



Patterns in Estuarine Vegetation Communities in Two Regions of California: Insights from a Probabilistic Survey

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Abstract Monitoring wetlands at the ecoregion level provides information beyond the site scale and can inform regional prioritization of management and restoration projects. Our study was a component of the United States Environmental Protection Agency's 2002 Environmental Monitoring and Assessment Program Western Pilot and is the first quantitative comparison of regional condition of California estuarine wetland plant communities. We measured indicators of estuarine emergent wetland condition in southern California and San Francisco Bay at probabilistically selected sites. In southern California, we also assessed

potential anthropogenic stressors (presence of modified tidal hydrology, intensity of surrounding land use, and population density). Southern California salt marsh exhibited higher species diversity and greater percent cover of invasives. Seven of eight common plant species showed less variation in their distributions (zonation) across the marsh in southern California than in San Francisco Bay. Modified tidal hydrology was associated with absence, in our data, of certain native species, and higher relative percent cover of invasives across the marsh; however, our measures of landscape-level anthropogenic stress did not correlate with cover of invasives. We discuss lessons learned regarding the use of probabilistic site selection combined with our spatially complex data-collection arrays, and comment on utility of our protocol and indicators.

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Introduction

Wetlands worldwide are threatened by filling, fragmentation, hydromodification, and the urbanization of surrounding watersheds (Zedler and Kercher 2005) and impacts are often particularly severe in estuarine wetlands due to intense coastal development. Anthropogenic disturbances can alter wetland physical structure, hydrology, and biotic communities, leading to ecosystem-wide degradation of habitat quality (Kennish 2001). Monitoring can reveal changes in wetland extent and condition (Callaway et al. 2001; Steyer et al. 2003), help identify responsible factors, and provide guidance for management; nonetheless, well-established regional/statewide programs are rare in the United States, due in part to lack of clarity on

indicators and sampling designs that provide cost-effective assessments.

Over the past two decades, the United States Environmental Protection Agency's (US EPA) Environmental Monitoring and Assessment Program (EMAP) has been developing state capacity for ambient monitoring of aquatic resources via research on indicators of habitat quality and appropriate sampling designs, and by demonstrating the value of survey-based monitoring for solving problems of regional and state interest. A key element of the EMAP approach is the use of probability-based surveys, which are intended to generate statistically unbiased estimates of regional conditions and stressors (US EPA 2001).

For many years, the EMAP Western Pilot conducted a comprehensive monitoring program along the United States west coast that focused mostly on contaminant-related management issues in nearshore and estuarine subtidal habitats (Lamberson and Nelson 2002). In 2002, estuarine wetland condition assessment was added, which entailed sampling intertidal flats and salt marshes. As an "intensification" of this effort, additional sites and indicators were incorporated in southern California and San Francisco Bay (SF Bay) in order to address local coastal-zone management concerns (Sutula et al. 2002). One goal of this increased regional sampling was to demonstrate appropriate sampling designs and indicators of salt marsh condition in order to provide data to inform management decisions. Previously, no vegetation-focused wetland survey in California had used an EMAP probabilistic sampling design.

The plant community is often used to assess estuarine wetland biological integrity because vegetation is an excellent habitat-quality indicator. Vegetation community characteristics are relatively easy to assess, compared to those of most animal assemblages. Furthermore, vegetation integrates aspects of wetland condition including hydrology and salinity (Beare and Zedler 1987; Squires and van der Valk 1992; Visser et al. 1999; Chambers et al. 2003; Greer and Stow 2003), and habitat fragmentation and sedimentation (Sager et al. 1998; Wardrop and Brooks 1998). Vegetation condition also reflects a site's ability to support estuary-dependent animal species, including many that are listed as either threatened or endangered under the California and/or United States Endangered Species Act(s) (Powell 1993; Zedler 1993). Therefore, vegetation was selected as the primary indicator of salt marsh condition for the California intensification of the EMAP 2002 intertidal assessment.

Species-specific competitive ability and stress tolerance can interact to influence species presence and abundance in estuarine plant communities (Bertness 1992; Pennings and Bertness 2001; Grewell et al. 2007), and presence of tidal channels can significantly influence salt marsh vegetation spatial patterns of distribution, or zonation, across elevation

gradients (Zedler et al. 1999; Sanderson et al. 2000). Hydrologic modifications altering inundation and salinity regimes may cause shifts in the abiotic factors that structure intertidal plant communities, thus leading to shifts in characteristic patterns of species composition within the marsh. In this sense, the presence of distinctive vegetation patterns (zonation) could be a valuable indicator of estuarine wetland condition, at least as related to hydrology.

Vegetation monitoring within wetlands has taken many approaches, often involving data collection along transects (Henry et al. 2002; Luckeydoo et al. 2002; Leck 2003), and sometimes the use of stratified random sampling with plots (e.g., Moore and Keddy 1989; Galatowitsch and van der Valk 1996). Design specifics may vary, from use of point- or line-intercept (Edwards and Proffitt 2003; Kercher et al. 2003) to that of multiple plots at specific elevation intervals (e.g., Galatowitsch and van der Valk 1996; Leck 2003). With the growing importance of long-term monitoring in the context of anthropogenic influences such as pollution and climate change, great value is placed on accurately and quantitatively describing vegetation (Kercher et al. 2003; Carlsson et al. 2005; Milberg et al. 2008), and for wetlands, various methods can differ in the total effort required to reach the same level of accuracy (VT Parker, unpublished).

While the traditional salt marsh vegetation sampling approaches discussed above are widely used, they have rarely been employed within an EMAP-style probability-based survey. Sampling designs for the EMAP West Coast Pilot assessments facilitate reporting of condition of estuarine subtidal and nearshore habitats in terms of the areal coverage of the resource that is associated with varying levels of condition (Walter et al. 2002). 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 that frame. Sampling associated with the survey then occurs within a 1-m² plot centered on each randomly selected point. In contrast, typical salt marsh vegetation studies are often conducted at targeted sites selected by best professional judgment, or at those that fit prescribed criteria of the study (e.g., relating to geomorphic elements of the study design, prior knowledge of stressors, or logistics). Thus, the challenge is to develop a sample design for a probability-based survey of salt marsh vegetation that can be implemented across a broad geographic area and provide data on community structure and potential stressors. This topic is of great interest to those participating in the first US EPA National Wetland Condition Assessment (NWCA; <http://www.epa.gov/Wetlands/survey/>) to be conducted in 2011, which will use vegetation as a wetland condition indicator. Moreover, since the State of California lacks standardized methods to assess salt marsh condition, there is interest in testing protocols relevant to California's estuaries for the State's emerging wetland

monitoring program. At a broader level, it is our intention that lessons learned from our study will be informative, not only for large-scale wetland monitoring efforts within the United States, such as NWCA, but also for those in other parts of the world, where similar efforts have also been under development and refinement (e.g., the European Union Water Framework Directive; Best et al. 2007; Ferreira et al. 2007).

This paper presents baseline data, from regional assessments of salt marsh vegetation community structure in southern California and SF Bay estuaries, that were collected through an EMAP probability-based sampling design. The study had three objectives: 1) To describe basic patterns in species richness, percent cover, diversity, and zonation of salt marsh vegetation between southern California and SF Bay, 2) To explore relationships between salt marsh community structure and selected measures of anthropogenic stress at field (in terms of modified tidal hydrology) and landscape (in terms of percent developed land within the wetland buffer, and watershed population) scales, and 3) To assess the ability of the probabilistic sampling design and our vegetation sampling protocol to capture plant community structure differences across the two dissimilar regions. This final objective is important because estuarine geform (e.g., enclosed bay vs. lagoon vs. river mouth estuary; Madden et al. 2009) and tidal regime have been hypothesized to be important determinants of the occurrence of particular salt marsh species. MacDonald and Barbour (1974) presented qualitative data suggesting that typical salt marsh vegetation in southern California perennially tidal estuaries was distinct from that in seasonally closed, bar-built lagoons and river mouth estuaries, yet estuarine geform has not been considered in previous West Coast EMAP assessments. San Francisco Bay is a large enclosed bay with fringing salt marshes, representing approximately 75% of the total salt marsh extent in California. By contrast, southern California salt marsh occurs in approximately 40 small estuaries, most of which are coastal lagoons. Thus our goal in Objective #3 is to assess whether a single protocol can capture plant community structure among different classes of estuaries in California, for large-scale monitoring purposes.

Methods

Description of Study Regions

Our two study regions, southern California and SF Bay, are characterized by different estuarine geomorphology and climate, as well as different patterns of historical land use and ongoing anthropogenic disturbance. SF Bay is a large enclosed bay with substantial deep- and shallow-water

subtidal habitat fringed with intertidal mudflat and salt marsh, and has a salt marsh habitat mean tidal range of 1.8 m (Grewell et al. 2007). Because SF Bay is well flushed with a strong tidal prism and receives relatively high freshwater flows, SF Bay wetlands support complex, well developed networks of tidal channels (Sutula et al. 2008).

In contrast, southern California estuaries are mostly coastal lagoons, with salt marsh habitat mean tidal ranges varying from 1.6 to 1.75 m among the systems with full-tidal hydrology. Historically, several estuaries in the region may have been closed seasonally to tidal inundation (Grewell et al. 2007), and many are now structurally altered with restricted tidal flows, while others are managed to maintain perennial tidal connections. Many southern California estuaries have been heavily impacted by excess sedimentation (Greer and Stow 2003; Callaway and Zedler 2004). Furthermore, by definition, coastal lagoons have narrow ocean inlets that restrict exchange with the ocean, resulting in reduced tidal prisms relative to enclosed bays. As a result, southern California estuaries often exhibit poor development of tidal channel networks (Sutula et al. 2008). *Spartina foliosa* (a low-marsh species) is prevalent in only a handful of southern California estuaries (Tijuana Estuary, Newport Bay, and Seal Beach), and the remaining ones are dominated by salt marsh at mid-high- to high-marsh zones (PERL 1990), which are known to be more species rich, regardless of geomorphology (Day et al. 1989). The combination of lagoon morphology with poor channel network development superimposed on higher elevation gradients and invasion by upland species (Macdonald and Barbour 1974) may cause southern California estuaries to be more diverse than those of SF Bay, yet lacking in typical patterns of zonation.

Climatic variations interact with geomorphic differences. Rainfall in the SF 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 (~25–40 ppt; PERL 1990). Both southern California and SF Bay estuaries have been heavily impacted by urbanization. Southern California has lost approximately 91% of its estuarine wetland habitat (Ferren 1990), while the SF Bay estuary has lost approximately 85% of its salt marsh and 92% of its freshwater marsh habitat (Goals Project 1999; Dahl 2000). Many estuarine wetlands in both regions are embedded within intensive land development and fragmented by levees and transportation infrastructure. These conditions diminish the hydrological and ecological connectivity among the wetlands, disrupt vegetation zonation, diminish species diver-

sity, and encourage invasion by exotic species (Callaway and Zedler 2004, 2009). Such disturbances may have a greater impact on southern California estuarine wetlands because they are smaller with proportionately more edge, and are thus more susceptible to outside disturbance. Furthermore, restricted tidal hydrology in coastal lagoons may heighten the vulnerability of southern California estuarine wetlands to anthropogenic stress. Therefore, while SF Bay has experienced similar stressors, the larger wetland expanses in this region may buffer and reduce their relative impact.

Sampling Design, Site Selection, and Indicators

Thirty sampling points were randomly assigned to estuarine intertidal mudflat and salt marsh habitats within each of two strata: southern California and SF Bay. Three types of data were collected corresponding to each point falling within vegetated marsh (points falling in mudflats were excluded from the “intensification” data collection effort described in this paper): quantitative field data, field observations of modifications to tidal hydrology, and GIS data based on aerial photographs and land cover types. Depending upon the indicator, data collection associated with each point took place within either its corresponding third-order tidal drainage basin, the landscape immediately adjacent to the habitat patch containing the point, or the watershed containing the point (Table 1).

Field Data Collection

The drainage-basin-oriented sampling design of the 2002 EMAP Western Pilot regional intensification was based on the concept that well functioning estuarine ecosystems “self-organize”, and that their plant communities exhibit characteristic spatial patterns of species distributions (zonation) in response to hydrology, tidal elevation, and salinity regime. We assumed these patterns to be detectable at the level of third-order tidal drainage basins, because at this level, the marsh plain

can develop predictable patterns in wetland elevation relative to the foreshore (i.e., adjacent to the open water), the mid-marsh, and the backshore (i.e., near the wetland–upland transition boundary). We also assumed that proximity to tidal creeks would relate to plant community attributes.

Vegetation data collection followed a protocol designed to evaluate the following plant-community parameters: plant species richness, absolute cover, diversity, zonation (as indicated by the distribution of plant species among the sampling transects), and relative percent cover of invasive species. We collected vegetation data along an array of five, 15-m transects arranged objectively within the third-order tidal drainage basins corresponding to the randomly assigned sampling points (Fig. 1; Online Resource 1 provides details on transect placement rules). Transects “A” and “B” in each array represented the mid marsh adjacent to the mainstem tidal channel, and 20 m from the channel, respectively. Transects “C” and “D” represented the foreshore adjacent to the mainstem tidal channel, and 20 m from the channel, respectively. Transect “E” represented conditions near the marsh-upland boundary at the backshore. Our design sought to objectively sample a spectrum of moisture regimes 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 E.

A series of rectangular sampling plots (2×1 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. Transects C and D were assigned fewer plots than A, B, and E because low marsh is quite narrow in California. Each plot consisted of two adjacent 1-m² subplots. Within each subplot, absolute percent cover was estimated for: total vegetated area, bare ground, litter-covered area, and each individual plant species present. Visual estimates of absolute cover were made using a modified Daubenmire cover-class system (Daubenmire 1959) with a 7-point scale. Native vs. non-native status of plant species was based on Hickman (1993), and invasive vs.

Table 1 Indicators measured in southern California and SF Bay intensification regions of the 2002 EMAP Western Pilot

Basic Data Source; Geospatial Range	Indicator
Multiple-transect array; level of third-order drainage basin	<ul style="list-style-type: none"> ○ Absolute and relative percent cover (individual plant species and classes, such as native, invasive) ○ Plant species zonation (spatial distribution across the marsh) ○ Plant species richness ○ Shannon diversity index
Observation; level of third-order drainage basin GIS analysis (for southern California sites, only); level of the habitat patch or watershed	<ul style="list-style-type: none"> ○ Modification of tidal hydrology by weir or tide gate ○ Percent development in a series of 100-m intervals (up to 600 m) around habitat patch containing sampling station ○ Human population density per watershed

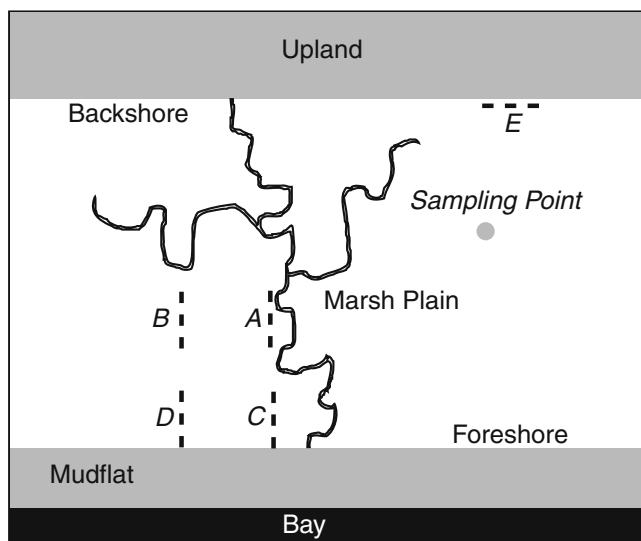


Fig. 1 Sampling array for the estuarine wetland vegetation community. The dot indicates where the probabilistically selected point fell. The tidal channels represent the closest third-order drainage network, whose basin contains the point. The dotted lines labeled A – E correspond to the five sampling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

non-invasive was based on the most recent designations by the California Invasive Plant Council (Cal IPC; <http://www.cal-ipc.org/ip/inventory/index.php>). Following the collection of the plant transect data, the hydrological regime of the site was determined as either fully tidal or modified tidal, the latter defined as a drainage basin whose hydrology was anthropogenically modified by a tide gate or weir.

Geographic Information System (GIS) Data Collection

The boundary of the largest intertidal drainage system (up to third-order) that contained each sampling point was delineated using ArcMap and digitized. US Geological Survey Digital Orthophoto Quarter-Quadrangles were used to identify and map the watersheds contributing to each third-order drainage basin by assigning each basin 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 min series quadsheets and USGS blue-line streams and urban channels. The watersheds were delineated into a geodatabase featureclass using ArcGIS ArcMap, with the TOPO! extension.

The GIS analyses were used to evaluate the effects of potential landscape-level anthropogenic stressors (watershed population and surrounding land development) on the vegetation community in estuarine wetlands. 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 of buffer extending outward from each patch boundary. Thus the relationship between vegetation community structure and percent developed land use within buffers ranging from 100 m to 600 m was tested.

Data Analysis

For estimates of plant cover, Daubenmire index values were used in calculations as surrogates for true percent coverage measurements, an approach that has been used in similar studies (McCune and Grace 2002). Mean absolute cover estimates were generated for each species at the level of each transect by taking the average of the Daubenmire scores for that species across all subplots within the transect, and expressing it as a percent of the maximum possible Daubenmire score. The resulting transect-level percent cover estimates for each species, for each array, were further pooled as necessary, depending upon the requirements of the analysis at hand (e.g., for drainage-basin-level estimates, the transects comprising each array were pooled by calculating weighted average cover values for each species). Most of the analyses presented here that use percent cover data were based on estimated absolute percent cover determined as described above. The exception to this was relative percent cover, which was calculated as the proportion of total vegetation cover (based on the summed absolute covers across all species) that was comprised of a certain class of interest, such as invasives.

For analyses requiring normalized sampling effort among sites, only those in which data were collected across the full complement of 42 subplots (i.e., five complete transects) were included. 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 significance of relationships at the level of the drainage basin (e.g., the relationship between tidal hydrology and plant-community parameters), when two sampling arrays occupied the same drainage basin, percent cover values were pooled across arrays within basins.

Because the probabilistically selected sites in SF Bay resulted in only three basins with modified tidal hydrology, only the results for southern California, in which nearly half the basins were modified, were included in analyses assessing the relationships between plant community composition and anthropogenic stress. Plants that were not identified to species level were eliminated from any analyses involving native/non-

native/invasive status designations. This entailed excluding only eight records, and no relationships between frequency of unidentified plants and any of the effects for which statistics were run were apparent.

Values for the Shannon diversity index (H') were calculated. Cumulative distribution functions (CDFs), which depict the estimated probability distribution of values of a given indicator relative to the cumulative proportion of the geographic unit of interest, were calculated for each of the two study regions using the Shannon diversity index data. Non-metric Multidimensional Scaling (NMDS) based on plant species absolute percent cover, and using Bray-Curtis distance, was employed to evaluate patterns of plant community zonation across the marsh plain between southern California and SF Bay. PC-ORD version 5 software was used for the NMDS (McCune and Mefford 2006). Zonation was assessed by evaluating similarity in plant community composition, as a function of marsh zone, among sites within a region. For this analysis, zones were collapsed into three categories from low to high elevation: the foreshore (Transects C+D), the mid-marsh plain (Transects A+B) and the backshore (Transect E). For each site within the two study regions, plant species percent cover data corresponding to these three categories were ordinated.

Inferential analyses were conducted to explore relationships between indicators of condition and stress. The Mann-Whitney U test was used to evaluate relationships between tidal hydrology and absolute percent cover of plant species. Analysis of variance (ANOVA) was used to evaluate the relationship between tidal hydrology and relative percent cover of invasive plant species. Regression was used to evaluate relationships between landscape-level stressors (watershed human population, and developed land cover surrounding the basin) and relative percent cover of invasive plant species. All determinations of statistical significance were based on an α level of 0.05. Multiresponse Permutation Procedure (MRPP; Biondini et al. 1985) using plant species absolute percent cover and Bray-Curtis distance was employed to test whether there was a significant difference in vegetation community composition between the foreshore, the mid-marsh plain, and the backshore, as well as to determine whether patterns of zonation differed between southern California and SF Bay.

Results

Probabilistically Selected Sampling Sites and Their Hydrology

Of the 30 probabilistically selected sites in each of the two regions, 29 sites in southern California and 21 sites in SF

Bay were deemed acceptable for vegetation data collection. The unacceptable sites were located in unvegetated mudflat areas, and while these were still usable for the broader EMAP study, they were not part of the intensification. 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 SF Bay, the sampling points fell within 21 unique third-order drainage basins and 16 unique watersheds. Nearly half of basins in southern California exhibited modified tidal hydrology, whereas only three SF Bay basins were modified by tidal gates or weirs.

Comparison of Plant Community Diversity and Composition Between Regions

Of the 81 plant species recorded across vegetation transects, 14 were found in both study regions (Online Resource 2), and of these, eight of the nine most common species were California natives. In order of descending estimated absolute percent cover across sampling arrays (for the two regions, combined), they were: *Salicornia virginica*, *Frankenia salina*, *Spartina foliosa*, *Jaumea carnosa*, *Distichlis spicata*, *Cuscuta salina*, *Atriplex triangularis*, and *Limonium californicum*. Three invasive plant species: *Carpobrotus edulis*, *Bromus diandrus*, and *Salsola soda*, as well as two other non-native species: *Beta vulgaris* and *Polypogon monspeliensis* were also common to both regions. Transect arrays in southern California basins supported, on average, almost two more species than those in SF Bay, and also exhibited a higher relative percent cover of invasive species (Table 2). CDF graphs based on Shannon diversity index values for the two study regions (Fig. 2) indicated that, although the range and heterogeneity of index values were greater across SF Bay than in southern California, actual index scores averaged lower. In general, a higher relative percent cover of invasive plant species was evident across drainage basins in southern California as compared to SF Bay (Table 2). *Carpobrotus edulis* was particularly common in southern California, exhibiting 25 times the absolute cover there as in SF Bay (Online Resource 2).

The majority of species observed during vegetation data collection were found in only one of the two study regions (Online Resource 3). A total of 34 unique species were found in southern California, and 33 in SF Bay, which had a higher proportion of species commonly associated with freshwater. In SF Bay, *Lepidium latifolium* was the invasive with the highest absolute percent cover (Online Resource 3), and it was present in nearly half of the transect arrays. We did not record this species in southern California.

Table 2 Plant species mean relative percent cover and richness at the level of transect arrays, and percent of the arrays supporting native, invasive, and non-native species classes in southern California and SF Bay. Standard error of the mean is provided in parentheses, followed by range. Only arrays with a full complement of subplots/transects sampled are included

Parameter	Plant Species Class	Southern California (N=25 arrays)	SF Bay (N=12 arrays)
Relative Percent Cover	Native	89.4 (2.2); 63.1–100	93.8 (1.1); 86.5–99.1
	Invasive	9.5 (2.1); 0–36.9	5.9 (1.2); 0–13.5
	Non-native	1.1 (0.6); 0–13.6	0.3 (0.3); 0–3.4
Species Richness	Native	8.5 (0.6); 4–14	6.8 (0.6); 3–10
	Invasive	1.4 (0.3); 0–4	1.5 (0.2); 0–3
	Non-native	0.3 (0.1); 0–1	0.1 (0.1); 0–1
Percent of Transect Arrays	Native	100	100
	Invasive	60	92
	Non-native	28	1

Regional Patterns of Plant Species Distributions Across Drainage Basins

Of the eight most common native plant species occurring in southern California and SF Bay, seven exhibited patterns of zonation that varied markedly between regions in fully tidal systems (Fig. 3). In general, species showed less variation across the five marsh transects in southern California, with more distinctive patterns of distribution or zonation apparent in SF Bay marshes. *Cuscuta salina* (3a), *L. californicum* (3b), and *F. salina* (3c) were present across all transects in southern California but were not encountered along the foreshore transects (C and D) in SF Bay. *Distichlis spicata* (3d) and *J. carnosus* (3e) behaved similarly, in that they were absent from Transect C in SF Bay but present across all transects in southern California. *Spartina foliosa* (3f) and *S. virginica* (3g) both exhibited similar levels of absolute

percent cover across Transects A through D in southern California. In contrast, in SF Bay along the foreshore, *S. foliosa* exhibited approximately five times the absolute percent cover that was present along the mid-marsh plain, while *S. virginica* exhibited almost twice the percent cover within the mid-marsh plain as along the foreshore.

Differential patterns of zonation between the two regions were also indicated by NMDS ordination of plant species absolute percent cover data (Online Resource 4). The data points in the plot represent the three marsh elevation zones (color coded) for each of the study sites, by region. Those points that are near one another on the plot are more similar in terms of their plant community composition than those that are further apart. If points of a similar elevation zone cluster together, this constitutes evidence for zonation corresponding to the elevation gradient in that study region. In the ordination space of the SF Bay plot, the foreshore vegetation was well separated from mid-marsh plain and backshore vegetation, indicating zonation within the intertidal zone. Conversely, foreshore and mid-marsh plain vegetation were not well separated in the southern California plot, but backshore was distinct. For SF Bay, MRPP analysis also revealed zonation within the intertidal zone based on significant dissimilarity of foreshore vs. mid-marsh plain vegetation, whereas in southern California, backshore vegetation was significantly dissimilar from intertidal vegetation, but there was no significant difference between the foreshore and mid-marsh plain (Table 3).

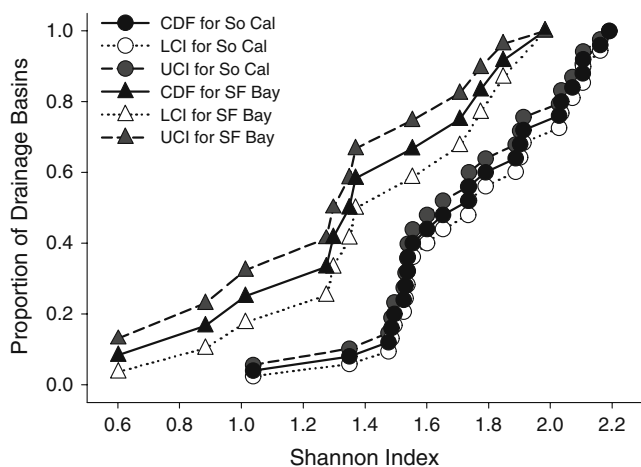
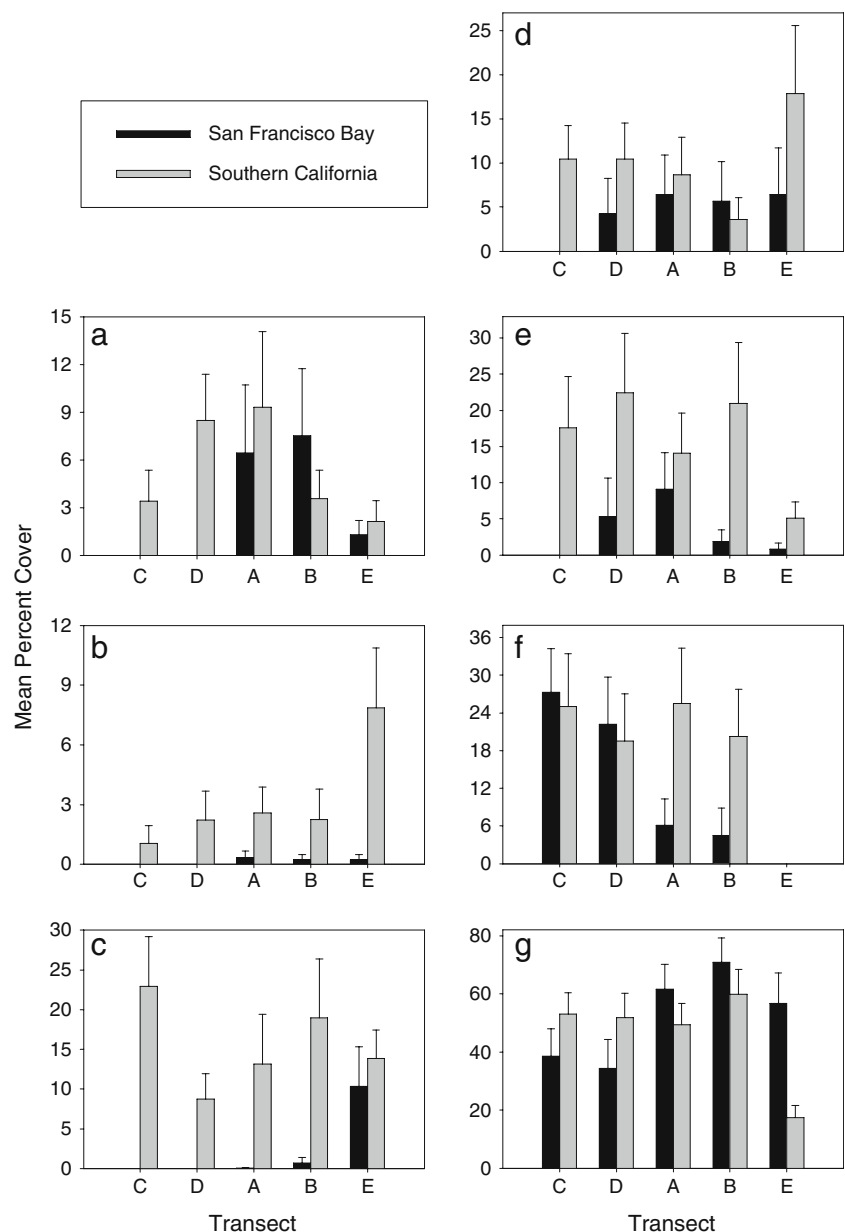


Fig. 2 Cumulative distribution functions (CDFs) for Shannon diversity index (H') values for the vegetation communities in southern California and SF Bay estuarine wetlands. These graphs show the probability distribution of index scores relative to the cumulative proportion of sample drainage basins. Upper and lower 95% confidence intervals (UCI and LCI) are provided for each regional estimate

Factors Relating to Plant Community Composition and Structure Within Southern California

Modification of tidal hydrology from weirs or tidal gates was a highly significant predictor of relative percent cover of invasive plant species in third-order drainage basins ($p < 0.001$; F-ratio=35.4; one-way ANOVA; Table 4). Systems with modified tidal regimes supported on average 8.5 times greater relative cover of invasive species than fully tidal systems.

Fig. 3 Regional patterns of zonation of common estuarine wetland plant species: **a**, *Cuscuta salina*; **b**, *Limonium californicum*; **c**, *Frankenia salina*; **d**, *Distichlis spicata*; **e**, *Jaumea carnosa*; **f**, *Spartina foliosa*; **g**, *Salicornia virginica*. Data shown are mean estimated absolute percent cover, by transect, across basins within each study region. For the purposes of comparison, only data from fully tidal drainage basins are shown. Refer to Fig. 1 and Online Resource 1 for a description of transect locations. Note: Transect C had greatest exposure to tidal flushing, as it occupied the lowest elevation position, followed by Transects D, A, B, and Transect E



Absolute percent cover of some species appeared unrelated to hydrology, but other species, including a number of native estuarine wetland taxa, exhibited lower cover in tidally modified systems relative to fully tidal (Fig. 4). *Cuscuta salina*, for example, exhibited six times higher cover in fully tidal systems than in modified (Mann-Whitney $U=31$, $Z=-2.1$, $p=0.035$), and other native estuarine species also exhibited greater cover in fully tidal systems, albeit non-significantly (e.g., *J. carnosa*, *S. foliosa*, and *Monanthochloe littoralis*). Some species with low cover in fully tidal systems were absent from our data in modified systems. These included *Salicornia bigelovii*, *Juncus acutus*, and *Triglochin concinna*. Species exhibiting higher percent cover in modified

systems were usually invasive. Examples include *C. edulis*, which was 137 times more abundant (based on absolute percent cover) in tidally modified systems than in fully tidal systems (Mann-Whitney $U=8$, $Z=-3.5$, $p<0.001$). Other invasive species that exhibited higher percent cover in tidally modified systems, albeit to a lesser degree than *C. edulis*, and non-significantly, include *B. diandrus*, *Brassica nigra*, and *Atriplex semibaccata*.

Not only was percent cover of the invasive *C. edulis* higher in tidally modified basins; it was found to be more widespread across the marsh plain. In southern California basins with modified tidal hydrology, this species was recorded at least once along each of the five transect positions of the sampling array, and was found in 10

Table 3 Results of MRPP analysis of plant species estimated absolute 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” is the chance-corrected within-group agreement. “P” is the probability of a smaller or equal δ , which is the overall weighted mean of the within-group means of pairwise dissimilarities among sampling units. For comparison purposes, only sites with fully tidal hydrology are included in the analysis

Region	Comparison	A	P
Southern California	Foreshore vs. Mid-marsh plain	-0.01	0.894
	Mid-marsh plain vs. Backshore	0.16	<0.0001
SF Bay	Foreshore vs. Mid-marsh plain	0.06	<0.001
	Mid-marsh plain vs. Backshore	0.01	0.121

different basins. However, in fully tidal basins, it exhibited much more limited distribution, occurring in only a single basin and within a single transect position. Other invasive species, such as *A. semibaccata* and *B. diandrus*, also exhibited wider distribution across the marsh plain when tidal influence was modified (Fig. 5).

No significant relationships were detected in our data between the landscape-level measures of anthropogenic stress we examined and the proportion of invasive plant species based on relative percent cover. Neither watershed-level human population density nor measures of percent developed land surrounding the habitat patch containing sample arrays was significantly associated with this characteristic of the vegetation community.

Discussion

Plant Community Patterns Within and Between Regions

Several major differences in vegetation community structure were noted between southern California and SF Bay salt marshes. First, southern California transect arrays supported more species on average, and were more consistently diverse from basin to basin, than in SF Bay. Second, several species more characteristic of freshwater habitats were found to occur in SF Bay. While these species are widespread throughout California and common in southern California freshwater wetlands, none were detected in southern California estuarine wetlands during this study. Third, southern California salt marshes exhibited higher relative percent cover of invasive plant species.

Another difference between regions involved salt marsh plant zonation, which was more consistent in SF Bay than in southern California. Even among fully tidal basins in southern California, the common species tended to occur throughout the intertidal zone with relatively little spatial heterogeneity in

their distributions, while in SF Bay there were distinctive patterns of individual species distributions or zonation. For example, the foreshore of SF Bay salt marsh was dominated by *S. foliosa*, a common low-marsh inhabitant requiring regular inundation with saline water (Josselyn 1983, Zedler et al. 1999). While *S. foliosa* was found principally along the foreshore in SF Bay, it was distributed fairly evenly across the intertidal zone in southern California.

Plant Community Responses to Anthropogenic Disturbances

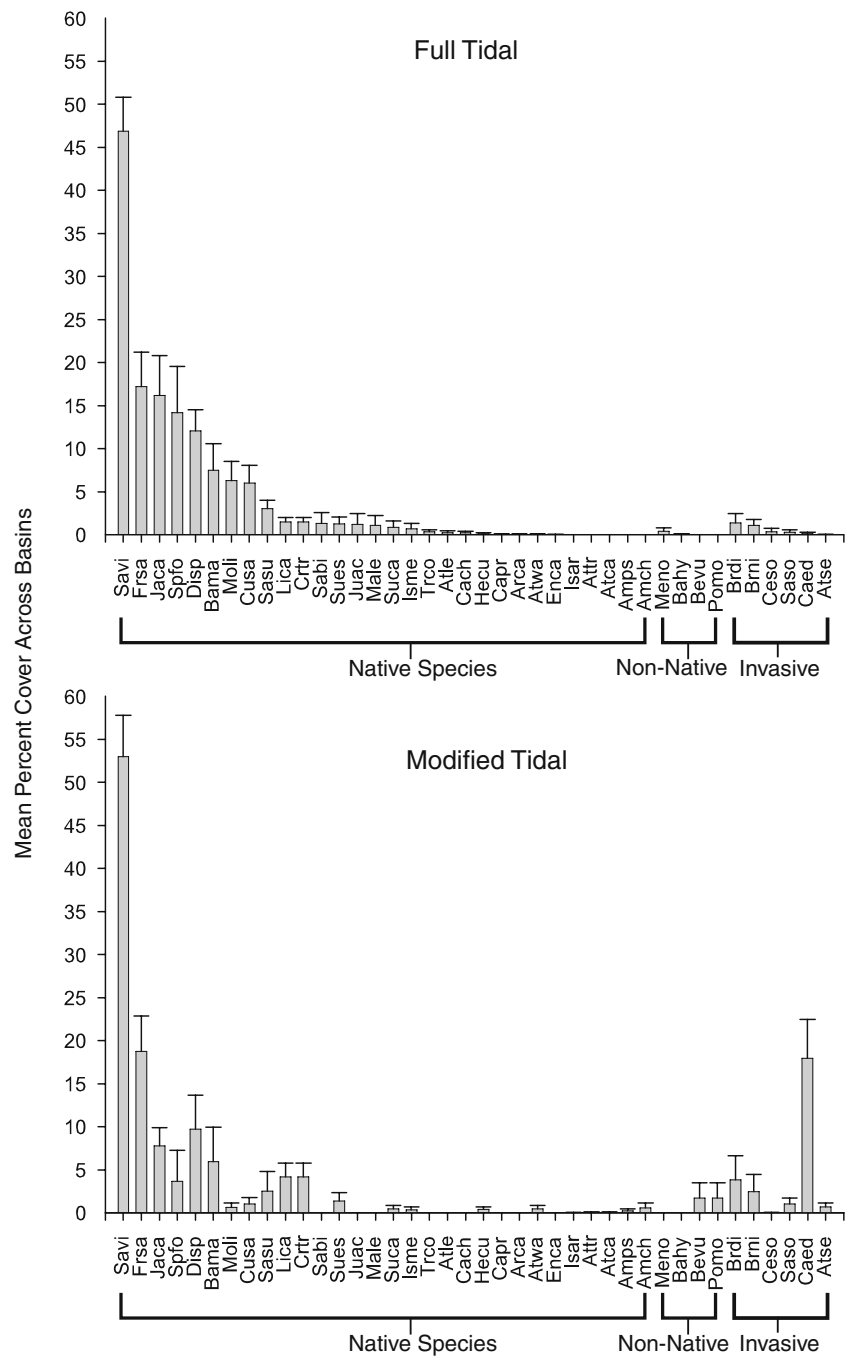
Almost all southern California coastal wetlands have been anthropogenically impacted to some degree (Marcus 1989), and wetland vegetation is known to be responsive to hydrological modifications (Rey et al. 1990; Ibarra-Obando and Poumian-Tapia 1991; Zedler and Callaway 2001). In sites with modified tidal hydrology, we found either that native species exhibited lower cover, or that no relationship between their cover and modification of tidal regime was apparent. The absence in our data of the low-marsh annual, *S. bigelovii*, in tidally modified basins is in agreement with previous work in Tijuana Estuary, where large sedimentation events were shown to reduce the micro-depressions important for supporting that species (Varty and Zedler 2008; Zedler and West 2008). As such, *S. bigelovii*, while historically common in Tijuana Estuary (and throughout southern California in general; MacDonald and Barbour 1974), has more recently been nearly extirpated from that location (J. Zedler, pers. comm.). These results are consistent with direct observation of species loss following hydrologic modification at Tijuana Estuary (Zedler et al. 1992) and Estero de Punta Banda in Baja California (Ibarra-Obando and Poumian-Tapia 1991).

We also found invasive species cover to be higher at southern California sites with anthropogenic modifications of tidal regime. For example, *C. edulis* exhibited significantly higher cover in tidally modified basins than in fully tidal. This species was also found throughout the marsh plain in third-order drainage basins with modified tidal hydrology but not in fully tidal systems, similar to the

Table 4 Relative percent cover of native, invasive, and non-native plant species from transect arrays in southern California, under modified and fully tidal conditions. Standard error of the mean is provided in parentheses, followed by range

Plant Species Class	Full Tidal (N=13)	Modified 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

Fig. 4 Mean estimated absolute percent cover of plant species in full vs. modified tidal drainage basins in southern California. Plant species are represented by 4-letter codes (see parentheses in species lists in Online Resources 2 and 3 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



findings of Zahn (2006). It is worth noting that *C. edulis* was planted throughout the state along railways in the early 1900s and has also been planted by CalTrans more recently (D'Antonio 1990). Railroad trestles and transportation infrastructure transect many southern California salt marshes, thus providing a mechanism for invasion. According to MacDonald and Barbour (1974), four decades ago, southern California estuaries exhibited higher plant species diversity than SF Bay, and, as was the case with our findings, a great number of these species were introduced. Factors proposed as contributing to this phenomenon were

habitat fragmentation and freshwater input. These authors pointed out that the seasonally closed systems are more likely to be invaded by exotic species. Based on the assertions of MacDonald and Barbour (1974), the historical seasonality of many of the southern California estuaries assessed in this study, in addition to severe habitat fragmentation in recent decades, may help explain the relatively high species diversity and high percent cover of invasive species that we found in this region.

Ecological restoration of estuaries often does not include removal of hydrological barriers to flow, in part because of

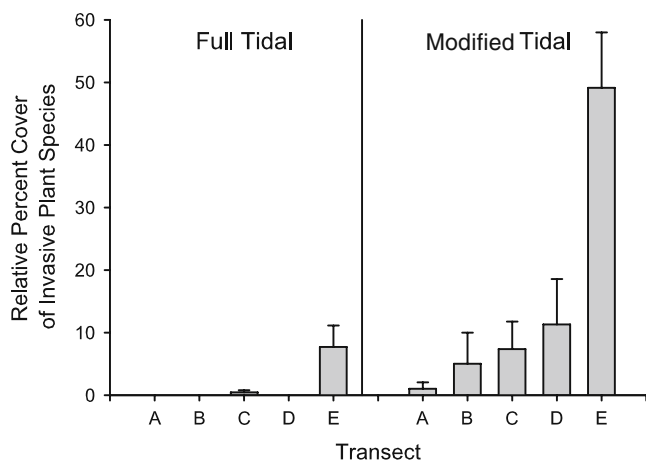


Fig. 5 Zonation of invasive plant species across the estuarine marsh plain in full vs. modified tidal drainage basins. Values are relative percent cover (expressed as percent of total vegetation cover) of invasive species, averaged across basins for each transect

the difficulties in balancing complex factors, including cost of dike removal and issues associated with flood control and habitat for threatened and endangered species. In this study, the absence of certain native species and higher relative percent cover of invasives across the marsh were associated with presence of modified tidal hydrology. This suggests that there are ecological benefits to the emergent plant community from restoring natural hydrology to tidally modified systems, by removing structures that impede or restrict tidal flows.

Previous studies have found that percent of developed land uses within a perimeter of the established assessment area of freshwater depressional wetlands are correlated with water quality (Craft et al. 2007; Trebitz et al. 2007) and indicators of wetland condition (e.g., Fennessy et al. 2007; Wardrop et al. 2007; Johnston et al. 2009). In contrast, we did not find strong evidence that percent developed land uses in the buffer (up to 600 m wide) surrounding the drainage basin was an important determinant of estuarine wetland plant community composition within southern California. Neither watershed population nor percent of adjacent land development were found to correlate significantly with plant community condition in terms of relative percent cover of invasive species. Additional exploration of stressors and appropriate, cost-effective means of measuring them is warranted.

Utility of Piloted Indicators and Sample Design

Probability-based surveys are becoming more commonly used within state and national monitoring programs. When coupled with appropriate indicators, they can provide unbiased, regional assessments of biological conditions along with quantitative estimates of sampling uncertainty.

With regard to the vegetation-community indicators piloted in this study, the multiple-transect array, embedded within a delineation of the third-order drainage basin, facilitated an understanding of plant-community zonation not achievable by sampling the 1-m² plot-per-site used in the standard regional EMAP intertidal wetlands assessment (US EPA 2001). In addition to sampling a larger area of vegetation, the multiple transect array piloted here was better able to characterize estuarine wetlands along elevation gradients, thus allowing the detection of differences in patterns of plant-community zonation between regions, as well as between fully tidal and modified tidal sites within a region (southern California).

Overall, we were satisfied with the performance of the indicators piloted for this study, based on several factors. We were able not only to establish a baseline data set for a number of vegetation community characteristics for our two study regions; we also were able to detect variations in species-specific patterns of cover at different locations in the marsh (corresponding to elevation/moisture regimes), and under different tidal hydrology scenarios (fully tidal vs. modified). In addition, we detected variation between regions in terms of dominant vegetation types, species diversity, and zonation. Our observations reflected expectations based both on our collective best professional judgment and on relevant mechanistic studies of factors driving salt marsh plant distributions, primarily focusing on salinity and inundation (Mahall and Park 1976a, b; Mendelssohn and Morris 2000). A related study of different assessment methods using random points, belt transects, and transects similar to our approach found that all three methods provided similar results, with a greater efficiency of sampling realized with transect methods (VT Parker, unpublished). Shannon index values generated from our data, and expressed in the form of cumulative distribution functions, were a powerful way of comparing probabilistic data across southern California and SF Bay. These analyses allowed us to estimate region-scale species diversity of vegetation communities, in terms of index values, ranges, distributions, and confidence limits.

What the results of our study could not answer is the question of how *sensitive* our indicators are to differences, whether they be between sampling locations, or within a single location over time. In order to assess this, we recommend that future surveys incorporate assessment of sampling error in order to quantify minimum detectable difference (MDD), and therefore the limits of meaningful resolution achievable with a specific combination of protocol and indicators. In addition, it would be of value to establish regional reference sites in order to assess marsh conditions in terms of deviation from reference. Both of these activities would increase the ability to use and fully interpret vegetation surveys with respect to meaningful

differences among sites, condition with respect to “minimally disturbed reference,” and MDD to interpret trends over time.

A key advantage of the probability-based survey is that it produces an unbiased, statistically representative estimate of the indicator employed. The concept of “unbiased” is important, because probability-based sampling forces the survey of areas typically not visited, due to difficult logistics or because the site does not fit the conceptual paradigm inherent in the protocol. A drawback of the multiple-transect array we used in the survey was that it was sometimes impossible to sample certain transects according to the protocol due to lack of a foreshore or backshore in the vicinity of the sampling point, resulting 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. Other approaches could mitigate the problem of unequal sampling effort *a priori*: 1) the sample frame could be established in such a way to reduce the likelihood that points would fall within unsampleable sites, 2) sites could be reconnoitered more carefully by aerial photography to ensure all sites can be comprehensively sampled, or 3) the data-collection protocol could be designed to be less restrictive in terms of areas of estuarine wetland where the full protocol can be carried out. However, corrective actions such as elimination of sites where our protocol did not completely work would have resulted in exclusion of certain types of estuaries. Likewise, design of a less restrictive protocol may have resulted in reduced ability to detect differences, because the protocol would ignore important gradients in vegetation community structure.

Other limitations of probability-based surveys are apparent. For example, while this approach is useful to generate hypotheses, it is not intended to test causal relationships. Probability-based surveys can provide insight into correlative relationships if the design includes proper stratification of the sample frame across “treatment” groups of interest (e.g., sites with fully tidal vs. modified tidal hydrology). However, stratification can increase sampling costs. Our ability to conduct powerful inferential analyses on plant-community relationships with tidal modification in SF Bay was hampered by the fact that our non-stratified (within regions) probabilistic site selection approach generated a sample set with only a small minority of tidally modified basins there. However, inclusion of tidal modification as a stratum in itself would have doubled the cost of the assessment.

Thus our study underscored the tension between adhering to a genuinely probabilistic approach to site selection, 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), and trade-offs between the need to stratify and the need to control costs. This reinforces the importance of careful planning and integration of the monitoring approach 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.

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