Patterns in vegetation communities of estuarine wetlands in two California regions: Insights from a probabilistic survey

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Abstract

Urban development in the California coastal zone has greatly impacted the ecological integrity of estuarine wetlands. Anthropogenic modifications to natural wetland structure and hydrology can have negative consequences for the composition of estuarine biotic communities. Monitoring wetlands at the ecoregion level is an important tool for understanding how wetland condition is changing over time and can be the basis for hypotheses about the causative factors influencing resource condition. It provides information for managers beyond the site scale and can better guide agency priorities for management and restoration region-wide. Our study was a component of the 2002 United States Environmental Protection Agency (USEPA) Environmental Monitoring and Assessment Program (EMAP) Western Pilot. We measured indicators of estuarine wetland plant community condition in two regions: southern California and the San Francisco (SF) Bay, with the goal of providing information of practical use to wetland managers. The regional surveys included a comprehensive assessment of the plant communities at probabilistically selected locations across the intertidal marsh plain. In addition, in southern California, an assessment of anthropogenic stressors was conducted determining the amount of tidal muting and by assessing the intensity of surrounding land use and human population density. Results indicate that the two regions differed substantially in terms of plant community composition and structure. Southern California wetlands supported a higher diversity of plant species, were more prone to invasion by exotic species, and exhibited less zonation of plant species within the intertidal zone than the SF Bay. There were negative effects of tidal muting on the marsh plant community within southern California, such as disappearance of certain native species and the propensity for invasive species to encroach the marsh plain. Conversely, indicators of anthropogenic stress in the surrounding landscape did not correlate with plant community structure. This paper evaluates the effectiveness of the indicators used in this study, explores the utility and drawbacks of the selected survey design, and discusses how results from such surveys may inform restoration and management actions in southern California estuarine wetlands.

Introduction

Worldwide wetlands are threatened by filling, fragmentation, hydromodification, and the urbanization of surrounding uplands and their respective watersheds (Zedler and Kercher 2005). Many of these impacts are most severe in estuarine wetlands because of large population pressures in coastal areas, and these anthropogenic disturbances often result in impacts to wetland physical structure, hydrology, and biotic communities, which can ultimately lead to ecosystem-wide changes in habitat quality (Kennish 2001). Monitoring is an important tool for understanding how wetland resource extent and condition are changing over time (Callaway *et al*. 2001, Steyer *et al*. 2003). It is critical to identify

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the factors responsible for these changes and provide guidance for management actions. However, despite the importance of wetland monitoring, few states have well-established wetland monitoring programs, due in part to lack of clarity on indicators and sampling designs that provide cost-effective assessments of wetland condition.

Over the past two decades, the USEPA EMAP has been working to develop state capacity for ambient monitoring of aquatic resources in order to generate statistically unbiased estimates of regional condition (USEPA 2001). This is accomplished through: 1) research on indicators of habitat quality and appropriate sampling designs and 2) work with state resource managers to demonstrate the value of survey-based monitoring via application of such approaches to problems of regional and state interest. The EMAP Western Pilot has conducted an integrated comprehensive coastal monitoring program along the west coast of the United States, focusing mostly on contaminant-related management issues (Lamberson and Nelson 2002). In 2002, EMAP conducted an assessment of the condition of estuarine wetlands in California, Oregon, and Washington. This effort expanded previous EMAP assessments of estuarine habitats to include intertidal flats and saltmarsh habitat. The study also incorporated additional sites and indicators in southern California and the SF Bay in order to serve the information needs of local, coastal-zone management units in those regions (Sutula *et al*. 2002). A goal of the regional intensification in California was to pilot alternative sampling designs and indicators of intertidal wetland condition that would provide data on emerging management concerns for wetland managers. Indicator development focused on community composition of estuarine wetland vegetation and measures of anthropogenic disturbance at different spatial scales.

The plant community is often used to assess the biological integrity of estuarine wetlands because it comprises a diverse assemblage of species with different adaptations, ecological tolerances, and life history strategies (Callaway *et al*. 2001, Steyer *et al*. 2003). Vegetation is an excellent indicator of habitat quality due to ease of its measurement and because it is an ecologically meaningful integrator of many different aspects of wetland condition, such as hydrology (Gosselink and Turner 1978, van der Valk 1981, Spence 1982, Squires and van der Valk 1992, Wilcox 1995), sedimentation (van der Valk 1981, 1986; Sager *et al*. 1998; Wardrop and Brooks 1998), salinity and freshwater influence (Beare and Zedler 1987, Visser *et al*. 1999), habitat fragmentation and hydrological modifications (Chambers *et al*. 2003, Greer and Stow 2003), and others. The condition of the vegetation community is also of interest because it reflects the ability to support numerous estuary-dependent animal species, many of which are state and/or federally listed (Powell 1993, Zedler 1993).

Furthermore, estuarine plant communities are characterized by zonation patterns across elevational gradients, which are thought to be controlled by the combination of competitive ability and stress tolerance (Chapman 1974, Bertness 1992, Pennings and Bertness 2001, Grewell *et al*. 2007). The presence of tidal channels has been shown to significantly affect vegetation distributions in both Baja California (Zedler *et al*. 1999) and the San Francisco Bay (Sanderson *et al*. 2000). Many human-related alterations to the environment that act to degrade estuarine ecosystems cause shifts in abiotic factors, such as salinity and inundation regimes, that structure intertidal plant communities and lead to alteration in characteristic patterns of zonation. This makes plant zonation a valuable indicator of estuarine wetland condition.

While protocols existed to measure vegetation community composition, they had not been piloted in an EMAP probability-based survey of estuarine wetlands. Moreover, because the State of California lacked standardized methods to assess the condition of estuarine vegetation, testing protocols for this purpose was desirable for facilitating statewide reporting of estuarine marsh condition. Historically, sampling designs for the EMAP West Coast Pilot assessments have been geared toward reporting on the condition of estuaries and nearshore habitats with respect to the percent of area of the resource sampled. Under this design, sites are chosen by developing a map or "sample frame" of the total habitat type of interest (e.g., estuarine wetland) and randomly selecting sampling points within the sample frame.

Anthropogenic disturbance, and wetland responses, can occur on various scales. In order to answer many of the questions of interest to local wetland managers, such as the health of the plant community, sampling may require a variety of approaches. The sampling design of the 2002 regional intensification was based on the concept that well functioning estuarine ecosystems "self-organize", and that their plant communities should therefore exhibit characteristic spatial patterns of species distributions in response to hydrology, material inputs, salinity regime, and tidal elevation. It also assumed that these patterns should be detectable at the level of third-order tidal drainage basins. In order to capture these patterns, the plant community was assessed by collecting vegetation data along a series of systematically arrayed transects within the basin corresponding to each randomly assigned sampling point.

This paper presents regional profiles of southern California and SF Bay estuarine wetland vegetation communities resulting from a survey that was designed to answer four key questions: 1) What is the condition of estuarine wetlands as indicated by the diversity and abundance of plant species? 2) What are the differences in species occurrence and patterns of zonation between southern California and the SF Bay? 3) Is the vegetation sampling protocol satisfactory across the regions (particularly in light of the fact that the two regions studied support categorically different type of estuaries)? and 4) Is there evidence of relationships between plant community characteristics and measures of anthropogenic stress? These data will be used to: 1) provide a means of comparing wetland condition between regions, and establishing baseline conditions for future surveys; 2) explore possible relationships between anthropogenic disturbance and condition that can, in turn, inform the design of future, more intensive studies relating to estuarine monitoring; and 3) demonstrate the utility and limitations of the piloted vegetation indicators within the context of standard EMAP probability-based surveys, in order to help managers choose the most appropriate monitoring approaches.

Methods

Sampling Design and Site Selection

A total of 90 sampling points were randomly assigned to estuarine intertidal mudflat and wetland habitat within California, encompassing both salt and brackish marshes. The sampling effort was intensified in SF Bay and coastal southern California estuaries by allocating 30 points to each of these two regions, whereas the remaining 30 points were allocated throughout the rest of California. Sampling at each site included a 1-m^2 plot, as well as the third-order tidal drainage basin, wetland habitat patch, and watershed containing the point. Because each point was randomly selected, the sequentially nested drainage basin, habitat patch, and watershed were, by extension, also randomly selected.

Indicators

Three types of data were collected corresponding to each sampling point: 1) quantitative field data, 2) field observations, and 3) GIS analysis of aerial photographs and land cover data. Depending on the indicator, data collection took place either within the third-order drainage basin, the landscape immediately adjacent to the habitat patch containing the point, or the watershed containing the point. Table 1 lists the set of indicators treated in the present paper, grouped by data source and the geospatial range within which the data were collected. Definitions and methods for measuring each indicator are given below.

Table 1. Intensification indicators.

Basic Data Source; geospatial range	Indicator
Field transect; level of third-order drainage basin	○ Native plant species percent cover and distribution (zonation) ○ Non-native and invasive plant species percent cover and distribution (zonation) ○ Shannon diversity index
Third-order drainage basin	○ Muting of tidal hydrology
GIS analysis; level of the habitat patch or watershed (for southern California sites, only)	○ % development in a series of 100-m intervals around habitat patch containing sampling station ○ Human population density per watershed

Field Data Collection

For the regional intensification effort, data collection for plants followed a protocol designed to evaluate three plant-community parameters: 1) species diversity, 2) zonation, and 3) encroachment by invasive species, based on designations by the California Invasive Plant Council (Cal IPC). Data collection consisted of assessing characteristics of the plant community along an array of five 15-m transects oriented relative to each of the randomly drawn sampling points (Figure 1).

Transects A and B in each array represented channel-side and marsh plain conditions for the mid marsh, respectively, and C and D represented channel-side and marsh plain conditions for the low marsh at the foreshore. Transect E represented conditions near the backshore along the upland boundary. The array design sought to objectively sample the spectrum of moisture regimes that exist across the marsh plain within the limits of third-order tidal marsh drainage systems. Transect C had greatest exposure to tidal flushing, as it occupied the lowest-elevation position, followed by Transects D, A, B, and Transect E, which was positioned at the highest elevation, and therefore experienced the least exposure to tidal hydrology.

Placement of each of these transects was based on the spatial relationship between each of the randomly drawn sampling points in the study and its nearest third-order tidal channel. The rules for determining the locations of each transect are detailed in Table 2.

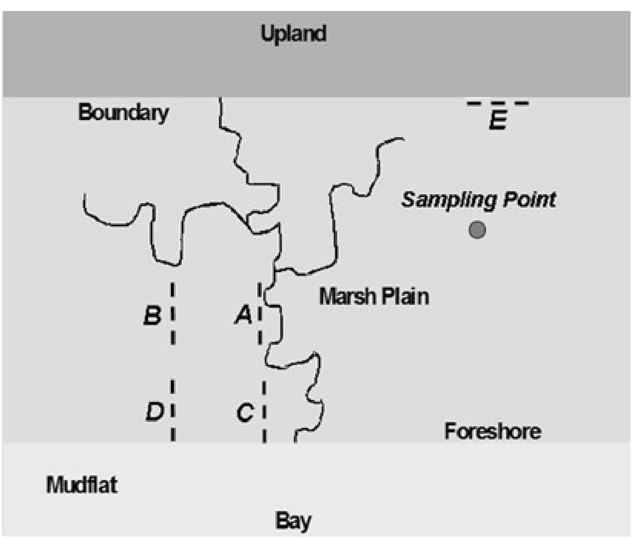

Figure 1. Sampling array for the estuarine wetland vegetation community. The dot indicates where the probabilistically selected point fell. The tidal channels represent the closest third-order drainage network, whose basin contains the point. The dotted lines labeled A - E correspond to the five sampling transects that comprise the array.

To collect vegetation data, a series of rectangular sampling plots (2 m x 1 m) were randomly placed along the length of each transect. Transects A, B, and E consisted of five sampling plots, each, whereas C and D consisted of three plots. Each plot consisted of two adjacent 1-m^2 subplots. Within each subplot, the percent cover of all non-vegetated areas was estimated, followed by bare ground and litter-covered area. Following this, the percent cover for each plant species was estimated separately. Visual estimates of cover were made using a modified Daubenmire cover-class system (Daubenmire 1959) using a seven-point scale. For the purposes of analyses in this study, native vs. non-native status of plant species was based on Hickman (1993), and invasive vs. non-invasive determination was made based on the most recent invasive plant inventory of the Cal IPC (see http://www.cal-ipc.org/ip/inventory/index.php).

Following the completion of the plant community composition surveys, a general reconnaissance of each marsh drainage basin in the study was conducted. The hydrological regime (fully tidal or muted) was determined, where muted was defined as a drainage basin whose hydrology was controlled by a tide gate or weir. Hydrological modifications to the wetland were noted. Where possible, collection of this information was aided by interviews and reviews of reports concerning the assessment area.

GIS Data Collection Methods

Each sampling point fell within an intertidal drainage system of a wetland habitat patch, and each habitat patch fell within a watershed. This inherently nested spatial hierarchy was used to assign data collected at wetland habitat patch, drainage system, or watershed scale to each sampling point. To this end, the boundary of the largest intertidal drainage system (up to third-order) that contained each sampling point was delineated and digitized. This involved locating the sampling point on a 1:12,000 scale United States Geological Survey (USGS) Digital Orthogonal Quarterly Quadrangle (DOQQ), identifying the channel nearest to the sampling point, tracing the largest channel network (up to third-order) to which the channel nearest the sampling point belonged, and then digitizing the boundary of the intertidal area that drained to the selected channel

Table 2. Rules for determining locations of vegetation sampling transects.

Transect	Transect Siting Rule
A	Adjacent to the mainstem tidal channel of the third-order drainage basin within which the sampling point fell Transect A's location was determined by selecting the shortest distance from the sampling point to the mainstem.
B	20 m from Transect A. as measured along an imaginary line running parallel to the foreshore.
C	Downstream from Transect A. adjacent to the mainstem where it meets the foreshore.
D	20 m from Transect C. as measured along an imaginary line running parallel to the foreshore.
E	Along the backshore of the third-order drainage basin at the location representing the shortest distance from the sampling point.

network. For each sampling point, sample drainages were delineated using ArcMap and exported to a shapefile.

The USGS DOQQs were used to identify and map the watersheds that contribute to each third-order drainage basin. Each third-order drainage basin was assigned to the watershed of the nearest perennial fluvial channel. Watershed boundaries from the California watershed layer (CALWATER) were used, when possible. New watershed boundaries were delineated by examining elevation contour lines from digital USGS 7.5 minute series quad-sheets and USGS blueline streams and urban channels. The watersheds were delineated into a geodatabase featureclass using ArcGIS ArcMap, with the TOPO! Extension and then exported to a shapefile.

The GIS analyses were used to evaluate the effects of landscape-level anthropogenic stressors on the vegetation community in estuarine wetlands. Watershed population and surrounding land development associated with each sampling array were determined as follows. The boundaries of local watersheds draining to third-order drainage basins containing sampling arrays were used to "cut" the US 2000 census data. If a census block was dissected by a watershed boundary, then a portion of the data was included from that block that was equal to the portion of the block that was included in the watershed. In addition, percent developed land in the surrounding landscape was determined for each habitat patch containing a sampling array. This was done for six concentric, 100 m wide intervals extending outward from each patch boundary.

Data Analysis

Preparing vegetation data

For estimates of percent cover, Daubenmire index values were used in calculations as surrogates for true percent coverage measurements, an approach that has been deemed acceptable by investigators in previous, similar studies (McCune and Grace 2002). The percent cover estimates were generated for each species by expressing its scored Daubenmire value as the percent of the maximum possible Daubenmire score, and these were averaged across each transect. Then transect-level percent cover estimates for each species for each array were further pooled as necessary, depending upon the requirements of the analysis or graph at hand (e.g., for drainage-basin-level estimates, the transects comprising each array were pooled by calculating weighted average percent cover values for each species).

Depending upon the analysis, certain additional modifications to the data set were required in order to ensure accurate interpretation of results. For analyses requiring normalized sampling effort among sites, only those in which data were collected across a full complement of 42 subplots across 5 transects were included. Conversely, for the preparation of transect-specific graphs to examine patterns in plant zonation across the marsh, sites were included even if their sampling arrays did not consist of the full complement of transects. For inferential analyses comparing "treatment groups", it was necessary to pool data in such a way as to avoid pseudoreplication (Hurlbert 1984). Specifically, for analyses testing effects at the level of the drainage basin (e.g., the effect of tidal hydrology on plant-community parameters), when two sampling arrays occupied the same drainage basin, percent-cover values were pooled across arrays within basins. Conversely, for any analyses that concerned the profiles of vegetation community parameters for comparisons between regions, arrays within common basins were not pooled.

Due to limitations in data availability, only data from southern California were used for the analyses assessing the relationships between plant community composition and anthropogenic stress. Plants that were not identified to species level (a total of eight) were eliminated from any analyses involving native/non-native/invasive status designations. This represented a very small minority of the plant data collected, and no relationships between frequency of unidentified plants and any of the effects for which statistics were run in this analysis were apparent.

Values for the Shannon diversity index (*H'*) were determined for the vegetation transect arrays associated with each sampling point in the study, among all sites from which a full data set was collected. Calculation of this index takes into account species diversity as well as proportion of total percent cover comprised by each species within a given vegetation sampling array to give a measure of diversity of the vegetation community (Kent and Coker 1992). It was calculated according to the following formula:

$$H' = -\Sigma(pi*\ln(pi))$$

Where p_i is the proportion of vegetation cover made up by species *i*.

Regional profiles

A highly informative type of data output for use in a regional survey is that of a cumulative distribution function (CDF), which depicts the estimated distribution of values of a given indicator per cumulative proportion of the geographic unit of interest, such as acres, drainage basins, or watersheds in each region. The CDFs were calculated for each of the two study regions using the Shannon diversity index data. Non-metric Multidimensional Scaling (NMDS), based on plant species percent cover and using Bray-Curtis distance, was employed to evaluate patterns of plant community zonation across the marsh plain between southern California and the SF Bay.

Inferential analyses

Inferential analyses were conducted on the dataset to explore relationships between indicators of condition and stress. Analyses included regression, analysis of variance (ANOVA), and the Mann-Whitney U test. All determinations of statistical significance were based on an a level of 0.05. Because the probabilistically selected sites in the SF Bay resulted in only a small minority (a total of three) of basins with muted tidal hydrology, only the results for southern California, in which nearly half the basins were muted, are included in these analyses. The Multiresponse permutaion Procedure (MRPP), based on plant species percent cover and using Bray-Curtis distance, was employed to test whether there was a significant difference in vegetation community composition between the foreshore (Transects C and D), mid-marsh plain (Transects A and B), and back-shore (Transect E) and whether patterns of zonation differed between southern California and the SF Bay.

Results

Probabilistically Selected Sampling Sites and Their Hydrology

Of the 30 probabilistically selected sites in each of the two regions, a total of 29 sites in southern California and 21 sites in the SF Bay were deemed acceptable for data collection. Larger estuaries had more sample sites due to their higher probability of inclusion in the sample frame. In southern California, the sampling points fell within 25 unique third-order drainage basins and 16 unique watersheds. In the SF Bay, the sampling points fells within 21 unique third-order drainage basins and 16 unique watersheds. Nearly one-half of basins in southern California exhibited muted tidal hydrology, whereas fewer than one-sixth of the SF Bay basins were muted.

Comparison of Plant Community Diversity and Composition between Regions

Transect arrays in southern California basins supported, on average, two more species than those in the SF Bay, and also exhibited a higher proportion of cover by invasive species (Table 3). Although the range of *H'* values was broader across the SF Bay than in southern California, it averaged lower. There was also more heterogeneity in species diversity values across basins in the SF Bay relative to southern California (Figure 2).

Of the 83 plant species recorded across vegetation transects, 14 of them were common to both study regions (Table 4). The eight most common plant species for the two regions combined were all California natives. However, both non-native and invasive plant species were also found in California estuarine wetlands. Three invasive plant species, *Carpobrotus edulis* (ice plant), *Bromus diandrus*

Table 3. Relative percent cover of native, invasive, and non-native plant species from transect arrays in the SF Bay and southern California. Standard error of the mean is provided in parentheses, followed by range. Only sites with a full complement of subplots/transects sampled are included.

Plant Species Class	San Francisco Bay (N = 12)	Southern California (N = 25)
Native	93.8 (1.1); 86.5 - 99.1	89.4 (2.2); 63.1 - 100
Invasive	5.9 (1.2); 0 - 13.5	9.5 (2.1); 0 - 36.9
Non-native	0.3 (0.3); 0 - 3.4	1.1 (0.6); 0 - 13.6

(ripgut brome), and *Salsola soda* (Russian thistle), as well as two other non-native species, *Beta vulgaris* (common beet) and *Polypogon monspeliensis* (rabbit's-foot grass), were common to both regions. Each of the remaining non-native and invasive species encountered in the study were found in only one or the other of the two regions.

The majority of species observed during the vegetation data collection were found in only one of the two study regions (for a total of 34 unique species in southern California, and 33 in the SF Bay; Table 5). The SF Bay had a higher proportion of plant species that are commonly associated with freshwater, as opposed to estuarine or brackish specialists. A higher rate of invasion by noxious weeds was evident in southern California as compared to the SF Bay. For example, *C. edulis* (ice plant) was 25 times more abundant in the former region than in the latter based on absolute cover across drainage basins. *Lepidium latifolium* (perennial pepperweed), another invasive species, was the most common non-native species in the SF Bay, and present in nearly half of the transect arrays. In addition to common estuarine wetland species, both regions also registered a number of species not characteristically (or exclusively) associated with such habitats.

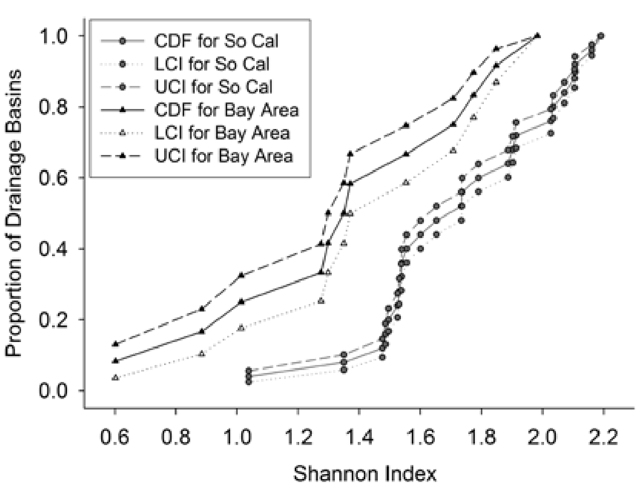

Figure 2. Cumulative distribution functions (CDFs) for Shannon diversity index (H') values for the vegetation communities in southern California and SF Bay estuarine wetlands. Upper and lower 95% confidence intervals (UCI and LCI) are provided for each regional estimate.

Regional Patterns of Plant Species Distribution across Drainage Basins

Of the eight most common species occurring in southern California and the SF Bay, seven exhibited patterns of zonation that varied markedly between regions in fully tidal systems. *Cuscuta salina* (salt

Table 4. Estimated percent cover of plant species by region, averaged across transect arrays, in order of descending abundance (based on the two regions combined). The table includes all species that were common to both study regions, along sampling transects. Four-letter codes presented behind species names are used in Figure 5.

Species	SF Bay	Southern California
Salicornia virginica (Savi)	58	49
Frankenia salina (Frsa)	4	17
Spartina foliosa (Spfo)	9	11
Jaumea carnosa (Jaca)	5	12
Distichlis spicata (Disp)	5	10
Cuscuta salina (Cusa)	5	4
Carpobrotus edulis ** (Caed)	<1	8
Atriplex triangularis (Attr)	7	<1
Limonium californicum (Lica)	<1	3
Bromus diandrus ** (Brdi)	<1	2
Polypogon monspeliensis * (Pomo)	<1	1
Salicornia bigelovii (Sabi)	<1	1
Salsola soda ** (Saso)	<1	1
Beta vulgaris * (Bevu)	<1	<1

* Non-native species

** Invasive species (also considered to be non-native)

Table 5. Estimated percent cover of plant species, averaged across transect arrays, in order of descending abundance. The table includes all species that were unique to each study region along the sampling transects. Four-letter codes presented behind southern California species names are used in Figure 5.

Southern California		SF Bay	
Species	**Percent Cover**	**Species**	**Percent Cover**
Batis maritima (Bama)	8	*Scirpus maritimus*	9
Monanthochloe littoralis (Moli)	4	*Grindelia stricta*	6
Salicornia subterminalis (Sasu)	3	*Scirpus acutus*	6
Cressa truxillensis (Crtr)	2	*Lepidium latifolium* **	5
Brassica nigra ** *(Brni)*	1	*Euthamia occidentalis*	4
Suaeda esteroa (Sues)	1	*Typha latifolia*	4
Atriplex sp	1	*Rosa californica*	3
Salicornia sp	1	*Baccharis pilularis*	3
Suaeda californica (Suca)	1	*Artemisia douglasiana*	2
Mesembryanthemum nodiflorum * *(Meno)*	1	*Juncus balticus*	2
Juncus acutus (Juac)	1	*Calystegia sepium*	2
Malvella leprosa (Male)	<1	*Achillea millefolium*	1
Isocoma menziesii (Isme)	<1	*Spartina alterniflora* **	1
Juncus sp	<1	*Spartina hybrid* **	1
Atriplex watsonii (Atwa)	<1	*Scirpus americanus*	1
Atriplex semibaccata ** *(Atse)*	<1	*Mesembryanthemum crystallinum* **	1
Ambrosia chamissonis (Amch)	<1	*Baccharis douglasii*	1
Heliotropium curassavicum (Hecu)	<1	*Typha angustifolia*	1
Baccharis sp	<1	*Scirpus californicus*	1
*Centaurea solstitialis*** *(Ceso)*	<1	*Picris echioides**	1
*Bassia hyssopifolia** *(Bahy)*	<1	*Phragmites australis*	<1
Triglochin concinna (Trco)	<1	*Polygonum lapathifolium*	<1
Atriplex lentiformis (Atle)	<1	*Raphanus sativus* *	<1
Camissonia cheiranthifolia (Cach)	<1	*Hirschfeldia incana* **	<1
Ambrosia psilostachya (Amps)	<1	*Salicornia europea*	<1
Gnaphalium sp	<1	*Dactylis glomerata* *	<1
Opuntia sp	<1	*Pluchea odorata*	<1
Carex praegracilis (Capr)	<1	*Lathyrus jepsonii*	<1
Artemisia californica (Arca)	<1	*Carduus pycnocephalus* **	<1
Atriplex californica (Atca)	<1	*Madia sp*	<1
Baccharis sarothroides (Basa)	<1	*Foeniculum vulgare* **	<1
Encelia californica (Enca)	<1	*Lolium multiflorum* **	<1
Isomeris arborea (Isar)	<1	*Rumex crispus* *	<1
Sonchus sp *	<1		

* Non-native species
** Invasive species (also considered to be non-native)

marsh dodder), Limonium californicum (western marsh-rosemary), and *Frankenia salina* (alkali heath) were present across all transects in southern California, but were not encountered along the foreshore transects (C and D) in the SF Bay. *Distichlis spicata* (saltgrass) and *Jaumea carnosa* (salty Susan) behaved similarly, in that they were absent from Transect C in the SF Bay, but present across all transects in southern California. *Spartina foliosa* (cordgrass) and *Salicornia virginica* (pickleweed) both existed in fairly even quantities across Transects A through D in southern California, but the former was approximately five times more prevalent along the foreshore than the mid-marsh plain (Transects A and B) in the SF Bay. Conversely, *S. virginica* was almost twice as abundant in the mid-marsh plain as along the shore in this region. Figure 3 shows the regional patterns of occurrence and abundance for these species across transects. *Atriplex triangularis* (arrowleaf saltbush), another native estuarine wetland species found in both regions, is not shown because it was recorded only in basins with muted tidal hydrology in southern California.

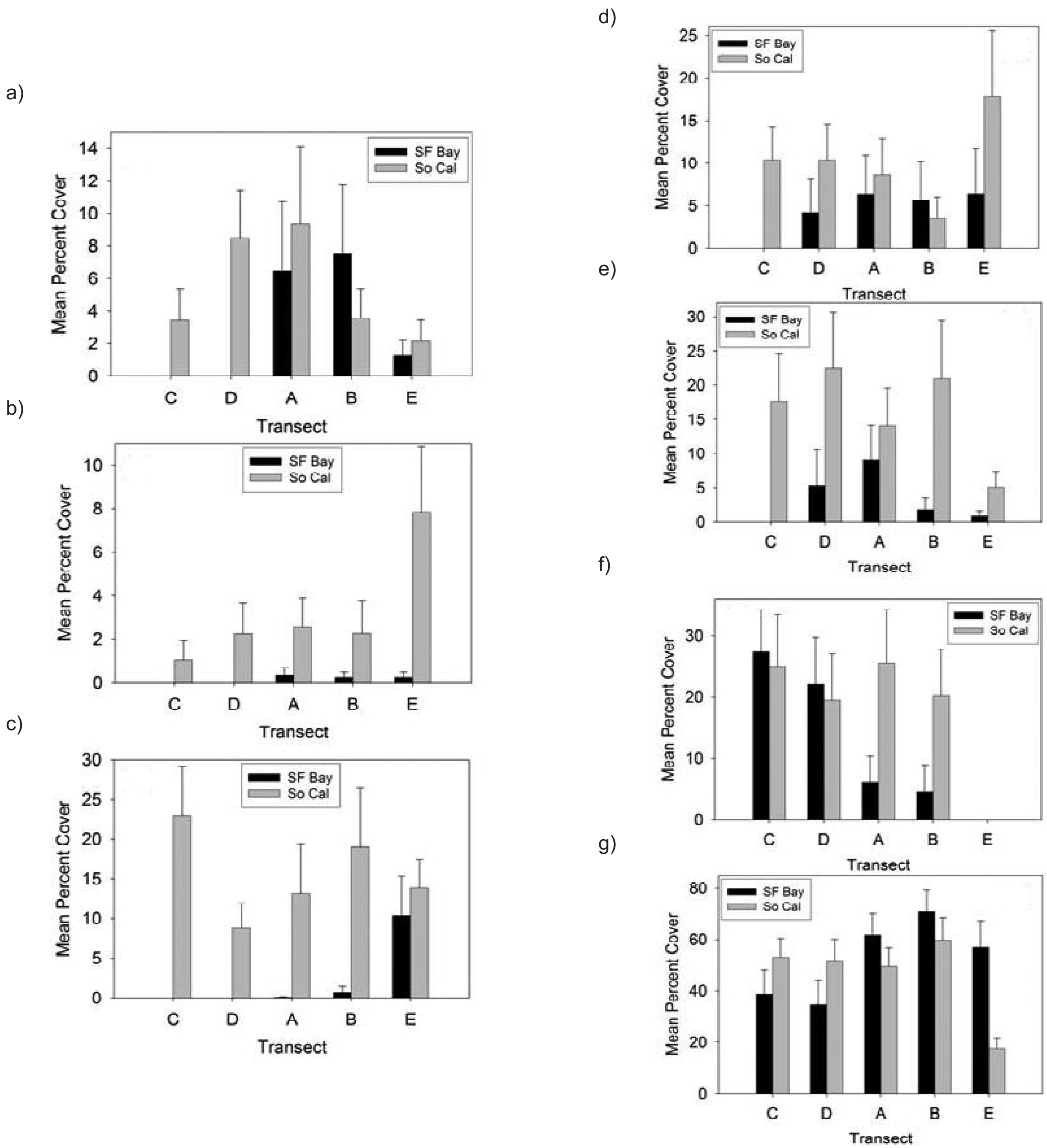

Figure 3. Regional patterns of zonation of common estuarine wetland plant species: *Cuscuta salina* (a); *Limonium californicum* (b); *Frankenia salina* (c); *Distichlis spicata* (d); *Jaumea carnosa* (e); *Spartina foliosa* (f); and *Salicornia virginica* (g). For the purposes of comparison, only data from fully tidal drainage basins are shown. Refer to Figure 1 and Table 2 for an explanation of transect locations.

The NMDS ordination of plant species percent cover for southern California and the SF Bay also indicated differential patterns of zonation between the two regions (Figure 4). In ordination space, foreshore vegetation was well separated from mid-marsh plain and backshore vegetation in the SF Bay, indicating zonation within the intertidal zone. Conversely, foreshore and mid-marsh plain vegetation were not well separated in southern California, but backshore was distinct. For the SF Bay, MRPP analysis also indicated signification zonation within the intertidal zone in that the dissimilarity of foreshore vs. midmarsh plain vegetation was statistically significant, whereas in southern California, backshore vegetation was significantly dissimilar from intertidal vegetation, but there was no difference between the foreshore and mid-marsh plain (Table 6).

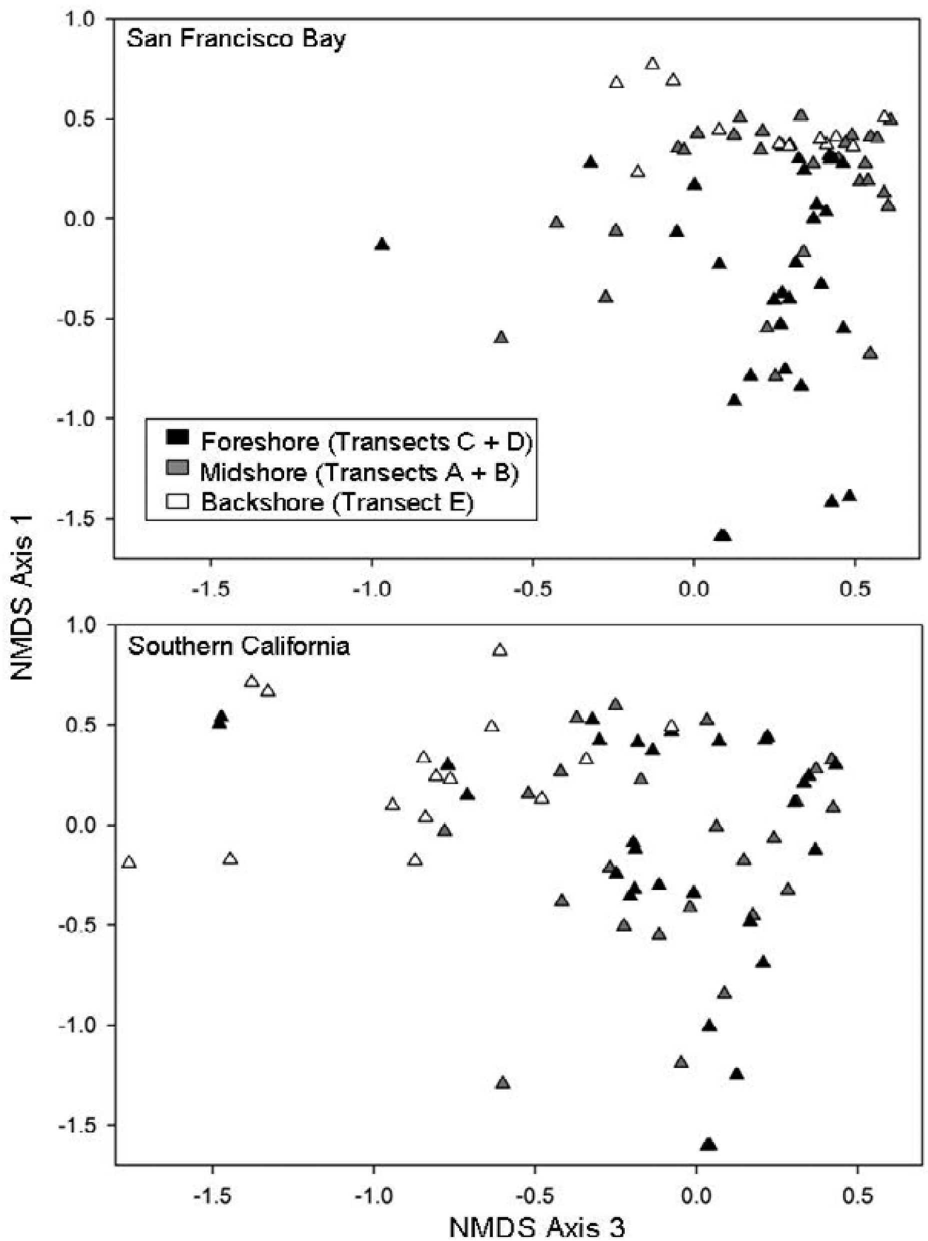

Figure 4. NMDS ordination axes 1 and 3 based on plant species percent cover for the SF Bay and southern California. Each data point corresponds to a single vegetation transect. Symbol shades refer to location of the transect within the estuarine wetland. For comparison purposes only; only sites with fully tidal hydrology included in analysis.

Factors Affecting Plant Community Composition and Structure within Southern California

Plant community composition relative to muted tidal hydrology

Tidal muting was a highly significant predictor of the proportion of invasive plant species in third-order drainage basins ($p < 0.0001$; one-way ANOVA; Table 7). Muted tidal systems had on average 8.5 times more invasive species cover than fully tidal systems.

Percent cover of some species appeared unaffected by hydrology, but other species, including a number of native estuarine wetland taxa, exhibited trends of lower abundance in muted systems relative to fully tidal (Figure 5). *C. salina*, for example, was 6 times more abundant in fully tidal systems than in muted systems ($p = 0.0301$; Mann-Whitney test), and other native estuarine wetland species exhibited a trend toward higher abundance in fully tidal systems, albeit non-significantly (e.g., *J. carnosa*, *S. foliosa*, and *Monanthochloe littoralis* (shoregrass)). Other species were recorded in some fully tidal systems

Table 6. Results of MRPP analysis of plant species percent cover. Groupings are according to location within the estuarine wetland, for each of the two study regions: foreshore = Transects C + D; mid-marsh plain = Transects A + B; and backshore = Transect E. A = the chance-corrected within-group agreement; and P = the probability of a smaller or equal *delta*, which is the overall weighted mean of the within-group means of pair-wise dissimilarities among sampling units. For comparison purposes only; only sites with fully tidal hydrology included in analysis.

Region	Comparison	A	P
SF Bay	Foreshore vs. Midshore	0.06003474	0.00019082
	Midshore vs. Backshore	0.01052304	0.1212253
Southern California	Foreshore vs. Midshore	-0.01021555	0.89363052
	Midshore vs. Backshore	0.15949069	0.00000001

(albeit in low abundances), but were not encountered in muted systems. These include *Salicornia bigelovii* (dwarf saltwort), *Juncus acutus* (spiny rush), and *Triglochin concinna* (arrow-grass). Conversely, certain others, particularly some of the invasive species, appeared much more likely to proliferate in muted systems. Examples include *C. edulis* (ice plant), which was 137 times more abundant in muted systems than in fully tidal ($p < 0.0001$; Mann-Whitney test). Other species that followed a similar trend, albeit to a lesser degree and non-significantly, include *B. diandrus* (ripgut brome), *Brassica nigra* (mustard), and *Atriplex semibaccata* (Australian saltbush).

Not only was the invasive *C. edulis* more abundant in muted tidal basins, it was found to be more widespread across the marsh plain (Figure 6). This species was recorded along all five of the transect locations in southern California among third-order drainage basins with muted tidal hydrology, but exhibited much more limited distribution in fully tidal basins. Other invasive species, such as *A. semibaccata* and *B. diandrus*, also exhibited wider distribution across the marsh plain when tidal influence was muted.

Plant community composition relative to landscape development in the watershed

Regression analyses were used to assess relationships between landscape-level measures of anthropogenic stress and aspects of southern California estuarine vegetation communities. No significant relationships were detected. Neither watershed-level human population density nor measures of percent developed land surrounding the habitat patch containing sample arrays was significantly associated with percent invasive plant species cover.

Discussion

Plant Community Profiles within and between Regions

This study assessed vegetation community structure in order to begin examining regional differences in the condition of SF Bay and southern California estuarine wetlands. Four major differences were noted. First, southern California estuarine wetlands supported on average two more species, and were more consistently diverse from basin to basin, than the SF Bay estuarine wetlands. Second, several species that are characteristic of freshwater habitats were found to occur in the SF Bay, indicating that

Table 7. Relative percent cover of native, invasive, and non-native plant species from transect arrays in southern California, under muted and fully tidal conditions. Standard error of the mean is provided in parentheses, followed by range.

Plant Species Class	Full Tidal (N = 13)	Muted Tidal (N = 10)
Native	96.7 (1.2); 87.2 - 100	79.9 (3.2); 63.1 - 100
Invasive	2.2 (0.9); 0 - 8.8	18.7 (2.9); 0 - 36.9
Non-native	1.1 (0.6); 0 - 6.9	1.4 (1.4); 0 - 13.6

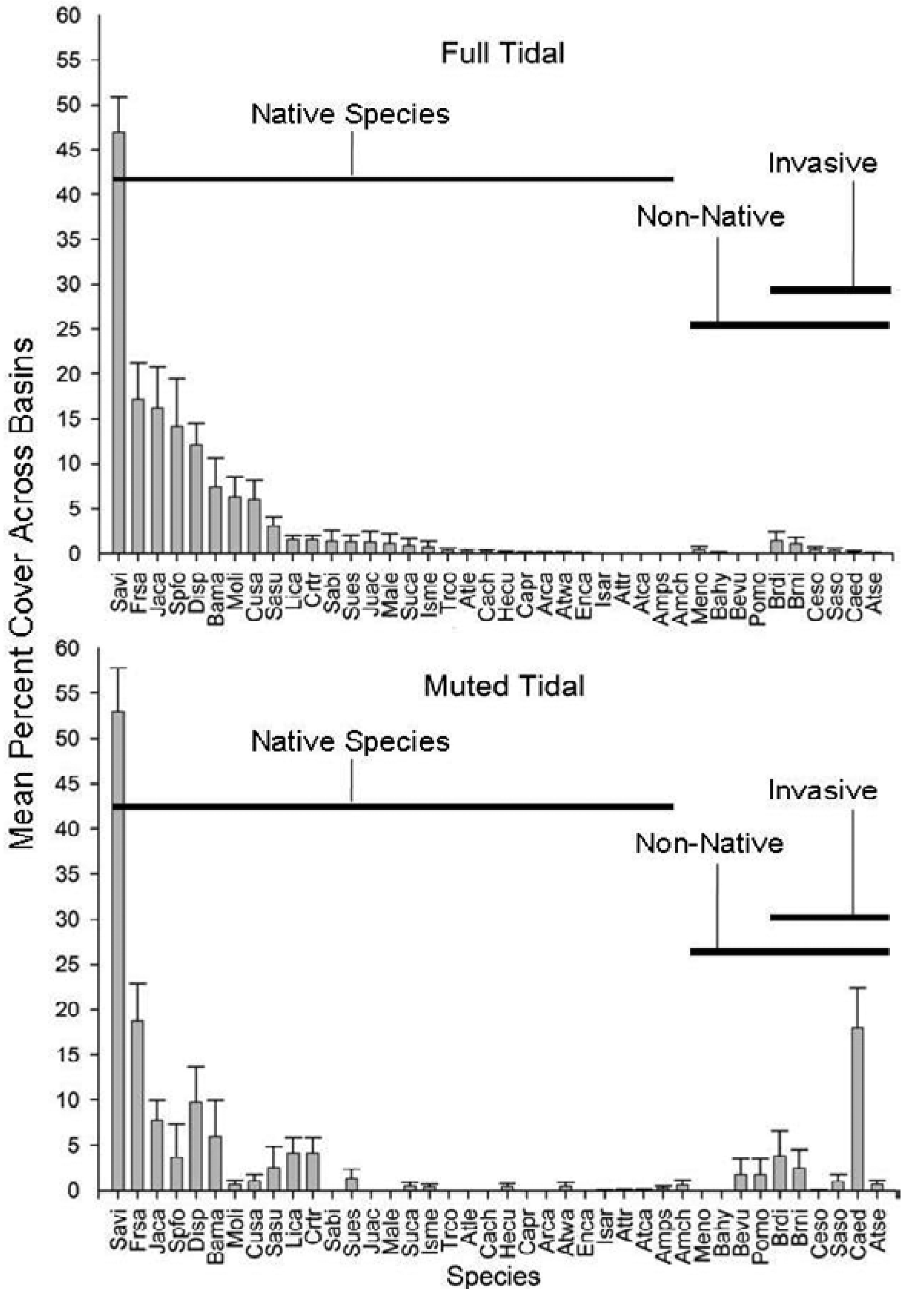

Figure 5. Mean percent cover of plant species in fully tidal *vs.* muted tidal drainage basins in southern California. Plant species are represented by four-letter codes (see parentheses in species lists in Tables 4 and 5 for full species names). Only data from full transect arrays are included. To facilitate comparison, plant species are listed in the same order for the top and bottom graphs.

estuarine wetlands in this region encompass a wider range of salinities, including brackish conditions. These species included *Scirpus acutus* (hard-stemmed bulrush), *Euthamia occidentalis* (western goldenrod), *Typha latifolia* (cattail), *Rosa californica* (California wild rose), and *Baccharis pilularis* (coyote brush), all of which were found in one-fifth or more of the SF Bay basins. While each of these species are widespread throughout California and are abundant in southern California freshwater wetlands, none of them were detected in southern California estuarine wetlands during this study. This regional difference is attributable to the fact that the SF Bay Estuary has a much greater freshwater influence than the relatively small estuaries of southern California. Third, southern California estuarine wetlands appeared to be more prone to invasion by exotic species. *C. edulis*, for example, was 25 times more abundant in the former region than in the latter.

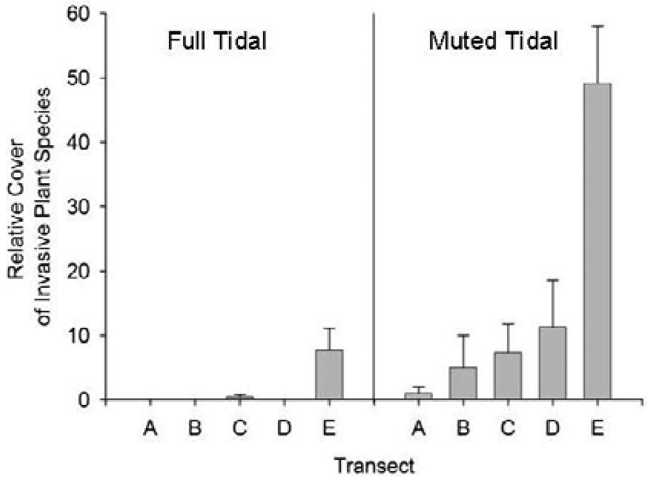

Figure 6. Zonation of invasive plant species across the estuarine marsh plain in fully tidal and muted basins. Values are expressed as the percent of total vegetation cover consisting of invasive species, and are averaged across basins for each transect.

Finally, regional profiles of the transect array data revealed that zonation of estuarine wetland plant species was more consistent across the SF Bay intertidal zone than that of southern California. Even among fully tidal basins in southern California, the common species tended to occur throughout the marsh plain with indistinct patterns of zonation. In contrast, the foreshore of SF Bay estuarine wetlands was dominated by *S. foliosa*, which is known to be a low-marsh inhabitant, requiring regular inundation with saline water (Josselyn 1983, Zedler *et al*. 1999). While *S. foliosa* existed in fairly even quantities across the marsh plain in southern California, this species was approximately five times more prevalent along the foreshore than the mid-marsh plain in the SF Bay area. In the SF Bay, *F. salina* was most limited in its distribution, followed by *L. californicum* and *C. salina*. *D. spicata* and *J. carnosa* were more widespread within basins, but were still absent from the foreshore of SF Bay estuarine wetlands. *S. virginica*, generally recognized as a mid-marsh species (Josselyn 1983, Zedler *et al*. 1999), was found within the SF Bay marsh plain but was largely absent from the foreshore.

The major differences in plant community profiles between the two regions are likely a function of patterns in historical land use and ongoing anthropogenic disturbance, superimposed on regional differences in estuarine geomorphology and climate. TheSF Bay and southern California estuaries, as a group, represent two distinct types of geomorphic environments that would be expected to greatly influence the zonation and species composition of estuarine wetland vegetation. The SF Bay is a large enclosed bay representing approximately 75% of California's total estuarine habitat (Sutula *et al*. 2008); it features substantial deep- and shallow-water subtidal habitat, with fringing intertidal mudflat and estuarine wetlands. Because the SF Bay is well flushed with a strong tidal prism, as well as relatively high freshwater flows, estuarine wetlands in this region support complex, well developed networks of tidal channels and characteristic zonation typical of many enclosed bays in the United States.

In contrast, southern California estuaries are mostly coastal lagoons, many of which historically may have closed to tidal inundation seasonally. However, many are now structurally altered in ways that restrict tidal flows, and many are managed to maintain perennial tidal connections. By definition, coastal lagoons have narrow ocean inlets which restrict exchange with the ocean, resulting in reduced tidal prisms relative to enclosed bays. In addition, many southern California estuaries have been heavily impacted by excess sedimentation. As a result, southern California estuaries are dominated by wetland habitat with poor development of tidal channel networks (Sutula *et al*. 2008). Low-marsh is only prevalent in a handful of southern California estuaries (Tijuana Estuary, Newport Bay, and Seal Beach); the remaining estuaries are dominated by estuarine wetlands at mid-high- to high-marsh elevational gradients (PERL 1990). Mid- and high-marsh zones are known to be more diverse, regardless of geomorphology (Day *et al*. 1989). Therefore, it is likely that the combination of lagoon morphology with poor channel network development, superimposed on higher elevation gradients, have caused southern California to be more diverse, yet lacking in typical patterns of zonation.

Climatic variations are superimposed on geomorphic differences. Rainfall in the Bay Delta region averages 130 cm per year and freshwater sources from the Bay Delta supply approximately two-thirds of the State's freshwater needs. In contrast, southern California freshwater flow to estuaries is significant only during the wet season, so the average salinities of the perennially tidal southern California estuaries are more characteristically polyhaline to euhaline, with relatively little brackish water marsh (~25 - 40 ppt; PERL 1990).

Both SF Bay and southern California estuaries have been heavily impacted by urbanization.

Southern California has lost approximately 91% of its estuarine wetland habitat (Ferren 1990), while the San Francisco Estuary has lost approximately 85% of its estuarine wetlands and 92% of its freshwater marsh habitat (Goals Project 1999, Dahl 2000). Many estuarine wetlands in both regions are embedded within intensive land use development and fragmented by levees and transportation infrastructure. These conditions diminish the hydrological and ecological connectivity among the wetlands, disrupt vegetation zonation, diminish species diversity, and encourage invasion by exotic species (Callaway and Zedler 2004, 2009). It is likely that these disturbances have had a greater impact on southern California estuarine wetlands, because southern California estuaries are smaller, with greater edge per unit area, and are thus more susceptible to outside disturbance. Restricted tidal hydrology in coastal lagoons may heighten the vulnerability of southern California estuarine wetlands to anthropogenic stress. Therefore, while the SF Bay has experienced similar stressors, the larger wetland expanses in this region have likely buffered and reduced the relative impact of these stressors.

Plant Community Responses to Anthropogenic Disturbances

In general, invasive species tended to increase in abundance with tidal muting, whereas the response of native estuarine wetland plants was highly variable. Some of the most common species in southern California estuarine wetlands (*S. virginica*, *F. salina*, *D. spicata*, and *Batis maritima*) seemed to be relatively unaffected by tidal muting, as their abundance did not vary significantly with tidal regime. This suggests that these species are well adapted to shifting estuarine conditions in terms of flooding, sedimentation, drought, and fluctuations in salinity, and have rather broad ranges of tolerance to a number of environmental parameters (Zedler *et al*. 1980). Conversely, some species such as *C. salina* decreased significantly in muted systems, and others such as *J. carnosa*, *S. foliosa*, and *M. littoralis* exhibited similar trends (albeit nonsignificantly). Other species (such as *S. bigelovii, J. acutus*, and *T. concinna*) were present in some tidal systems, but not recorded in muted systems. This is in agreement with previous studies indicating that *S. bigelovii*, an annual pickleweed, was likely extirpated from Tijuana Estuary as a result of large sedimentation events, which eliminated the micro-depressions important for supporting that species (Varty and Zedler 2008, Zedler and West 2008). Conversely, *C. edulis*, an invasive species, was significantly more likely to be found in muted basins (18% mean cover) than in fully tidal (0.14% mean cover). This species was also found to occur throughout the marsh plain in southern California third-order drainage basins with muted tidal hydrology. However, it was extremely limited in its distribution and significantly less abundant in fully tidal systems. Other investigators have also observed this phenomenon (Zahn 2006), which suggests that muting may facilitate the spread of some noxious invaders that might ordinarily be kept at bay in the face of a fully tidal hydrologic regime.

Wetland vegetation is known to be responsive to hydrological modifications (Rey *et al*. 1990, Ibarra-Obando and Poumian-Tapia 1991, Zedler and Callaway 2001). Almost all southern California coastal wetlands have been anthropogenically modified to some degree (Marcus 1989). In particular, hydrologic obstructions such as dikes, levees, and railroad and freeway crossings are widespread throughout estuarine wetlands, often resulting in tidal muting. This study found that tidal muting is an important factor in altering the composition and zonation of the southern California estuarine wetland plant community. Ecological restoration of the estuaries often does not include removal of levees and other hydrological barriers to flow, in part because of cost, but also due to a desire to balance the need for waterfowl habitat with other habitat considerations. In general, the results of this study suggest that restoration efforts in muted systems should seriously consider investing in restoring natural tidal hydrology by removing dikes, levees, and other structures that impede or restrict tidal flows.

Surprisingly, we did not find strong evidence for urbanization in the surrounding landscape as an important determinant of estuarine wetland plant community composition within southern California. Neither watershed population nor percent of adjacent land development were found to significantly affect the plant community condition in terms of relative percent cover of invasive species. These results suggest that estuarine wetland vegetation is more highly sensitive to hydrologic modifications, including those acting at a highly local level, than the more diffuse anthropogenic pressures from surrounding land use.

Utility of Sample Design and Piloted Indicators

Probability-based surveys are becoming a commonly used monitoring tool. When coupled with appropriate biological indicators, they can provide unbiased assessments of biological conditions along with quantitative estimates of sampling uncertainty at the level of the region. However, the implementation in this study of a probabilistic survey designed for the purpose of generating regional estimates of condition was not without disadvantages. For example, while this approach is useful to generate hypotheses, it is not intended to test causal relationships. In order to conduct such hypothesis testing, treatment groups need to be identified and an adequate number of sites within each treatment group need to be selected in such a way that provides sufficient statistical power to address the questions at hand. This can be achieved within a probabilistic survey if it includes proper stratification of the sample frame to capture sufficient numbers of sites within treatment groups of interest. Our ability to conduct powerful inferential analyses on the effects of tidal muting in the SF Bay was hampered by the fact that non-stratified probabilistic site selection generated a sample set with only a small minority of muted basins.

With regard to the vegetation-community indicators piloted in this study, the multiple-transect array facilitated an understanding of plant-community zonation not achievable by sampling the 1-m^2 plot-per-site used in the regional EMAP intertidal wetlands assessment (USEPA 2001). In addition to sampling a larger area of vegetation, the multiple-transect array piloted here was able to characterize estuarine wetlands along elevational gradients thus allowing the detection of differences in patterns of plant-community zonation between regions. A drawback of the multiple-transect array was that sometimes it was not possible to sample certain transects according to the protocol due to lack of a foreshore or backshore in the vicinity of the sampling point, and this resulted in an unequal sampling effort among sites.

In order to normalize effort, we excluded sites that lacked a full complement of transects from some of the analyses, but this resulted in a smaller data set relative to the amount of field work and expense incurred. Several other possibilities existed to mitigate the problem of unequal sampling effort *a priori*: 1) the sample frame could have been established in such a way to reduce the likelihood that points would fall within unsampleable sites; 2) sites could have been reconnaissanced before finalizing the sample set, in order to ensure that the full number of intended sites could be comprehensively sampled; or 3) the data-collection protocol could have been designed to be less restrictive in terms of areas of estuarine wetland in which the full protocol could be carried out completely.

Our study underscored the tension between: 1) adhering to a genuinely probabilistic approach to site selection; and 2) sampling only from sites that accommodate the full expression of the data-collection protocol so that all sites are sampled exactly the same, and with equal effort. This reinforces the need for careful planning of the monitoring approach, indicators, and data-collection protocols in order to generate survey results that speak directly to the targeted management questions, in the most cost-effective manner possible. Choice of protocols and study design will depend upon study objectives and how these align with the various pros and cons of each approach.

Literature Cited

Beare, P.A. and J.B. Zedler. 1987. Cattail invasion and persistence in a coastal salt marsh: the role of salinity reduction. *Estuaries* 10:165-170.

Bertness, M.D. 1992. The ecology of a New England salt marsh. *American Scientist* 80:260-268.

Callaway, J.C., G. Sullivan, J.S. Desmond, G.D. Williams and J.B. Zedler. 2001. Assessment and monitoring. pp. 271-335 *in*: J.B. Zedler (ed.), Handbook for Restoring Tidal Wetlands. CRC Press. Boca Raton, FL.

Callaway, J.C. and J.B. Zedler. 2004. Restoration of urban salt marshes: lessons from southern California. *Urban Ecosystems* 7:107-124.

Callaway, J.C. and J.B. Zedler. 2009. Conserving the diverse marshes of the Pacific Coast. pp. 285-307 *in*: B.R. Silliman, M.D. Bertness and D. Strong (eds.), Anthropogenic Modification of North American Salt Marshes. University of California Press. Berkeley, CA.

Chambers, R.M., D.T. Osgood, D.J. Bart and F. Montalto. 2003. Phragmites australis invasion and expansion in tidal wetlands: interactions among salinity, sulfide, and hydrology. *Estuaries* 26:398-406.

Chapman, V.J. 1974. Salt marshes and salt deserts of the world. pp. 3-19 *in*: R.J. Reimold and W.H. Queen (eds.), Ecology of Halophytes. Academic Press. New York, NY.

Dahl, T.E. 2000. Status and trends of wetlands in the conterminous United States, mid-1986 to 1997. United States Department of Interior, Fish and Wildlife Service. Government Publication Office. Washington, DC.

Daubenmire, R. 1959. A canopy-coverage method of vegetation analysis. *Northwest Science* 33:43-64.

Day, Jr., J.W., C.A.S. Hall, W.M. Kemp and A. Yánez-Arancibia. 1989. Estuarine Ecology. John Wiley & Sons. New York, NY.

Ferren, W.R. 1990. Recent research on and new management issues for southern California estuarine wetlands. pp. 55-79 *in*: A.A. Schoenherr (ed.), Endangered plant communities of southern California (Special Publication No. 3). Southern California Botanists. Claremont, CA.

Goals Project. 1999. Baylands Ecosystem Habitat Goals. A report of habitat recommendations prepared by the San Francisco Bay Area Wetlands Ecosystem Goals Project. United States Environmental Protection Agency, San Francisco, California/San Francisco Bay Regional Water Quality Control Board. Oakland, CA.

Gosselink, J.G. and R.E. Turner. 1978. The role of hydrology in fresh water wetland systems. pp. 63-67 *in*: R.E. Good, D.F. Whigham and R.L. Simpson (eds.), Freshwater Wetlands, Ecological Processes and Management Potential. Academic Press. New York, NY.

Greer, K. and D. Stow. 2003. Vegetation type conversion in Los Peñasquitos Lagoon, California: an examination of the role of watershed urbanization. *Environmental Management* 31:489-503.

Grewell, B.J., J.C. Callaway and W.R. Ferren, Jr. 2007. Estuarine wetlands. pp. 124-154 *in*: M.G. Barbour, T. Keeler-Wolf and A.A. Schoenherr (eds.), Terrestrial Vegetation of California. University of California Press. Berkeley, CA.

Hickman, J.C. 1993. The Jepson Manual. University of California Press. Berkeley, CA.

Hurlbert, S.H. 1984. Pseudoreplication and the design of ecological field experiments. *Ecological Monographs* 54:187-211.

Ibarra-Obando, S.E. and M. Poumian-Tapia. 1991. The effect of tidal exclusion on salt marsh vegetation in Baja California, México. *Wetlands Ecology and Management* 1:131-148.

Josselyn, M. 1983. The ecology of San Francisco Bay tidal marshes: a community profile. United States Fish and Wildlife Service, Division of Biological Services. Washington, DC.

Kennish, M.J. 2001. Coastal salt marsh systems in the US: a review of anthropogenic impacts. *Journal of Coastal Research* 17:731-748.

Kent, M. and P. Coker. 1992. Vegetation Description and Analysis: A Practical Approach. Belhaven Press. London, United Kingdom.

Lamberson, J. and W. Nelson. 2002. Environmental Monitoring and Assessment Program National Coastal Assessment Field Operations: West Coast Field Sampling Methods Intertidal 2002 (Amendment to: Environmental Monitoring and Assessment Program National Coastal Assessment Quality Assurance Project Plan 2001-2004). US Environmental Protection Agency, Office of Research and Development, National Health and Environmental Effects Research Laboratory, Western Ecology Division, Coastal Effects Branch. Newport, OR.

Marcus, L. 1989. The Coastal Wetlands of San Diego County. California State Coastal Conservancy. Oakland, CA.

McCune, B. and J.B. Grace. 2002. Analysis of Ecological Communities. MjM Software Designs. Gleneden Beach, OR.

Pennings, S.C. and M.D. Bertness. 2001. Salt marsh communities. pp. 289-316 *in*: M.D. Bertness, S.D. Gaines and M.E. Hay (eds.), Marine Community Ecology. Sinauer Associates. Sunderland, MA.

Pacific Estuarine Research Laboratory (PERL). 1990. A manual for assessing restored and natural coastal wetlands with examples from southern

California. California Sea Grant Report T-CSGCP-021. PERL. La Jolla, CA.

Powell, A.N. 1993. Nesting habitat of Belding Savannah sparrows in coastal salt marshes. *Wetlands* 13:219-223.

Rey, J.R., J. Shaffer, R. Crossman and D. Tremain. 1990. Above-ground primary production in impounded, ditched, and natural Batis-Salicornia marshes along the Indian River Lagoon, Florida. *Wetlands* 10:151-171.

Sager, E.P.S., T.H. Whillans and M.G. Fox. 1998. Factors influencing the recovery of submersed macrophytes in four coastal marshes of Lake Ontario. *Wetlands* 18:256-265.

Sanderson, E.W., S.L. Ustin and T.C. Foin. 2000. The influence of tidal channels on the distribution of salt marsh plant species in Petaluma Marsh, CA, USA. *Plant Ecology* 146:29-41.

Spence, D.H.N. 1982. The zonation of plants in freshwater lakes. pp. 37-113 *in*: A. Macfayden and E.D. Ford (eds.), Advances in Ecological Research Volume 12. Academic Press. New York, NY.

Squires, L.A. and A.G. van der Valk. 1992. Water depth tolerances of dominant emergent macrophytes. *Canadian Journal of Botany* 70:1860-1867.

Steyer, G.D., C.E. Sasser, J.M. Visser, E.M. Swenson, J.A. Nyman and R.C. Raynie. 2003. A proposed coast-wide reference monitoring system for evaluating wetland restoration trajectories in Louisiana. *Environmental Monitoring and Assessment* 81:107-117.

Sutula, M.A., J. Collins, J. Callaway, T. Parker, M. Vasey and E. Wittner. 2002. Quality assurance project plan for Environmental Monitoring and Assessment Program West Coast Pilot 2002 Intertidal Assessment: California intensification. United States Environmental Protection Agency. San Francisco, CA.

Sutula, M., J.N. Collins, A. Wiskind, C. Roberts, C. Solek, S. Pearce, R. Clark, A.E. Fetscher, C. Grosso, K. O'Connor, A. Robinson, C. Clark, K. Rey, S. Morrissette, A. Eicher, R. Pasquinelli, M. May and K. Ritter. 2008. Status of perennial estuarine wetlands in the state of California. Final report to the Surface Water Ambient Monitoring Program, State Water Resources Control Board. Technical Report 571. Southern California Coastal Water Research Project. Costa Mesa, CA.

United States Environmental Protection Agency (USEPA). 2001. Environmental Monitoring and Assessment Program (EMAP): National Coastal Assessment Quality Assurance Project Plan 2001-2004. EPA Report 620/R-01/002. USEPA, Office of Research and Development, National Health and Environmental Effects Research Laboratory, Gulf Ecology Division. Gulf Breeze, FL.

van der Valk, A.G. 1981. Succession in wetlands: a Gleasonian approach. *Ecology* 62:688-696.

van der Valk, A.G. 1986. The impact of litter and annual plants on recruitment from seed bank of a lacustrine wetland. *Aquatic Botany* 24:13-26.

Varty, A.K. and J.B. Zedler. 2008. How water-logged microsites help an annual plant persist among salt marsh perennials. *Estuaries & Coasts* 31:300-312.

Visser, J.M., C.E. Sasser, R.H. Chabreck and R.G. Linscombe. 1999. Longterm vegetation change in Louisiana tidal marshes, 1968-92. *Wetlands* 19:168-175.

Wardrop, D.H. and R.P. Brooks. 1998. The occurrence and impact of sedimentation in central Pennsylvania wetlands. *Environmental Monitoring and Assessment* 51:119-130.

Wilcox, D.A. 1995. Wetland and aquatic macrophytes as indicators of anthropogenic hydrologic disturbance. *Natural Areas Journal* 15:240-248.

Zahn, E.F. 2006. Invasive of southern California's coastal salt marshes by exotic iceplants (*Aizoaceae*). Master's Thesis, California State University, Long Beach, CA.

Zedler, J.B., T. Winfield and P. Williams. 1980. Salt marsh productivity with natural and altered tidal circulation. *Oecologia* 44:236-240.

Zedler, J.B. 1993. Canopy architecture of natural and planted cordgrass marshes: selecting habitat evaluation criteria. *Ecological Applications* 3:123-138.

Zedler, J.B., J.C. Callaway, J.S. Desmond, G. Vivian-Smith, G.D. Williams, G. Sullivan, A.E. Brewster and B.K. Bradshaw. 1999. Californian salt marsh vegetation: an improved model of spatial pattern. *Ecosystems* 2:19-35.

Zedler, J.B. and J.C. Callaway. 2001. Tidal wetland functioning. *Journal of Coastal Research* 27:38-64.

Zedler, J.B., J.C. Callaway and G. Sullivan. 2001. Declining biodiversity: why species matter and how their functions might be restored in Californian tidal marshes. *Bioscience* 51:1005-1017.

Zedler, J.B. and S. Kercher. 2005. Wetland resources: status, trends, ecosystem services, and restorability. *Annual Review of Environment and Resources* 30:39-74.

Zedler, J.B. and J.M. West. 2008. Declining diversity in natural and restored salt marshes: a 30-year study of Tijuana Estuary. *Restoration Ecology* 16:249-26.

Acknowledgements

The authors thank Diana Benner, Emily Briscoe, Xavier Fernandez, Amy Langston, Leslie Lazarotti, and David Wright for their assistance with field work. Stephen Weisberg provided valuable input on the conceptual approach and statistical design. Eric Stein, Kenneth Schiff, and Allen Herlihy gave valuable comments on this manuscript; Raphael Mazor provided assistance with graphics. This work was supported by a National Coastal Assessment Grant from the United States Environmental Protection Agency.