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Tidal Wetland Vegetation in the San Francisco Bay-Delta Estuary

Michael C. Vasey^{1,4}, V. Thomas Parker¹, John C. Callaway², Ellen R. Herbert,¹ and Lisa M. Schile³

ABSTRACT

We analyzed tidal wetland vegetation patterns in the San Francisco Bay-Delta estuary (Bay-Delta) and discuss their significance for future conservation. Our objective was to conduct a balanced, random sample of six historic “remnant” tidal wetlands along a salinity gradient that ranged from southern San Pablo Bay to the lower Delta. We also wanted to compare diversity among these sites at five different scales, ranging from small subplots to total species per site. We randomly established twenty 0.1-ha plots at each site, and sampled ten 7-m² circular subplots (subplot scale) in each plot for species presence and cover. We calculated total species per plot (plot scale) and total species per site (site scale) based on these subplot data. We calculated importance values for each species found in subplots based on frequency of occurrence and proportion of total cover at each site. In addition, we recorded species found within the 0.1-ha plot but not sampled in subplots (plot_all scale), and calculated the total species for each site

based on these plot_all data (site_all scale). Thus, richness at each site was evaluated at five different scales that ranged from 7 m² to 20,000 m². We conducted a one-way ANOVA that compared mean richness among three scales with continuous data: subplot, plot, and plot_all. At lower estuary (San Pablo Bay) sites, richness values at these three scales were significantly lower than upper estuary (Suisun-Delta) sites. In Suisun-Delta sites, significant differences in richness varied, depending on sampling scale. Rush Ranch, a brackish wetland, had the highest average number of species per plot, whereas Sand Mound Slough, a freshwater wetland, had the highest average number of species at the subplot scale and the most total species at the site_all scale. Sand Mound Slough also had the highest number of unique species (22) compared to the other sites. We found a strong negative correlation ($r^2 = 0.99$) between total species number and salinity (the most in the Delta at the lowest salinity, and the least at China Camp with the greatest salinity). Our analysis suggests the following conservation recommendations: (1) restore habitat for freshwater plant species diversity in the Delta; (2) restore transitional brackish wetland habitat in salt marshes of the San Pablo Bay and San Francisco Bay; and (3) focus on control of pepperweed (*Lepidium latifolium*) in brackish marshes.

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San Francisco Bay–Delta, tidal wetland vegetation, sampling scale, species richness, importance value, salinity gradient, conservation strategies

INTRODUCTION

At approximately 3,400 km² (Atwater and others 1979), the San Francisco Bay–Delta (Bay–Delta) is the largest and most complex embayment along the Pacific coast of North America. Over 55% of the historic tidal wetlands in California were originally located in this once vast estuary (Macdonald and Barbour 1974). Subsequently, approximately 95% of Bay–Delta tidal wetlands have been modified by various human practices (Atwater and others 1979). Hardest hit was the freshwater Delta region that once covered ca. 140,000 ha (Atwater and others 1979) and was diked and “reclaimed” for agriculture by the early 1920s. In the late 1800s and early 1900s, the margins of the Suisun, San Pablo, and San Francisco Bays were impacted by a variety of land use practices, including agriculture, creation of seasonal duck hunting ponds, salt pond production, and bay fill for urban development. By some estimates, thirty percent of the open water of the Bay–Delta has been lost through diking and filling (Goals Project 1999). During the 20th century, tidal wetlands began to regenerate in the Bay–Delta as levees degraded and former wetlands were reclaimed by natural processes. Wetland plant species colonized extensive outboard mudflats created by the legacy of sediments deposited by upstream hydraulic gold mining, so called “centennial marshes” (PWA and Faber 2004). This marsh recovery has been augmented in the latter part of the century by intentional restoration, at first for mitigation purposes (Josselyn 1982) and, as the ecological importance of tidal wetland habitats became more fully appreciated, through large-scale wetland restoration projects (Williams and Faber 2001; Callaway and others 2011).

The floristic composition of Bay–Delta tidal wetlands is still poorly documented (Macdonald and Barbour 1974). Given the size and complexity of the Bay–Delta, difficulties of access, and the scale of

historic human impacts, we have limited knowledge of tidal wetland species composition from relatively few localities (e.g., Atwater and others 1979). In San Francisco and San Pablo bays, transitional habitats between salt marsh plains and adjacent uplands have been so heavily affected by human practices that their former species are now largely extirpated, and the flora of these transitional areas is not generally recognized as part of the Bay–Delta wetland ecosystem (Baye and others 2000). One of the reasons China Camp State Park and Rush Ranch Open Space Preserve are valuable is because they both contain upland-wetland transition habitats, which are now extremely rare (Baye in press; Whitcraft and others 2011). Both of these sites are components of the San Francisco Bay National Estuarine Research Reserve (NERR) and the focus of this special issue.

Salt and brackish wetlands of Suisun Bay, San Pablo Bay, and San Francisco Bay have received the most study, while there has been much less focus on freshwater tidal wetlands of the Delta (e.g., Josselyn 1983; Goals Project 1999; Baye and others 2000; Grewell and others 2007). This focus on the more saline portions of the estuary has confounded a deeper understanding of the Bay–Delta wetland ecosystem as a whole. Today, Delta tidal wetlands are the poorest known element of Bay–Delta vegetation, despite their former widespread extent, and their contribution to the broad intermingling of freshwater, brackish, and saltwater wetland species that occur in the Bay–Delta.

In this study, we employed a balanced, random quantitative analysis of six historic remnant wetlands that span the salt-to-freshwater gradient that characterizes the Bay–Delta region (Figure 1). While we have multiple research goals and activities, we present preliminary results of ongoing tidal wetland vegetation studies. Although these sites were selected for a variety of research purposes, they reflect the extent of historic remnant wetlands along the Bay–Delta regional salinity gradient. We explored different scales of vascular plant species richness. We used frequency of occurrence and proportion of total cover to calculate an importance value (IV) index to characterize dominance and diversity relationships for each individual species at each site. While we recognize that many factors influence local vegetation patterns

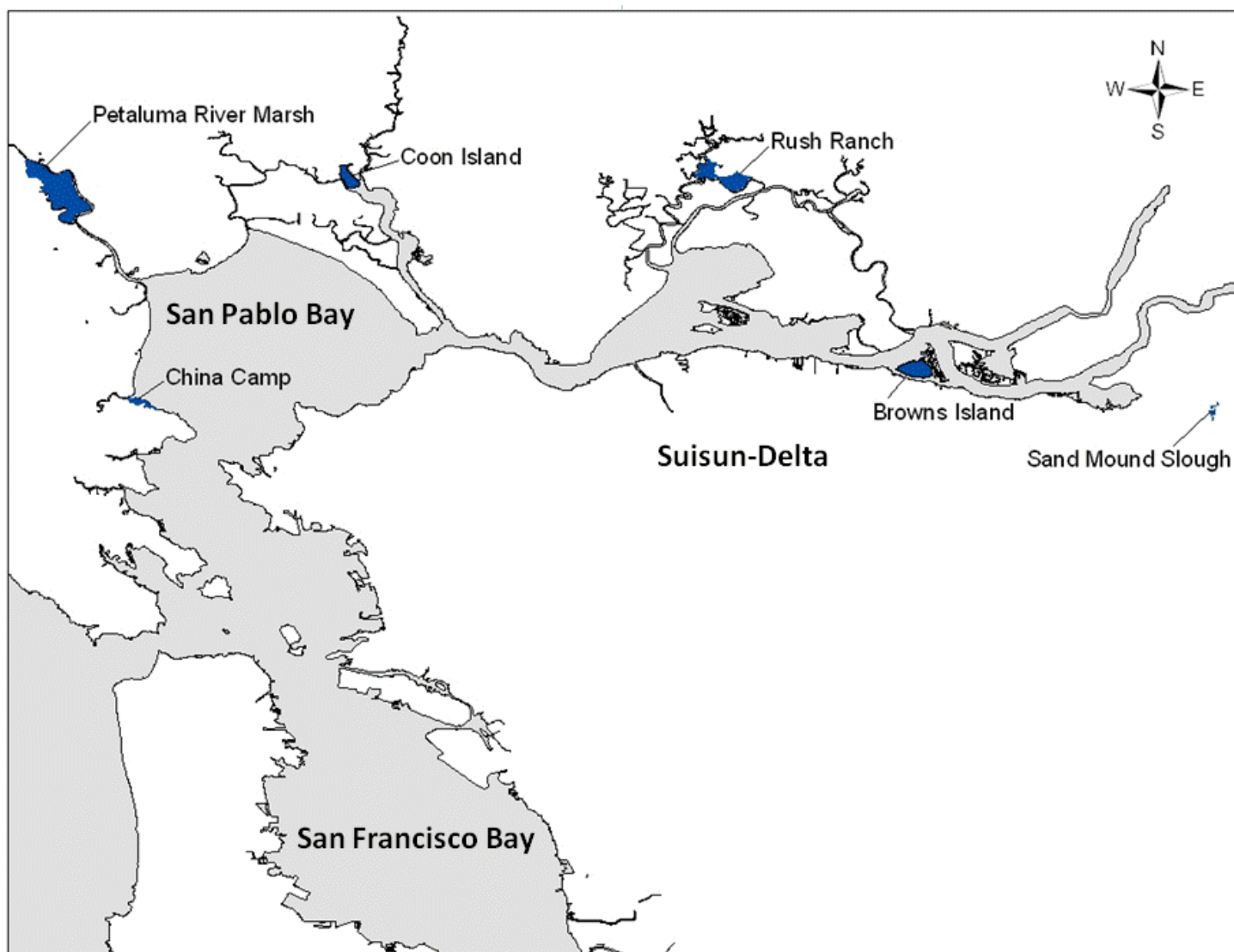


Figure 1 Distribution of six sample sites in the San Francisco Bay-Delta estuary. Different subregions are identified in bold font.

other than ambient salinity regimes (e.g., duration of inundation; see Schile and others 2011), we focused on a regional scale at which salinity generally drives compositional shifts within the tidal wetland species pool throughout the Bay-Delta (Grewell and others 2007). One of the primary concerns about rapid climate change is its potential to shift salinity gradients at a regional scale (Parker and others 2011). Based on our findings, we offer some recommendations for regional conservation actions that apply to Bay-Delta tidal wetland vegetation.

METHODS

We investigated six sites across the Bay-Delta salinity gradient: three sites in the lower estuary (hereafter referred to as San Pablo Bay) that have been influenced by relatively high salinity regimes and three sites in the Upper Estuary (hereafter referred to as Suisun-Delta) that have been influenced by brackish and freshwater conditions (Table 1). The San Pablo Bay sites included China Camp State Park (China Camp), Petaluma Marsh State Reserve (Petaluma Marsh), and Coon Island State Reserve (Coon Island).

Table 1 Geographic and salinity profiles for the six study sites sampled in two subregions of the San Francisco Bay-Delta estuary. Salinity regimes are based on the Venice system (Anonymous 1959). Salinity ranges were obtained at tidal creek margins for each site during summer and fall 2008 to 2010.

Code	Site	Area	Subregion	Latitude	Longitude	Salinity	ppt
CC	China Camp	125 ha	San Pablo Bay	38° 0.745 N	122° 29.300 W	Polyhaline	28±4
PM	Petaluma Marsh	800 ha	San Pablo Bay	38° 11.315 N	122° 33.550 W	Polyhaline	27±4
CI	Coon Island	175 ha	San Pablo Bay	38° 11.630 N	122° 19.500 W	Polyhaline	21±3
RR	Rush Ranch	400 ha	Suisun-Delta	38° 12.000 N	122° 2.000 W	Mesohaline	6±2
BI	Browns Island	200 ha	Suisun-Delta	38° 2.350 N	121° 51.800 W	Oligohaline	4±2
SMS	Sand Mound Slough	25 ha	Suisun-Delta	38° 0.275 N	122° 37.400 W	Limnetic	0±0

The Suisun–Delta sites included Rush Ranch Open Space Preserve (Rush Ranch), Browns Island Regional Shoreline (Browns Island) and Sand Mound Slough. China Camp, located in western San Pablo Bay, is the most saline of these tidal wetlands, and its vegetation is generally typical of central and south San Francisco Bay wetlands (Josselyn 1983, Grewell and others 2007). It is dominated by a large high marsh plain with fringing low marsh and an elaborate, dendritic network of channels. Petaluma Marsh occurs at the upper reaches of Petaluma River Slough, a major tidal slough that drains a watershed in northwestern San Pablo Bay and consequently receives seasonal freshwater influence. Petaluma Marsh is the largest remnant historic salt marsh in the San Francisco Bay estuary and also has a well-developed system of tidal creeks. Coon Island is a brackish wetland in the tidally influenced portion of the Napa River that enters northeastern San Pablo Bay. The larger watershed of the Napa River provides more freshwater influence than that received by the Petaluma Marsh.

Of the three Suisun–Delta sites, Rush Ranch is the most saline, and occurs along the upper reaches of Suisun Slough in the western Suisun Marsh. Rush Ranch is the largest remnant tidal wetland in the Suisun region. Browns Island is a large island at the margin of the eastern Suisun Bay and western Delta, while Sand Mound Slough is an archipelago of six small islands in the south-central Delta between diked former freshwater wetlands. Tidal creeks in the Suisun–Delta tend to be fewer and less dendritic than those in San Pablo Bay, and all three of these sites

have lower annual salinity regimes than the three San Pablo Bay sites (Table 1).

For each of these six sites, we randomly chose pairs of spatial coordinates on ArcMap version 8.0 (ESRI Anaheim, CA, USA) using Hawth's tools (Beyer 2004). Sampling was not stratified by a preconceived vision of vegetation types because our intention was to randomly sample twenty 20 × 50 m plots at each site within intact natural wetland vegetation, incorporating less than 10% open water, and with no obvious human disturbances. We navigated to sample sites using a hand-held Garmin 76S GPS receiver (1- to 5-m accuracy), and established 20 × 50 m plots (0.1 ha) (long axis east to west). Within each 0.1-ha plot, all species present were identified; abundance was assessed using ten randomly positioned, 3-m diameter (~7.0 m²) circular subplots employing a modified Daubenmire cover class approach (Daubenmire 1959). Sampling was conducted during the summers of 2007 and 2008. Teams of two to four people sampled each plot. Additionally, we sampled pore-water salinity concentrations at tidal creek margins from each site during late summer and fall 2008 to 2010 using a refractometer. We obtained 5 to 12 readings from each site during this interval. Although salinity at these sites shifts annually and seasonally, the regional salinity gradient is generally consistent, and provides a relatively robust context in which to compare species composition in these widely spaced sites (Table 1).

Data from each wetland were analyzed at different spatial scales (see Figure 2 for design). Richness (i.e.,

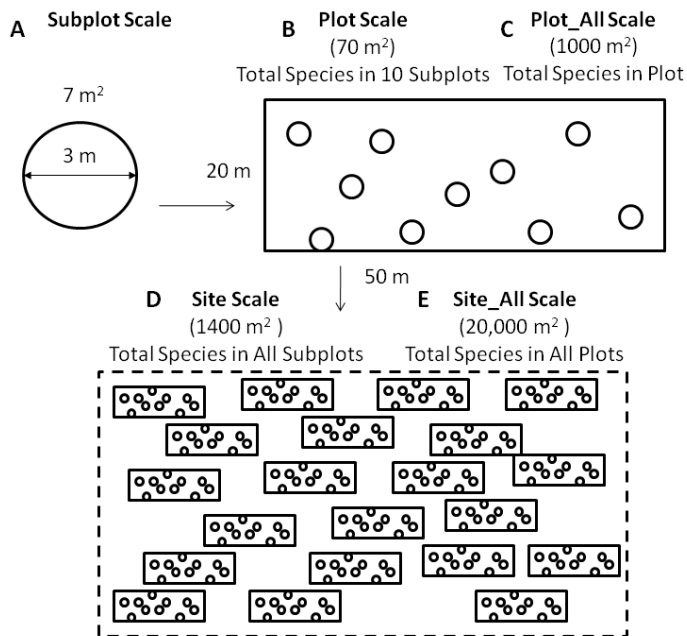


Figure 2 Sampling scales for species richness. **A.** Subplot scale: circular plots 3-m diameter, 7-m² area; **B.** Plot scale: 10 subplots within 0.1-ha plot, 70-m² area; **C.** Plot_all scale: all species found within 0.1-ha plot, both in and out of subplots, 1,000-m² area; **D.** Site scale: total of all subplots (200) within 20 plots at each site, 1,400 m² area; **E.** Site_all scale: all species found in and out of subplots within 20 plots at each site, 20,000 m² area.

the number of species per sample unit) was based on species presence-absence at each scale. We calculated the mean number of species per subplot (subplot scale = 7.0 m²), mean number of species per 0.1-ha plot using only subplot data (plot scale = 70 m²), and total number of species per 0.1-ha plot (plot_all scale = 1,000 m²), including all species recorded in subplots as well as species found in the 0.1 ha plot but not in subplots. We then calculated the total number of species per site based on the 200 subplot data (site scale = 1,400 m²), and total number of all species found in the sites, including those not found in the subplots (site_all scale = 20,000 m²).

At each site, we added midpoint cover class values for all species in all subplots ($n = 200$), summed these values for all species, and then divided each species total by the sum of the total cover for all species, yielding a proportion of total cover for each species

(relative abundance). We then totaled the number of subplot occurrences for each species and divided this total by 200 to yield the relative frequency of occurrence for each species. An IV was then calculated for each species as: [(relative abundance + relative frequency) / 2 × 100]. This IV index ranges from 0 to 100, and integrates both the proportion of total abundance and frequency of occurrence data for individual species so that, for example, widespread species with relatively low cover values (e.g., herbaceous dicots) are given greater weight than if only species abundance values were considered (Barbour and others 1987).

We analyzed data with JMP 8.0 (SAS Cary, NC, USA) for differences between sites at subplot, plot, and plot_all scales by separate one-way ANOVAs. We estimated differences among sites using a Tukey HSD test of *post hoc* contrasts. Before running the one-way ANOVAs, data were analyzed for normality. Plot and plot_all data met the assumptions of normality, but sub-plot data required square root transformation. To explore the possible relationship between total number of species per site (site_all scale), salinity, and area, we ran two linear regression models with total species per site as the dependent variable, and area or salinity as independent variables. In both models, residuals were normal, and Cook's Distance values were less than one (i.e., there was no problem with outliers). We collected voucher specimens of sampled species and deposited them at San Francisco State University.

RESULTS

At all sampling scales, the more saline San Pablo Bay sites contained significantly fewer species than the Suisun-Delta sites (Table 2, Figure 3). For example, at the subplot (7 m²), plot (70 m²), and plot_all (1,000 m²) scales, San Pablo Bay sites contained approximately half the number of species as Suisun-Delta sites. While the greatest contrast in species richness occurs between San Pablo Bay and the Suisun-Delta, there are more subtle contrasts between the three Suisun-Delta sites at different scales (Table 2). At the plot and plot_all scales, for example, Rush Ranch averaged significantly more species than

Table 2 Mean and standard error values for species richness from six sites at subplot (7 m²), plot (70 m²), and plot_all (1,000 m²) scales. Site (1,400 m²) and site_all (20,000 m²) values represent total species from all subplots per plot and all species per plot (including species not found in subplots), respectively. Superscript letters for subplot, plot, and plot_all represent significant differences based on one-way ANOVA and post hoc Tukey HSD tests. F values and subscript df are provided where applicable.

Site	CC	PM	CI	RR	BI	SMS	F value	P
Subplot	2.5ab±0.1	2.8b±0.1	2.3a±0.1	5.2cd±0.2	4.7c±0.2	5.4d±0.2	5,1191=31.4	<0.0001
Plot	5.2a±0.5	5.8a±0.5	4.8a±0.6	12.4c±0.6	10.4b±0.6	10.8bc±0.8	5,1141=29.8	<0.0001
Plot_All	6.2a±0.4	7.1a±0.7	6.2a±0.7	15.9b±0.7	13.2b±0.8	13.4b±1.1	5,1141=32.4	<0.0001
Site	10	14	21	39	48	44	NA	NA
Site_All	10	17	23	44	55	56	NA	NA

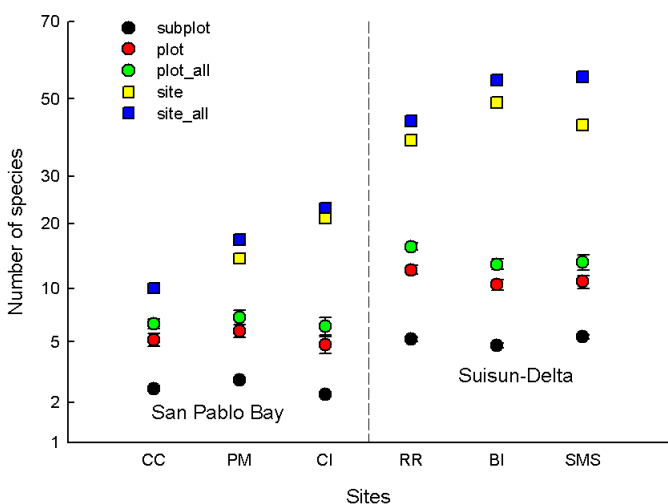


Figure 3 Mean (± S.E.) species richness at subplot, plot, and plot_all scales, and total number of species at site and site_all scales for each site.

either Browns Island or Sand Mound Slough. Yet, at the site and site_all scales, Browns Island and Sand Mound Slough contained more total species based on all twenty plots. Sand Mound Slough had the highest number of species recorded (56) for all sites, slightly greater than Browns Island (55). We found no relationship between site area and total number of species per site. On the other hand, there was a significant relationship between salinity levels and all sample scales for richness. This relationship is the most robust at the site_all scale (total species per site), where the regression coefficient is $R^2 = 0.99$ ($P < 0.0001$) (Figure 4).

The table of IV differences (Table 3) also illustrates the scope of the distinction between San Pablo Bay and Suisun-Delta sites. An IV value above 10 is relatively high (the species is either encountered relatively frequently or is relatively abundant wherever it is encountered). All three San Pablo Bay sites were dominated by *Sarcocornia pacifica* with IVs above 60. China Camp and Petaluma Marsh host four additional species that all had IVs greater than 10—*Distichlis spicata*, *Jaumea carnosa*, *Grindelia stricta*, and *Cuscuta salina*—all typical of high salt marsh plains. Tidal wetland vegetation in the three Suisun-Delta sites was more rich and diverse than in the San Pablo Bay sites. Both Rush Ranch and Browns Island retain species that are characteristic of the high marsh plain in San Pablo Bay (*Sarcocornia pacifica*, *Distichlis spicata*, and *J. carnosa*); however, *D. spicata* had a higher IV than *S. pacifica* at these two Suisun-Delta localities, and *J. carnosa* had a higher IV than *S. pacifica* at Browns Island. An unusual tidal wetland species in the Bay-Delta found only at Browns Island during this survey, *Anemopsis californica*, was located in this high marsh habitat. The great majority of the tidal marsh plain in these two Suisun-Delta sites, however, is dominated by a middle marsh assemblage consisting primarily of *Schoenoplectus americanus* and species such as *Juncus balticus*, *Triglochin maritima*, *Euthamia occidentalis*, *Symphotrichum lentum*, *Epilobium ciliatum*, *Eleocharis macrostachya*, and *Glaux maritima*. A listed species largely confined to Rush Ranch, *Cirsium hydrophilum*, occurs along shallow channels in this habitat. At the margins of deep channels and low areas where water stands, a third low-marsh

assemblage contributes to the heterogeneity of these sites. Here, species such as *Schoenoplectus acutus*, *Typha latifolia*, *Typha domingensis*, *Typha angustifolia*, and *Schoenoplectus californicus* provide a structural matrix in which species such as *Calystegia sepium*, *Persicaria maculosa* and *Samolus parviflorus* occur.

The eight species with highest IVs (> 10) at Sand Mound Slough in descending order were *Schoenoplectus acutus*, *Schoenoplectus americanus*, *Calystegia sepium*, *Phragmites australis*, *Typha latifolia*, *Rubus discolor*, *Salix lasiolepis*, and *Typha domingensis*. Together, these species create tall, dense thickets that are difficult for people to penetrate; however, many species such as the fern *Atherium felix-femina*, flowering plants such as *Potentilla palustris*, *Hibiscus lasiocarpus*, *Lycopus asper*, *Stachys albus* and *Mimulus guttatus*, emergent wetland species such as *Sparganium eurycarpum* and *Sagittaria latifolia*, sedges such as *Carex obnupta* and *C. pellita*, and other woody species such as *Cephalanthus occidentalis* and *Cornus sericeus* were interwoven within and between these dominants (Table 3).

In total, 82 species were found in the combined subplot samples for all sites (site scale, Table 3), and 94 species were observed in all 120 plots, including those species not picked up in the subplot sampling (site_all scale, Table 4); therefore, although the site samples covered an area of only 1400 m² compared to the 20,000 m² for the site_all samples (i.e., about 7% of the total area surveyed), the subplot sampling picked up 87% of the total number of species observed in all plots per site. Twenty-nine species occurred in San Pablo Bay: six were restricted to San Pablo Bay and 23 species were shared among one or more Suisun-Delta sites (Table 4). Conversely, 88 species occurred in the Suisun-Delta sites and 65 of these were restricted to the Suisun-Delta region. Of the shared 23 species, 12 were shared only by Coon Island and other Suisun-Delta sites. No species were found exclusively at China Camp, two (both exotics) were found at Petaluma Marsh, none at Coon Island, seven at Rush Ranch, five at Browns Island, and 22 (23% of all species picked up in the survey) at Sand Mound Slough. There were far more native spe-

cies found in these wetlands than exotic species (81 native to 13 exotic; 86% to 14%; Table 4) and, with the exception of *Lepidium latifolium*, these all had low IVs (Table 3).

DISCUSSION

The results of this analysis were generally consistent with past studies that include quantitative vegetation samples from the Bay-Delta (Atwater and Hedel 1976; Atwater and others 1979; Watson and Byrne 2009). At a regional scale, tidal wetland vegetation in the Bay-Delta is influenced by ambient salinity regimes (Figure 4). At different sampling scales, species richness tends to increase from salt marshes (low richness) to mild brackish and freshwater wetlands (high richness; Table 2, Figure 3). In terms of frequency of occurrence and proportion of total abundance per occurrence, there is a distinct shift of species composition and dominance from a narrow suite of salt-tolerant species in salt marshes to a diverse array of species in the brackish and freshwater tidal wetlands of the Suisun-Delta (Table 3). These findings have important implications for understanding patterns of plant species diversity in Bay-Delta wetlands, and, potentially, for the future conservation management of Bay-Delta wetlands to maintain and increase this diversity in the face of rapid environmental change.

Patterns of Bay-Delta Tidal Wetland Plant Species Diversity

Despite the pioneering work by Atwater and others (1979), there has been a persistent belief that brackish wetland vegetation of the Suisun Bay region is more diverse than the freshwater Delta. For example, Byrne and others (2001, p. 66) state:

Brackish wetlands are floristically distinctive and contain a greater diversity of plant species than either the salt marshes of San Francisco Bay or the freshwater wetlands of the Sacramento-San Joaquin Delta. [emphasis added]

A recent paper reiterates this perspective, and argues that with anticipated sea-level rise resulting from

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Table 3 Species codes, species names, and Importance Values (IVs) for species found in subplots at all six sites. Relatively high IVs (above 10) are highlighted in bold. Species are generally arranged in descending ranks from highest IV to lowest IV at each site, except where species are found in more than one site. Note that out of 82 species sampled, 57 were sampled only in the Suisun-Delta, 2 in San Pablo Bay, and 23 were found in both subregions.

	Code	Species	Status	CC	PRM	CI	RR	BRI	SMS
1	Sapa	<i>Sarcocornia pacifica</i>	N	85.4	86.5	64.9	28.9	6.2	
2	Disp	<i>Distichlis spicata</i>	N	20.6	17.5	3.3	34.1	30.2	
3	Jaca	<i>Jaumea carnosa</i>	N	17.5	18.7	4.0	13.7	11.7	
4	Grst	<i>Grindelia stricta</i> var. <i>angustifolia</i>	N	12.7	9.9	6.2	20.4	2.5	
5	Cusa	<i>Cuscuta salina</i>	N	15.0	23.3		0.5		
6	Frsa	<i>Frankenia salina</i>	N	5.2	16.1				
7	Lica	<i>Limonium californicum</i>	N	6.5	1.1				
8	Cusu	<i>Cuscuta subinclusa</i>	N	3.0	3.7		1.3		
9	Boma	<i>Bolboschoenus maritimus</i>	N	1.6	2.3	36.3		0.3	
10	Spfo	<i>Spartina foliosa</i>	N	7.2		1.1			
11	Acmi	<i>Achillea millefolium</i>	N		2.2	0.3	2.1	1.0	
12	Lela	<i>Lepidium latifolium</i>	E		7.3		12.6	2.0	
13	Bapi	<i>Baccharis pilularis</i>	N		2.2				
14	Attr	<i>Atriplex triangularis</i>	N		0.8	1.9	13.8		
15	Rucr	<i>Rumex crispus</i>	N		0.3	0.3	0.8	0.3	0.8
16	Scam	<i>Schoenoplectus americanus</i>	N			11.0	41.8	64.2	48.9
17	Scac	<i>Schoenoplectus acutus</i>	N			6.5	4.1	23.3	56.0
18	Poan	<i>Potentilla anserina</i>	N			5.6	15.7	14.4	3.7
19	Tyan	<i>Typha angustifolia</i>	N			4.9	4.9		6.7
20	Juba	<i>Juncus balticus</i>	N			2.6	36.5	9.9	
21	Ardo	<i>Artemisia douglasiana</i>	N			1.3		1.2	
22	Scca	<i>Schoenoplectus californicus</i>	N			1.5		0.3	0.9
23	TySp	<i>Typha</i> spp.	N			9.0			5.7
24	Tyla	<i>Typha latifolia</i>	N			0.8	0.3	0.8	19.5
25	Tydo	<i>Typha domingensis</i>	N			0.8	6.4	19.7	10.6
26	Bado	<i>Baccharis douglasii</i>	N			0.3	0.9	0.3	
27	Chmu	<i>Chenopodium multifidum</i>	E			0.3			
28	Case	<i>Calystegia sepium</i>	N				10.7	12.0	31.3
29	Trma	<i>Triglochin maritima</i>	N				16.4	15.5	
30	Euoc	<i>Euthamia occidentalis</i>	N				4.0	15.3	0.3
31	Pepu	<i>Persicaria punctata</i>	N				4.0	1.9	6.1
32	Epci	<i>Epilobium ciliatum</i>	N				4.1	3.3	0.5
33	Plod	<i>Pluchea odorata</i>	N				1.3	2.1	0.3
34	Glma	<i>Glaux maritima</i>	N				8.4	1.5	
35	Asle	<i>Aster lentus</i>	N				6.8	0.8	
36	Elma	<i>Eleocharis macrostachya</i>	N				0.4	8.8	1.4
37	Sapar	<i>Samolus parviflorus</i>	N				0.8	1.5	0.8
38	Gatr	<i>Galium triflorum</i>	N				0.5	1.6	
39	Sysu	<i>Symphyotrichum subulatum</i>	N				0.5	0.3	

	Code	Species	Status	CC	PRM	CI	RR	BRI	SMS
40	Ruca	<i>Rumex californicus</i>	N				0.3		
41	Apgr	<i>Apium graveolens</i>	E				3.0		
42	Sool	<i>Sonchus oleraceus</i>	E				1.0		
43	Trco	<i>Triglochin concinnum</i>	N				2.0		
44	Asra	<i>Aster radulina</i>	N				0.8		
45	Sodo	<i>Solanum douglasii</i>	N				0.3		
46	Sasu	<i>Salicornia subterminalis</i>	N				0.3		
47	Cihy	<i>Cirsium hydrophilum</i>	N				0.3		
48	Heec	<i>Helminthotheca echiodes</i>	E				0.5		
49	Lyca	<i>Lythrum californicum</i>	N					2.7	0.3
50	Migu	<i>Mimulus guttatus</i>	N					5.5	
51	Lyam	<i>Lycopus americanus</i>	N					3.1	1.9
52	Caob	<i>Carex obnupta</i>	N					2.3	0.4
53	Cape	<i>Carex pellita</i>	N					2.0	8.1
54	Hyve	<i>Hydrocotyle verticillata</i>	N					1.3	1.0
55	Lyas	<i>Lycopus asper</i>	N					1.4	0.8
56	Hyum	<i>Hydrocotyle umbellata</i>	N					1.2	0.3
57	Rudi	<i>Rubus discolor</i>	E					0.9	17.3
58	Peam	<i>Persicaria amphibia</i>	N					0.8	6.7
59	Lima	<i>Lilaeopsis masonii</i>	N					0.5	0.5
60	Mear	<i>Mentha arvensis</i>	N					0.6	1.9
61	Irps	<i>Iris pseudacorus</i>	E					0.3	2.6
62	Anca	<i>Anemopsis californica</i>	N					1.2	
63	Sisu	<i>Sium suave</i>	N					0.3	
64	Laje	<i>Lathyrus jepsonii</i> var. <i>jepsonii</i>	N					1.1	
65	Soam	<i>Solanum americanum</i>	N					0.3	
66	Dece	<i>Deschampsia cespitosa</i>	N					0.3	
67	Pema	<i>Persicaria maculosa</i>	N					8.3	8.9
68	Phau	<i>Phragmites australis</i>	N						24.3
69	Sala	<i>Salix lasiolepis</i>	N						13.6
70	Atfi	<i>Athyrium filix-femina</i>	N						8.5
71	Popa	<i>Potentilla palustris</i>	N						7.0
72	Salat	<i>Sagittaria latifolia</i>	N						6.8
73	Speu	<i>Sparganium eurycarpum</i>	N						6.5
74	Stal	<i>Stachys albens</i>	N						2.4
75	Lupe	<i>Ludwigia peploides</i>	N						1.4
76	Juxi	<i>Juncus xiphioides</i>	N						0.3
77	Cima	<i>Cicuta maculata</i> var. <i>bolanderi</i>	N						0.3
78	Hila	<i>Hibiscus lasiocarpus</i>	N						0.5
79	Cose	<i>Cornus sericeus</i>	N						0.9
80	Scmi	<i>Scirpus microcarpus</i>	N						0.8
81	Ceoc	<i>Cephalanthus occidentalis</i>	N						0.3
82	Hyra	<i>Hydrocotyle ranunculoides</i>	N						0.3

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Table 4 Species codes, species names, and species status (N=native, E=exotic) present at each site, including species not recorded in the subplots (site_all scale). Presence of a species at a site is indicated by a “+”.

	Code	Species	Status	CC	PRM	CI	RR	BRI	SMS
1	Frsa	<i>Frankenia salina</i>	N	+	+				
2	Lica	<i>Limonium californicum</i>	N	+	+				
3	Spfo	<i>Spartina foliosa</i>	N	+	+	+			
4	Cusu	<i>Cuscuta subinclusa</i>	N	+	+		+		
5	Cusa	<i>Cuscuta salina</i>	N	+	+		+		
6	Boma	<i>Bolboschoenus maritimus</i>	N	+	+	+		+	
7	Disp	<i>Distichlis spicata</i>	N	+	+	+	+	+	
8	Jaca	<i>Jaumea carnosa</i>	N	+	+	+	+	+	
9	Grst	<i>Grindelia stricta</i> var. <i>angustifolia</i>	N	+	+	+	+	+	
10	Sapa	<i>Sarcocornia pacifica</i>	N	+	+	+	+	+	+
11	Chal	<i>Chenopodium multifidum</i>	E		+				
12	Coma	<i>Conium maculatum</i>	E		+				
13	Bapi	<i>Baccharis pilularis</i>	N		+	+			
14	Lela	<i>Lepidium latifolium</i>	E		+	+	+	+	
15	Acmi	<i>Achillea millefolium</i>	N		+	+	+	+	
16	Attr	<i>Atriplex triangularis</i>	N		+	+	+	+	
17	Rucr	<i>Rumex crispus</i>	N		+	+	+	+	+
18	Tyso	<i>Typha</i> spp.	N			+		+	+
19	Ardo	<i>Artemisia douglasiana</i>	N			+		+	
20	Tyan	<i>Typha angustifolia</i>	N			+	+		+
21	Bado	<i>Baccharis douglasii</i>	N			+	+	+	
22	Juba	<i>Juncus balticus</i>	N			+	+	+	
23	Scac	<i>Schoenoplectus acutus</i>	N			+	+	+	+
24	Poan	<i>Potentilla anserina</i>	N			+	+	+	+
25	Scca	<i>Schoenoplectus californicus</i>	N			+	+	+	+
26	Scam	<i>Schoenoplectus americanus</i>	N			+	+	+	+
27	Tyla	<i>Typha latifolia</i>	N			+	+	+	+
28	Tydo	<i>Typha domingensis</i>	N			+	+	+	+
29	Euoc	<i>Euthamia occidentalis</i>	N			+	+	+	+
30	Pomo	<i>Polypogon monspeliensis</i>	N				+		+
31	Sasu	<i>Salicornia subterminalis</i>	N				+		
32	Civu	<i>Cirsium vulgare</i>	E				+		
33	Sool	<i>Sonchus oleraceus</i>	E				+		
34	Loco	<i>Lotus corniculatus</i>	E				+		
35	Trco	<i>Triglochin concinnum</i>	N				+		
36	Cihy	<i>Cirsium hydrophilum</i>	N				+		
37	Heec	<i>Helminthotheca echioides</i>	E				+		
38	Glma	<i>Glaux maritima</i>	N				+	+	
39	Asle	<i>Aster lentus</i>	N				+	+	
40	Apgr	<i>Apium graveolens</i>	E				+	+	
41	Gatr	<i>Galium triflorum</i>	N				+	+	
42	Sysu	<i>Symphotrichum subulatum</i>	N				+	+	
43	Sodo	<i>Solanum douglasii</i>	N				+	+	
44	Ruca	<i>Rumex californicus</i>	N				+	+	
45	Sisu	<i>Sium suave</i>	N				+	+	
46	Trma	<i>Triglochin maritima</i>	N				+	+	+

	Code	Species	Status	CC	PRM	CI	RR	BRI	SMS
47	Case	<i>Calystegia sepium</i>	N				+	+	+
48	Epci	<i>Epilobium ciliatum</i>	N				+	+	+
49	Pepu	<i>Persicaria punctata</i>	N				+	+	+
50	Plod	<i>Pluchea odorata</i>	N				+	+	+
51	Sapar	<i>Samolus parviflorus</i>	N				+	+	+
52	Lyca	<i>Lythrum californicum</i>	N				+	+	+
53	Elma	<i>Eleocharis macrostachya</i>	N				+	+	+
54	Anca	<i>Anemopsis californica</i>	N					+	
55	Laje	<i>Lathyrus jepsonii</i>	N					+	
56	Soam	<i>Solanum americanum</i>	N					+	
57	Dece	<i>Deschampsia cespitosa</i>	N					+	
58	Pema	<i>Persicaria maculosa</i>	N					+	
59	Migu	<i>Mimulus guttatus</i>	N					+	+
60	Lyam	<i>Lycopus americanus</i>	N					+	+
61	Caob	<i>Carex obnupta</i>	N					+	+
62	Carex	<i>Carex pellita</i>	N					+	+
63	Hyve	<i>Hydrocotyle verticillata</i>	N					+	+
64	Lyas	<i>Lycopus asper</i>	N					+	+
65	Hyum	<i>Hydrocotyle umbellata</i>	N					+	+
66	Rudi	<i>Rubus discolor</i>	E					+	+
67	Peam	<i>Persicaria amphibia</i>	N					+	+
68	Lima	<i>Lilaeopsis masonii</i>	N					+	+
69	Juxi	<i>Juncus xiphioides</i>	N					+	+
70	Cima	<i>Cicuta maculata</i> var. <i>bolanderi</i>	N					+	+
71	Irps	<i>Iris pseudacorus</i>	E					+	+
72	Mear	<i>Mentha arvensis</i>	N					+	+
73	Phau	<i>Phragmites australis</i>	N						+
74	Sala	<i>Salix lasiolepis</i>	N						+
75	Atfi	<i>Athyrium filix-femina</i>	N						+
76	Popa	<i>Potentilla palustris</i>	N						+
77	Salat	<i>Sagittaria latifolia</i>	N						+
78	Speu	<i>Sparganium eurycarpum</i>	N						+
79	Stal	<i>Stachys albens</i>	N						+
80	Lupe	<i>Ludwigia peploides</i>	N						+
81	Hila	<i>Hibiscus lasiocarpus</i>	N						+
82	Cose	<i>Cornus sericeus</i>	N						+
83	Scmi	<i>Scirpus microcarpus</i>	N						+
84	Ceoc	<i>Cephalanthus occidentalis</i>	N						+
85	Bila	<i>Bidens laevis</i>	N						+
86	Oesa	<i>Oenothera sarmentosa</i>	N						+
87	Vebo	<i>Verbena bonariensis</i>	E						+
88	Hyra	<i>Hydrocotyle ranunculoides</i>	N						+
89	Asle	<i>Aster radulina</i>	N						+
90	Eicr	<i>Eichornia crassipes</i>	E						+
91	Lesp	<i>Lemna</i> sp.	N						+
92	Vela	<i>Verbena lasiostachys</i>	N						+
93	Vebo	<i>Verbena bonariensis</i>	E						+
94	Scga	<i>Scutellaria galericulata</i>	N						+

climate change, “increasing salinity may just move the center of diversity eastward” (Watson and Byrne 2009, p. 126). Yet, based on original wetland vegetation surveys by Atwater and Hedel (1976), Atwater and others (1979, p. 363) state:

Diversity generally increases from San Francisco Bay to the Delta. Whereas individual marshes around San Francisco Bay typically contain 13 or 14 species of native plants, specific sites in the Delta contain 40 species. Composite regional lists imply even greater differences in diversity: only 15 native species reportedly live in tidal marshes around San Francisco Bay but about 30 reportedly live around San Pablo Bay and Carquinez Strait, 40 around Suisun Bay, and 80 in the Delta.

Atwater and others (1979, p. 369) continue:

Tidal-marsh plants of San Pablo Bay, Carquinez Strait, and Suisun Bay provide an intricate, mutable transition between salt marshes of San Francisco Bay and freshwater marshes of the Delta ... Species from opposite ends of the spectrum overlap to varying degrees in the middle ...

These observations by Atwater and others (1979) are consistent with our findings. While all of the Suisun-Delta sites are significantly richer than San Pablo Bay sites in terms of species richness, we recorded the greatest total species richness at Sand Mound Slough in the Delta (56) and Browns Island in the western Delta (55), and the least species richness in the more brackish wetlands of Rush Ranch in the western Suisun Bay region (44) (Table 2, Figure 3D). We also found that Rush Ranch and Browns Island contain a rich mixture of species, characteristic of the eastern San Pablo Bay site (Coon Island) as well as the Suisun-Delta sites, perhaps constituting the heart of the “intricate, mutable transition” vegetation described by Atwater and others (1979) above. If Sand Mound Slough is a reasonable indicator of Delta plant species diversity compared to these other wetlands, and there is little data to suggest otherwise, many species that occur in Delta freshwater wetlands simply do not establish in more saline reaches of the

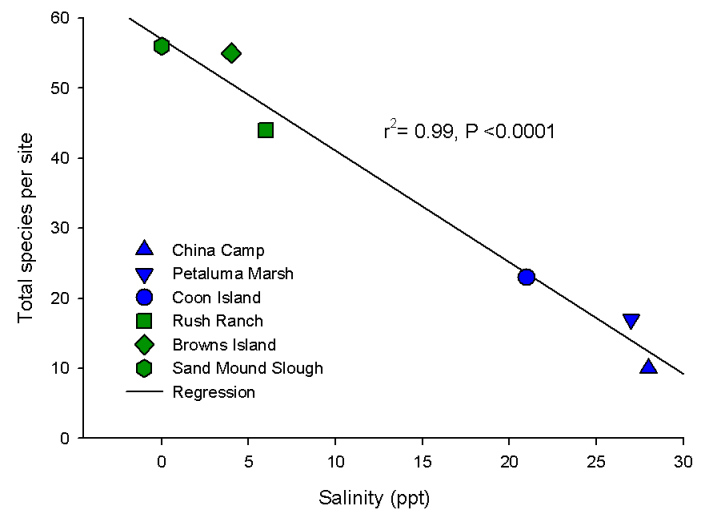


Figure 4 Linear regression comparing total number of species (site_all scale) as dependent variable and mean salinity (ppt) as independent variable.

estuary. For example, Sand Mound Slough had 22 species that were not found downstream (Table 4). This suggests that the species pool for vegetation in the Bay-Delta ecosystem is richest in the Delta and progressively attenuates as higher levels of ambient salinity are encountered. The significant correlation between ambient salinity and total number of species per site in this limited study strongly suggests this relationship (Figure 4).

We suspect that the reason Watson and Byrne (2009) found more species at South Hampton Bay and Hill Slough in the Suisun Bay region, compared to Sand Mound Slough in the Delta, is that the area they sampled at Sand Mound Slough was not sufficient to detect the greater number of species that we found there. Since their design was based on Atwater and Hedel (1976), who originally sampled a comparatively small transect at Sand Mound Slough compared to South Hampton Bay and Hill Slough, this is understandable. As pointed out, in a comparison of richness at the 1,000-m² plot scale between Rush Ranch, Browns Island, and Sand Mound Slough, Rush Ranch had the highest richness; whereas at the site_all scale (20,000 m²), Sand Mound Slough had 12 more species than Rush Ranch (Table 2). These data suggest that Rush Ranch has more species that are fre-

quently encountered at local scales, but that Sand Mound Slough has more species that are infrequently encountered at the larger site scale.

While our study provides evidence that the greatest number of tidal wetland plant species occurs in the Delta, this is not to say that the brackish wetlands of Suisun Bay are not diverse, but rather that their diversity, compared to the Delta, may be more a function of species endemism than species numbers. Suisun Bay is well known for its concentration of local endemic plant species in Bay-Delta tidal wetlands. A good example is *Cirsium hydrophilum*, and there are other brackish wetland examples, such as *Lathyrus jepsonii* var. *jepsonii* and *Chloropyron molle* (CNPS 2009). Conversely, none of the species we encountered at Sand Mound Slough are classified as local endemics. Rather, the Delta species are more widespread freshwater wetland plants that present a greater diversity of life histories than Suisun wetlands, including trees, shrubs, vines, ferns, floating aquatic species, and other more typical wetland herbaceous plants.

Another important source of Bay-Delta tidal wetland plant diversity that has been generally overlooked formerly occurred in the salt marshes of the historic San Pablo Bay and San Francisco Bay. As Baye and others (2000) describe, many locally rare herbaceous species today were once found in wetlands historically concentrated on the edges of tidal salt marshes where seasonal pools, freshwater springs, and intermittent creeks created a system of small, brackish, tidally influenced wetlands. Unfortunately, most of these marginal wetland habitats are now gone because the Bay-Delta has been transformed by human activity in the post-European settlement era. Our tidal wetland sampling of the San Pablo Bay sites did not record any of these species, and, clearly, the more saline regions of the estuary would be regarded as a more diverse wetland ecosystem if these species were still present. This potential for incomplete sampling, and the previous discussion of brackish and freshwater wetlands, raises the issue of sampling methods that we address below.

The Benefits and Costs of Balanced, Random Sampling

In this study, we intentionally designed a balanced, random sample of tidally influenced vegetation at each historic wetland site that represented a range of positions along the salinity gradient within the Bay-Delta (Figure 1, Table 2). The advantage of this approach is that it provides an unbiased estimate of species richness, relative abundance, and frequency of occurrence at a variety of scales, to ensure an equal comparison among sites. As such, we can state with some confidence that species numbers in the Suisun-Delta are more likely greater than in San Pablo Bay, and that there appears to be a strong correlation between ambient (water column) salinity and numbers of species at tidal wetlands arrayed along the estuarine salinity gradient (Figure 4). One cost of random sampling, especially in a system with strong local gradients such as tidal wetlands, is that it is inherently biased toward recording species that are relatively abundant and spatially well-distributed (Greig-Smith 1983). Rare species that are patchily distributed—particularly in uncommon, specialized habitats—generally require large numbers of randomly distributed samples (Greig-Smith 1983). For example, while the Coon Island tidal wetland is more species-rich than either China Camp or Petaluma Marsh at the site scale, richness is obscured when the data is viewed at smaller sampling scales, such as subplots and plots (Table 2, Figure 3). This may be an example of how brackish species found more commonly in Suisun Bay wetlands are more patchily distributed on Coon Island, and therefore more likely to be missed in small-scale, random samples. The balanced random-sampling approach, for similar reasons, would not be effective at detecting fine-scale diversity of transitional brackish habitats such as those described by Baye and others (2000). Consequently, for large-scale questions—such as those that address the potential effects of climate change on Bay-Delta plant species along the estuarine salinity gradient—the balanced, random approach is useful. However, for more local-scale questions, and for questions that involve species in specialized habitats, a more targeted approach is likely to be more effective (Parker and others 2011).

Conservation Implications

Our study has implications for the conservation of Delta tidal wetland vegetation. The Sacramento–San Joaquin Delta once encompassed approximately 260,000 ha of wetlands, of which approximately 140,000 ha were tidally influenced (Atwater and others 1979). According to Hart (2010), this Delta wetland habitat was not monolithic. The north Delta was shaped by powerful flows of the Sacramento River. Natural levees, 6 to 7 m high, were deposited by these flows, and colonized by tall gallery forests of valley oak, cottonwoods, sycamores, and alders. The south Delta was shaped by more moderate flows of the San Joaquin River, levees were lower, and riparian woodlands sparser. Behind these natural levees were extensive stands of freshwater wetlands, characterized by tules, cattails, and other tidal wetland species that gradually gave way to seasonal wetlands, vernal pools, grasslands, and oak savanna. This mosaic of freshwater wetland plant diversity must have been extraordinary; however, as the Delta was “reclaimed,” over 95% of this habitat was lost. Today, small remnants of this diversity persist in remote corners of the Delta, such as at Sand Mound Slough, and one compelling question is: If conditions in the Delta become more saline with sea-level rise and potentially greater diversion of freshwater from upstream, where will these species go? At the moment, conservation alternatives are limited by the lack of available habitat and restoration opportunities; however, an expanding restoration movement exists in the Delta (<http://www.deltacouncil.ca.gov/>), and we hope that the broader community of the public, scientists, and policy-makers recognize that plant species diversity in the Delta is remarkable, despite its general appearance to the contrary (as one cruises by on a boat). While the vegetation of Sand Mound Slough may not represent the entire Delta, its high diversity compared to other historic wetlands in the Bay–Delta provides the impetus to recognize that future Delta restoration efforts should be viewed as an opportunity to re-create this diversity, as well as to provide for vegetation structure and ecosystem services that support other wildlife and microbial organisms.

This study also highlights the importance of the Suisun Bay region for plant diversity at a variety of

scales. Tidal wetlands in the Suisun are a convergence between salt tolerant and freshwater dependent plant species, including several species that are endemic to this region. Although partially salt-tolerant species in the brackish portion of the estuary should be able to retreat upstream in the face of salinity intrusion (Watson and Byrne 2009), this presupposes that marsh plain habitat will be (or become) available to colonize. Of possibly greater conservation concern for Bay–Delta brackish wetlands is the spread of an invasive non-native species, *Lepidium latifolium*. We found that this species has a relatively high IV at Rush Ranch compared to other species, was well established at Browns Island and Petaluma Marsh, and also was present at Coon Island (Table 3, Table 4). *Lepidium latifolium* is particularly problematic at Rush Ranch, where it dominates habitat in which *Cirsium hydrophilum* occurs. Invasive *L. latifolium* has become so well integrated into sensitive brackish wetland habitat that it poses a particularly onerous control challenge. Further research and pilot control studies are under way and need full support.

Although our assessment did not sample the kinds of marginal brackish habitat in San Pablo Bay and San Francisco Bay that Baye and others (2000) have highlighted, and which have been largely extirpated, it does underscore the importance of brackish habitat to greater plant diversity in the Bay–Delta. Landscapes with intact transition habitat at the margin of salt and brackish wetlands are highly limited, and this is one of the reasons San Francisco Bay NERR components such as China Camp and Rush Ranch are so valuable from a conservation perspective. The greatest opportunity for large-scale habitat restoration in the Bay–Delta is currently focused on these more saline portions of the estuary. Given the importance of these marginal brackish habitats to plant diversity in the Bay–Delta as a whole, we advocate that more effort be made to establish conditions favorable for these marginal habitats in tidal wetland restoration projects in San Francisco Bay and San Pablo Bay. This could greatly enhance the potential for greater plant diversity in the Bay–Delta.

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