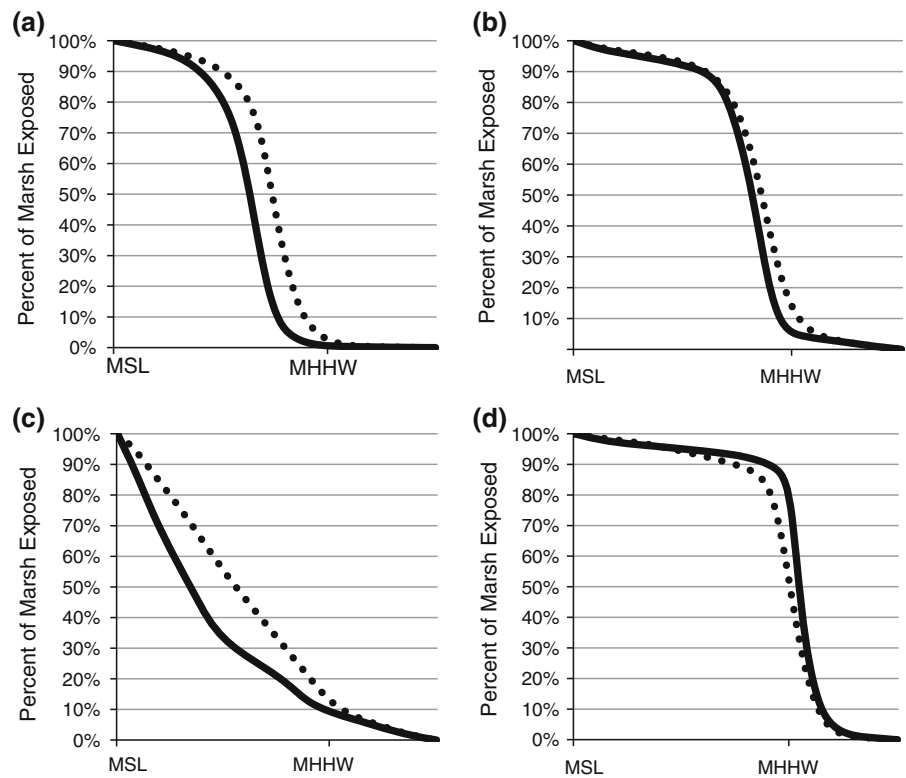


Table 2 Known-fate model results from program MARK version 5.1 run on 108 California clapper rails (*Rallus longirostris obsoletus*) radio marked in South San Francisco Bay, January 2007–March 2010

Model rank	Model	Delta AICc	AICc weight	Model likelihood	# of Parameters	LR ^{2a}
1	Constant survival + seasonal MaxHHW + treatment group	0.0000	0.2304	1.0000	6	0.2420
2	Constant survival + seasonal MaxHHW	0.3727	0.1912	0.8300	4	0.2105
3	Seasonal survival + MaxHHW	1.0325	0.1375	0.5967	4	0.2057
4	Seasonal survival	1.9638	0.0863	0.3746	3	0.1837
17	Constant survival (null model)	19.8424	0.0000	0.0000	1	N/A
26	Week specific survival (global model)	177.261	0.0000	0.0000	166	0.9238

Only competing models (Delta AICc < 2.0), global, and null models are presented. All models incorporating average weekly higher high water, annual, site or sex specific survival rates were poorly supported (AICc weight < 0.03, Model Likelihood < 0.1). A full explanation of variables used and candidate model set is available online (Supplement 1)

$R^2 = (1 - (L(\text{intercept model [17]})/L(\text{full model}))^{2/N}) / (1 - (L(\text{intercept model [17]})))$; where L() is the likelihood of the model and N = number of samples [N = 108]

^a Likelihood pseudo-R² calculated using the method of Nagelkerke (1991)

0.97–0.992 and 0.990; 95 % CL: 0.976–0.995, respectively). Seasonal risk of mortality (i.e. $1-\hat{S}$) was more than twice as great in the winter than in other seasons.

Weekly MaxHHW was negatively correlated with survival in four of the six competing models

($\Delta\text{AICc} < 2.0$). Seasonally varying tidal effects outperformed models allowing only a constant effect of tide level throughout the year; these models likely represent the influence of vegetation structure which differed in each season. The effect of maximum tide

Table 3 Tidal characteristics and high tide refuge habitat at four salt marshes in South San Francisco Bay

Marsh	Size (ha)	MSL	MHHW	Tide rise	Proportion of marsh above MHHW 2004 (%)	Proportion of marsh above MHHW 2010 (%)
Arrowhead	19.1	1.09	2.03	0.94	2.6	0.6
Colma	32.2	1.15	2.14	0.99	12.8	9.3
Cogswell	78.2 ^a	1.16	2.28	1.12	13.5	5.5
Laumeister	39.2	1.24	2.31	1.07	50.5	77.7

Habitat characteristics determined by LiDAR first-return surface elevation maps and represent minimum elevation of habitats in 2004 and in 2010

^a Cogswell Marsh is 84.8 hectares but due to gaps in the flightline of LiDAR data only 78.2 hectares were assessed

level was greatest during the winter (model averaged, logit scale $\beta = -1.27$) relative to equivalent tides during other seasons (Breeding season $\beta = -0.891$; Post-breeding $\beta = 0.841$; Fig. 5). Qualitatively similar patterns were estimated when weekly MaxHHW was modeled as an additive effect with seasonal survival differences (Supplement 1). Contemporaneous seasonal vegetation structure data were not available to test their effect in models of survival.

The best performing model differentiated survival probability into the three treatment groups, and all models including this effect outperformed the null model and reduced models without treatment effects (Supplement 1). The model averaged weekly survival in marshes prior to initial efforts to eradicate hybrid *Spartina* (0.985; 95 % CL 0.973–0.992) was greater than after eradication efforts began (0.975; 95 % CL 0.960–0.985) and compared to Laumeister Marsh (0.972; 95 % CL 0.947–0.985) which did not contain hybrid *Spartina* (Fig. 6). Survival in marshes with untreated hybrid *Spartina* was associated with annual survival rates that were one and a half to two times as greater than survival rates after eradication or in native marsh. Extrapolated annual survival in marshes with hybrid *Spartina* prior to treatment was 0.466 (95 % CL 0.419–0.518) and was 0.275 (95 % CL 0.235–0.321) after eradication began. Extrapolated annual survival at Laumeister Marsh was 0.227 (95 % CL 0.185–0.279) where only native vegetation was available to clapper rails. Native marsh had the lowest estimated mean survival rates in our study, but was not significantly different than survival following herbicide treatment to remove hybrid *Spartina* (difference in model averaged weekly survival = 0.0034; SE 0.00864; $p = 0.679$). This may have reflected residual hybrid *Spartina* that often remained as shorter

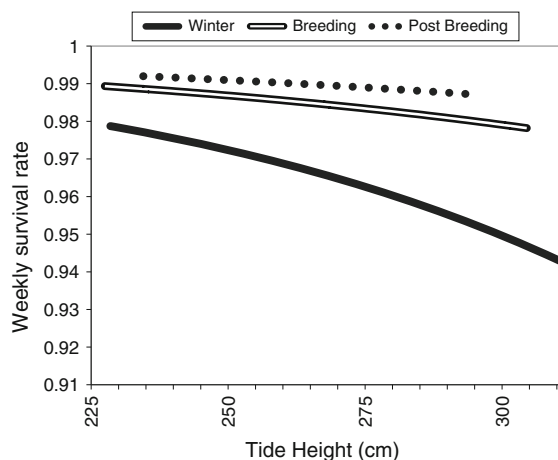


Fig. 5 Model averaged weekly California clapper rail (*Rallus longirostris obsoletus*) survival estimates for three seasonal periods in relation to Maximum Higher High Water (MaxHHW). Seasonal periods included Winter (November 15–March 14), Breeding (March 15–July 14), and Post Breeding (July 15–November 14). Plotted lines represent observed tide range for each season during this study, 2007–2010

refuge cover in marshes during the first years following treatment (McBroom 2012; USGS unpublished data). Clapper rails within the native marsh had significantly lower mean survival than rails in hybrid *Spartina* invaded marshes that had not yet been treated (difference in weekly survival 0.0135; SE = 0.00751; $p = 0.036$; Fig. 6). Our results also suggest that survival prior to eradication was greater than survival following herbicide application within hybrid *Spartina* invaded marshes (difference in weekly survival = 0.00994; SE = 0.00634; $p = 0.059$).

As we have noted, models evaluating survival rate differences among marsh treatments outperformed reduced models without treatment effects (Supplement 1) and model average parameter values estimating

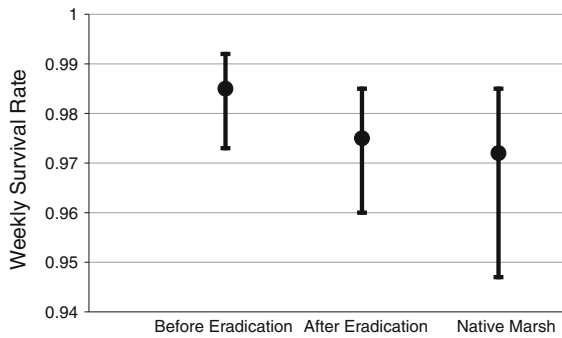


Fig. 6 California clapper rail (*Rallus longirostris obsoletus*) weekly survival rates between January 2007 and March 2010 were analyzed for differences between hybrid *Spartina* (*S. foliosa* × *alterniflora*) treatment groups. Model averaged parameters indicated that survival in marshes with hybrid *Spartina* prior to eradication activities (before) was greater than both survival following eradication (after) and at Laumeister which contained virtually no hybrid *Spartina* (native). Native marsh survival rates were similar to survival after herbicide treatment in invaded marshes. However, available data was limited and model selection indicated nearly equal support for models with and without treatment effects on survival rates. Error bars represent 95 % confidence limits

differences between marsh treatments indicated that hybrid *Spartina* marshes prior to herbicide application had significantly greater survival rates than native marsh or the same marshes following eradication. However, AICc ranking of models indicated competition (ΔAICc values < 2.0) between nested models that included and excluded marsh treatments. This led to contradictory support for our hypotheses between traditional p value and information theoretic approaches to statistical inference suggesting caution to avoid overinterpreting the available data (Burnham and Anderson 1998).

Discussion

California clapper rail population trends mirrored the invasion of South San Francisco Bay by hybrid *Spartina*. Increase in the clapper rail population abundance from a few hundred individuals to a few thousand individuals coincided with expansion of hybrid *Spartina* throughout South San Francisco Bay (Albertson and Evens 2000). Clapper rail populations have declined following efforts to eradicate hybrid *Spartina* (Liu et al. 2009). Furthermore, the highest clapper rail densities frequently occur in invaded areas. One exception was

Laumeister marsh which contained the only known large clapper rail population in South San Francisco Bay and was not invaded by hybrid *Spartina* (Invasive *Spartina* Project 2003, Liu et al. 2009). Altered survival is a likely mechanism that accounts for these patterns, and the highest survival rates we estimated occurred in marshes with substantial infestation by hybrid *Spartina*. Following herbicide application, these same marshes had survival rates equivalent to a marsh with native vegetation only. The patterns of differences in survival rates among treatments are consistent with rail survival due to hybrid *Spartina* removal. Native-dominated marsh occupied by clapper rails could not be replicated; therefore, we cannot exclude the possibility that marsh identity is responsible for these patterns. For example, native-dominated marsh typically occurs at higher average elevation than invaded marsh due to the greater inundation tolerance of hybrid *Spartina*. However, survival after *Spartina* eradication was not significantly different than survival in native-dominated Laumeister marsh. The data led to considerable model selection uncertainty (Supplement 1), and competing models both with and without treatment effects were produced by our analysis with both information theory criteria and hypothesis testing. Hybrid *Spartina* could have facilitated greater survival in California clapper rails, although our results are inconclusive.

The environmental mechanisms influencing clapper rail survival, which hybrid *Spartina* was expected to ameliorate (i.e., tidal inundation and seasonal vegetation senescence), were significant correlates to survival estimates. Survival of clapper rails decreased during periods of greater tidal inundation in all marshes, but the impact of tide level was greatest in the winter when senesced vegetation reduced available refuge cover. In concordance with this seasonal pattern, Albertson (1995) also found similarly low California clapper rail survival rates during the winter in saltmarshes with native vegetation. We believe that it is differences in the vegetation structure provisioned by hybrid *Spartina*, rather than species composition *per se*, which facilitated higher clapper rail survival within invaded marshland.

Invasive species can ameliorate harsh environments by creating novel habitats through ecosystem engineering (Rodriguez 2006; Watling et al. 2011). This facilitation may be particularly important to mediate persistence in stressful environments (Stachowicz 2001). Extreme tidal inundation, though

occupying a small portion of the year, dramatically alters the suitability of habitats to provide escape cover. Clapper rails use tall vegetation as refuge from predation, which becomes less available during tidal inundation and during the winter when vegetation senesces. We found that hybrid *Spartina* used by radio-marked California clapper rails in 2007 was taller than similarly used native marsh vegetation, but within two years after application of herbicide, the height of hybrid *Spartina* had dropped and native vegetation regrown sufficiently for no differences to have been evident between treated and native marshes (USGS unpublished data). The rapid return of native plant species following herbicide treatment (McBroom 2012) suggests that within the highly fragmented and greatly altered marshlands in San Francisco Bay, hybrid *Spartina* provides higher quality tidal refugia, and refuge over a greater range of environmental conditions than native vegetation. Even with active restoration of saltmarsh vegetation, eradication of hybrid *Spartina* could have negative consequences for California clapper rails. The impact on the endangered southwestern willow flycatcher of large-scale control efforts of tamarisk offers interesting parallels to the current hybrid *Spartina* effort. Willow flycatchers benefit from the structure provided by non-native tamarisk particularly where native riparian plant communities are absent (Sogge et al. 2013). Tamarisk was also the focus of a major removal effort involving biological control by the tamarisk leaf beetle (*Diorhabda oblongata*), which defoliates tamarisk during the summer coinciding with the flycatcher's breeding activities (Paxton et al. 2011). Concerns about the effect of defoliation during this critical reproductive period were compounded by uncertainty on the pace and ability of native riparian woodlands to replace tamarisk and led to cessation of biological control efforts by the U.S. Department of Agriculture (Sogge et al. 2013). The potential impacts of hybrid *Spartina* removal on clapper rails have raised similar concerns.

Sea-level rise is a recognized concern that may influence clapper rail survival and suitability of already degraded habitats (U.S. Fish and Wildlife Service 2010). San Francisco Bay saltmarshes exhibit extreme spatial and seasonal variation in tidal cycles (Fig. 1). During our study, mean tide range at the Golden Gate Bridge was 1.25 m, but this increased to 2.20 m at the extreme southern reach of our study area,

Laumeister Marsh (National Oceanic and Atmospheric Administration 2011). The highest tides inundate large sections of marshland and constituent vegetation. Coupled with seasonal vegetation senescence patterns and damage from storm surges, the habitat available as refuge cover for saltmarsh obligate species is highly variable and becoming more limited as sea level increases (Flick et al. 2003; National Oceanic and Atmospheric Administration 2009). Even when fully mature, native vegetation would not replace losses of the novel refuge cover provided by hybrid *Spartina* given the current level of habitat fragmentation and degradation of San Francisco Bay marshlands. Our analysis of habitat elevation, relative to local tidal patterns, corroborates this. Following hybrid *Spartina* eradication, the proportion of marshland that provided potential refuge cover during the winter declined in all treated marshes (Fig. 4) despite the presence of vegetation that was structurally similar to native marshes (USGS, unpublished data). The relative loss of refuge habitat was often more pronounced at higher tide levels and suggests that the pattern of sea level rise may influence quality of salt marsh habitats. For example, sea-level rise scenarios typically assess increases in mean sea level (Flick et al. 2003). However, some research suggests that tidal maxima (high and higher high water) are increasing faster than mean sea level and indicates limitation of tidal refuge may become more severe in the future (Cayan et al. 2008). Habitats that currently provide refuge cover during extreme tides may fail to do so in the future even with relatively minor increases in mean sea level. *Spartina* species are known ecosystem engineers highly valued for maintaining shorelines, largely through increased sediment deposition (Strong and Ayres 2009). Loss of tidal refugia could be minimized if sedimentation rates can offset sea level rise. However, under all projected climate scenarios, San Francisco Bay is expected to lose high marsh habitat that serves as refuge during extreme tides (Stralberg et al. 2011; Takekawa et al. 2013).

Our findings do not discount the potential for larger scale and extrinsic factors to influence clapper rail survival. California clapper rail populations declined substantially between 2007 and 2008; this pattern was also noted for the light-footed clapper rail (*R. l. levipes*) in southern California (Zemba et al. 2009). No specific process has been investigated that would cause such wide-scale regional synchrony in terrestrial

population regulating mechanisms, but large-scale climate patterns are associated with changes in communities of marine species in San Francisco Bay and off the California coast (Cloern et al. 2010; Sydesman et al. 2013). Continued monitoring for population synchrony between these subspecies is warranted. Predator–prey relationships are also likely to play a role in regulating individual populations. Avian predator abundance in California increases markedly for some key species in the winter compared to other seasons (Wilkinson and Debban 1980). In particular, the short-eared owl (*Asio flammeus*) and peregrine falcon (*Falco peregrinus*) are known predators of California clapper rails and both achieve their highest local abundances during the winter. Most mammalian predator species do not migrate into saltmarsh habitats during the winter, but seasonal changes in diet, either behavioral (e.g. prey switching) or through additional opportunity provided by decreased vegetation cover, could result in increased depredation by generalist predators.

Density-dependent survival is a third mechanism that could explain seasonal survival differences. Rail populations reach their highest annual densities late in the breeding season. Lower winter survival could represent population regulation following fledging of young that are independent of adults at six weeks of age (Adams and Quay 1958). Survey methods that rely on indices of abundance from pre-breeding call counts may not accurately reflect changes in numbers of breeding individuals or represent post-breeding population abundance, particularly across variable habitat types (Anderson 2001; Conway et al. 1993). Regardless, we feel this explanation falls short since clapper rail density was generally declining during our study. If density-dependent survival was operating, survival should have increased when rail abundance declined, but there was no support for that pattern in our survival models.

Implications

California clapper rail populations have been declining for over 50 years (Albertson and Evens 2000; Liu et al. 2009). Our survival estimates represent the lowest known survival rates for any clapper rail subspecies and appear consistent with recent levels of decline. Current clapper rail management plans to

reverse the population trajectory and recover the species focus mainly on protection and restoration of native saltmarsh habitats previously converted to salt production (U.S. Fish and Wildlife Service 2010). Negative effects of hybrid *Spartina* in the tidal environment are well-documented (Daehler and Strong 1996; Grosholz et al. 2009) and threaten restoration activities. Eradication of hybrid *Spartina* is viewed as a prerequisite to prevent establishment of this invasive species in newly restored tidal marshes. However, there is increasing recognition that invasive species control may have unintended negative consequences for native bird communities, particularly where seasonal changes in vegetation structure affect demographic rates (Paxton et al. 2011). Recommendations for mitigating the negative effects of invasive species control have included maintaining existing uninvaded native habitats, restoring native vegetation, and balancing loss of non-native habitat with adjacent native habitat (Paxton et al. 2011). Our results suggest that high quality habitat for clapper rails should recognize both short term (3–5 h), and seasonal (3–4 months) limitation in tidal refuge cover that reflect a bottleneck in annual survival rates.

The remaining natural habitats in San Francisco Bay may not currently provide high quality habitat for clapper rails, and nearly 96 % may convert to mudflat under projected sea-level rise scenarios (Cayan et al. 2008; Takekawa et al. 2013). Short vegetation, or that which occurs at the lowest elevations of the marsh, may provide suitable habitat for the majority of the year but be unsuitable during critical high tide periods. Since native vegetation does not attain the same biomass or height as hybrid *Spartina*, restoration with native species (e.g. *S. foliosa*) following hybrid *Spartina* eradication may still not provide sufficient tidal refugia for clapper rails to achieve the population sizes apparent in invaded marshes. Habitat modification that decreases available refuge during these critical periods should be considered when assessing effects on clapper rails. Long-term changes to the intertidal marsh ecosystem are ultimately responsible for California clapper rail populations that are not self-sustaining (Albertson and Evens 2000). Around 90 % of marshlands in San Francisco Bay have been lost or converted to other land uses causing reduction and fragmentation of remaining marshlands (Goals Project 1999). Since larger marshes are more likely to have heterogeneous elevations, and given that most of the

conversion for development occurs from the upland transition areas into the high elevation marsh, it is reasonable to assume that tidal refuge was disproportionately affected by past land use changes. Restoration actions, particularly conversion back to tidal salt-marsh, should seek to develop habitats that provide tidal refuge cover throughout the year by restoring heterogeneity in marsh elevations as well as native vegetation communities.

The effects on clapper rail survival and habitat suitability from sea-level rise are likely to vary between San Francisco Bay subregions. The tidal prism moving water in and out of San Francisco Bay determines high-tide level. The natural lateral constriction and shallow depth of South San Francisco Bay leads to a greater tidal range than in North San Francisco Bay marshes, which creates microhabitat conditions suitable for different plant communities in the two areas (Fig. 1). These different plant communities may respond differently to increased inundation frequency and depth, unless vertical sediment accretion can keep pace. In most portions of San Francisco Bay, upslope migration of marshes is no longer possible due to levees, and failure to achieve suitable accretion is likely to result in changes in vegetation composition. Since native *S. foliosa* typically grows among the lowest elevations, replacement of high and mid-marsh vegetation by *S. foliosa* may occur with sea-level rise. *Spartina foliosa* is much taller than most species, which occur higher in San Francisco Bay intertidal marshlands. This could result in increased rail survival, particularly in breeding and post-breeding seasons if *S. foliosa* provides more tidal refugia than existing vegetation. However, this effect may be lost when *S. foliosa* senesces and degrades in the winter. The results from this study suggest a need for future conservation of California clapper rails to address the loss of novel ecosystem function that hybrid *Spartina* provided as refugia during tidal inundation.

We recommend additional research assessing the impacts of habitat structure and modification on recruitment of California clapper rails. Tide height may also affect the reproductive ecology of clapper rails (De Groot 1927; Harvey 1988; Kozicky and Schmidt 1949). Although prior research in San Francisco Bay indicated little nest failure due to inundation (Schwarzbach et al. 2006), this pattern may change as a result of habitat modification toward shorter vegetation species or with sea-level rise. The greater tidal range in South San Francisco Bay compared with North San

Francisco Bay (Fig. 1) is likely to make density independent (abiotic) population regulation through tide height and available cover a greater factor. Additional research is needed into alternatives to existing tidal refugia that facilitate survival rates equivalent those provisioned by hybrid *Spartina*, such as islands. Levees have replaced these natural features in most remaining San Francisco Bay marshlands while mammalian predators have proliferated in the highly urbanized landscape of San Francisco Bay (Foin et al. 1997; Lewis et al. 1999). Easily accessible terrestrial refugia may present rails with greater exposure to mammalian predators than flooded intertidal refugia, as seen in other waterbirds (Pierluissi 2010). Increased terrestrial refugia could result in increased predation rates, compared with intertidal refugia, if anthropogenically subsidized predators can gain easier access to clapper rails. Predator management for red fox coincided with expansion of hybrid *Spartina* in South San Francisco Bay and eradication of hybrid *Spartina* may change the effectiveness of predator control (Harding et al. 2001). Due to the low clapper rail survival rates documented in this study, and implications of hybrid *Spartina* eradication, we advise that predator management (including red fox control) be reevaluated to determine if California clapper rail populations have continued to respond positively following eradication of hybrid *Spartina*.

Acknowledgments We thank Tobias Rohmer, Peter Coates, Brian Halstead, and Mark Herzog for helpful suggestions in preparing this manuscript and during analyses; Peggy Olofson, Jen McBroom and the Invasive *Spartina* Project staff for data contributions; Steve Bobzien, Mark Taylor, and Ralph Trujillo for assistance and access to East Bay Regional Park District properties; Joy Albertson and Cheryl Strong for assistance accessing Don Edwards San Francisco Bay National Wildlife Refuge properties; and Jeffrey Lewis, Whitney Thornton, Annie Shultz, Christina Crabtree, and the USGS San Francisco Bay Field Station staff for assistance with field work. We also thank Valary Bloom and Josh Hull of the U.S. Fish and Wildlife Service for facilitating work on California clapper rails. This project was funded by the USGS Western Ecological Research Center, grants from the U.S. Fish and Wildlife Service, Region 8, Coastal Programs Branch and Recovery Branch and by grants from the California State Coastal Conservatory. It was also partially funded through the South Bay Salt Pond Restoration Project Graduate Fellowship Program. California clapper rail studies were permitted under FWS endangered species permit TE-020548, California Department of Fish and Game Memorandum of Understanding and scientific collecting permits, U.S. Geological Survey Bird Banding Laboratory permit 21142, and the U.S. Geological Survey Western Ecological Research Center Animal Care and Use Committee.

Use of trade names is for descriptive purposes only and does not imply government endorsement.

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