Invasion of San Francisco Bay By Smooth Cordgrass, *Spartina alterniflora*: A Forecast of Geomorphic Effects On the Intertidal Zone

Report Prepared for US EPA Region 9
By

Joshua N. Collins, Ph.D.
San Francisco Estuary Institute
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Purpose and Focus of Report

This report describes the existing and likely future effects and related uncertainties of the invasion of the non-native cordgrass, *Spartina alterniflora* Loisel, on the geomorphology of the intertidal zone of San Francisco Bay, based on field studies.

Summary of Results, Conclusions, and Outstanding Questions

Summary of Results

The study results are summarized below. These results pertain to the saline bayshore and salinity gradients of tidal creeks of South San Francisco Bay. The results should not be extrapolated to brackish or freshwater bayshores that have not yet been invaded. For the purpose of brevity, the invasive *S. alterniflora* and the hybrids *S. alterniflora* x *S. foliosa* are both referred to as NIS cordgrass.

1. NIS cordgrass grows at higher and lower elevations than the native cordgrass in the saline intertidal zone of San Francisco Bay.
2. Colonization by NIS cordgrass usually begins between its minimum and maximum elevations and then expands down-slope and up-slope. Older patches extend to higher and lower elevations than younger patches.
3. NIS cordgrass can form a continuous foreshore below the elevation of native cordgrass.
4. NIS cordgrass can colonize offshore shoals that are within the elevation range of onshore colonies.
5. The maximum observed elevation of NIS cordgrass was about 3 inches (8 cm) below local Mean Higher High Water (MHHW), and at least 6 inches (15 cm) below the maximum elevation of tidal marsh vegetation.
6. The minimum observed elevation of NIS cordgrass was about 29 inches (73 cm) above local Mean Lower Low Water (MLLW), which by definition is the lower limit of the intertidal zone.

7. The minimum elevation of NIS cordgrass, relative to MLLW, increases with Mean Tide Range (MTR = MHW – MLW). That is, it grows lower where the mean tide range is smaller.
8. The minimum elevation of NIS cordgrass can be reasonably well predicted based on Mean Tide Range.
9. For each of three sites examined, the predicted minimum elevation of NIS cordgrass corresponds to about the 40th percentile of the probability density function for duration of tidal inundation during June.
10. NIS cordgrass colonizes saline tidal marsh channel beds between the upper reaches of third-order channels and the lower reaches of first-order channels.
11. The minimum elevation of NIS cordgrass decreases with decreasing water salinity. That is, it grows lower where the Estuary is less saline.
12. NIS cordgrass colonizes the channel beds of the brackish tidal reaches of fluvial channels between the head of tide (i.e., the usual upstream limit of the tide) and the local Mean Tide Level (MTL).
13. *S. alterniflora* does not occur upstream of the tides in small creeks around San Francisco Bay.
14. There is no correlation between the genetic similarity of hybrids to *S alterniflora* and the minimum tidal elevation of hybrids.
15. Non-hybrid *S. alterniflora* is more common in the fresh-brackish zones of local streams than in the more saline zones.

Summary of Conclusions

If it is assumed that the NIS cordgrass has achieved its maximum elevation range at the study sites, and that conditions among the sites indicate how the invasion will proceed elsewhere in the San Francisco Estuary, then the results summarized above lead to the following conclusions about the geomorphic effects of NIS cordgrass on the intertidal zone. *However, continuing evolution of NIS cordgrass may select for genotypes that change the spatial pattern of the invasion, resulting in different endpoints.*

1. NIS cordgrass is unlikely to invade more than the upper half of the saline tidal flats and will tend to invade a smaller proportion of the tidal flats in Far South Bay then in South Bay or Central Bay.
2. NIS cordgrass will probably not dominate the saline high marsh above MHW.
3. The invasion of existing mid- and high-elevation marsh channels by NIS cordgrass will tend to isolate the headward reaches of first-order channels from the rest of their channel networks.
4. NIS cordgrass can cause second- and third-order tidal marsh channels to retrogress, thus shortening and simplifying intertidal channel networks and the shoreline of the Estuary as a whole.

5. NIS cordgrass can obstruct tidal flow and fluvial discharge in the upper tidal reaches of fluvial drainages.
6. The upper tidal reaches of local streams can serve as refugia for non-hybrid *S. alterniflora* and as sources of new recruits for continued invasion around San Francisco Bay.

Summary of Outstanding Questions

The following three basic questions about the nature of the NIS cordgrass invasion must be answered before the geographic extent of the invasion within the Estuary and the general ecological effects of the invasion within its extent can be predicted.

1. *How low will NIS cordgrass grow in Suisun and perhaps the western Delta?* Studies are needed to show the minimum elevation of NIS cordgrass when suitable substrate is available in the lower intertidal zone under brackish to freshwater conditions.

2. *Will NIS Cordgrass meadows evolve into high marsh dominated by native plants?* The regional model of marsh evolution from tidal flat through low marsh to high marsh needs to be tested when the low marsh is dominated by NIS cordgrass rather than native cordgrass.

3. *How will native plants and animals adjust to the Invasion by NIS cordgrass?* The hydro-geomorphic processes of the intertidal zone create a dynamic physical template for ecological interactions. Seasonal production of emergent intertidal vegetation and changes in its physical structure are prominent aspects of this dynamic template. The invasion by NIS cordgrass is altering the template and thus will affect the ecology of the intertidal zone. Since the invasion is ongoing and unprecedented in the region, its ecological effects are evolving and the future ecological character and functions of the intertidal system are uncertain.

Key Definitions

The following definitions are used in this report

NIS Cordgrass

Spartina alterniflora Loisel. (smooth cordgrass) is an emergent intertidal grass that is endemic to the East Coast of North America (1). In San Francisco Bay, *S. alterniflora* readily hybridizes with the native cordgrass, *Spartina foliosa* L. (2). While the degree of hybridization can be quantified through genetic analysis of leaf tissue (2), hybrids and pure stands of *S. alterniflora* can be difficult to distinguish in the field. Field keys can usually be used, however, to distinguish native *S. foliosa* from pure stands of *S. Alterniflora* and hybrids (3). For the purposes of this report, *S. alterniflora* and *S. alterniflora x S. foliosa* hybrids are both referred to as NIS cordgrass. NIS cordgrass is regarded as an ecological engineer because it can significantly alter ecosystem processes and change the habitats of other species of plants and animals (2).

Geomorphology

Geomorphology combines aspects of geology and ecology in the scientific study of the configuration and evolution of landforms (4).

Tide

The tide is the periodic rise and fall of a body of water resulting from gravitational interactions between the Sun, Moon, and Earth (5).

Water Level or Height

The tide plus other phenomena, such as wind, barometric pressure, and runoff from uplands, account for the observed daily and shorter-term changes in estuarine water heights (6).

Tidal Datum

A tidal datum is a base elevation defined in terms of a certain phase of the tide, such as high tide or low tide, and used as a reference from which to reckon marine and estuarine heights or depths. A tidal datum is calculated as the average height of a certain phase of the tide for a tidal epoch period of 19 years. For San Francisco Bay, zero tide height for any locale is defined as the 19-year average height of the lower of the two low tides of each lunar day for that locale, termed local Mean Lower Low Water (MLLW) (5).

Tidal Benchmark

A tidal benchmark is a fixed physical object or mark used as a reference for a tidal datum. The standard tidal benchmark of the National Ocean Service (NOS) of NOAA is a brass, bronze, or aluminum alloy disk 3-½ inches in diameter containing the inscription NATIONAL OCEAN SERVICE together with other individual identifying information. The exact locations and official tidal elevations of NOS benchmarks are published by the NOS in Tidal Benchmark Sheets (5).

Foreshore

The foreshore lies between the ordinary low water and ordinary high water contours of the marine or estuarine shore (7). For the purposes of this report, the foreshore is defined as the boundary between unvegetated tidal flat and vegetated tidal marsh.

Backshore

The backshore lies between the ordinary high water and extreme high water contours of the marine or estuarine shore (7). For the purposes of this report, the backshore is defined as the boundary between tidal marsh and upland. The backshore is reached only by the highest tides.

Tidal Flat

For the purposes of this report, tidal flats are landforms between zero tide (local MLLW) and the adjacent foreshore that do not support vascular plants except for eelgrass (*Zostera* spp.). Tidal flats can consist of clays, silts, sands, gravel, cobble, or shell hash (a slurry of shell fragments from marine or estuarine shellfish).

Tidal Marsh

For the purposes of this report, tidal marshes are landforms between the foreshore and backshore that support abundant vascular vegetation.

Tidal Marsh Channel

For the purposes of this report, a tidal marsh channel is a natural or man-made feature that conveys the tides to and from a tidal marsh and that does not directly receive any upland runoff that measurably affects the volume or salinity of the water that it conveys.

Tidal Reach of Creek

For the purposes of this report, the tidal reach of a creek is that segment of a natural or man-made upland drainage channel where the water height is measurably affected by the tide.

Intertidal Zone

For the purposes of this report, the intertidal zone is defined as an area of an estuary between zero tide (i.e., local MLLW) and the backshore.

History and Nature of the Invasion

The chronology, mechanisms, and regional geography of the invasion by smooth cordgrass in San Francisco Bay are fairly well known (2, 8, 9, 10, 11). It was purposefully introduced as part of a tidal marsh restoration project near Alameda Creek in South Bay in the mid 1970s (8), and for shoreline erosion control near the entrance to the San Leandro Channel in South Bay in the late 1970s (11). Undocumented introductions probably occurred elsewhere in South Bay during the 1970s and 1980s (12). The primary means of invasion seem to be tidal distribution of seeds and hybridization due to wind-carried pollen (2), although rhizomes and seeds might be inadvertently distributed by wildlife (especially waterfowl) and heavy equipment (especially clamshell dredges).

The regional distribution of smooth cordgrass was mapped in 1998 (13) and in 2000-01 (10). Since 1998, the invasion has reached from South Bay into Far South Bay and into Central Bay and North Bay (Figure 1).

Colonies along the foreshore seem to expand downslope, upslope, and laterally from their colonization sites at mid-elevation in the intertidal zone (14). Colonies of smooth cordgrass on tidal flats away from the foreshore tend to form doughnut-shaped patches that expand concentrically outward at early stages of expansion and then elongate along elevation contours. The purity and stature of *S. alterniflora* stands seem to increase upstream within the tidal reaches of local creeks, which suggests that the upper reaches might function as sources of pollen, seed, and rhizomes of relatively pure *S. alterniflora* for invasion, or re-invasion, downstream (14). There are large uncertainties about the probable future extent of the invasion because it has not proceeded far enough along the main axis of the Bay to reveal the effects of both tidal hydroperiod (sensu 6) and salinity regime on vertical range of the invasion (14).

Conceptual Models

Conceptual models of natural systems are useful tools to organize existing information, identify information gaps, and, when the information base is adequate, predict system response to internal perturbations or changes in boundary conditions. Recent empirical studies of tidal marsh geomorphology based in San Francisco Bay serve as a foundation for building conceptual models of tidal marsh form and evolution. Less is known about the tidal flats in the region, but their fundamental nature can be surmised from studies of similar systems elsewhere. The models presented below are used to help predict the local and regional geomorphic effects of the NIS cordgrass invasion on the intertidal zone.

Geomorphic Models for the Inception of Tidal Flats and Tidal Marshes

Tidal Flats

Tidal flats store estuarine and terrigenous sediments along their pathway between the open bays or rivers and tidal marshes. In San Francisco Bay, the structure of tidal flats consists of fine silts and clays, sand, shell hash, and an invertebrate in-fauna (17, 22, 23, 91). The amount of sand in tidal flats depends on their proximity to fluvial inputs or ancient sand deposits.

The distribution of tidal flats within an estuary relates directly to tidal range, salinity regime, and nearshore bathymetry (24). Tidal flats tend to be narrower under fresher conditions than under saline conditions. This is partly due to the decrease in tidal range with distance upstream within the Bay, and partly to the tendency of vascular vegetation to extend lower into the intertidal zone under fresher conditions.

Estuarine tidal flats represent a dynamic equilibrium between sediment supply and the erosive energy of the tides. They form where wave action, currents, and the duration of tidal inundation inhibit vascular plant growth (16, 25, 26, 27), but promote the deposition of fine sediments (20, 27, 28). There are three places in a shallow estuary where this dynamic equilibrium tends to be achieved: along the foreshore (especially along the windward shore and along the largest sloughs in tidal marshes); within the brackish zones of maximum sediment entrapment (19, 29), and within the convergence zones of large sloughs subject to two or more tidal sources (30, 31). It is not certain that tidal flats will naturally evolve into tidal marsh, or that the evolution from tidal flat to marsh is irreversible, even as sea level rises. Marsh plains can be swamped by rapid sea level rise and thusly converted into tidal flats or shallow bays.

Tidal Marshes

In the saline areas of San Francisco Bay, the upper limit of tidal marshland exceeds Mean Higher High Water (31, 32, 33). Under natural conditions, there is a transition zone from marshland to upland (i.e., the backshore), which is indicated by changes in plant community composition across the contour of extreme tide height. The backshore is narrow where the land is steep, and broad where the uplands slope gradually to the marshland. Wind that blows salt from the estuary into the uplands can widen the backshore. The transition from tidal marsh to tidal flat (i.e., the foreshore) corresponds to the rather abrupt lower limit of vascular plant growth. The form and ecological nature of tidal marshes vary with tidal regime and salinity regime (6, 27, 34, 35).

Tidal marshes form when tidal flats or the backshore is colonized by vascular plants (85). Plant colonies decrease local wave action and currents and thus increase inorganic sedimentation. Over time, the plants contribute organic material to the sedimentary process, thus increasing the rate of upward development of the marsh through the intertidal zone. This upward development is closely followed by changes in plant community composition (27, 36, 37, 85). In other words, the low marsh plant community is succeeded by a mid-marsh community, which in turn is succeeded by a high marsh community (40, 85).

The initial formation of tidal marshland depends upon a high sediment supply and a low rate of sea level rise (38, 39, 40). Tidal marshes will not evolve if the sediment supply or the rate of sea level rise does not provide a substrate and appropriate tidal regime for plants to colonize and survive.

Under conditions of a slowly rising sea, tidal marshes tend to evolve upwards in approximate equilibrium with sea level rise (40). They can expand both downslope, due to plant colonization of the adjacent tidal flat, and upslope as sea level transgresses the land (85). The oldest area of a patch of tidal marsh therefore tends to be somewhere between the foreshore and the backshore (42, 85).

The high-order drainage networks of large saline tidal marshes have two origins. Most of the larger channels originate on the pre-existing tidal flats (31, 92, 93). As the tidal marsh develops upward, these antecedent channels become deeper and longer (41, 42). The smaller channels of tidal marshland evolve on the marsh plain, and have no place of origin on the pre-existing tidal flat (30, 31).

Models for Intertidal Zone as Transitional Environment

Hydrological Model

The intertidal zone influences watershed outputs to the Bay. Most of the local outputs of terrigenous sediments and freshwater are transported from watersheds through the intertidal zone to shallow bays by fluvial discharge and ebb tides. Some of the sediment from local watersheds is stored within mudflats and trapped within tidal marshlands before reaching the Bay. Tidal marshes can also delay the downstream distribution of freshwater by spreading out the riverine floodwaters (94), or by providing areas for re-circulation of freshwater between neap and spring tide series. The relative importance of watershed outputs of sediment and water therefore increases with distance away from the Golden Gate and into the local watersheds. This model applies to the tidal reaches of watersheds throughout the Bay.

Tidal marshes and tidal flats represent a net landward direction of estuarine sediment transport from the open bays. Some portion of the terrigenous sediments and the marine sediments that are mixed within the open bays is transported onto tidal flats and into tidal marshes. Daily and seasonal sequences of sediment deposition and scour produce a net landward flux of sediment across the tidal flats (43). This transport is punctuated seasonally due to re-suspension of tidal flat sediments by wind-generated waves (20, 29). A portion of the suspended sediment that reaches the marsh drainage system may wash back and forth between the marsh and the Bay, with temporary storage on the tidal flats. But most of the sediment that enters the marsh drainage system is eventually trapped within the channels or on the marsh plain.

The tidal prism of marshes helps maintain the hydraulic geometry of the larger tidal channels that connect the marshlands to the tidal flats and open bays (44, 45). The loss of tidal marshes through reclamation has therefore caused the shoaling and narrowing of these channels (46, 47). Large-scale restoration of tidal marshland would begin to reverse the historical pattern of shoaling.

The tidal and fluvial processes that affect the transitional nature of the intertidal zone vary on many time scales. Fluvial processes vary seasonally, annually, and in relation to the irregular schedules el niño or la niña climatic episodes. Tidal processes vary minute-to-minute (i.e., the velocity pulses that characterize ebb and flood flows in tidal marsh channels) (95, 96); hourly (i.e., on the mixed-diurnal cycle of the daily tides), bi-weekly (i.e., on the neap-spring tidal cycle); monthly, seasonally, and on longer scales of years and tens of years (6).

Chemical Model

The intertidal zone is generally regarded as a retentive environment that serves to filter throughputs of water. It also tends to retain materials that are atmospherically deposited (48). In this way, the intertidal zone serves as a filter and as a place of storage for materials that enter the zone from local watersheds or open bays. The storage function might be greatly enhanced in mudflats by the filtering action of the benthic infauna, and in tidal marshes by the uptake of materials by rooted plants (98, 99, 100, 101).

Tidal marshlands are recognized to be very productive environments, owing to the high levels of primary production by vascular plants on the marsh plain, algae on the exposed tidal flats and channel banks, and phyto-plankton in the channel waters (6, 37, 58). While most of this production fuels endogenic processes, the production is so great that there may be some seasonal leakage downstream or bayward. Most of the output from the intertidal zone occurs in autumn and winter, during the period of maximum decay of detritus and aerial portions of marsh plants (49, 50). Tidal marshes can be either a source or a sink for carbon, depending on the relationship between aerobic microbes and their consumers (51).

Under special circumstances, the intertidal zone may yield sediment and contaminants. Tidal flats and the foreshore can erode due to increased water supply (i.e., increased sea level and/or increased wave energy), decreased sediment supply, or both. Sequential wetting and drying of shallow water sediments may promote the release of contaminants in soluble forms, depending upon the concentration of the contaminants in the sediments, the size of the organic soil faction, and exposure of the contaminants to export processes. The small channels of tidal marshes are dynamic features that are continuously cutting headward or retreating (30, 31), and thus both exhuming and storing sediment. In this regard it should be remembered that the small channels comprise most of the flux boundary between the land and the water.

It is expected from work in other estuaries that there is generally no net annual output of nutrients and particulate organic matter from tidal marshland (37, 49). There may be net inputs or outputs seasonally, and some leakage as suggested above, but on an average annual basis the inputs and outputs are roughly in balance.

Food Web Model

The movements of plants and animals in and out of intertidal habitats represent important ecological linkages between these habitats and adjacent environments (36). Upland wildlife frequently commutes to and from tidal marshes to feed. Mammals and birds that are mainly residents of tidal marshes use the adjacent uplands to escape tidal flooding (65). Some fishes spend their lives in tidal marsh channels, but other fishes follow the tide in and out of marsh channels from adjacent bays and rivers (56).

Saline tidal marshes in San Francisco Bay seem to support two or three food webs that are weakly linked. The marsh plain supports a food web that is linked to terrestrial energy pathways through predacious birds and mammals that feed across tidal marsh plains as well as in the uplands. There is a separate food web for large tidal marsh channels that is essentially an extension of the food web of tidal flats and shallow bays. And there seems to be a food web centered on small tidal marsh channels that is weakly linked to the marsh plain through resident marsh birds that feed in the small channels at low tide, and to the large channels though predation by fishes that move from large channels to small channels during high tide (79). Detritus is an important energy source throughout the intertidal zone (58, 79).

Geomorphic Models for Ongoing Development of Tidal Flat and Tidal Marsh

Plan Form

Tidal marshes and stable tidal flats consist of channels large and small in well-organized drainage networks, and broad plains of low relief between the channels. Mature tidal marshes contain shallow ponds or pannes on the low-gradient plains.

The drainage networks of tidal flats and marshes are typically dendritic and fractal in plan view (30, 52). The termini of first-order channels delineate the headward reaches of the drainage network. These are the narrowest channels that do not branch. Two or more first-order channels that come together form a second-order network; two or more second-order channels that come together form a third-order network, and so forth.

The amount of meander of tidal marsh channels varies with marsh elevation (or age) and slope of the marsh plain. The most sinuous channels and most complex drainage networks are maintained in higher marshes with less slope. Lower marshes with steeper slopes have less sinuous channels in parallel drainage networks that are mostly perpendicular to the foreshore.

Channel density varies with salinity regime, as mediated by the vertical extent of vascular plant growth in the intertidal zone (35). The tendency of vegetation to grow lower in the intertidal zone under fresher conditions extends the marsh plain bayward (narrows the tidal flats), and therefore also moves the tidal source further from the marsh interior (31). As a result, the tidal marsh channels tend to shorten in their headward reaches. Freshwater tidal marshes have simpler and shorter drainage system with broader plains between channels than saline marshes (35).

The average form of tidal flats and marshes in plan view varies slowly over time. Long-term changes in the distribution of tidal flats may signal a major change in local or regional supplies of suspended sediment (53). Cross-sections of the foreshore in many parts of the Bay reveal alternating strata of mudflat and marsh sediments, indicating alternating periods of foreshore advance and retreat (i.e., horizontal accretion and erosion).

Changes in channel density or meander geometry of mature tidal marsh drainage networks depend on changes in plant vigor or plant community composition, and can signal a local or regional change in water supply (i.e., sea level) and salinity regime. Large seasonal variations around the average conditions have been noted, however. For example, the elevation and bayward extent of tidal flats varies seasonally with sediment supply, with winter and spring gains being offset by summer and fall losses (54). The width of the channel-side plant zone in brackish marshes can much wider in wet years of low salinity than in dry years of high salinity (27).

Cross-sectional Form

Plants and wildlife show vertical zonation within the intertidal zone. The zonation is due to complex interaction among biotic and abiotic influences (6, 27, 55). These interactions vary among species and life stages. While the mechanisms of zonation are not well known for many species, the patterns of zonation correlate strongly with tidal elevation, distance from tidal source (i.e., distance upstream along tidal marsh channels or distance away from the channel banks), and aqueous salinity regime.

The cross-sectional form and dimensions of natural tidal channels can be predicted based upon headward tidal prism (57, 102, 103), tidal range, and salinity regime (56). With decreasing tidal range and increasing freshwater influences, the width-to-depth ratio of tidal channels tends to increase. For any tidal marsh or tidal flat, channel cross-sectional area and depth decrease headward (31, 56, 57, 92, 93).

Natural levees only attend the downstream reaches of the largest channels in tidal marshes (31) and along tidal reaches of local rivers and streams. The distribution of natural levees in tidal marsh systems is explained in part by the greater supply of suspended sediment and vertical mixing of the flood tide waters in the downstream reaches of the drainage networks (56). Natural levees are common features along major channels leading from the foreshore into mudflats. These levees are apparently created by the deposition of larger sediments near the channel bank during flood tide.

Large tidal marsh channels have internal berms created by slump blocks produced by bank undercutting (31, 93,104). Slumps occur on the outside of meander bends and on both sides of strait reaches. Large supplies of suspended sediment and its entrapment by vegetation on the slump blocks can cause them to evolve upward faster than they can be eroded, such that banks rebuild themselves in place rather migrate across the marsh plain (30, 31). Smaller channels that evolve on the marsh surface are more dynamic, variously retrogressing bayward due to plant capture in their headward reaches, or elongating headward to accommodate local increases in tidal prism (30, 31).

The relative influence of abiotic tidal influences decrease with intertidal elevation, while the relative influences of non-tidal biotic processes increase (30, 31). At the lower limits of the tides, the structure of habitats is mainly controlled by the direct tidal action, especially through deposition or scour of inorganic sediment. At the higher limits of the tides, habitat structure is mainly controlled by vascular plant growth, especially the development of peaty soils. The geomorphic work of the tides and plant growth are approximately co-equal near the Mean High Tide datum (31).

This cross-sectional model and the plan form model (see above) comprise a three-dimensional model of tidal marsh form. The model predicts that elevation and the geomorphic influences of biotic processes in a tidal marsh increase together with distance away from a tidal source, such as the mouth or bank of a tidal channel. Based upon this model, it might be predicted that the organic faction of tidal marsh sediments increases with elevation, for example. It also suggests that the dynamics of the headward reaches of the first-order tidal channels is due to their spatial correspondence to the co-equal give-and-take of the erosive actions of the tides and constructive actions of plants near the MHW datum.

Ecological Models

Temporal Variability of Plant and Animal Communities

Patches of intertidal habitat support resident populations of non-native as well as native plants and animals, plus populations of migratory and transient species (66). Native species comprise most of the vascular flora (65), although non-native species can dominate the aerial extent of the vascular plant community at some locales, especially along the foreshore and backshore.

The temporary use of intertidal habitats by transient or migratory wildlife may relate to their breeding or rearing, foraging or refuge, or resting (66). For some animal species, especially aquatic insects (67, 68, 69), anadromous fishes (70, 71), and migratory waterfowl (72), the use of intertidal channels is restricted to certain life stages or seasons. Some species of estuarine fishes (73) and shorebirds (64) only use tidal marshes during high tides. Changes in the local or regional mosaic of intertidal and adjacent habitats can either disrupt or enhance their support of wildlife, depending upon habitat patch size, shape, the distance between patches of like kind, and the mix of habitat types (74). Terrestrial predators, including feral dogs and non-native fox that occasionally target tidal marshes can significantly affect the distribution and abundance of native animals, especially resident birds and small mammals (65).

For any salinity regime, the species composition of intertidal communities changes over time as the landforms evolve upward from tidal flats to high marsh. Except for truly freshwater tidal marshes, soil salinity and the abundance of salt-tolerant plants generally increase as habitats gain elevation and age (40).

At any elevation within the intertidal zone, the species composition of plant and animal communities varies over time due to such things as invasions, changes in salinity (32), changes in tidal hydroperiod (6), and disturbance by people. Drought and deluge can affect significant increases and decreases in salinity, with concomitant shifts in species abundance (32, 75).

Intertidal Zonation

Ecological zonation is an obvious feature of the intertidal zone (36, 86). Horizontal zonation between tidal marshes is indicated by predictable variations in plant community composition at any elevation contour along the salinity gradient of the Estuary (75, 32). Vertical and horizontal zonations within a marsh are correlated to elevation and distance from tidal source (i.e., distance away from the foreshore or distance from channel banks) (80, 81). Soil salinity and duration of tidal inundation are the two interacting factors that seem to account for these correlations (6, 27, 36, 75, 77, 81, 82, 83, 84, 86, 97). The horizontal and vertical zones expand and contract due to variations in freshwater supplies that control soil salinity within and between marshes. Abundant freshwater inflows through the Delta can push the brackish zone of the estuary downstream (32, 40, 75), and can cause the channel-side vegetation within tidal marshes to expand onto the marsh plains (27).

Integrated Tidal Marsh and Tidal Flat Ecology and Geomorphology

Intertidal habitats tend toward an average form in dynamic equilibrium with local or regional changes in sediment and water supplies, as affected by climate, geology, and land use. They are highly organized landscapes with well-defined physiographic features that are predictably distributed through space and over time.

The relative geomorphic importance of abiotic and biotic processes varies with elevation and distance from tidal sources in the intertidal zone. Biotic processes, such as production of peats and vegetative (i.e., non-sexual) plant reproduction, increase with tidal elevation, distance upstream within drainage networks, and distance away from channel banks. Abiotic and biotic controls fluctuate in dominance within small channels that dewater at low tide. Weak tides above Mean High Water tend to permit channel capture by vascular vegetation, resulting in channel retrogression. But in large tidal marshes, there tends to be a compensatory relationship between natural losses and gains in the total length of all small channels. Individual retrogression events are incompetent to affect the cross-sectional area of the much larger channel system at its tidal source. Therefore, the system is subject to the same tidal prism before and after individual retrogression events. The tidal prism displaced from retrogressing channels moves headward along the hydraulic gradient generated by channel friction to other channels that consequently elongate, such that the overall tidal prism and amount of channels large and small are conserved. The hydraulic gradient is slight, and a large system is required to generate sufficient hydraulic head to move enough water headward to cause channel elongation. Lesser systems tend to experience chronic retrogression, with overall loss of channel capacity and ecological function over time.

Restricting the tidal source or moving it away from the interior reaches of the system promotes retrogression, expansion of areas that lack channels (i.e., loss of habitat for estuarine fishes and other aquatic resources), and expansion of natural ponds or pannes on drainage divides (i.e., gain in habitat for shorebirds and waterfowl). Increasing the tidal source or moving it more interior promotes headward channel erosion and loss of ponds.

Vascular vegetation plays a critically important ecological role because it affects the physical structure of habitats and because it functions as a food resource throughout most of the intertidal zone.

Tidal marshes are where the estuary and the uplands meet. The intersection is not fixed in time or space because marsh elevations are constantly changing, relative to estuarine water heights. The intersection is always between the foreshore and backshore, however, and may be more narrowly delineated. Conditions above MHW and below MTL seem to be more terrestrial than estuarine, and more estuarine than terrestrial, respectively (6, 78). In small channels of saline marshes that have base elevations above MTL, tidal velocities tend to be too weak to prevent channel capture by marsh plants (30). Elevation boundaries between dominant plant assemblages tend to correspond to local MHW (78). Tidal marshes seem to support three nearly independent food webs, one for large tidal marsh channels, one for the marsh plain and backshore, and one for small channels (79). The latter food web might provide a weak link between the other two. Detritus is expected to be an important source of energy at elevations above MHW, but is largely replaced by attached and epiphytic algae at lower elevations (58). Beds of filter-feeding bivalves are also expected to strongly influence suspended sediment supplies for tidal flats and large tidal marsh channels. Based on this evidence, the actual boundary between bays and uplands in tidal marshes seems to trace the beds of small channels, between MTL and MHW.

The conservation of native biological diversity of the intertidal zone depends on the natural, or naturalistic variability of the tides, freshwater supply, sediment supply, and salinity regime (75, 80).

Study Methods

Bayshore and Tidal Marsh Studies

Site Descriptions

The purpose of these studies was to measure the vertical distribution of NIS cordgrass for different bayshore and tidal marsh conditions. To minimize the error of the elevation surveys, sites had to include a NOS Primary or Subordinate Tide Station with multiple NOS tidal benchmarks that could be recovered.

Four suitable sites were chosen: San Leandro Channel, Arrowhead Marsh, Coyote Point Marsh, and Coyote Hills Slough (see Figure 1). These sites differ with regard to tidal range, length of adjacent fetch, and topographic steepness of the intertidal zone (see Table 1). All site-specific tide statistics are taken from NOS published benchmark sheets available at http://co-ops.nos.noaa.gov/bench_mark.shtml?region=ca.

Table 1: Identifying characteristics of the four sites studied in the field.

	San Leandro Channel	**Arrowhead Marsh**	**Coyote Point Marsh**	**Coyote Hills Slough**
NOAA Tide Station Code	941 4724	941 4711	941 4449	941 4621
Mean Tide Range	4.98 feet (1978 epoch)	4.95 feet (1978 epoch)	5.61 feet (1978 epoch)	5.63 feet (1978 epoch)
Length of Adjacent Windward Fetch	0.5 miles	0.75 miles	3.0 miles	5.5 miles
Average Foreshore Steepness	1:30	1:10	1:20	1:30
Age of Invasion (estimated from interviews)	20-25 years	10-15 years	5-10 years	15-20 years

In addition to these sites that were surveyed in the field, additional sites were used to investigate the relationships between tidal statistics and expected minimum elevations of NIS cordgrass. The emphasis on minimum elevation is due to the concern that NIS cordgrass might take over all or most of the existing tidal flats, at least under saline conditions. The investigation relied on published water heights to construct cumulative duration curves for three NOS Tide Stations. These stations are: Alameda in San Francisco Bay (NOS code 9414750), Redwood City Wharf # 5 (NOS code 9414523), and Dumbarton Bridge West (NOS code 9414509). These data are available from NOS at http://co-ops.nos.noaa.gov/data_retrieve.shtml?input_code=100111111vwl.

Elevation Surveys

All elevation surveys were conducted using a Zeis self-leveling level with a 20x scope and a survey rod readable to about 0.01 ft (3.0 mm). The instrument was serviced and calibrated just prior to the surveys. All surveys were conducted during June and July, when annual above-ground growth of NIS cordgrass is obvious.

At each site, two or more benchmarks were recovered. In all cases, the recovered benchmarks were within 0.001 ft (3.0 mm) of their published relative elevations. The nearest benchmark to the foreshore with NIS cordgrass was selected as the survey starting point. Surveys were conducted along the foreshore and backshore from the benchmark. At least 30 readings of NIS cordgrass elevations were made along each shoreline. For example, to begin a vegetation survey of the foreshore, a point along the foreshore was randomly chosen. From that starting point, the elevation at the base of the lowest-elevation NIS cordgrass was surveyed at 3 m intervals until 30 points had been surveyed. The process was repeated for the backshore, except that the highest-elevation NIS cordgrass was surveyed. Where possible, an additional 30 points were surveyed along the up-slope extent of the highest-elevation native marsh vegetation. Each survey was closed to its starting benchmark. Closure error never exceeded 0.003 ft (1.0 mm).

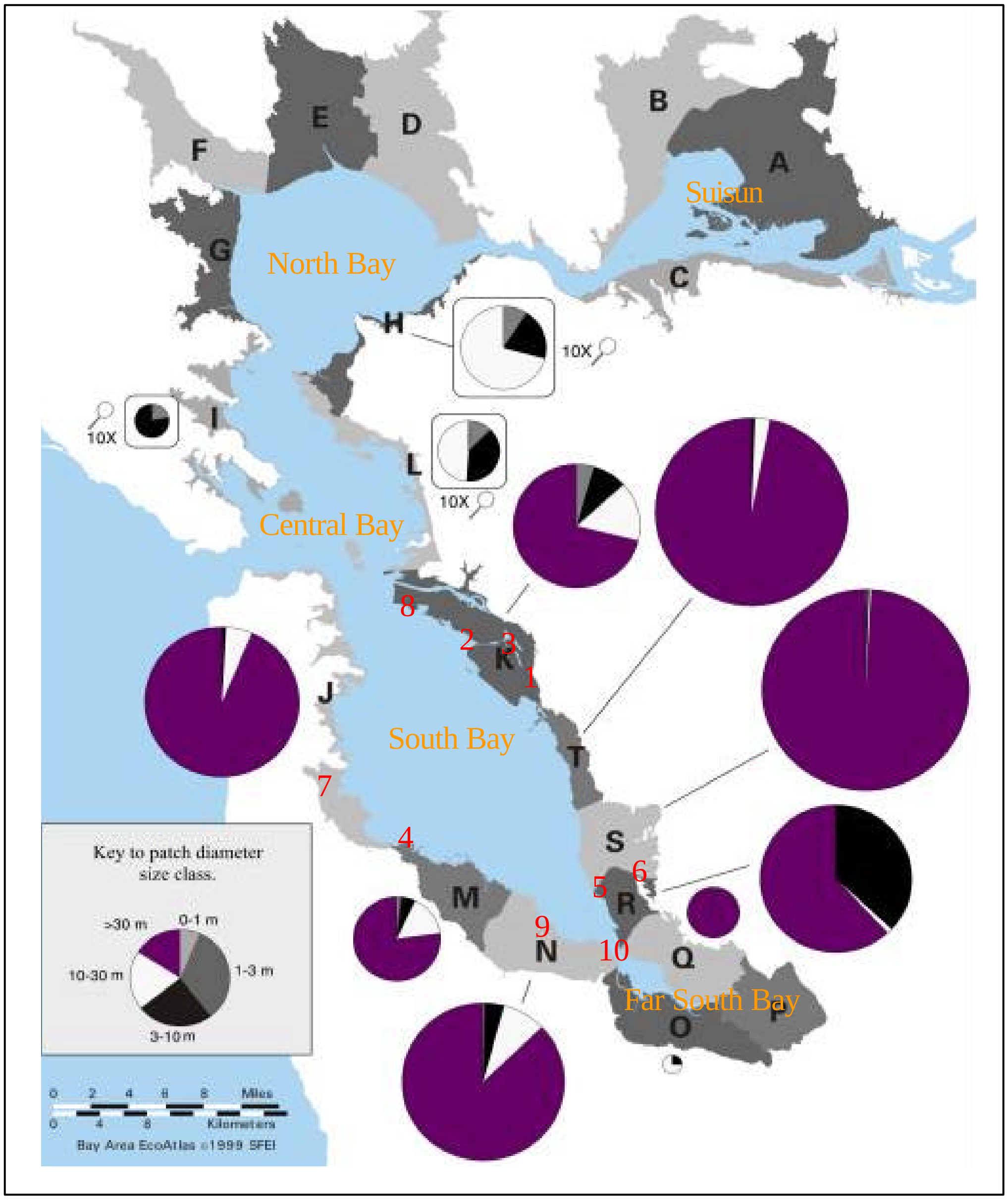
Each survey data point represents the elevation of the substrate surface at the base of living NIS cordgrass. The survey rod was prevented from either resting above or settling below the substrate surface. Some foreshore data for minimum elevation of NIS cordgrass pertain to plants growing at the edge of a wave-cut bench, with an exposed root zone. In these cases, the survey rod was carefully held at the top edge of the bench, since it represents the surface that was colonized by the NIS cordgrass.

Local Stream Studies

Site Descriptions

The purpose of these study sites was to describe the relationship between the minimum elevation of NIS cordgrass and aqueous salinity regime along tidal reaches of local streams. Candidate sites had to be accessible, extensively invaded, have complete salinity gradients of such length that each site could be surveyed in a day, and reasonably close to a dependable NOS Tide Stations or NOS tidal benchmarks for controlling the elevation surveys. Three suitable sites were selected: Alameda Flood Control Channel in Newark (i.e., the upper tidal reach of Coyote Hills Slough), San Leandro Creek in Oakland, and Colma Creek in South San Francisco (see Figure 1). All three sites are perennial streams that drain to South Bay.

Figure 1: Patch size distribution of NIS cordgrass in different Segments A-T of the San Francisco Estuary (see reference #14), and the locations of (1) San Leandro Creek, (2) San Leandro Channel; (3) Arrowhead Marsh; (4) Coyote Point Marsh; (5) Coyote Hills Slough; (6) Alameda Flood Control Channel, (7) Colma Creek; (8) Alameda Tide Station; (9) Redwood City Tidal Station; and (10) Dumbarton Bridge Tide Station.



Tidal Datum Reckoning

For all three study sites, the nearest tidal benchmarks were too far away from the study reaches to survey directly between the reaches and the benchmarks. The "alternate height different method" (87, 88) was used to reckon the local MHW datum at the study reaches. This method treats the slack high stage of the tide as a leveling devise between a reference site of known tidal elevation and a study site with unknown elevations.

The alternate method of tidal datum reckoning assumes that the height attained by a tide at the reference site is the same as the height attained by the same tide at the study site, relative to local MHW. In other words, if a tide reaches ten inches above MHW at the reference site, then the same tide should also reach ten inches above MHW at the study site. To test this relationship, the heights of slack high tides at the study site are regressed on the heights of the same high tides at the reference site. The regression line should be straight with a small residual error.

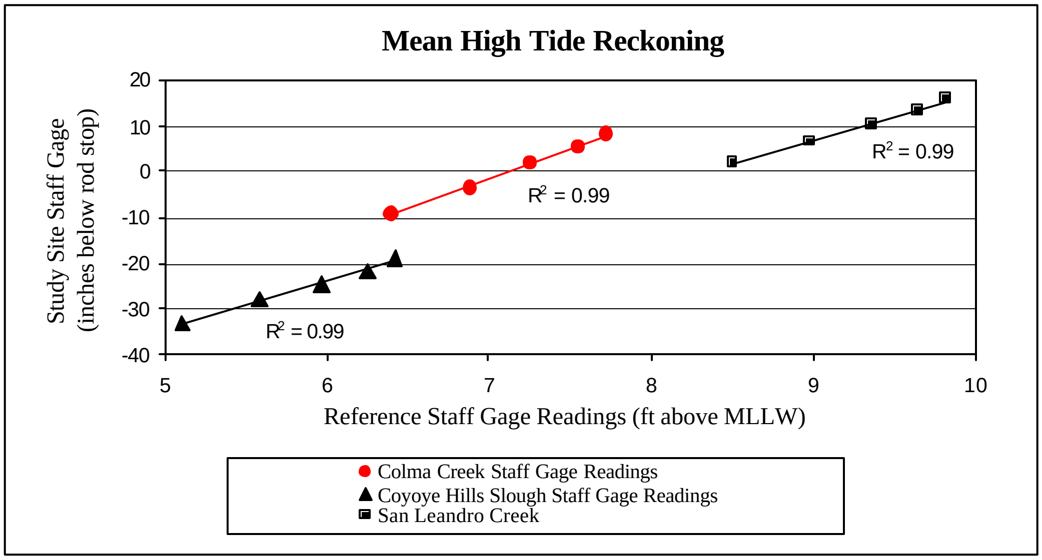
At the study sites and their reference sites, temporary staff gages were installed. Each gage consisted of a metal tape ruler and rod-stop attached to 1-in OD schedule 40 PVC pole installed in a stillwell. For each of five days, the temporary staff gages were painted with a mixture of potassium dichromate crystals and water-soluble glue. The mixture dissolves rapidly in water but does not wick. The height of a high tide is easily read as the lower limit of the undissolved mixture on the staff gage.

For the San Leandro Creek and the Alameda Flood Control Channel study sites, the rod-stops of the reference gages were referred to tidal benchmarks set by NOS at its Tide Stations near the creek mouths (Coyote Hills Slough Station 9414621 for the Alameda Flood Control Channel; Oakland Airport Station 9414711 for San Leandro Creek). Multiple benchmarks were reoccupied at each site and their relative differences in elevation were within 0.06 in (1.5 mm) of the published values. For these two creeks, the study site staff gages were installed within 0.5 miles (1.73 km) of the NOS benchmarks, and the total survey error from the benchmarks to the staff gages was less than 0.14 in (3.6 mm). There was no nearby NOAA Tide Station or NOS benchmark for Colma Creek. For this site, a temporary benchmark was installed at the study site and later referenced to the nearest permanent NOS Tide Station (Alameda Station 9414750).

The staff gage readings for the Alameda Flood Control Channel and San Leandro Creek were regressed on the readings for their downstream reference staff gages. Since there was no nearby reference station for Colma Creek, its staff gage readings were regressed on the NOS record for the same period at the permanent station at Alameda. The distance between Colma Creek and the Alameda station is greater than recommended for the alternate method (87). However, the correlation coefficient (R^2) was greater than 0.99 for all three sites (Figure 2), and the residual error was smaller than the survey error.

The five high tides recorded at each site were from a spring tide series. Four of the high tides were higher than the MHW datum at the NOAA reference gages. The use of relatively high tides reduces some of the effect of channel friction and the geomorphic irregularities of channels on tide height, and this improves the precision of the reckoning.

Figure 2: Results of Mean High Water reckoning for the three stream study sites.



Elevation Surveys

All elevation surveys were conducted using a Zeis self-leveling level with a 20x scope and a survey rod readable to about 0.01 ft (3.0 mm). The instrument was serviced and calibrated just prior to the surveys.

Plant Surveys

The surveys of plant vertical distribution focused on the lowermost vascular vegetation in the intertidal zone. Each study site was surveyed in one day during late July 2001. Each survey started in the saline part of a site and proceeded upstream to the freshwater zone during the slack low water of a minus tide (i.e., a tide below MLLW at the NOS reference station). The survey of plant elevation at each site was closed to the starting benchmark. Closure error was less than about 0.03 ft (9 mm) at each site.

The vegetation in the lower intertidal zone along either bank of each site tended to be patchy and variable in its lowermost extent. The survey proceeded from one plant patch to the next. The lowermost elevation of each patch was surveyed, and the plant species that comprised the patch was noted. Other plant species that comprised at least 25% of the plant cover near the surveyed patch were identified as co-dominants for the patch. The most downstream and upstream positions of co-dominant species were noted.

The identification of dominant species was made easy by the simplicity of the low marsh plant community. Patches and bands of a few species of tall emergent monocots characterize the low marsh zone of the Estuary. Point measures of elevations were taken at the lowermost extent of obvious patches of a species, and the species composition of neighboring patches was also obvious. Percent cover of dominant plant species was estimated by visual inspection without using quadrats, point frames, or other sampling devices. All the estimates of plant cover were conducted by the same person.

Hybrid Identification

Special attention was given to the genetic composition of *Spartina* patches. Tissue samples were taken from each surveyed patch of *Spartina*. The percent *S alterniflora* for each sample was determined by the Spartina Laboratory at the University of California at Davis using Randomly Amplified Polymorphic DNA (2). Samples of known *S. foliosa* collected from outside the range of the NIS cordgrass were used as blind tests of the laboratory analyses. All *S foliosa* samples were correctly identified.

Defining the Salinity Gradient

Many past studies of the distribution and abundance of vegetation in the intertidal zone of the San Francisco Estuary have shown general correlations between aqueous salinity regime and plant community composition (e.g., 32). The low marsh plants are especially sensitive to salinity changes during the growing season (75), and can therefore be used as indicators of the salinity regime. The convention has been to use the plant distribution data to approximately delimit the saline, brackish, and fresh zones.

Although spatial changes in plant community composition can be used to delimit salinity regimes in a general way, the spatial limits of the indicator species do not necessarily indicate their salt tolerances. Their distributions may be the result of many factors interacting with salinity (36, 75). However, physical factors tend to be more influential at lower elevations, and biotic interactions, including competition, tend to be more important at higher elevations (36). For the lower intertidal zone, the distribution of NIS cordgrass relative to other plant species that are strongly associated with different salinity regimes can be used to infer the potential upstream and downstream extent of the NIS cordgrass invasion within the Estuary.

Study Results

Bayshore and Tidal Marshes

The basic data for average elevations of NIS cordgrass at the four bayshore field sites are presented in Table 2. The data show that the maximum and minimum elevations of NIS cordgrass relative to maximum elevation of the backshore as well as high and low tidal datums differ between sites. Although the values for mean minimum elevation relative to Mean Tide Level (MTL) are the same for the two sites closest together (i.e., San Leandro Channel and Arrowhead Marsh), the relationship does not remain the same for the other two sites.

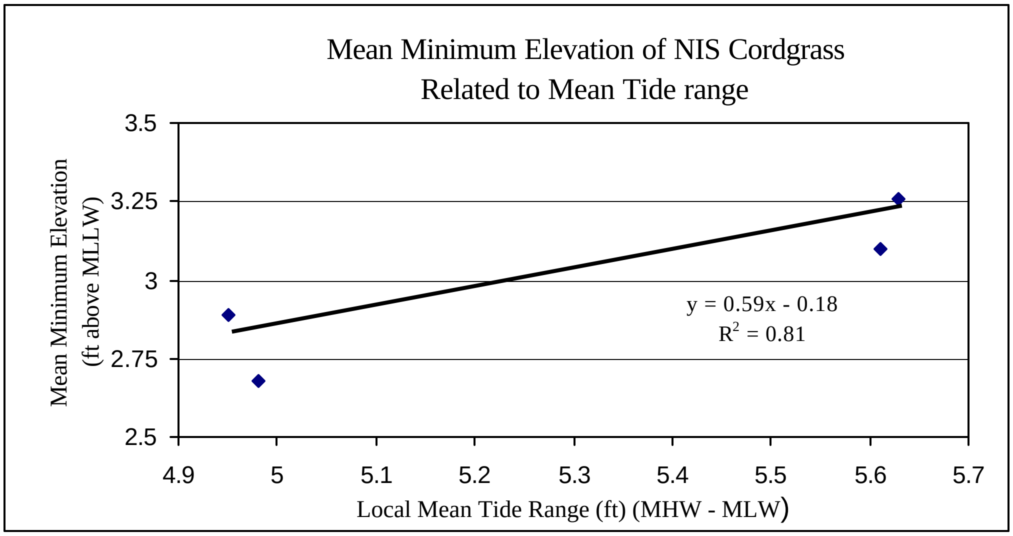
While there are consistent maximum and minimum elevations for NIS cordgrass within a site, there are no consistent maxima or minima between sites.

There is, however, a strong positive correlation between minimum elevation of NIS cordgrass and local Mean Tide Range (MHW minus MLW). That is, as MTR increases, the distance between local MLLW and the minimum elevation of NIS cordgrass also increases (see Figure 3 below).

Table 2: Mean and variance of elevation of NIS cordgrass relative to local tidal datums, and maximum elevation of native marsh vegetation at four saline bayshore study sites in South San Francisco Bay.

	San Leandro Channel	**Arrowhead Marsh**	**Coyote Point Marsh**	**Coyote Hills Slough**
Mean maximum elevation (ft) of NIS Cordgrass relative to local MHHW n = 30	- 0.25 ? 0.3	- 0.44 ? 0.2	- 0.93 ? 0.4	-0.36 ? 0.4
Mean maximum elevation (ft) of NIS Cordgrass relative to maximum elevation of marsh vegetation (*Grendelia* zone) n = 30	- 0.87 ? 0.4	- 0.91 ? 0.4	- 1.46 ? 0.4	1.41 ? 0.5
Mean minimum elevation (ft) of NIS Cordgrass relative to local MHW n = 30	- 3.41 ? 0.3	- 3.14 ? 0.3	- 3.65 ? 0.3	- 2.88 ? 0.4
Mean minimum elevation (ft) of NIS Cordgrass relative to local MTL n = 30	- 0.92 ? 0.3	- 0.92 ? 0.3	- 0.84 ? 0.3	- 0.04 ? 0.4
Mean minimum elevation (ft) of NIS Cordgrass relative to local MLLW n = 30	+ 2.68 ? 0.3	+ 2.89 ? 0.3	+ 3.10 ? 0.3	+ 3.26 ? 0.4

Figure 3: Correlation between Mean Minimum Elevation of NIS Cordgrass and local Mean Tide Range at the four saline bayshore study sites in San Francisco Bay.



Isolated patches of NIS cordgrass on tidal flats in the San Leandro Channel were initially thought to represent the lowest elevations of the invasion simply because they are offshore (see Figure 4 below). However, elevation surveys of these patches and examination of historical aerial photos revealed that the isolated patches have colonized relatively high shoals within the same elevation range as the foreshore invasion. The minimum elevations of offshore colonies are within the range of minimum elevation for the foreshore colonies (compare Table 3 below to the last row of Table 2 above).

It may be important to note that the offshore colonies occupy the bayward edge of the shoals at the end of a long fetch. The windward side of each colony is marked by a wave-cut bench that exposes the root zone of the colony. Whether or not the colonies have eroded on their windward sides in not known. But the roots apparently protect the shoals enough to support a vertical cut face. The unvegetated portions of the shoals slope away from the colonies on their leeward sides (see Figure 4).

It is not clear from the historical aerial photos whether or not the shoals are growing downwind of the colonies. The elevation and extent of tidal flats vary seasonally and from year to year, such that changes in their plan form cannot be easily attributed to the plant colonies or to other factors, such as changes in sediment supply, wind regimes, or nearshore currents. If the shoals are accreting downwind of the plant colonies, then the colonies might also expand downwind, and perhaps coalesce along the contour of their minimum elevation.

The surface of each offshore colony varies in elevation. In general, the colonies are higher near their windward edges. There was a general topographic low near the middle of each colony. Overall topographic relief from one patch to another varied from about 1.2 ft to about 1.7 ft (36.5 cm to 51.8 cm) (see Table 3 below).

Table 3: Mean and variance for maximum and minimum elevations of offshore patches of NIS cordgrass at San Leandro Channel in South San Francisco Bay. Patch numbers are taken from tags placed on each patch by researchers working through the University of California at Davis on NSF Grant DEB-0083583.

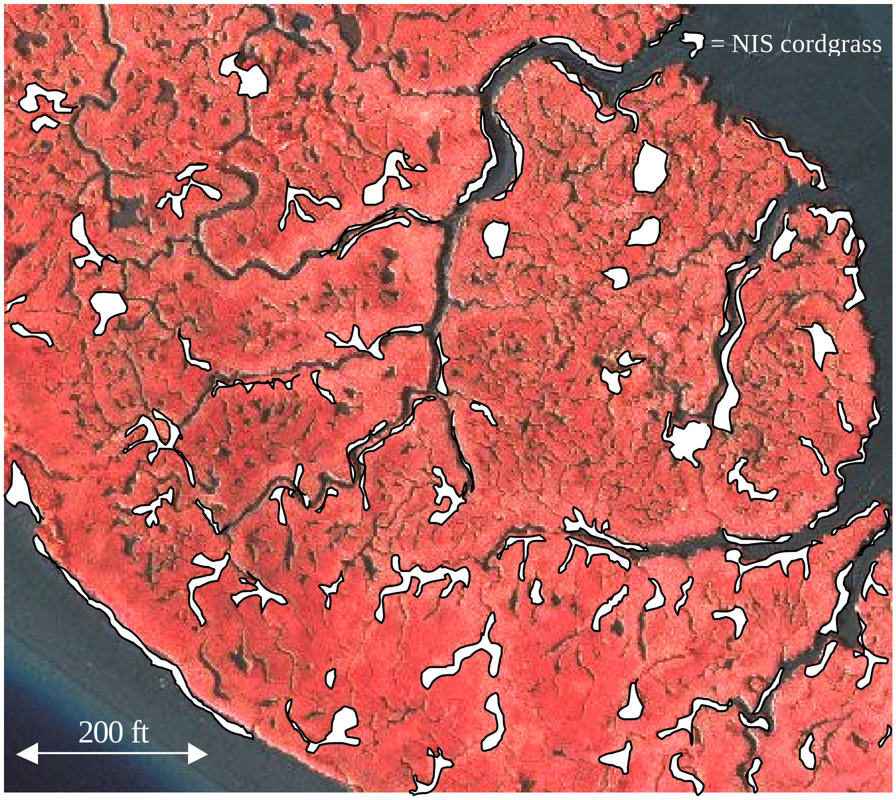
	Patch 6	**Patch 7**	**Patch 8**
Mean minimum elevation (ft) of NIS cordgrass relative to local MLLW n =5	+ 2.52 ? 0.2	+ 2.54 ? 0.2	+ 2.77 ? 0.2
This is the mean difference in feet between maximum and minimum patch elevations n = 5	+ 1.68 ? 0.1	+ 1.66 ? 0.3	+ 1.22 ? 0.4

Figure 4: Offshore colonization by NIS cordgrass of tidal flat shoals of relatively high elevation at San Leandro Channel. The shoals existed before the offshore colonies. Note that the unvegetated portions of the shoals extend downwind from the colonies. The foreshore in front of the buildings is also dominated by NIS cordgrass.

The vertical range of NIS cordgrass had been previously surveyed at Coyote Hills Slough (54). Resurveys near this site suggest a local change in the vertical range of NIS cordgrass. However, in the previous study, tidal elevations were based on a benchmark of unknown integrity (i.e., "a permanent Alameda County Flood Control District benchmark") (54). If it is assumed that the previous elevation survey is correct, then NIS cordgrass near the mouth of Coyote Hills Slough has advanced upslope about 0.4 ft (12.2 cm), and has advanced downslope about 0.9 ft (27.4 cm) in about eight years. These are site-specific data of unknown accuracy that mostly illustrate the need to use standard methods of tidal elevation surveys.

It is obvious from a general reconnaissance of tidal marshes in South Bay that NIS cordgrass invades saline marsh drainage systems. The lower elevation limits of NIS Cordgrass correspond to the slump blocks and lower banks of large channels (i.e., third-order and larger channels that do not de-water at low tide and are V-shaped in cross-section), and to the beds of medium-sized channels (i.e., second-order channels and the upper reaches of third-order channels that de-water and are U-shaped in cross-section). NIS cordgrass does not tend to colonize the steep-sided banks of U-shaped channels. This invasion pattern produces a discontinuous but predictable distribution of NIS cordgrass within tidal marshes, with some first-order and second-order channels being isolated from the rest of their channel networks (see Figure 5 below)

Figure 5: Example map of the distribution of NIS cordgrass among channels at Arrowhead Marsh, San Leandro Bay of South San Francisco Bay.



Tidal Reaches of Local Creeks

Geomorphic Controls on Species Distributions

Each of the three study sites consisted of the tidal reach of a small perennial stream. The bed of each stream slopes downward into the Estuary from elevations above the tides. This means that the low tide may not extend throughout the brackish or freshwater zones of the intertidal salinity gradient. The minimum vertical distribution of estuarine plants is therefore constrained by the height of the bed upstream of the intersection of the bed and the low tide.

Plant elevations were surveyed relative to local MHW because it extends upstream through the intertidal salinity gradient. However, the MHW datum is not a horizontal plane along these small streams. During the wet season, stream discharge adds water to the tides and can cause the height of the MHW datum to increase upstream. During the dry season, when there is very little discharge at any of the study sites, channel friction can cause the MHW datum to decrease upstream. It is assumed that salinity has the greatest effects on plant distribution during the growing season, which begins near the end of the wet season. The MHW datum was therefore adjusted along each study site for the effect of channel friction in the absence of wet season discharge. A slope of 0.00004 (decreasing upstream) was applied, based on surveys of high water marks at the sites and a previous study of water surface slopes in tidal marsh channels in the region (56).

Vertical and Longitudinal Distribution of Species

The minimum elevations of all cordgrass decrease with distance upstream from saline to brackish conditions, and the minimum elevations of *Scirpus and Typha* decrease with distance upstream from brackish to fresh conditions. In the absence of NIS cordgrass, the minimum elevation of native vegetation decreases with distance upstream. Native *Scirpus acutus*, *Scirpus californicus* and *Typha spp,* which are restricted to brackish and fresh conditions, grow lower than the native cordgrass (*S. foliosa),* which is restricted to saline conditions. This pattern has been observed elsewhere in the Estuary (15, 32, 54).

For all three study sites, the NIS cordgrass occurred at lower elevations than any other low marsh plant species. The NIS cordgrass grows lower in the intertidal zone and further upstream along the salinity gradient than the native *Spartina foliosa*. Local differences in minimum elevation between native and non-native *Spartina* may reflect site history (see Discussion), but the NIS cordgrass can grow at least 0.7 ft (21.3 cm) further below the local MHW datum than the native cordgrass (see Table 4 below).

At the San Leandro Creek site and at the Colma Creek site, there are cement aprons below bridges that constrain the upstream extent of low tide and saline conditions. In San Leandro Creek, the apron below the bridge at Hegenberger Road is above the MLLW datum. Bed load from upstream has filled the channel to elevations above the apron for a distance of almost 1,000 ft (about 328 m) upstream of the bridge (see Figure 6). Low tide does not extend above this barrier. Freshwater discharge across the elevated sediments upstream of the bridge during low tide helps to flush salts from the sediments. Saline conditions therefore only extend a few hundred feet upstream of the bridge.

In areas upstream of the bridge, where the channel bed is less than 4 feet (about 1.2 m) below the local MHW datum, NIS Cordgrass has begun to extend onto the bed from the channel banks. Some patches are entirely restricted to mid-channel bars of sediment. No other plant species is exhibiting this tendency to grow across the intertidal channel, except under nearly freshwater tidal conditions at the head of the tide, where the invasive giant reed, *Arundo donax*, and the NIS cordgrass are both encroaching onto the channel bed. These encroachments withstood the scouring flood flows of the subsequent wet season.

Figure 6: Spatial distribution of intertidal plants along San Leandro Creek. Horizontal arrows at the top of the graph show the maximum observed longitudinal distribution of species indicative of saline, brackish, or freshwater tidal regimes. Dotted vertical bars show approximate boundaries between these regimes. Plots show longitudinal distributions of species co-dominant along the down-slope edge of the foreshore.

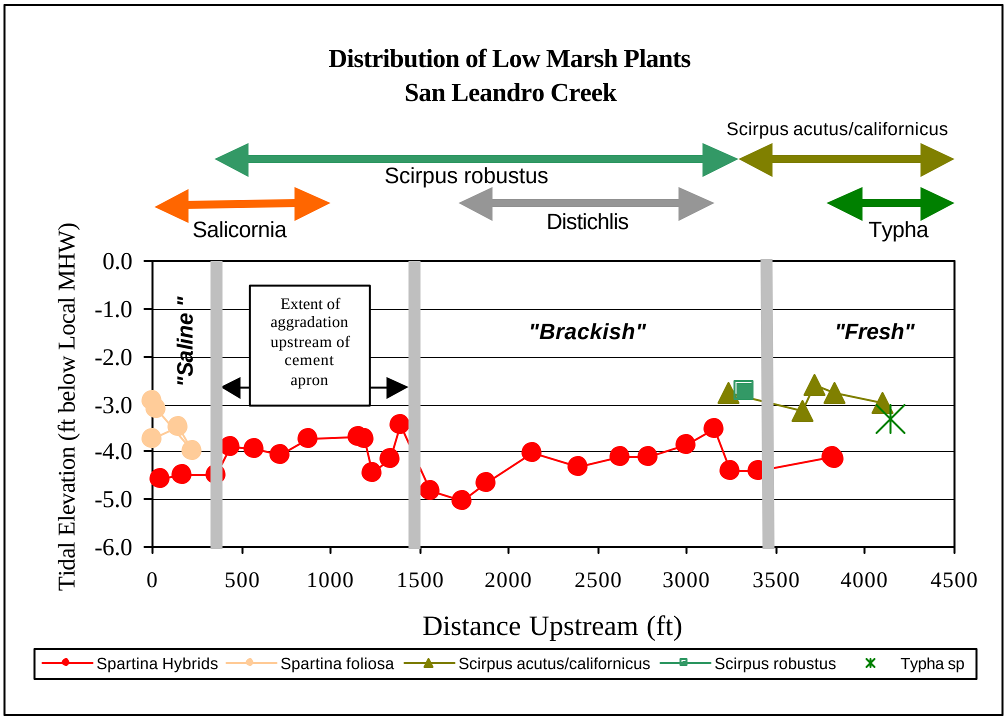
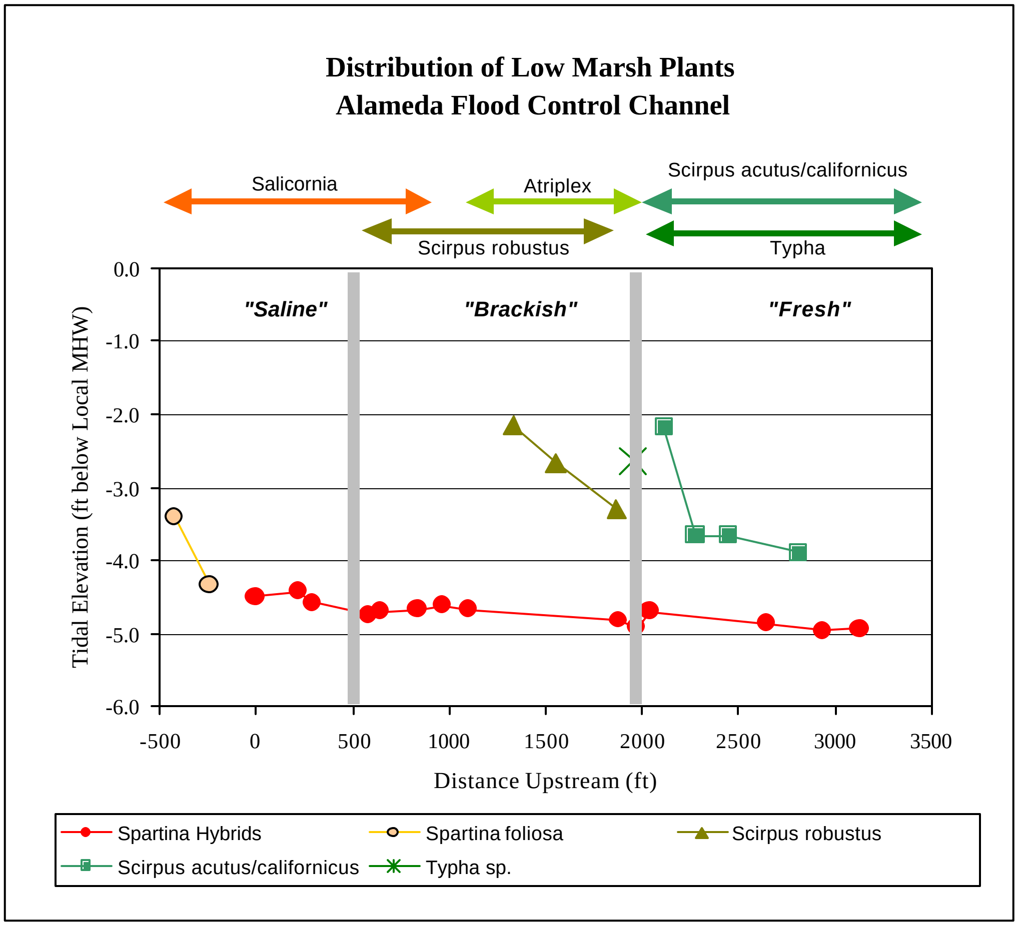


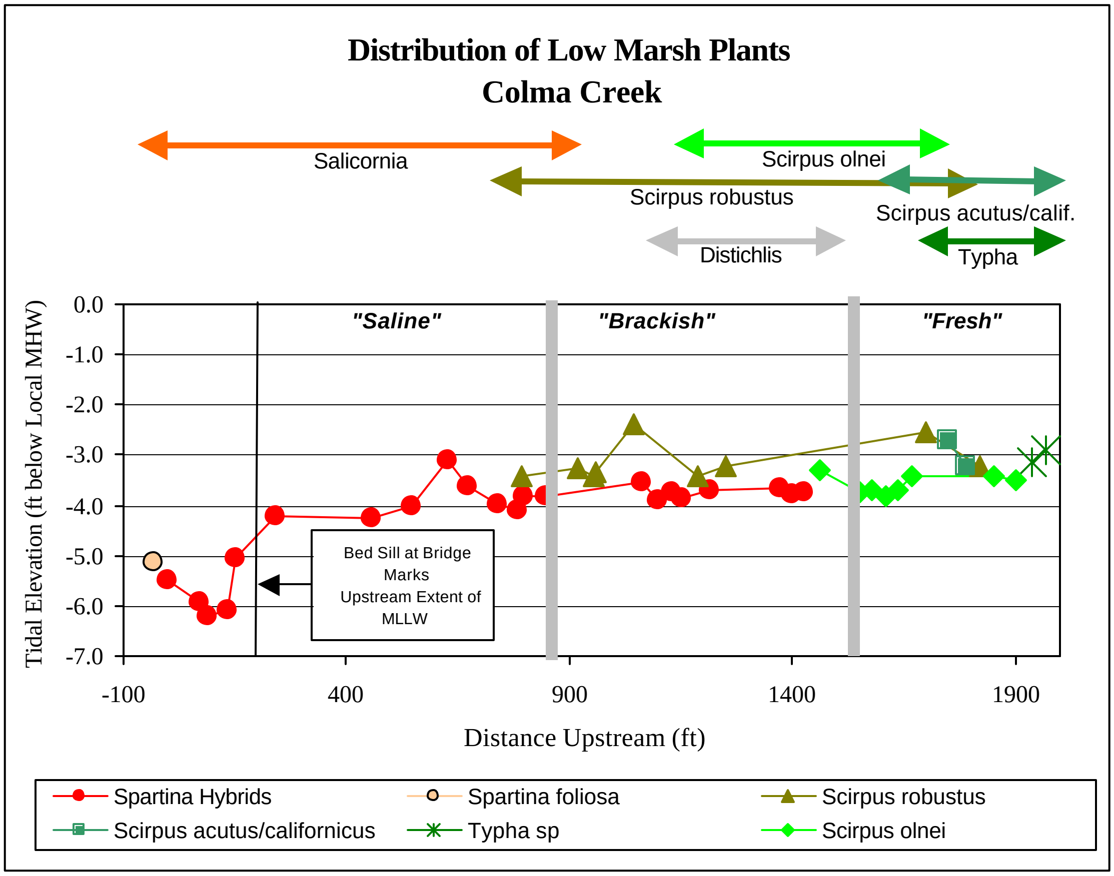
Figure 7: Spatial distribution of intertidal plants along the Alameda Flood Control Channel. Horizontal arrows at the top of the graph show the maximum observed longitudinal distribution of species indicative of saline, brackish, or freshwater tidal regimes. Dotted vertical bars show approximate boundaries between these regimes. Plots show longitudinal distributions of co-dominant species along the down-slope edge of the foreshore.



In the Alameda Flood Control Channel, where the channel bed is deep enough to allow the low tide to extend upstream into the fresh-brackish zone, the minimum elevation of plants decreases upstream (see Figure 7 above).

At the Colma Creek site (Figure 8 below), the cement apron below the bridge at Spruce Street has elevated the bed above the MLLW datum. The bed has apparently aggraded for at least 500 ft (about 160 m) upstream of the bridge. The bed is less than four feet below the local MHW datum for most of the brackish and freshwater zones of the study site. The upstream change in minimum elevation of NIS cordgrass through the brackish zone generally parallels the gradient of the channel bed. Encroachment by NIS Cordgrass onto the bed from the banks is evident. Other species are not encroaching onto the bed, except in the freshwater zone, where both *Scirpus acutus/californicus* and *Typha* have established small mid-channel patches. The NIS cordgrass barely extends into the freshwater zone, perhaps because of the steepness of the channel gradient near the head of the tide.

Figure 8: Spatial distribution of intertidal plants along Colma Creek. Horizontal arrows at the top of the graph show the maximum observed longitudinal distribution of species indicative of saline, brackish, or freshwater tidal regimes. Dotted vertical bars show approximate boundaries between these regimes. Plots show longitudinal distributions of species co-dominant along the down-slope edge of the foreshore.



The minimum elevation of NIS cordgrass has been calculated for each study site, relative to MHW. Estimates of elevations relative to MLW or MLLW are not relevant because the channel beds of tidal reaches are mostly above the low water datums. The high variance around the estimate of mean minimum elevation of NIS cordgrass for the creeks reflects the tendency of NIS cordgrass to grow lower upstream than downstream.

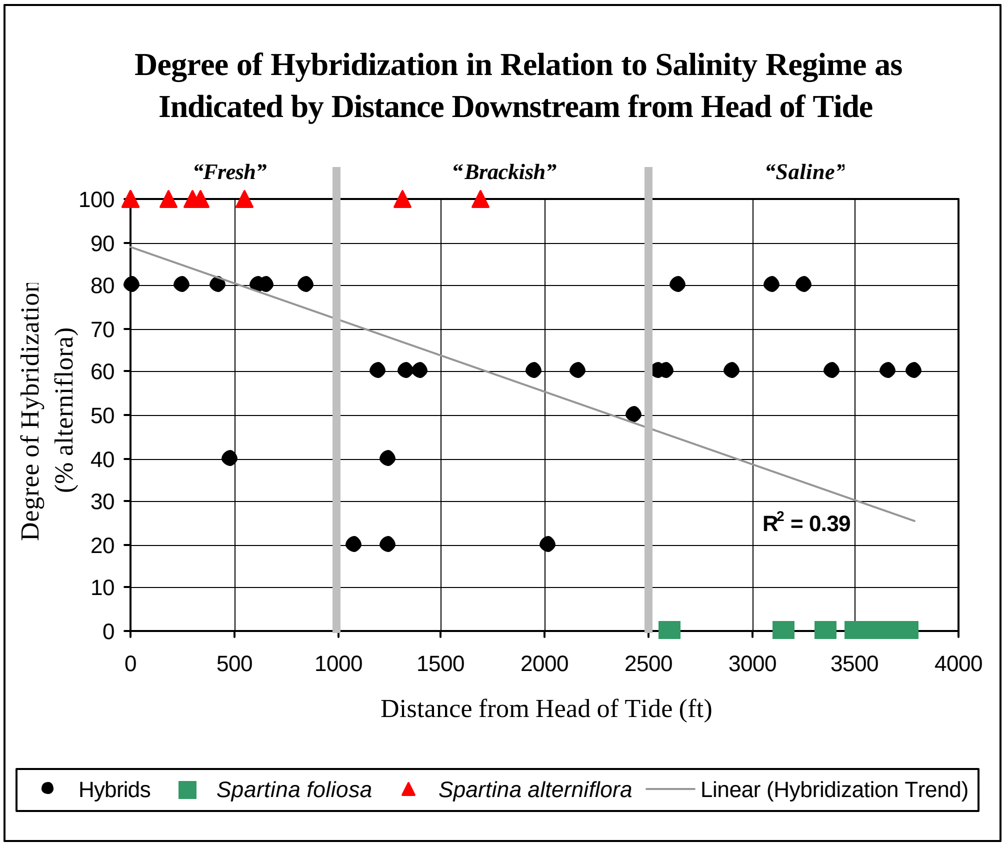
Table 4: Minimum elevations of NIS cordgrass relative to MHW for fresh-brackish tidal reaches of three creeks of South San Francisco Bay.

Site	Elevation Relative to Local MHW
Colma Creek n = 23	-4.24 ? 0.9
Alameda Flood Control Channel n = 14	-3.85 ? 0.7
San Leandro Creek n = 13	-3.31 ? 0.6

Variation in Spartina Hybridization along the Salinity Gradient

Hybrids of *S. alterniflora* and *S. foliosa* occurred all along the salinity gradients of the three tidal reach study sites (14). There appears to be no strong correlation between percent hybridization and salinity within the brackish zones (see Figure 9 below), although the methods for representing salinity might have influenced the fit of the data (see Discussion). However, the native *Spartina*, which was coded as 0.0 percent hybridization in Figure 9, only occurs in the saline zone. In contrast, most of the pure *Spartina alterniflora*, which was coded as 100 percent hybridization, occurs in the freshwater zone. This produces a slight inverse relationship between salinity regime and degree of hybridization.

Figure 9: Spatial relationship between degree of *Spartina alterniflora* x *Spartina foliosa* hybridization and aqueous salinity regime. Salinity regime is represented by distance downstream from the upstream start of the freshwater regime, as indicated by species composition of the low marsh plant community (see Figures 6-8 above). Degree of hybridization is measured as percent genetic similarity to *S. alterniflora*. Zero percent similarity indicates pure *S. foliosa*. One hundred percent similarity represents pure *S. alterniflora*.



Discussion

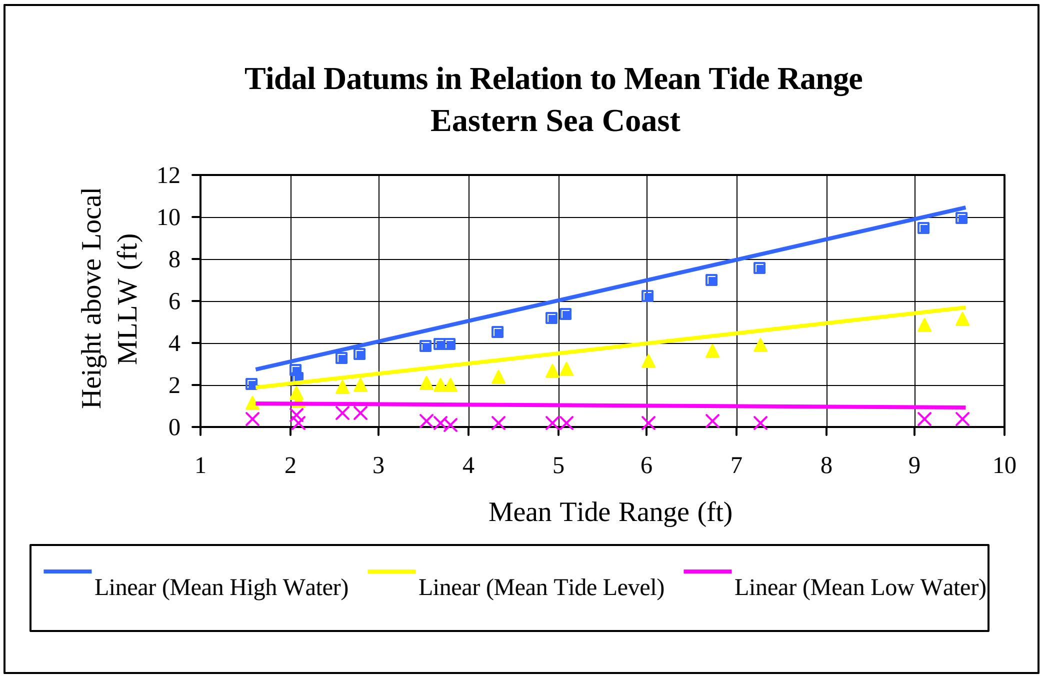
Bayshore and Tidal Marshes

Vertical Distribution of NIS Cordgrass

Other studies have reported poor correlation between the elevation limits of *Spartina* and tidal datums (e.g., 59), but better correlation between *Spartina* limits and Mean Tide Range (MTR) (42, 59, 60, 61, 105). A regression model relating MTR to vertical range of *S. alterniflora* along the U.S. East Coast (59) has been used to predict the distribution of NIS cordgrass in the San Francisco Estuary (62). However, the *Spartina* hybrids in the Estuary behave differently than non-hybridized *S. alterniflora* (2), and the earlier predictions relied on transplant experiments rather than volunteer (i.e., "natural") colonization to determine the elevation limits of NIS cordgrass (59, 15). The correlation between MTR and minimum elevation of NIS cordgrass reported here is the first predictive model for San Francisco Bay that is based on local empirical data.

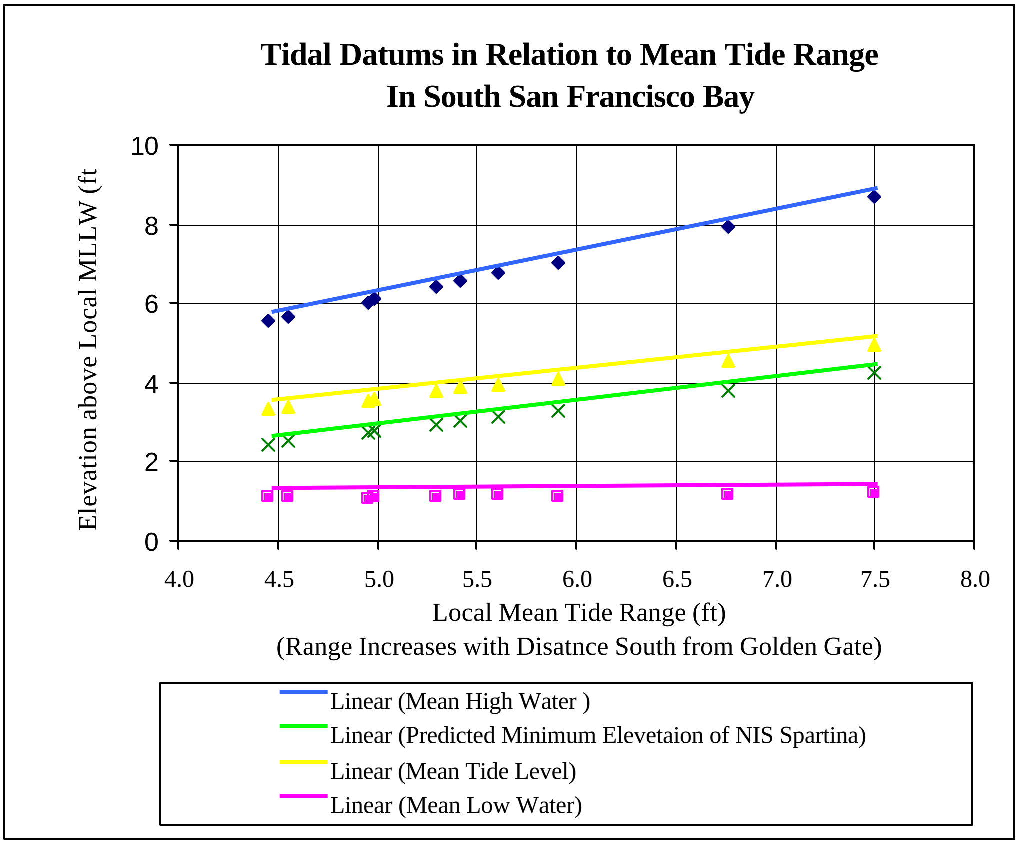
The conceptual models for intertidal zonation and some of the studies of correlations between MTR and vertical distribution of *Spartina* (e.g., 63, 90) suggest that the correlations relate to physiological tolerances of the plants to tidal exposure or inundation. To examine this further, the relationship between MTR and tidal datums was investigated. For the East Coast of the United States (Figure 10), and for South San Francisco Bay (Figure 11), spatial variations in MTR are due to variations in high tide datums. By convention, MLLW is held constant at zero elevation, but MLW also varies little compared to the high tide datums. In essence, MTR varies with MHW.

Figure 10: Variation in MHW, MLW, and Mean Tide Level (MTL) in relation to MTR along the East Coast. Data are from published NOS Benchmark Sheets for sixteen tide stations between Maine and South Florida.



The relationship between MTR and minimum elevation of NIS cordgrass in the San Francisco Estuary (see Figure 3 above) was used to predict the minimum elevation of NIS cordgrass at NOS Tide Stations throughout the South Bay. The relationship between MTR and the minimum elevation of NIS cordgrass is not constant. MHW (and hence MTR) increases faster than the minimum elevation of NIS cordgrass with distance south from the Golden Gate (see Figure 11 below).

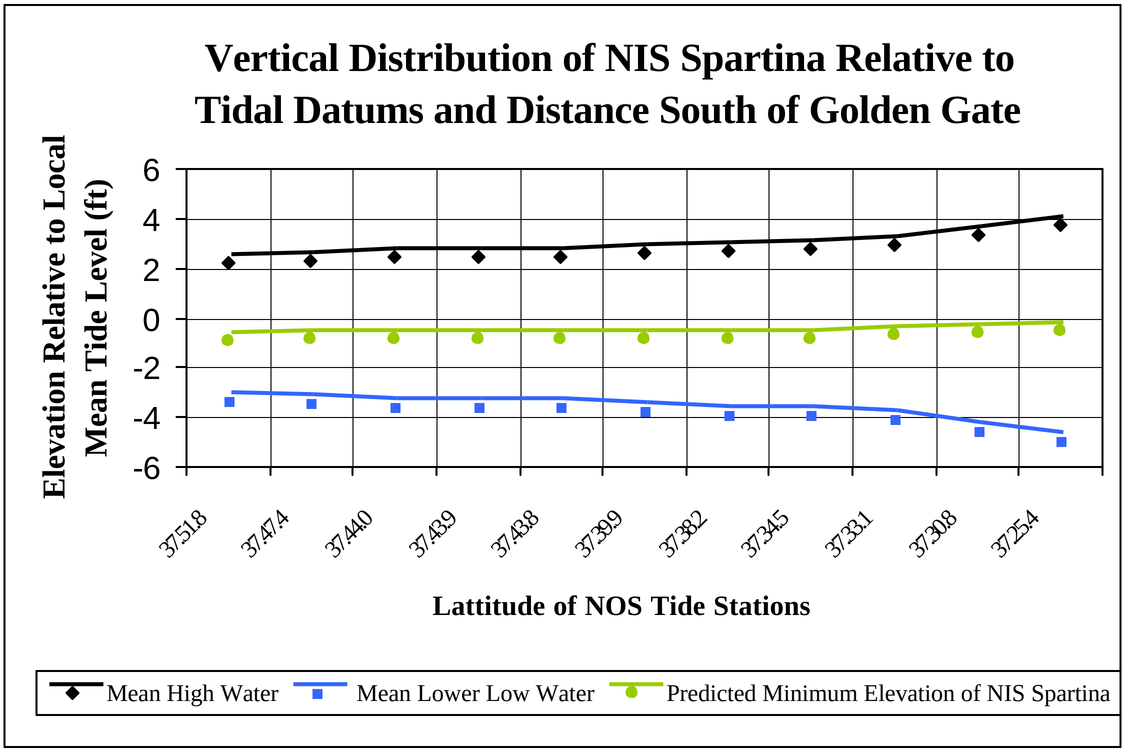
Figure 11: Variation in Mean High Water, Mean Low Water, Mean Tide Level, and predicted minimum elevation of NIS *Spartina* in relation to Mean Tide Range for NOS Tide Stations between Central San Francisco Bay at Berkeley and Far South Bay at Alviso.



In the San Francisco Estuary, as sea level rises, the high tide datums, especially MHHW, are rising faster than MLW (6). This means that the tidal range is increasing. The minimum elevation of NIS cordgrass, relative to MLLW, might therefore also increase as sea level rises. The effect of this change on the overall vertical range of the NIS cordgrass is unstudied. The effect on the distribution of NIS cordgrass among the tidal flats is difficult to surmise because the distribution and abundance of the tidal flats might also be affected by the change in tide range.

The predicted minimum elevation of NIS cordgrass and the high and low datums were also plotted relative to Mean Tide Level (see Figure 12 below). The high and low datums represent the approximate boundaries of intertidal flats. The well known fact that the amount of flats increases with distance south of the Golden Gate in represented by the divergent high and low datums on the right end of Figure 12. According to this graph, NIS cordgrass will colonize less than the upper half of the flats in far South.

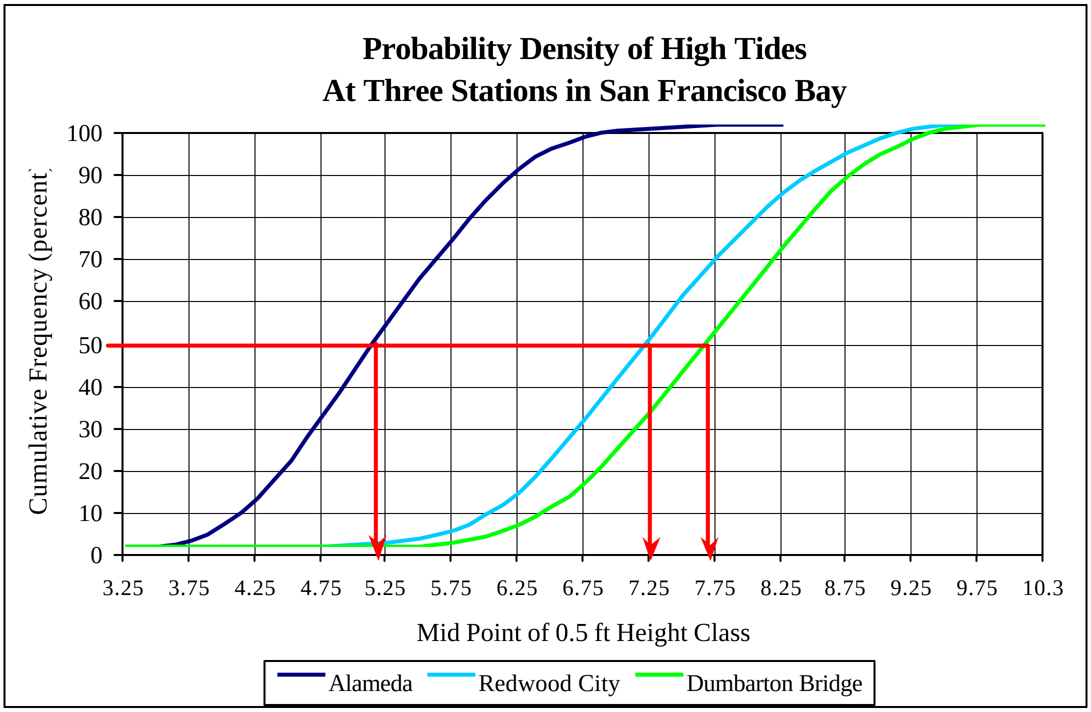
Figure 12: Variation in Mean High Water, Mean Lower Low Water, and predicted minimum elevation of NIS *Spartina* in relation to Mean Tide Level (MTL) for NOS Tide Stations between Central San Francisco Bay at Berkeley and Far South Bay at Alviso.



Since MTR varies with MHW, then the frequency and duration of inundation varies with MTR (see Figures 12 and 13 below). That is, plants growing at any given elevation relative to MLLW will tend to be inundated more frequently and for longer periods of time where the tidal range is greater.

The correlation between MTR and minimum elevation of NIS cordgrass may represent a relationship between minimum elevation and duration of tidal inundation. As noted in the conceptual models, many intertidal phenomena, including the distribution and abundance of organisms, are strongly correlated to tidal inundation regime. For plants, the duration of inundation affects metabolic processes as well as exposure to herbivory, desiccation, wave action, etc. Given the physiological importance of inundation regime on intertidal vegetation, then the elevation thresholds of plant growth probably relate more to inundation regime than to elevation per se.

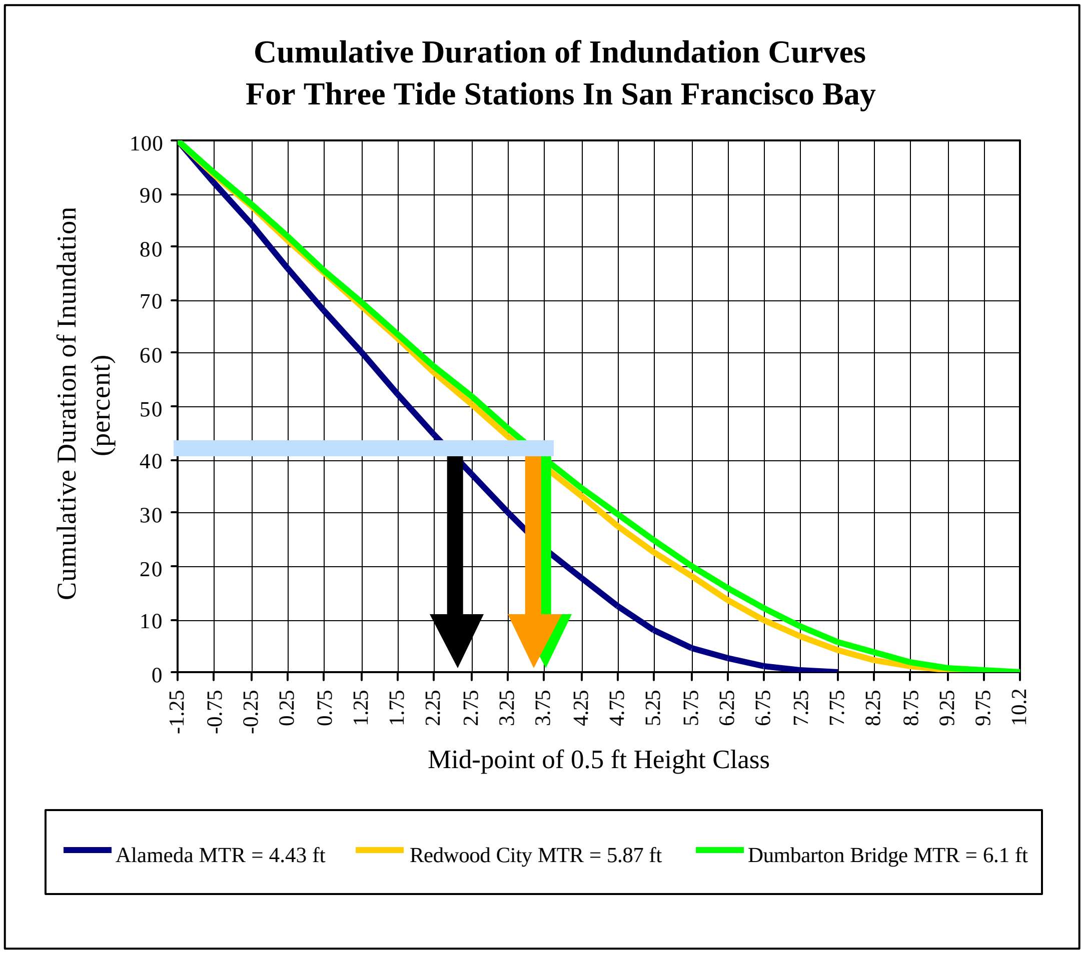
Figure 13: Cumulative frequency of daily tidal maxima for three NOS Tide Stations, showing that as Mean Tide Range increases, the elevation that corresponds to any given percentile of the high tides also increases. For example, 50% of the high tides are below about 5.2 ft at Alameda, 7.25 ft at Redwood City, and 7.7 ft at Dumbarton Bridge, where the MTR is about 4.4 ft, 5.9 ft, and 6.1 ft, respectively. Elevations are relative to local MLLW.



To further explore the possible relationship between the vertical distribution of NIS cordgrass and tidal regime, the minimum elevation of NIS cordgrass, as predicted from empirical data (see Figure 3 above), was plotted against cumulative duration of inundation at three NOS Stations for which adequate data were available. Mean Tide Range (MTR) differs between these Tide Stations. The predicted minimum elevation corresponds to about the 40th percentile of the cumulative inundation curve for June, regardless of MTR (see Figure 13 below). June data were analyzed because June is about the middle of the growing season for NIS cordgrass, and because the duration of inundation is greater in June than during other months of the growing season (i.e., June has a high value for monthly mean high tide). No relationships between NIS cordgrass distribution and tidal regime have been investigated for other months. Duration of inundation may be one of many factors underlying the correlation between elevation of NIS cordgrass and MTR.

The fact that the empirical data for minimum elevation of NIS cordgrass at the four study sites (see Figure 3 above) yield predictions for the same threshold of duration of inundation, even though the sites have different invasion dates (see Table 1 above), suggests that the invasion has reached its lower elevation limit at each site.

Figure 14: Relation between predicted minimum elevation of NIS cordgrass (see Figure 3) and cumulative duration of tidal inundation at three stations with different Mean Tide Range (MTR), showing that the predicted minimum elevations of NIS cordgrass (see vertical red arrows) correspond to about the 40th percentile of duration of inundation during June (see horizontal red arrow), regardless of MTR. The width of the arrows represents the confidence limits of the regression used to predict minimum elevation of NIS cordgrass (see Figure 3).



Discussion of Tidal Reaches of Local Creeks

Sources of Error in Surveying Relative Elevations

The level line surveys along the study sites were not significant sources of error for describing variations in plant patch elevations. Survey closures were always less than 0.025 ft (0.3 in). The range in plant elevations was more than two orders of magnitude grater than this survey error.

Sources of Error in Reckoning Tidal Datums

Based on the NOS standards for tidal datum determination, the reported values for MHW at the NOS reference stations for San Leandro Creek and the Alameda Flood Control Channel are within 0.1 ft (1.2 in) of the true datum (33, 89). However, a recent treatise on tidal statistics suggests that the results of tidal datum reckoning are sensitive to the seasonality of the data (6). The NOS values used for San Leandro Creek and the Alameda Flood Control channel are based on 5 months (February to June 1977) and 4 months (December 1976 to March 1977) of data, respectively. The error due to length of record and its seasonality has not been determined. The residual error of the alternate method of tidal datum reckoning was less than 0.1 ft (1.2 in) for all sites. This indicates that the maximum known error of the MHW determinations for the staff gages at each site was about 0.2 ft (2.4 in). This is probably close to the error rate that is introduced when trying to position the survey rod at the lowermost edges of plant patches, given that the sediments are typically very soft and the lowermost plant shoots or roots may not always be obvious. Furthermore, most of the differences in vertical distribution of plants as revealed by the surveys are more than a magnitude greater than the estimated error of datum reckoning (the NOS error of datum reckoning notwithstanding). Since the error of reckoning is a constant, it would not alter the apparent relative spatial patterns among plant patches.

Sources of Error in Tidal Reach Longitudinal Surveys

The maximum upstream adjustments in MHW to account for friction of the channel are less than the maximum error of datum reckoning and not significant with regard to the general findings of the study. The adjustment is proportional to the distance upstream from the staff gage at each site, and therefore has the greatest potential to introduce error in the upstream, freshwater zones. For the longest study site, the maximum adjustment was 0.16 ft (about 5 cm). For San Leandro Creek and Colma Creek, the adjustment slightly mediates the apparent upstream increase in minimum plant elevation. For the Alameda Flood Control Channel, the adjustment slightly exaggerates the apparent upstream decrease in minimum elevation. In all cases, the observed variations in plant elevation are more than a magnitude greater than the survey adjustment for friction.

The errors of the level line surveying, of the MHW reckoning at the staff gages, and maximum upstream adjustments in MHW sum to about 0.285 ft (about 8.5 cm). This maximum possible error only pertains to the most upstream reaches of the longest study site (Alameda Flood Control Channel), and does not significantly affect the observed patterns in vertical distribution for any plant species at any site.

It would be useful to report plant elevation relative to MLLW, rather than MHW, since by convention MLLW represents zero tide. But for most of the fresh-brackish portions of the tidal reaches, the MLLW datum is below the channel bed. In other places, where the bed is below the MLLW datum, the effect of channel form and friction on the height of slack low water is unknown. It is expected that the effect of friction is greater on low tides than high tides, and that the effect of friction increases upstream, because the efficiency of the channel decreases with decreasing volume of the tide. Since the NOS reference stations are very near the bayshore and not in small channels, the difference in height between MHW and MLLW at the reference stations may not be the same as the difference in height of these datums at the study sites. All elevations are therefore best reported relative to MHW.

Sources of Error in Estimating Salinity Regime

The distribution and abundance of the dominant and co-dominant plant species of the low marsh at each study site vary predictably with salinity regime in the San Francisco Estuary. The presence or absence of these species along the longitudinal axis of each study site provides a general description of the extent and steepness of its salinity gradient. The results of the field surveys reflect the most obvious characteristic of the study sites, which is that salinity increases downstream from fresh to saline conditions.

The areas of overlap for species that indicate different salinity regimes are probably due to inter-annual variability in freshwater discharge. During years of abundant discharge, the freshwater zone of these small estuaries can expand downstream, but the saline zone can only be compressed. The saline zone cannot expand downstream beyond the channel mouth. During years of scant discharge, the saline zone can expand upstream, but the freshwater zone can only be compressed. The freshwater zone cannot expand upstream unless sea level rises or the channel incises upstream of the head of the tide. Temporal shifts in the relative abundance of plant species along the channel correspond to shifts in salinity regime. The shifts in plant distribution lag behind the shifts in salinity, however, and are never complete, since conditions continue to change. As a result, species that are indicative of different salinity regimes can have overlapping distributions. The extent of overlapping distributions reflects the steepness of the site. Steeper sites have narrower salinity zones with less overlap.

Since the study sites differ in annual discharge and overall steepness, the lengths of their salinity gradients and the proportions of the salinity zones also differ. The reported large variability in the relationship between percent hybridization and salinity regime (see Figure 9) may, in part, be an artifact of the differences in site steepness and annual discharge. A less variable relationship might be reported if percent hybridization were compared directly to average water salinity, rather than to distance from the head of the tide. Which might be a sloppy proxy for aqueous salinity.

Possible Effects of Site History

The vegetation patterns at the study sites probably reflect the history of site management. The low marsh along the Alameda Creek Flood Control Channel appeared to be in early stages of invasion by NIS cordgrass and secondary succession by native plant species. As indicated for Segment R in Figure 1, many of the patches were small or moderately sized. And there was very little encroachment onto the channel bed, even in areas where the bed was above MLLW. The channel is maintained by dredging, and although the timing of the last dredging relative to the initial invasion is unknown, the dredging disturbs the vegetation at low elevations along the banks and increases the opportunity for new colonization by NIS cordgrass. Portions of San Leandro Creek and the Alameda Flood Control Channel have also been subjected to chemical control of NIS cordgrass. The control efforts killed some patches and reduced the stature of others, but the invasion has continued and ample evidence of the vertical distribution of NIS cordgrass remains. The Colma Creek site seemed to be the least disturbed by dredging or plant management. Shopping carts and other large urban debris were deeply embedded in the channel, and the channel-side vegetation included mature willows with dense undergrowth. The relative lack of disturbance in the Colma Creek site may help explain why NIS cordgrass grows at lower elevations (relative to local MHW) in Colma Creek than in the other tidal reach study sites (see Table 4 above).

Future Scenarios

The field data in combination with the conceptual models of the form and functions of intertidal habitats provide a basis for a set of general forecasts about the effects of NIS cordgrass on the intertidal zone as a physical system.

The basic spatial patterns of the invasion within local settings seem clear enough to summarize. And the physical responses of the intertidal system to date seem to agree well with what would be predicted from the conceptual models.

However, the regional spatial patterns of the invasion and the speed of the invasion within a locale and from place to place are mostly unknown because the various observations from different time periods have not been made using consistent methods. The lack of standardization among studies of NIS cordgrass in San Francisco Bay severely limits their usefulness for assessing change over time.

There is a basic need to monitor the invasion along the environmental gradients from saline to brackish conditions and from small to large tidal ranges, using standard methods with closely controlled reference to qualified vertical and horizontal controls for the spatial measurements. The time interval of the measurements is less critical than the spatial controls. However, a fixed time interval for measurements among randomly chosen sites along the primary environmental gradients seems most appropriate. A protocol for monitoring NIS cordgrass in the San Francisco Estuary has been produced that might prove useful (91).

While there is evidence that, in the few sites studied, the vertical limits of NIS cordgrass have been achieved (see page 13), this is not a conclusion, and elsewhere the invasion is apparently progressing both vertically within the intertidal zone and along the main axis of the Estuary. As the invasion progresses, its hydro-geomorphic effects may differ from what has been observed. The following forecasts of the likely endpoints of the invasion should be considered in the context of this uncertainty.

Bayshore and Tidal Marsh Scenarios

Figure 14: Conceptual model of changes in plan-form of the saline intertidal zone of existing mid- to high-elevation marshland, due to invasion by NIS cordgrass.

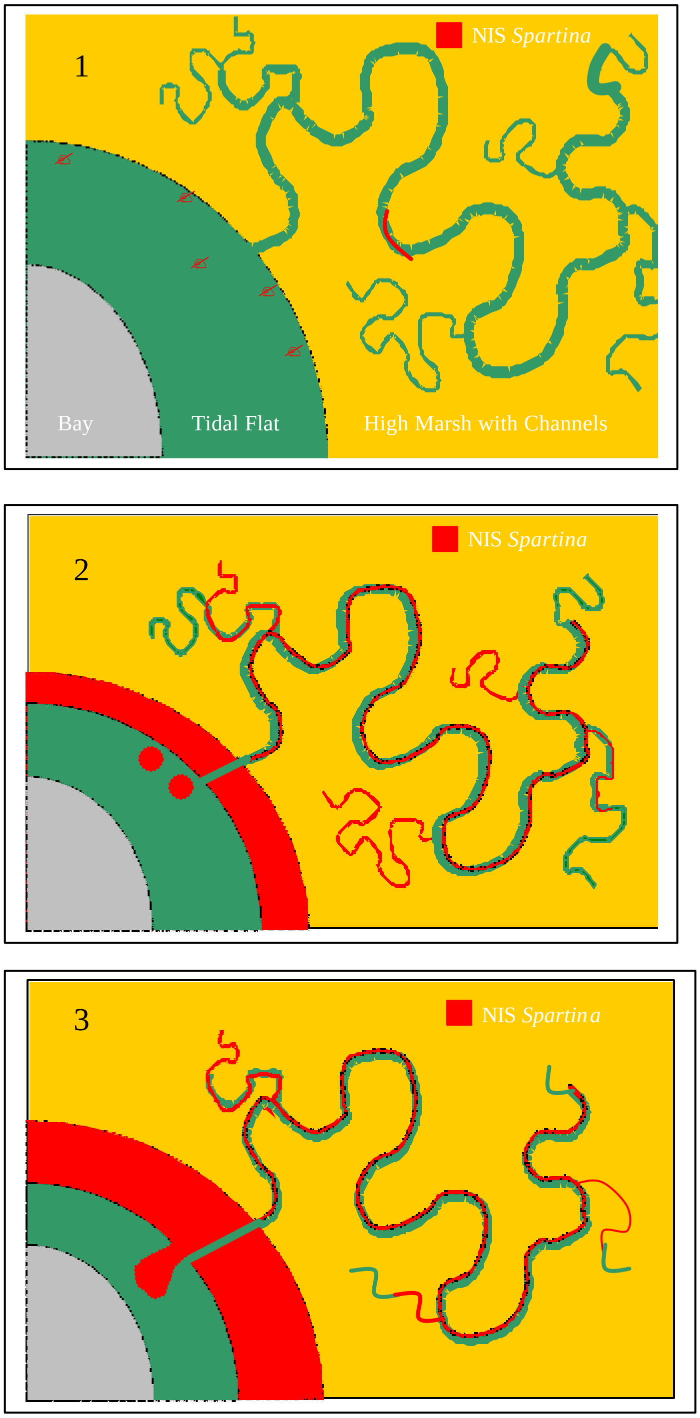


Figure 14 illustrates the basic pattern of NIS cordgrass invasion along the foreshore and channel network of an existing high-elevation tidal marsh (average height of the marsh plain is greater than local MHW) in the saline part of San Francisco Bay.

In the early stage of invasion (frame 1 of Figure 14), pioneering individuals of NIS cordgrass colonize the middle reaches of its vertical range along the foreshore and along the side slopes of the larger channels. Offshore shoals of tidal flats, such as those associated with the mouths of creeks, can also be colonized. The pioneers can be isolate from each other.

As the invasion progresses, (frame 2 of Figure 14), NIS cordgrass colonies expand upslope and downslope within the intertidal zone, forming a new foreshore at lower elevations than the old foreshore. Colonies also expand along the lower and middle reaches of the channel network.

Near the final stage of invasion, (frame 3) the NIS cordgrass has expanded throughout its vertical range along the foreshore and on the offshore shoal. The channel network is simplified, with isolated remnants of the most headward channels.

Figure 15 below illustrates in profile two possible end points of the NIS cordgrass invasion of existing mid-elevation saline tidal marsh (average height of the marsh plain is between MHW and MHHW). In the initial stage (frame 1 in Figure 15), NIS cordgrass colonizes the middle of its vertical range along the foreshore. As the invasion progresses (frame 2 in Figure 15), it expands throughout its vertical range along the foreshore. At the same time, the marsh is building upward above MHW. If the NIS cordgrass expands across the marsh plain, then it might form a cordgrass meadow that sustains itself near its upper limit, which is below the MHHW plain (frame 3 in Figure 15). Or, it might not expand across the plain, or it might be succeeded by native high marsh plant species (e.g., *Salicornia virginica*, *Distichlis spicata*, *Jaumea carnosa*) that can colonize organic substrates near the MHW datum and continue to build the marsh upward above MHHW, above the vertical limits of NIS cordgrass.

Figure 15: Conceptual model of changes in profile of the saline bayshore and tidal marsh due to invasion by NIS *Spartina*, showing two possible endpoints.

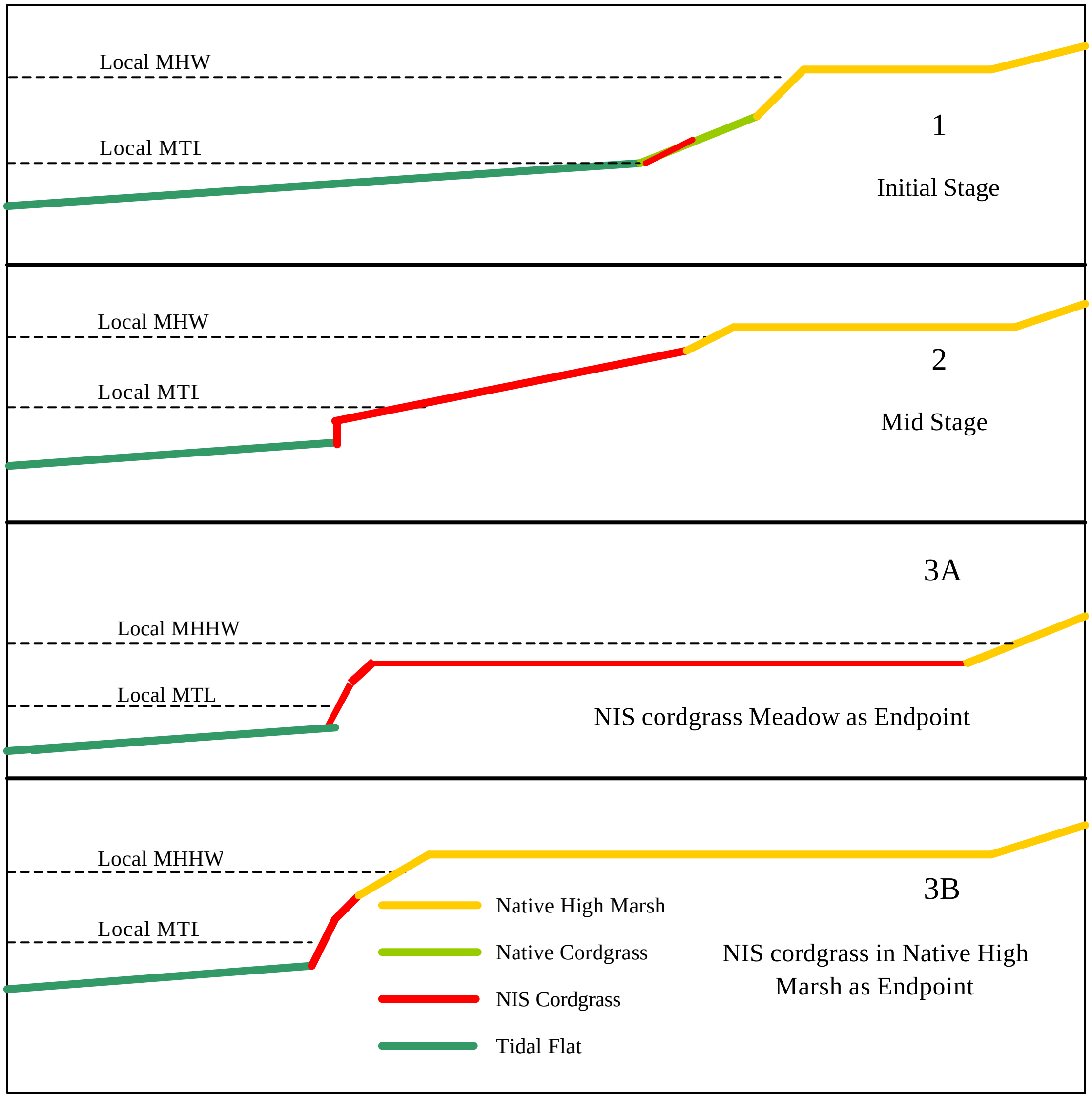
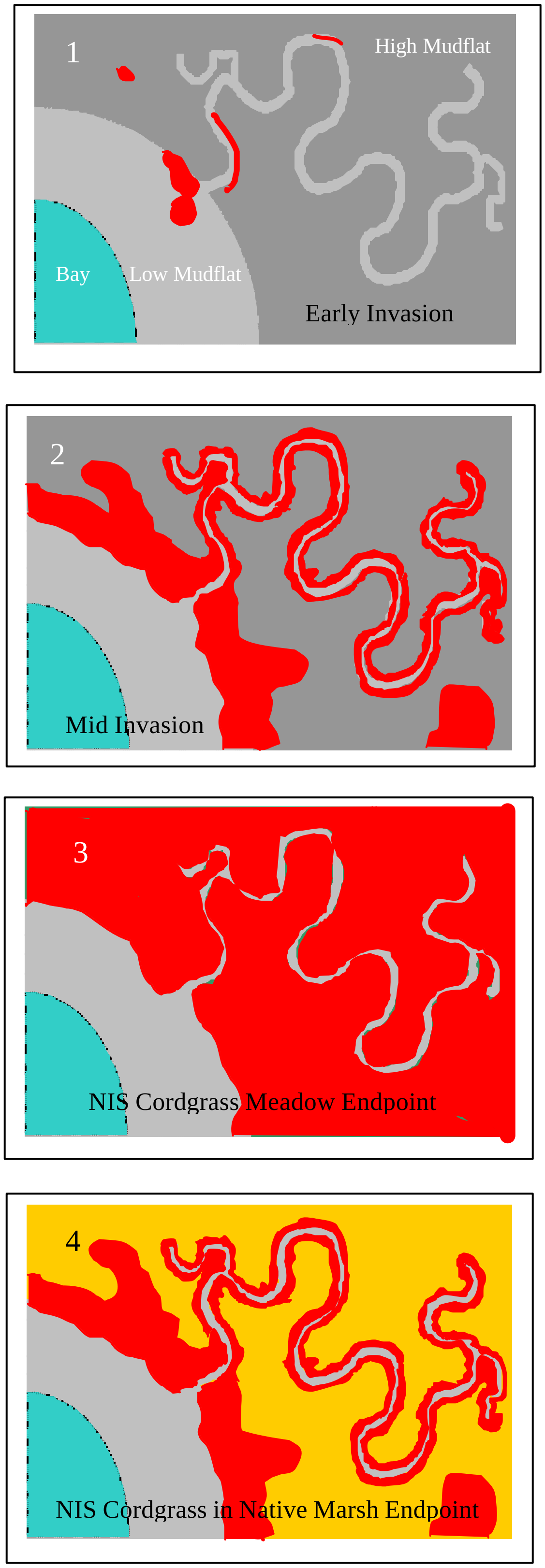


Figure 16: Conceptual model of two possible endpoints of tidal marsh development from mud flat, as influenced by NIS cordgrass.



At the earliest stage of invasion of the mudflat (Frame 1 in Figure 16), pioneer NIS cordgrass colonizes the relatively high-elevation shoals and the banks on the outside of meander bends of the lager channels.

As the invasion progresses (frame 2 of Figure 16), NIS cordgrass traps sediment and creates new habitat for itself along the foreshore and drainage network of the high-elevation tidal flat.

The NIS cordgrass eventually expands across the high tidal flat (Frame 3 of Figure 16), constraining the tidal channel network. This could be the endpoint of marsh development, with the marsh plain represented by a cordgrass meadow at elevations between MHW and MHHW. Another possibility is that the cordgrass meadow will succeed to a high marsh at elevations above MHHW due to colonization of the cordgrass meadow by native high marsh plants (see text for Figure 15 above).

In the latter case, the NIS cordgrass would probably persist as the dominant emergent plant of the foreshore and along the channel network (frame 4 of Figure 16), which would be simpler and lack the smaller channels of the native high marsh. That is, the evolution of high marsh from a NIS cordgrass meadow would probably have less channel habitat per unit area and the channel order would be lower for the channel network as a whole.

Tidal Reaches of Creeks Scenario

Figure 17: Conceptual model of changes in local creek profile and plan-form, as influenced by NIS cordgrass. Head of tide means upstream limit of tidal action.

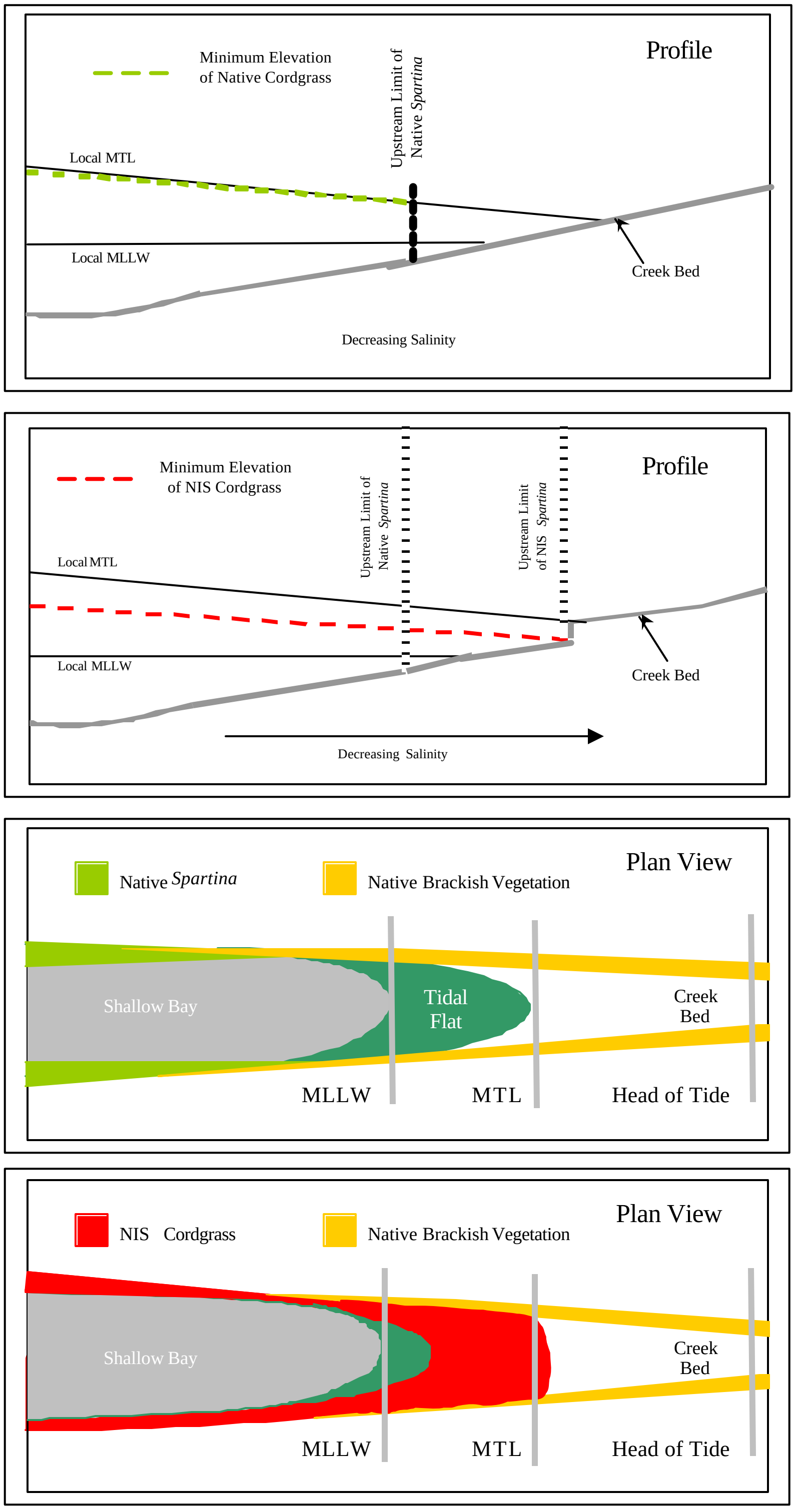


Figure 17 illustrates the potential effects of the NIS cordgrass invasion on creek profiles at the transition from fresh-tidal to saline-tidal conditions.

The NIS cordgrass grows at lower elevations than the native cordgrass, and can tolerate less saline conditions.

Brackish conditions prevent native cordgrass from growing as far upstream in creeks as the tidal regime would otherwise permit. Along the saline foreshore of the Bay, native cordgrass can grow at MTL. But creek beds intersect MTL upstream of saline habitat. Native cordgrass therefore does not grow across creek beds

NIS cordgrass grows below MTL, tolerates brackish conditions, and therefore can grow further up the creeks and across their beds. The ability of NIS cordgrass to trap sediment and to withstand flood flows can cause the creek beds to aggrade upstream, and thus shorten their tidal reaches.

Outstanding Questions

The hydrological and geomorphic processes of the intertidal zone create a dynamic physical template for ecological interactions. The production and physical structure of emergent intertidal vegetation are prominent aspects of this dynamic template. The invasion by NIS cordgrass will significantly alter the template and thus affect the ecology of the intertidal zone.

The following questions are fundamental and must be answered before the overall extent and general ecological effects of the NIS cordgrass invasion can be forecasted.

1. How low will NIS cordgrass grow in Suisun and perhaps the western Delta? Studies are needed to show the minimum elevation of NIS cordgrass when suitable substrate is available in the lower intertidal zone under brackish to fresh water conditions. To date, field studies of the effect of aqueous salinity on the vertical distribution of NIS cordgrass have been restricted to the tidal reaches of local creeks, where channel bed elevations are above low tide. These studies cannot indicate how low NIS cordgrass will grow under freshwater conditions where the lower intertidal zone is available to be colonized. The existing data do not indicate, for example, how low NIS cordgrass will grow along the foreshores of North Bay or Suisun. This question would be addressed best with laboratory studies of the survivorship of NIS cordgrass under controlled regimes of inundation and aqueous salinity.

2. Will NIS Cordgrass meadows evolve into high marsh dominated by native plants? The regional model of marsh evolution from tidal flat through low marsh to high marsh needs to be tested when the low marsh is dominated by NIS cordgrass rather than native cordgrass. It is apparent that NIS cordgrass readily traps suspended inorganic sediment and produces large amounts of organic debris. Retention of these materials within areas that are colonized by NIS cordgrass might raise the areas into the elevation range of other plant species, including native high-marsh species that might be able to compete with NIS cordgrass in the upper intertidal zone. There is evidence from the San Francisco Estuary of natural succession from low marsh that is dominated by native cordgrass to high marsh dominated by other native vegetation. The existing data do not indicate, however, whether an area of NIS cordgrass will be subject to plant community succession or if the area will remain unsuitable for other plant species despite being within their vertical range. If areas of NIS cordgrass build up rapidly to mid marsh or higher elevations, and if the areas are then colonized by native vegetation, then the NIS cordgrass might increase the rate of evolution of acceptable marsh conditions from tidal flats. The resulting marsh would have fewer small channels and a lesser density of channels overall, but the marsh plain might be dominated by native vegetation. This question could be addressed by monitoring elevation and plant species composition at a low marsh plain

that is presently dominated by NIS cordgrass, has an adequate supply of suspended sediment, and is allowed to develop upward through the intertidal zone.

3. What will be the ecological effects of the hydro-geomorphic changes? Some general effects of the NIS cordgrass invasion on the ecological functions of the intertidal zone might be hypothesized, based upon the expected geomorphic effects and the natural histories of the plants and animals involved. For example, the isolation of the headward reaches of first-order channels may increase mosquito production, until the channel remnants are colonized by plants and become part of the marsh plain. The retrogression or shortening the channel networks will tend to increase the size of broad pannes on the marsh plain that can serve as refugia and perhaps feeding areas for shorebirds and dabbling waterfowl. The increased width of the low marsh zone and the increased height of foreshore vegetation might represent more habitat for low marsh birds, such as rails, wrens, and song sparrows, although interactions among these taxa might offset the benefits of more habitat. The foreshore may be more stable and able to resist erosion. Shorebirds that feed along the tidal front as it rises and crosses the tidal flats will encounter the foreshore at lower tidal elevation and thus be forced off tidal flats sooner during a rising tide. Whether or not this will significantly affect shorebird energetics and fitness is unknown. The overall reduction in channel density and shoreline length might reduce the rate of exchange of water-borne materials between the marshes and the Bay. That is, the overall filtering function of the marshes and their role as habitat for some fishes is likely to be reduced. These are examples of basic ecological processes that might be affected by the NIS cordgrass invasion as mediated by hydro-geomorphic changes in the habitat. The important details of such effects remain to be elucidated.

References

1. Hickman, J.C. 1993. Jepson manual. University of California Press, Berkeley, CA.

2. Ayers, D.R., D Garcia-Rossi, H.G. Davis, and D. Strong. 1999. Extent and degree of hybridization between exotic (*Spartina alterniflora*) and native (*S. foliosa*) cordgrass (Poaceae) in California, USA determined by random amplified polymorphic DNA (RAPDs). Molecular Ecology 8: 1179-1186.

4. American Geological Institute. 1976. Dictionary of geological terms. Anchor Press/Doubleday, Garden City, NY.

5. Steacy D. Hicks, 1989. Tide and current glossary. National Ocean Service. NOAA, Washington, D.C.

6. Malamud-Roam, K.P. 2000. Tidal regimes and tide marsh hydroperiod in the San Francisco Estuary: theory and implications for ecological restoration. Doctoral dissertation, Department of Geography, University of California, Berkeley, CA.

7. NOAA Coastal Services Center. 2001. Shoreline Mapping Web Site, Shoreline Terms, United States Department of Commerce, National Oceanic and Atmospheric Administration, National Ocean Service, Charleston, SC. http://www.csc.noaa.gov/shoreline/term.html

8. Faber, P. 2000. Grass wars good intentions gone awry why would anyone bring and alien cordgrass into S.F. Bay? California Coast and Ocean 16(2).

9. Spicher, D. and M. Josselyn. 1985. *Spartina* (Gramineae) in Northern California: distribution ands taxonomic notes. Madrono 32: 158-167.

10. Collins, J.N. and M. May. 2001. Basic regional spatial analysis of NIS *Spartina* invasions in the San Francisco Estuary. Report to the California State Coastal Conservancy, San Francisco Estuary Institute, Oakland, CA

11. USCOE (undated). Shoreline erosion control demonstration program Alameda, California. Brochure produced by the U.S. Army Corps of Engineers, Public Affairs Office, San Francisco District, Navigation and Coastal Planning Section.

12. Personal communication. 2001. Debra Smith, Director, San Francisco Bay Invasive Spartina Project, California Coastal Conservancy, Oakland, CA.

13. Grossinger, R., J. Alexander, A.N. Cohen, and J.N. Collins. 1998. Introduced tidal marsh plants in the San Francisco Estuary regional distribution and priorities for control. San Francisco Estuary Institute, Richmond, CA.

14. Collins, J.N. 2001. The effects of invasive *Spartina alterniflora on* the elevation of tidal marsh shorelines: evidence from three small estuaries of San Francisco Bay. Report to the California State Coastal Conservancy, San Francisco Estuary Institute, Oakland, CA

15. Callaway, J.C. and M.N. Josselyn. 1992. The introduction and spread of smooth cordgrass (*Spartina alterniflora*) in South San Francisco Bay. Estuaries 15(2): 218-226.

16. Conomos, T.J., R.E. Smith and J.W. Gartner. 1985. Environmental setting of San Francisco Bay. In: Temporal dynamics of an estuary San Francisco Bay, J.E. Cloern and F.H. Nichols (eds.). Hydrobiologia 129: 1-12.

17. Peters, D.D. and J.A. Bohn. 1987. National Wetlands Inventory mapping for San Francisco Bay, California. American Society of Engineers, Coastal Zone '87: 1171-1182.

18. DWR (California Department of Water Resources). 1957. Salinity control barrier investigation. California Department of Water Resources, Bulletin No. 60, Sacramento, CA.

19. Arthur, J.F. and M.C. Ball. 1979. Factors influencing the entrapment of suspended material in the San Francisco Bay-Delta Estuary. In: San Francisco Bay: the urbanized estuary, T.J. Conomos (ed.). Proceedings of the 58th annual meeting of the Pacific Division of the American Association for the Advancement of Science, San Francisco, CA.

20. Krone, R.B. 1979. Sedimentation in the San Francisco Bay system. In: San Francisco Bay: the urbanized estuary, T.J. Conomos (ed.). Proceedings of the 58th annual meeting of the Pacific Division of the American Association for the Advancement of Science, San Francisco, CA.

21. Buchanan, P.A. and D.H. Schoellhamer. 1996. Summary of suspended-solids concentration data, San Francisco Bay, California, water year 1995. U.S. Geological Survey, Open File Report 96-591.

22. Helley, E.J. K.R. Lajoie, W.E. Spangle, and M.L. Blair. 1979. Flatland deposits of the San Francisco Bay region, California - their geology and engineering properties and their importance to comprehensive planning. U.S. Geological Survey, Professional Paper 943.

23. Nichols, F.H. and M.M. Pammatmat. 1988. The ecology of the soft-bottom benthos of San Francisco Bay: a community profile. U.S. Fish and Wildlife Service, Biological Report 85(7.19).

24. Davis, R.A., Jr. 1996. Coasts. Prentice Hall, Upper Saddle River, NJ.

25. Harvey, T.E., K.J. Miller, R.L. Hothem, M. Rauzon, G.W. Page, and R.A. Keck. 1992. Status and trends report on the wildlife of the San Francisco Estuary. U.S. Fish and Wildlife Service, Sacramento, CA.

26. Ustin, S.L., R.W. Pearcy, and D.E. Bayer. 1982. Plant water relations in a San Francisco Bay salt marsh. Botanical Gazette 143(3): 368-373.

27. Culberson, S.D. 2001. The interaction of physical and biological determinants producing vegetation zonation in tidal marshes of the San Francisco Bay Estuary, California, USA. Doctoral dissertation, Department of Ecology, University of California, Davis, CA

28. Reed, D.J. 1988. Sediment dynamics and deposition in a retreating coastal salt marsh. Estuarine, Coastal and Shelf Sciences, 26: 67-79.

29. Shoellhamer, D.H. and J.R. Burau. 1998. Summary of findings about circulation and the estuarine turbidity maximum in Suisun Bay, California. U.S. Geological Survey, Sacramento, CA.

30. Collins, J.N., L.M. Collins, L.B. Leopold, and V.H. Resh. 1986. The influence of mosquito control ditches on the geomorphology of tidal marshes in the San Francisco Bay Area: evolution of salt marsh mosquito habitat. Proceedings and Papers of the California Mosquito and Vector Control Association 54: 91-95.

31. Collins, L.M., J.N. Collins, and L.B. Leopold. 1987. Geomorphic processes of an estuarine tidal marsh: preliminary results and hypotheses. In: International Geomorphology 1986 Part I. V. Gardner (ed.). John Wiley and Sons, LTD.

32. Atwater, B.F. and C.W. Hedel. 1976. Distribution of seed plants with respect to tide levels and water salinity in the natural tidal marshes of the northern San Francisco Bay Estuary, California. U.S. Geological Survey, Open File Report 76-389.

33. NOAA (U.S. National Oceanic and Atmospheric Administration). 1980. The relationship between the upper limit of the coastal wetlands and tidal datums along the pacific coast. National Ocean Survey, U.S. National Oceanic and Atmospheric Administration, Rockville, MD.

34. Jones and Stokes Associates, Inc. 1979. Protection and restoration of San Francisco Bay fish and wildlife habitat, Volumes I and II. Jones and Stokes Associates, Inc., Sacramento, CA.

35. Grossinger, R.M. 1995. Historical evidence of freshwater effects on the plan form of tidal marshlands in the Golden Gate estuary. Masters of science thesis, Department of Marine Sciences, University of California, Santa Cruz, CA.

36. Allen, J.R.L. and K. Pye. 1992. Saltmarshes morphodynaimcs, conservation and engineering significance. Cambridge University Press, Cambridge, Great Britain.

37. Mitsch, J.W. and J.G. Gosselink. 1993. Wetlands. Van Nostrand Reinhold, New York, NY.

38. Wells, L.E. 1995. Environmental setting and quaternary history of the San Francisco estuary. In: E.M. Sangines, D. Anderson, and A.V. Bushing (eds.), Recent geological studies in the San Francisco Bay Area. Pacific Section of Economic Paleontologists and Mineralogists, Fullerton, CA.

39. Atwater, B.F., S.G. Conrad, J.N. Dowden, D.W. Hedel, R.L. MacDonald, and W. Savage. 1979. History, landforms, and vegetation of the estuary's tidal marshes. In: San Francisco Bay: the urbanized estuary, T.J. Conomos (ed.). Proceedings of the 58th annual meeting of the Pacific Division of the American Association for the Advancement of Science, San Francisco, CA.

40. Byrne, R., B.L. Ingram, S. Starratt, F. Malamud-Roam, J.N. Collins, and M.E. Conrad. 2001. Carbon-isotope, diatom, and pollen evidence for late Holocene salinity change in a brackish marsh in the San Francisco Estuary. Quaternary Research 55: 66-76.

41. Ahnert, F. 1960. Estuarine meanders in the Chesapeake Bay area. Geography Review 50: 390-401.

42. Redfield, A.C. 1972. Development of a New England salt marsh. Ecological Monographs, 42(2): 201-237.

43. Postma, H. 1967. Estuaries. American Association for the Advancement of Science publication 83.

44. Dyer, K.R. 1979. Estuarine hydrography and sedimentation. Cambridge University Press, Cambridge, Great Britain.

45. Dedrick, K.G. 1979. Effects of levees on tidal currents in marshland creeks. Abstracts of the G.K. Gilbert Symposium: San Francisco Bay its past, present, and future. Annual meeting of the Geological Society of America, 1979, San Jose, CA.

46. Dedrick K.G. and L.T. Chu. Historical atlas of tidal creeks San Francisco Bay, California. Proceedings of the eighth symposium on coastal and ocean management (Coastal Zone 93). American Society of Engineers, New York, NY.

47. Gilbert, G.K. 1917. Hydraulic-mining debris in the Sierra Nevada. US Geological Survey, Professional Paper 105. Washington, DC.

48. Collins, J.C. and M. May. 1996. Contamination of tidal wetlands. Pages 257-280 in: RMP 1996 Annual Report, San Francisco Estuary Institute, Oakland, CA.

49. Nixon, S.W. 1980. Between coastal marshes and coastal waters - a review of twenty years of speculation and research on the role of salt marshes in estuarine productivity and water chemistry. In: Estuarine and wetlands processes, P. Hamilton and K.B. MacDonald (eds.). Plenum, New York, NY.

50. Odum, E.P. and A.A. de la Cruz. 1967. Particulate organic detritus in a Georgia salt marsh-estuarine ecosystem. In: Estuaries, G.H. Lauff (ed.). American Association for the Advancement of Science, Washington, D.C.

51. Chalmers, A.G., R.G. Wiegert, and P.L. Wolf. 1985. Carbon balance in a salt marsh: interactions of diffusive export, tidal deposition and rainfall-caused erosion. Estuarine, Coastal and Shelf Sciences, 21: 757-771.

52. Marani, A.R., R. Rogon, and A Rinaldo. 1991. A note on fractal channel networks. Water Resources Research, 27(12): 3041-3049.

53. Huffman & Associates, Inc. 1994. An analysis of shoreline erosion rates in relation to oil spill events in Suisun Bay, California. Huffman & Associates, Inc., Larkspur, CA.

54. Larsson, B. 1996. A comparative investigation of accretion rates in *Spartina alterniflora* and *Spartina foliosa*. Masters of arts thesis in marine biology, San Francisco State University, San Francisco, CA.

55. Foin, T.C. and J.L. Benchley-Jackson. 1991. Simulation model evaluation of potential recovery of endangered light-footed clapper rail populations. Biological Conservation, 58: 123-148.

56. Leopold, L.B., J.N. Collins and L.M. Collins. 1993. Hydrology of some tidal marsh channels near San Francisco, California. Catena, 20: 469-493.

57. Siegel, S.W. 1993. Tidal marsh restoration and dredge disposal in the San Francisco Estuary, California. Masters thesis, Department of Geography, University of California, Berkeley, CA.

58. Josselyn, M.N. 1983. The ecology of San Francisco Bay tidal marshes: a community profile. U.S. Fish and Wildlife Service Report FWS/OBS-83/23.

59. McKee, K.L. and W.H. Patrick. 1988. The relationship of smooth cordgrass (*Spartina alterniflora*) to tidal datums: a review. Estuaries, 11: 143-151.

60. Hardaway, C.S., G.R. Thomas, A.W. Zacherle, and B.K. Fowler. 1984. Vegetation erosion control project. Virginia Institute of Marine Sciences, Gloucester Point, VA.

61. Gray, A.J. 1992. Salt marsh plant ecology: zonation and succession revisited. In: Saltmarshes: morphodynamics, conservation and engineering significance, J.R.L Allen and K Pye (ed.). Cambridge University Press, Cambridge, Great Britain.

62. Daehler, CC and D.R. Strong. 1996. Status, prediction, and prevention of introduced cordgrass *Spartina* spp. invasions in Pacific estuaries, USA. Biological Conservation 78: 51-58.

63. Mahall, B.E. and R.B. Park. 1976. The ecotone between *Spartina foliosa* Trin., and *Salicornia virginica* L. in salt marshes of northern San Francisco Bay. III. Soil aeration and tidal immersion. Journal of Ecology 64:811-819.

64. Stenzel, L.E. and G.W. Page. The results of the first comprehensive shorebird census of San Francisco and San Pablo bays. Wader Study Group, Bulletin 54: 43-48.

65. U.S. Fish and Wildlife Service 1984. Salt marsh harvest mouse and California clapper rail recovery plan. In cooperation with H.S. Shellhammer. T.E. Harvey, M.D. Knudsen, and P. Sorensen, Region 1, Portland, OR

66. Goals Project. 2000. Bayland ecosystem species and community profiles: life histories and environmental requirements of key plants, fish and wildlife. Prepared by the San Francisco Bay Area Wetlands Ecosystem Goals Project. P.R., Olofson (ed). San Francisco Bay Regional Water Quality Control Board, Oakland, CA.

67. Lane, R.S. 1969. The insect fauna of a coastal salt marsh. Masters of arts thesis, San Francisco State University, San Francisco, CA.

68. Barnby, M.A., J.N. Collins, and V.H. Resh. 1985. Aquatic macroinvertebrate communities of natural and ditched potholes in a San Francisco Bay salt marsh. Estuarine, Coastal and Shelf Sciences, 20: 331-347.

69. Balling, S.S. and V.H. Resh. 1991. Seasonal patterns in a San Francisco Bay, California, salt marsh arthropod community. Pan-Pacific Entomologist 67(2): 138-144.

70. Herbold, B. A.D. Jassby and P.B. Moyle. 1992. Status and tends report on aquatic resources in the San Francisco Estuary. U.S. Environmental Protection Agency, Region IX, San Francisco, CA.

71. Hoss, D.E. and G.W. Thayer. The importance of habitat to the early life history of estuarine dependent fishes. American Fisheries Society Symposium 14: 147-158.

72. Takekawa, J.Y., D.S. Gilmer, C.M. Marn, H.M. Ohlendorf, L.M. Acurso, and J.E. Takakawa. 1988. Abundance, distribution and habitat use of wintering waterfowl in the San Francisco Bay ecosystem, 1987-1988. U.S. Fish and Wildlife Service, Northern Prairie Wildlife Research Field Station, Dixon, CA, and Patuxent Wildlife Research Center, Davis, CA.

73. Balling, S.S., T. Stoehr, and V.H. Resh. 1980. The effects of mosquito control recirculation ditches on the fish community of a San Francisco Salt Marsh. California Fish and Game 66: 25-34.

74. Goals Project. 1999. Bayland ecosystem habitat goals. A report of habitat recommendations prepared by the San Francisco Bay Area Wetlands Ecosystem Goals Project. USEPA, San Francisco/SFBRWQCB, Oakland, CA.

75 Collins, J.N. and T.C. Foin. 1992. Evaluation of the impacts of aqueous salinity on the shoreline vegetation of tidal marshlands in the San Francisco Estuary. In: Managing freshwater discharge to the San Francisco/Sacramento-San Joaquin Delta Estuary, J.R, Schubel (ed). S EPA Region IX, San Francisco, CA.

76.Wilson, J.B., W.M. King, M.Y. Sykes, and T.R. Partridge. 1996. Vegetation zonation as related to the salt tolerance of species of brackish riverbanks. Canadian Journal of Botany, 74: 1079-1085.

77. Callaway, R.M., S. Jones, W.R. Ferren Jr., and A Parikh. 1990. Ecology of a Mediterranean-climate estuarine wetland at Carpenteria, California: plant distributions and soil salinities in the upper marsh. Canadian Journal of Botany, 68:(1990): 1139-1146.

78. Chapman, V.J. 1974. Salt marshes and salt deserts of the world 2nd edition. Verlag Von J. Cramer. Bremerhaven, Germany.

79. Grenier, L. 2002. The salt marsh food web. Technical report of the San Francisco Estuary Institute, Oakland, CA.

80. 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.

81. Sanderson, E.W., T.C. Foin, and S.L. Ustin. 2001. A simple numerical model of salt marsh plant spatial distributions with respect to a tidal channel network. Ecological Modeling 139: 293-207.

82. Josselyn, M.N., S.P. Faulkner, and W.H. Patrick, Jr. 1990. Relationships between seasonally wet soils and occurrence of wetland plants in California (USA). Wetlands 10(1): 7-26.

83. Adam, P. 1990. Salt marsh ecology. Cambridge University Press, Cambridge, Great Britain.

84. Sanderson, E.W., T.C. Foin, S.L. Ustin and S.D. Culberson. 1997. Tidal channel influence describes the zonation and distribution of plant species in Petaluma marsh, California. Bulletin of the Ecological Society of America 78.

85. Niering, W.A., R.S. Warren and C.G. Weymouth. 1977. Out dynamic tidal marshes vegetation changes as revealed by peat analysis. Bulletin No. 22 The Connecticut Arboretum, Connecticut College, New London, CT.

86. Rickets, F. R and J Calvin. 1968. Between Pacific tides, 4h edition (revised by Joel Hedgpeth). Stanford University Press, Stanford, CA.

87. LABINS, 2000. Height difference methodology, Land Boundary Information System, Florida Department of Environmental Protection, Tallahassee, FL.

88. NOAA, 1973. Variability of tidal datums and accuracy in determining datums from short series of observation. Technical Report NOS 64, National Oceanic and Atmospheric Association, Washington DC.

89. NOAA, 2000. NOS Hydrographic Surveys Specifications and Deliverables. National, Ocean Survey, National Oceanic and Atmospheric Association, Washington, DC.

90. Adams, J.B., Bate, G.C. 1995. The ecological implications of salinity and inundation tolerance in the estuarine halophyte, *Spartina martima* (Curtis) Fernald. Aquatic Botany 52: 183-191.

91. Collins, J.N., M. May, D. Smith, S. Klohr, and K. Zaremba. 2001. Guidelines to monitor the distribution, abundance, and treatment of non-indigenous species of cordgrass in the San Francisco Estuary. Report to the California Coastal Conservancy, Oakland, CA.

92. Pestrong, R. 1972. Tidal-flat sedimentation at Cooley Landing, southwest San Francisco Bay. Sedimentary Geology 8: 251-288.

93. Pestrong, R. 1965. The development of drainage patterns on tidal marshes. Stanford University Publications in the Geologic Sciences 10(2). Stanford University, Palo Alto, CA.

94. Collins, L. 1998. Sediment sources and fluvial geomorphic processes of lower Novato Creek watershed. Report to Marin County Flood Control and Water Conservation District, San Rafael, CA.

95. Bayliss-Smith, T.P., R. Healy, R. Lailey, T. Spencer, and D.R. Stoddart. 1979. Tidal flows in salt-marsh creeks. Estuarine and Coastal Marine Sciences 9: 235-255.

96. Boon, J.D., III. 1975. Tidal discharge asymmetry in a salt marsh drainage system. Limnology and Oceanography 20: 71-80.

97. Doty, M.S. 1946. Critical tide factors that are correlated with the vertical distribution of marine algae and other organisms along the Pacific coast. Ecology 27: 315-328.

98. Otto, S., P.M. Groffman, S.E.G. Findlay, and A.E. Arreola, 1999. Invasive plant species and microbial processes in a tidal freshwater marsh. Journal of Environmental Quality 28(4): 1252-1257

99. Caldwell, F.A., and G.E. Crow. 1992. A floristic and vegetation analysis of a freshwater tidal marsh on the Merrimack River, West Newbury, Massachusetts. Rhodora. 94(877): 63-97.

100. Alberts, J.J., M.T. Price, and M. Kania. 1990. Metal concentrations in tissues of *Spartina alterniflora* (Loisel) and sediments of Georgia salt marshes. Estuarine and Coastal Shelf Sciences 30: 4 - 58.

101. Otte, M. L. 1991. Heavy metals and arsenic in vegetation of salt marshes and floodplains. PhD Thesis. Vrije Universiteit, Amsterdam.

102. Haltiner, J. and P.B. Williams. 1987. Hydraulic design in salt marsh restoration. In: The national wetlands symposium: wetland hydrology, J.A. Kusler and G. Brooks (eds.). Association of State Wetland Managers, Chicago, IL.

103. Langbein, W.B. 1963. The hydraulic geometry of a shallow estuary. International Association of Scientific Hydrologists 8: 84-94.

104. Gabet, E.J. 1998. Lateral migration and bank erosion in a salt marsh tidal channel in San Francisco Bay, California. Estuaries 21 (4B): 745-753.

105. Adams, D.A. 1963. Factors influencing vascular plant zonation in North Carolina salt marshes. Ecology 44: 445-456.