

Tidal Marsh Vegetation of China Camp, San Pablo Bay, California

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ABSTRACT

China Camp (Marin County, California) preserves extensive relict stands of salt marsh vegetation developed on a prehistoric salt marsh platform with a complex sinuous tidal creek network. The low salt marsh along tidal creeks supports extensive native stands of Pacific cordgrass (*Spartina foliosa*). After hydraulic gold mining sedimentation, the outer salt marsh accreted. It consists of a wave-scarped pickleweed-dominated (*Sarcocornia pacifica*) high salt marsh terrace, with a broad fringing low marsh dominated by *S. foliosa*, including intermittent, variable stands of alkali-bulrush (*Bolboschoenus maritimus*). Most of the extensive prehistoric salt marsh plains within the tidal creek network also support mixed assemblages of *S. pacifica*, but high marsh zones along tidal creek banks support nearly continuous linear stands of gumplant (*Grindelia stricta*) and saltgrass (*Distichlis spicata*) with more diverse salt marsh forb assemblages. Salt pans with submerged wigeongrass (*Ruppia maritima*) are scarce, local, and small. The landward edge of the tidal marsh forms rare examples of ecotones with adjacent terrestrial vegetation, including those of alluvial valleys (riparian scrub and woodland, freshwater marsh, sedge-rush meadows) and hillslope grassland and oak woodland

vegetation. Narrow high tidal marsh ecotones that borders terrestrial grasslands are locally dominated by creeping wildrye (*Elymus triticoides*) and Baltic rush (*Juncus balticus*), mostly on south-facing slopes. Brackish tidal marsh ecotones above ordinary high tides are associated with freshwater discharges from groundwater and surface flows. Brackish marsh ecotones support large clonal stands of sedge, bulrush, and rush vegetation (*Carex praegracilis*, *C. barbarae*, *Bolboschoenus maritimus*, *Juncus phaeocephalus*, *Schoenoplectus acutus*), intergrading with terrestrial freshwater wetlands and salt marsh. The terrestrial ecotone assemblages at China Camp are comparable with those of other prehistoric tidal marshes in the San Francisco Estuary, but China Camp lacks most native clonal perennial Asteraceae and halophytic annual forbs of the region's remnant high tidal marsh ecotones. Few globally-rare salt marsh plant populations have been reported from China Camp within the National Estuarine Research Reserve (NERR) and state park boundaries, but some species occur that are regionally uncommon in San Francisco Bay tidal marshes. To date, non-native tidal marsh plant invasions have been relatively minor and localized within China Camp.

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KEY WORDS

China Camp, San Pablo Bay, tidal marsh, brackish marsh, salt marsh vegetation, terrestrial ecotone

INTRODUCTION

China Camp State Park (San Rafael, Marin County, San Pablo Bay, California (38°02'37" N 122°30'12" W)) includes a tidal salt marsh approximately 40.5 ha in area (Goman 2001; Goman and others 2008). Tidal marsh vegetation at China Camp is well known for its “old-growth” component: it contains a large remnant prehistoric marsh area with a complex, sinuous tidal channel network that escaped 19th- and 20th-century diking and agricultural reclamation, and preserved a nearly continuous stratigraphic record of estuarine marsh peat and mud deposition during the late Holocene epoch (Goman and others 2008; Malamud–Roam and Ingram 2004). Less well-known is another distinctive relict tidal marsh feature of China Camp tidal marsh that escaped diking and intensive agricultural modification in the 19th century: the tidal marsh vegetation gradients (ecotones) with adjacent terrestrial vegetation (oak woodland, valley grassland, freshwater marsh) on mostly intact soil profiles. Among San Pablo Bay’s few relict tidal prehistoric tidal marshes (Petaluma Marsh [Petaluma River], Fagan Slough [Napa River], Whittell Marsh [Point Pinole]), China Camp retains the greatest extent and diversity of terrestrial (upland and wetland) ecotone vegetation, with high native plant species diversity and complex vegetation patterns.

The following is a qualitative descriptive account of China Camp tidal marsh vegetation conditions based primarily on long-term field observations between 1991 and 2011, a period that included prolonged intervals of drought and high rainfall associated with long-term marsh salinity fluctuations, and one extreme storm erosion event (1997–1998 El Niño). The aims of this account include the following:

1. to describe vegetation patterns in relation to geomorphic and hydrologic patterns and processes

(tidal marsh landforms, dynamics, substrates, and drainage patterns), comparable with other prehistoric remnant tidal marshes of the Bay Area (Whitcraft and others 2011);

2. to identify qualitative short-term patterns of vegetation change;
3. to provide a local flora for the vascular plant species of the prehistoric China Camp tidal marsh plain and its terrestrial ecotones (see [Appendix A](#)), and
4. to summarize regionally distinctive or unique aspects of plant species composition of China Camp tidal marsh vegetation.

The physical landforms of the tidal wetlands can provide a meaningful eco-geomorphic framework to interpret and compare of San Francisco Estuary tidal marsh vegetation structures, and the many physical processes that influence it (Whitcraft and others 2011). The following description of the tidal marsh vegetation is organized primarily in relation to the diverse geomorphic structure and processes of the compound prehistoric remnant and modern tidal marsh ecosystem.

Historical and Prehistoric Tidal Marsh Units

The relict prehistoric (late Holocene) tidal marsh platform, and its terrestrial ecotones, occur within interior and landward portions of China Camp Marsh, including the partially drowned alluvial valleys (Back Ranch Meadows, Miwok Meadows) that are enclosed by North San Pedro Road and connected to tidal flows by culverts ([Figure 1](#)). The late Holocene marsh platform is associated with the original, highly sinuous, tidal marsh creek networks that extend between drowned hills, forming hillslope islands and island-like peninsulas ([Figure 1](#)), and grade into the alluvial valleys. The outer (eastern) portion of the tidal marsh, in contrast, consists of two younger and distinct marsh sub-units developed in historical times: a broad, fringing high tidal marsh platform or terrace, bounded by an active or relict wave-cut marsh scarp; and a highly-dynamic, outer fringing, low tidal

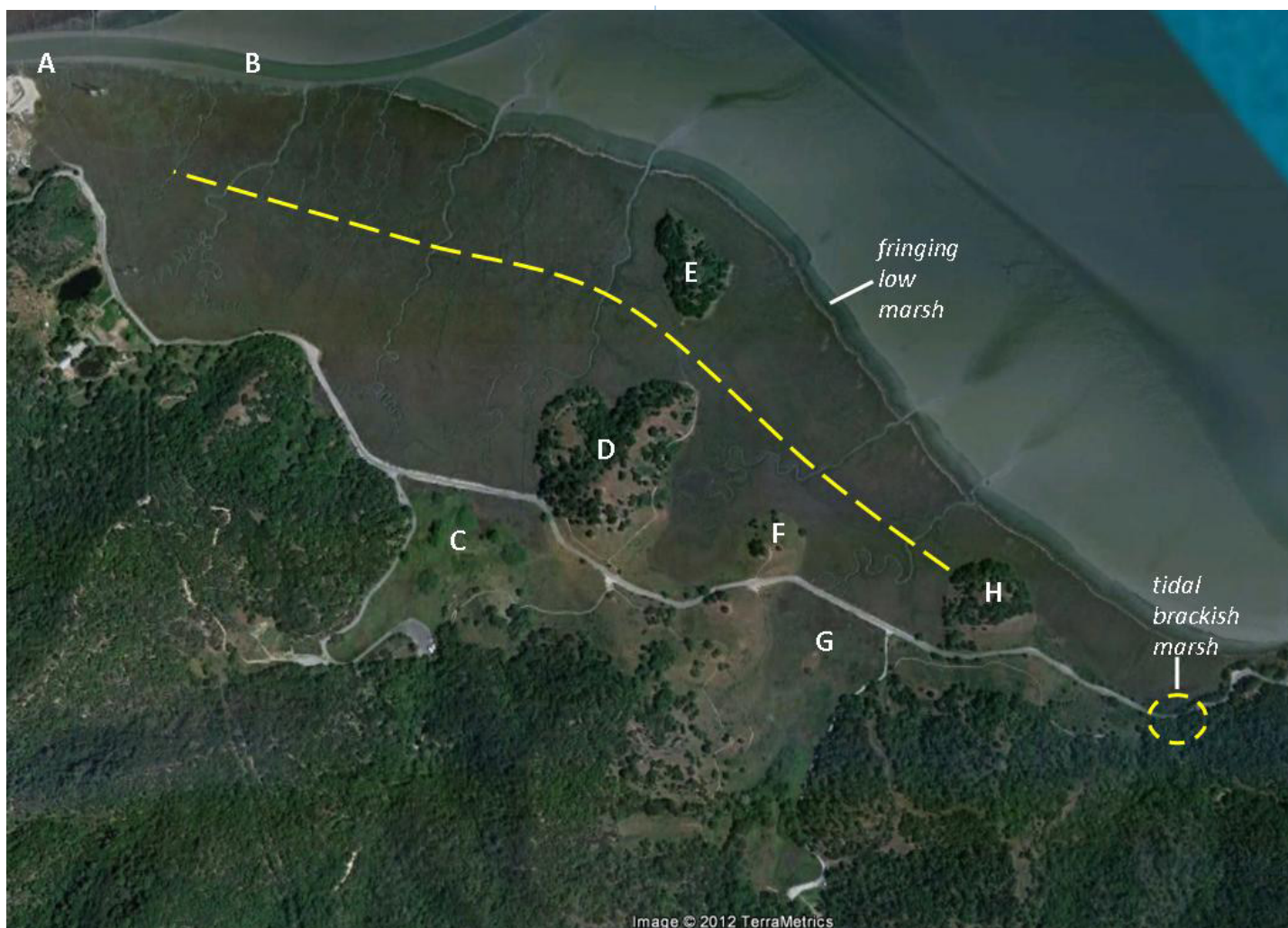


Figure 1 China Camp Marsh with local geographic place-names. Image Google Earth, May 6, 2012. Yellow dashed line represents approximate transition between late Holocene (prehistoric) interior tidal marsh platform with sinuous tidal creeks, and historically prograded outer salt marsh terrace with shore-normal, narrowly dendritic drainage patterns. **(A)** Buck's Landing. **(B)** Gallinas Creek. **(C)** Back Ranch Meadows. **(D)** Turtle Back Hill. **(E)** Jake's Island. **(F)** Bullet Hill. **(G)** Miwok Meadows. **(H)** Chicken Coop Hill.

marsh that cyclically erodes and progrades into tidal mudflats (Figures 1 and 2).

The outer high salt marsh terrace vegetation is historical: it formed bayward of the prehistoric tidal marshes in San Pablo Bay as a result of tidal marsh progradation. This progradation was initially induced by Gold Rush sedimentation (19th-century hydraulic mining outwash) under the influence of both tidal and wave deposition of fine sediment that accumulated from hydraulic mining spoils discharged from the Sacramento River (Atwater and others 1979; Doane 1999). Net progradation of the outer salt

marsh terrace at China Camp continued throughout most of the 20th century, interrupted by marsh–shoreline retreat episodes that began to prevail over progradation by the 1990s (Jaffe and others 1998; Doane 1999). The outer marsh terrace lacks the complex sinuous tidal channel network and high channel density of the prehistoric tidal marsh platform. The break between the contrasting tidal drainage patterns—widely spaced, shore-normal channels with limited dendritic branching of the historical outer salt marsh, and the highly irregular, branched, sinuous, late-Holocene tidal channel system—approximately demarcates the age and structural boundaries



Figure 2 Prograded modern high tidal salt marsh terrace (*Sarcocornia pacifica* dominant) with fringing low salt marsh spreading across mudflats below the relict erosional wave-cut scarp (*Bolboschoenus maritimus* landward and *Spartina foliosa* bayward dominant), southwest end of China Camp Marsh. **(A)** Aerial view of multiple relict erosional scarp boundaries between high salt marsh terrace above remains of *Spartina* litter wrack-lines (arrow; wrack accumulated around the break in slope at the oldest, inner scarp), transitional and low salt marsh, Google Earth image October 25, 2009. **(B)** Well-defined *Spartina* litter wrack-lines along scarp in spring, delineating high marsh terrace and low fringing marsh gradient, May 20, 2007. **(C)** Oblique view along fringing low marsh, north to Jake's Island (center background). Note low marsh extending into few, simple straight shore-normal tidal channels. **(D)** Ground view of scarp-defined abrupt *Sarcocornia/Spartina* zonation. View to southwest, southwest end of China Camp Marsh. April 2011.

between these two marsh sub-units (Figure 1). The high salt marsh terrace is approximately 200 m wide along most of China Camp Marsh between Jake's Island and Chicken Coop Hill, where it fronts the original prehistoric tidal marsh platform and creek system. Southwest of Chicken Coop Hill, the high marsh terrace narrows to less than 120 m wide, and occupies almost the entire tidal marsh profile.

Vegetation of the Outer High Salt Marsh Terrace and Fringing Low Marsh

Two vegetation sub-units of contrasting age, structure and dynamics have developed in the prograded outer tidal marsh: the inner high salt marsh terrace with nearly monotypic stands of robust *Sarcocornia pacifica* (syn. *Salicornia pacifica*; *S. virginica* misap-

plied) and an outer low fringing salt marsh composed of monotypic *Spartina foliosa* (Hopkins and Parker 1984; Li and others 2005) and annually variable, mixed stands of *S. foliosa* and *Bolboschoenus maritimus*, transitional between salt and brackish marsh (Goman 2001). The high salt marsh terrace substrate is composed of stiff bay mud (silty estuarine clay; Reyes clay soils) deposited by both tidal and wave processes, enriched with fibrous organic matter (Goman 2005; Goman and others 2008). Fresh bay mud deposits on top of matted pickleweed litter are evident on the outer terrace after winter storms that also deposit wave-transported wracks of tidal litter. The low fringing salt marsh, approximately 40 to 50 m wide most years, is formed by direct rhizome spread of *S. foliosa* into the soft muds of adjacent bay mudflats, and is subject to cyclic storm wave erosion followed by tidal sediment accretion during post-storm recovery phases. Wave action in winter generally strips the *S. foliosa* stands of senescent leaf litter, leaving the high salt marsh terrace relatively exposed to winter storm wave attack. The two zones are bounded by a relict wave-cut scarp.

High Salt Marsh Terrace Vegetation. *S. pacifica* growth forms on the high marsh terrace are tall (0.3 to 0.4 m), dense, highly branched, and shrubby, rather than prostrate or decumbent low forms common on peaty middle marsh plains of the prehistoric tidal marsh platform. Most *S. pacifica* stands on the terrace are either nearly monotypic or low in diversity (Hopkins and Parker 1984). Regionally, *S. pacifica* is associated with the middle and high salt marsh zones, where it is usually dominant (Grewell and others 2007; MacDonald 1977; Peinado and others 1994).

Vegetation gaps with exposed peaty bay mud, but minimal persistent wrack deposits, appear to be either recolonized by *S. pacifica*, or occasionally by less common perennial halophytic marsh forbs, including *Limonium californicum*, *Distichlis spicata*, *Frankenia salina*, and *Jaumea carnosa*. Other species comprising the high salt marsh terrace vegetation include *Polypogon monspeliensis*, *Cotula coronopifolia*, *Spergularia salina*, and *Spergularia macrotheca*. *Grindelia stricta* is uncommon in the high salt marsh terrace most years. Native salt marsh forbs are generally uncommon on the strongly *Sarcocornia*-

dominated terrace, and are associated with gaps in pickleweed canopies, and well-drained banks of tidal channels and ditches that occur infrequently within the high salt marsh terrace southwest of Jake's Island. Intermittent heavy litter wrack deposits persisting through the growing season appear to initiate dieback patches (vegetation gaps) in the thick pickleweed canopy. Dieback patches are often initially colonized by annual *Atriplex prostrata* while thick wrack debris persists. Vegetation gaps with bare bay mud substrate, exposed after litter mats are dispersed or decomposed, appear to become local, infrequent sites of native salt marsh forb colonization. Large areas of *Sarcocornia* dieback (conspicuous "gray marsh" patches), were evident on segments of the high marsh terrace that were influenced by prolonged waterlogging from high rainfall and frequent over-marsh tidal flooding, and by heavy wrack deposits in the El Niño winter of 1997–1998. *Sarcocornia* dieback in waterlogged and wrack-deposited marsh areas was followed by high abundance of *A. prostrata* the following summer (personal observation). Old wrack deposits in the outer marsh terrace include very old, persistent (embedded in marsh sediment), large woody debris, which consist of trunks and limbs of trees, wrecked docks, and pilings. Large woody debris provide topographic highs in the outer high marsh terrace, and support erratic occurrences of upland weeds perched above the marsh, rooted in the decaying wood, such as *Bromus diandrus*.

Cuscuta pacifica var. *pacifica* (syn. *C. salina* var. *major*), a leafless annual shoot-parasite of *Sarcocornia* and other halophytes (Grewell 2008), is episodically abundant in the high salt marsh terrace, but with high variability among years. It forms conspicuous, brilliant orange mats that temporarily shroud or smother *Sarcocornia*, usually reaching peak abundance in mid- to late summer, particularly in dry, hot summers (Figure 3). *Cuscuta* mats are usually most frequent and extensive on the landward portions of the high salt marsh terrace, often where marsh soil is visibly drying and cracking (likely indicators of hypersalinity). Vegetation gaps in *Sarcocornia* (local dieback or reduced cover and density that influence competition and species diversity) may follow severe *Cuscuta* infestations in California



Figure 3 Extensive infestation of *Sarcocornia*-dominated prehistoric salt marsh by annual parasitic *Cuscuta salina* during a drought year (July 2008). View southeast from Turtle Back Hill. (Photograph courtesy of Amelia Ryan, National Park Service.)

coastal salt marshes (Callaway and Pennings 1998; Grewell 2008), and *Cuscuta* appears to contribute to the vegetation gaps in the high salt marsh terrace of China Camp, along with wrack-deposition processes. Because of the strong seasonality and annual variability in *Cuscuta* cover, it has sometimes been under-estimated as an important or seasonally co-dominant component of China Camp's tidal marsh vegetation (e.g., Li and others 2005).

The geomorphic setting (marsh shoreline orientation to dominant winds, wide mudflats, and open water wave fetch) of China Camp Marsh appears to influence the density and complexity of tidal channel development in the outer high marsh terrace, and thus indirectly influences channel-patterned, local high marsh vegetation structure and plant diversity. The relative homogeneity of the outer high marsh terrace's nearly monotypic *S. pacifica* vegetation is related to its scarcity of natural tidal channels and associated drainage gradients that support the local higher frequency of *Grindelia stricta*, *Distichlis spicata*, *Frankenia salina*, and other high salt marsh forbs. Low-density, simplified tidal drainage patterns are typical of prograded salt marshes subject to strong wave action along the north shore of San Pablo Bay (Atwater and others 1979), including China Camp

(Doane 1999). The density of narrow, closely spaced, short ("herringbone" pattern) shore-normal tidal channels at the outer marsh edge increases westward towards Gallinas Creek, as the marsh edge becomes increasingly sheltered from exposure to the wave erosion and deposition processes (maximum open bay fetch) of San Pablo Bay. The channel-deficient, wave-exposed marsh edge of China Camp Marsh is similar to the structure of prograded, flat, relatively featureless fringing salt marsh terraces between Sonoma Creek and Petaluma River on the northeastern shore of San Pablo Bay. These marsh terraces increase in channel density, and channel-patterned high salt marsh diversity, as they grade toward the wave-sheltered mouths of Sonoma Creek and the Petaluma River, as China Camp Marsh does along Gallinas Creek.

Relict Wave-Cut Scarp: Vegetation Patterns and Physical Processes. There is a relatively sharp vegetation and topographic boundary between the high salt marsh terrace and the fringing, low, salt marsh vegetation, rather than a continuous elevation gradient and ecotone. The outer boundary of the high marsh terrace is marked by relict wave-cut scarp (marsh cliff), which is formed in cohesive bay mud, with dense *Sarcocornia* root mesh supplying the relatively high shear strength (Pestrong 1965, 1972) sufficient to maintain near-vertical eroded slopes. The scarp maintains a dynamic and relatively straight outer edge of the high marsh terrace vegetation, and a sharp discontinuity with the wide, low marsh zone below it (Doane 1999; Figure 2). The scarp is approximately 0.3 to 0.5 m high, varying with phases of accretion or erosion. Stepped marsh terrace topography is typical of relict wave-cut salt marsh terrace scarps that have cyclic erosion and progradation (Allen 1989, 2000; Pringle 1995). Wave-induced marsh scarp retreat rates are a function of wave power and sediment supply (Schwimmer 2001), modified by wave attenuation from the width and seasonally variable structure of fringing marsh vegetation below the scarp (Yang and others 2012; Möller and Spencer 2002). The low marsh fringe is, therefore, ecologically and geomorphically important in maintaining the relict marsh scarp profile and dynamics. Salt marsh terrace scarps may be masked by vegeta-

tion during the recovery or progradation phase or slow erosional retreat (Moreira 1992). The high marsh terrace scarp at China Camp is visible mostly within the inaccessible outer marsh, in aerial images, and a few roadside viewing points (Figure 2).

Microtopographic indicators of intermittent erosion (rills, spurs, and furrows; Allen 2000) occur along the scarp, despite the closed canopy of vegetation above and below the scarp. Erosional microtopography within the scarp is often evident in the scarp in spring, after winter storms, indicating partial reactivation of the scarp in some years. Wave scour and thinning or leveling of *Sarcocornia* canopies is often evident a few meters landward of the scarp crest in spring, after winter storm wave activity, and before vegetative regeneration. No other species are common in the wave-scoured zone within and behind the scarp, other than occasional *Atriplex prostrata*. The now-relict scarp was particularly active during the El Niño storm erosion event of 1997–1998, which caused scour of the fringing cordgrass marsh, scarp retreat, and large wrack deposits on the high marsh terrace. Some years, dense wracks of *Spartina* leaf litter are episodically concentrated along the topographic break at the toe of the scarp (Figure 2), where they may either delay re-emergence of the *Bolboschoenus* or *Spartina* canopy, or cause temporary dieback, depending on the thickness and duration of the wrack deposit.

Low Fringing Tidal Marsh. The low fringing tidal marsh below the relict wave-cut scarp is mostly dominated by California cordgrass (*Spartina foliosa*; Li and others 2005), often with an intermediate and usually inconspicuous zone of abundant *Bolboschoenus maritimus*, which is mixed with *Spartina* or *Sarcocornia* in years of high rainfall and relatively low salinity (Figure 2). Since the 1997–1998 El Niño event, the outer edge of the fringing *Spartina* marsh below the relict scarp has been dynamically stable or prograding (clonal spread into mudflats on a continuous gradient), with relatively minor cyclic erosion and recovery of the bayward edge. Most years, after winter wave erosion events, the outer rhizome front of the *Spartina* belt appears to be spreading into the mudflat. Smaller wave-cut scarps also form within the low fringing *Spartina*-

dominated salt marsh as it accretes bay mud, increasing its elevation and steepness. Monotypic stands of *S. foliosa* consistently occur bayward of the intermittent internal low marsh scarp, but mixed stands of *S. foliosa* and *B. maritima* can dominate the inner zone. Multiple salt marsh scarps that form stepped terrace profiles (erosional unconformities in marsh zone age) and associated vegetation zonation, are not common in San Francisco and San Pablo bays, where strong net scarp erosional retreat of tidal marsh is prevalent; examples of stepped tidal marsh terraces occur at Triangle Marsh (Tiburon), Emeryville Crescent, and at the headland-bound pocket salt marshes north of China Camp Beach (south of Buckeye Point), but China Camp Marsh exhibits one of the clearest and largest examples of this dynamically stable vegetation structure.

The development of *Bolboschoenus maritima* stands below the high marsh terrace scarp, in the inner zone of the fringing low marsh, appears to correspond with brackish phases in years of high rainfall and low salinity. *B. maritima* colonies or zones in the fringing low marsh are visually distinguishable from cordgrass in brackish years by their slightly darker-green foliage, but have not been detected by remote sensing, at least in some years (Li and others 1995). The error rate of *Bolboschoenus* stand classification by remote sensing methods is significantly higher than that of *Spartina* (Zhang and others 1997). In drought years of high salinity (particularly high salinity early in the growing season), *B. maritimus* remains mostly vegetative, and its culms scarcely exceed the height of cordgrass before they become senescent in late spring or early summer. Variable development of bulrush canopy height and density, especially in years of high marsh salinity, may limit discrimination of bulrush stands within the *Spartina*-dominated low marsh at China Camp. *B. maritimus* can remain dormant as corn-like buds on rhizomes through several years of excessive salinity (Percy and Ustin 1984; Ustin 1984), so its lack of emergence each year does not imply absence or extirpation in the fringing low marsh. At China Camp, mean winter and summer aqueous salinities in the 1970s were reported to range from approximately 20‰ to 30‰ (Atwater and others 1979), a range which are inhibitory to

growth of *Bolboschoenus maritimus* (Kantrud 1996; Ustin 1984). Average annual salinity at China Camp from 1988 to 1994 was also relatively high, ca. 27‰ (Malamud–Roam and Ingram 2004, citing USGS data), which suggests that the relative abundance and visibility of *Bolboschoenus* in the fringing low marsh may have been low (or practically undetectable) until after the series of wet years that followed the major El Niño event of 1997–1998.

Vegetation of the Prehistoric Tidal Marsh Platform

The inner belt of prehistoric tidal marsh vegetation is developed on the more complex environmental gradients and substrates that are associated with sinuous networks of stable prehistoric tidal creeks, and contacts terrestrial soils of alluvial valleys and hillslopes along its landward edges. The interior prehistoric marsh is late Holocene: the basal strata of the marsh developed since sea level stabilized near modern elevations during the last 4,500 yr BP, but the modern upper marsh soil horizons are only a few centuries old (Goman 2005; Goman and others 2008; Malamud–Roam and Ingram 2004). Pollen and sediment stratigraphy (long cores to depths up to 6 m below the modern marsh surface) reveals that most (67%) of the marsh's depositional history was dominated by relatively brackish—rather than saline—tidal marsh conditions (Goman 2005; Goman and others 2008) as well as by alternating unvegetated mud and marsh deposition episodes, which have been interpreted as disequilibrium phases of rapid sea-level fluctuations (Goman 2005). The stratigraphy of China Camp reveals that even in its brief (ca. 4,000 yr) late-Holocene history, its vegetation composition has fluctuated markedly in response to climate and sea level (Malamud–Roam and others 2007), and has not maintained a steady-state or dynamic equilibrium vegetation that resembles familiar historical conditions.

Modern salt marsh vegetation is established on geomorphically mature tidal marsh landforms and soils, including low-relief natural levees along larger tidal sloughs, nearly flat peaty marsh plains (higher organic matter content than the young bay mud of the historic prograded high marsh terrace) and

dynamic steep tidal creek banks with high turnover of slump blocks and scarps (Gabet 1998; Fagherazzi and others 2004). Depressional marsh-plain salt pans (pools, ponds), such as those of Petaluma Marsh, are a typical feature of the geomorphically mature or prehistoric tidal marsh plains of the San Francisco Estuary (Grossinger 1995; Baye and others 2000), but they do not occur in the prehistoric salt marsh platform of China Camp, and there is no indication that salt marsh pan features ever developed here. The distribution of tidal marsh pans correlates with their position along the stream-influenced gradients of tidal sloughs in other San Pablo Bay tidal marshes (Grossinger 1995). Only poorly drained marsh plains with prostrate *Sarcocornia* and *Distichlis* vegetation occupy the large drainage divides where pans potentially form.

Salt Marsh Plains of Drainage Divides. The middle marsh zone, occupying the broad, flat drainage divides between tidal channels, is a mosaic of relatively decumbent, low (0.2 to 0.3 m high) *Sarcocornia pacifica* assemblages, which include native salt marsh zone forbs and *Distichlis spicata* (Figure 4). The patchiness and species diversity of the prehistoric marsh plain contrasts with the extensive tall, dense, shrubby near-monotypic stands of *S. pacifica* on the outer high marsh terrace. Relatively common associates of *S. pacifica* in the interior marsh plain include *Distichlis spicata*, *Cuscuta pacifica* var. *pacifica*, *Jaumea carnosa*, and *Frankenia salina*. Infrequent species of the middle salt marsh plain include *Triglochin concinna*, *T. maritima*, *Spergularia salina*, *S. macrotheca*, *Polypogon monspeliensis*, *Limonium californicum*, *Cotula coronopifolia*, and *Atriplex prostrata*. The relative abundance of *Sarcocornia* and associated salt marsh forbs and *Distichlis* varies among years, typically with the increasing relative abundance of *Sarcocornia* during years of low rainfall/high salinity, which is consistent with local experimental investigations (Ryan 2009; Ryan and Boyer 2011).

High Salt Marsh Vegetation Bordering Tidal Creeks. One of the most conspicuous salt marsh vegetation patterns corresponds with the drainage, elevation, and sedimentation gradient patterns associated with tidal creeks (Allen 2000). Narrow and often dense and continuous bands of robust, semi-evergreen *Grindelia*



Figure 4 (A) Tidal creek patterning of the prehistoric interior salt marsh plain vegetation: shrubby *Sarcocornia* and *Grindelia* dominate the high marsh that borders creek banks; patchy mosaics of *Sarcocornia* (dominant), *Distichlis*, and common salt marsh forbs comprise the plain's vegetation. June 2006. (B) Nearly complete submergence of marsh platform vegetation during winter perigeon high tide during El Niño winter. View southeast from Turtle Back Hill, January 30, 2010.

stricta var. *angustifolia*, a perennial subshrub, delineate a zone of tall, dense, diverse high salt marsh that borders the banks of tidal creeks (Figures 4, 5, and 6). Tidal channels are associated with a narrow high marsh zone of tidal drainage and sedimentation gradients that support increased plant species diversity in Petaluma Marsh (Sanderson and others 2000), the other large remnant prehistoric tidal marsh in San Pablo Bay. The zone of creek-patterned high salt marsh vegetation at China Camp extends up to several meters from the edge of creek banks, similar to zonation of the lower-order channels of Petaluma Marsh, in relation to channel size and depth (Hopkins and Parker 1984; Sanderson and others 2000). The tall, semi-evergreen canopy of *G. stricta* on creek banks at China Camp rises up to approximately 1.0 m above the marsh substrate of natural creek bank levees, and is the only emergent vegetation during the extreme high (perigeon) tides of winter that completely submerge the marsh plain (Figure 4), particularly in years of El Niño-elevated mean sea level. *Grindelia* is almost entirely absent in the marsh plain vegetation of drainage divides, and when it does occur there, it does not develop the robust, tall sub-shrub growth form of tidal creek banks. The abundance and continuity of local, channel bank *Grindelia* stands, and the size of individual plants, has been observed to decline

markedly during high salinity and drought periods of the 1970s to 1980s (Phyllis M. Faber, consulting botanist, pers. comm., 2000; V. Thomas Parker, San Francisco State University, pers. comm., 2012) and early 1990s. The continuous, tall, flood-emergent canopy structure of *Grindelia* is important flood escape cover habitat for endangered California clapper rails that travel and forage along tidal channels (Albertson and Evens 2000), as well as for small mammals that inhabit the marsh plain, which include the endangered salt marsh harvest mouse (Shellhammer 2000). *Sarcocornia* also develops shrubby, tall growth forms (up to approximately 0.6 m high) in the high marsh zone that borders tidal creeks, similar to its growth forms on the high salt marsh terrace. It occurs in sporadic, discontinuous patches, often with low vigor, along the high marsh ecotones that border hillslopes. *Frankenia* and *Distichlis* stands are also relatively abundant, robust, and frequent near the crests of channel scarps and natural creek levees.

Low Salt Marsh Vegetation Dynamics of Tidal Creek

Banks. The structure of tidal creek bank vegetation is influenced by cyclic erosion and accretion processes that are driven by the tidal hydrology of channels. Erosional slump blocks are frequent along China Camp's mature tidal creeks (Figures 5 and 6), particularly after stormy winters. Cohesive, peaty

slump blocks displace high salt marsh vegetation from bank tops and natural levees to intertidal elevations too low to sustain them, causing dieback and death. Slump blocks subsequently become colonized by *Spartina foliosa* (Gabet 1998) and trap fine sediment (Figure 7), causing localized cyclic salt marsh succession back to *Sarcocornia* and associated species (Gabet 1998). This process results in the dynamic stability of creek banks, with a high turnover of low- and high-marsh vegetation types, and unstable intermediate stages of conversion between them, at any given creek bank location. Channel bank edges vary from near-vertical erosional scarps with overhanging dense *Sarcocornia*-*Distichlis*-*Frankenia* canopies, to dense *Spartina* low marsh (Figures 5 and 6).

During years of high rainfall and low channel salinity during the growing season, *Bolboschoenus maritimus* locally establishes or regenerates in sporadic but sometimes large (up to 5 m long) colonies within tidal creek banks, among dominant *Spartina foliosa* stands. *B. maritimus* is otherwise restricted to brackish marsh ecotones associated with terrestrial ecotones of the prehistoric marsh platform.



Figure 5 Tidal marsh creek vegetation. *Grindelia*, *Distichlis*, and *Sarcocornia* occupy high marsh above the bank crest. *Spartina foliosa* occupies the banks and slump blocks.

Brackish Tidal Marsh

Extensive areas of transitional salt-to-brackish tidal marsh occur in Miwok Meadows and Back Ranch Meadows (Figures 1 and 7), landward of N. San Pedro Road, where daily tidal flows are partially choked but maintained by culverts connected to tidal creeks bayward of the road, resulting in a damped tidal range of about 60 cm in channels. Choked tidal flows, combined with substantial terrestrial freshwater discharges (shallow groundwater, runoff, and ephemeral streams), reduce salinity in the brackish marsh. The brackish tidal marsh plains of Miwok Meadows Marsh and Back Ranch Meadows Marsh are also remnants of the prehistoric tidal marsh platform that intergrades with a drowned alluvial valley that support freshwater marsh and willow riparian scrub.

The Miwok Meadows Marsh plain supports a mosaic of patches dominated by *Distichlis*, *Sarcocornia*, *Bolboschoenus*, and *Jaumea*, with *Grindelia* again dominating narrow zones that borders tidal creeks. Beneath the *Sarcocornia* canopy, a sparse ground layer of *Isolepis cernua* and *Juncus bufonius* occurs sporadically, particularly near the terrestrial ecotone. During drought years, saline or hypersaline condi-



Figure 6 Tall (>0.6 m), dense *Sarcocornia* and *Grindelia* stands dominate the high marsh above a relict channel scarp along a large tidal creek. *Spartina foliosa* dominates the slump blocks below the scarp, accreting recent sediment deposits in the sheltered lee of the blocks and in the canopy.

tions can develop locally in the brackish marsh, causing dieback of *Bolboschoenus* and expansion of *Sarcocornia* stands. Brackish marsh and pans also support local or intermittently abundant stands of non-native *Cotula coronopifolia*, *Juncus bufonius*, and *Polypogon monspeliensis* that are otherwise minor elements in the fully tidal salt marsh. Back Ranch Meadows Marsh brackish marsh vegetation is distinct in supporting large monotypic and mixed stands of *Juncus balticus*, extensive monotypic stands of *Carex praegracilis*, and the only population of *Potentilla anserina* at China Camp.

Back Ranch Meadows and Miwok Meadows marshes lack the characteristic dominant coarse tules, bulrushes, and cattails (e.g., *Schoenoplectus acutus*, *S. californicus*, and *S. americanus*) that are found in the low, intertidal brackish marsh of northern San Pablo Bay. *Typha latifolia* is restricted to the fresh-brackish terrestrial ecotone of these brackish marsh areas, where it is subject to dieback and recovery cycles in relation to drought and wet climate cycles (see “Terrestrial Ecotones of Tidal Marsh”).

A few tidal marsh pans (marsh plain salt pans) occur in the brackish Miwok Meadows Marsh landward of

North San Pedro Road (Figure 8), but pans are otherwise very rare in the fully tidal marsh bayward of the road. Pan beds in the brackish marsh are persistently flooded by spring tides and winter rainfall for most of the year. They support dense stands of *Ruppia maritima* (submerged aquatic vegetation beds) in spring and early summer. *Ruppia* usually develops abundant epiphytic filamentous algal growth by summer, and goes dormant. The relatively stable marsh edges of brackish pans are associated with *Distichlis*, *Sarcocornia*, and *Jaumea*. *Bolboschoenus* marsh edges invade pan beds in years of low salinity. In contrast, the few small and shallow salt marsh channel pans at China Camp lack *Ruppia*.

A fully tidal brackish marsh with local dominance by tules and cattails occurs at the south end of China Camp Marsh (Figure 1), where local canyon drainage and a seep has established a narrow, dense stand of sharply zoned *Schoenoplectus acutus*, *Typha latifolia*, and *Bolboschoenus maritimus*, which grades directly into a *Sarcocornia* marsh that supports locally frequent *Triglochin maritima*—apparently the largest and most robust populations of *T. maritima* at China Camp (Figure 9). This disjunct occurrence of tule-bulrush tidal marsh occurs immediately below a wil-



Figure 7 Brackish tidal marsh, China Camp. **(A)** Brackish tidal marsh (choked tidal flows through culverts beneath San Pedro Road) of Miwok Valley Marsh exhibits a patchwork of *Bolboschoenus*, *Distichlis*, and *Sarcocornia*-dominated vegetation. *Grindelia* dominates channel and ditch bank crests. Oak woodland and valley grassland flank the marsh. Note riparian woodland and freshwater marsh in background, associated with alluvial fan of a small canyon stream. **(B)** Brackish marsh gradient between terrestrial riparian thickets (*Salix lasiolepis*) and *Sarcocornia* salt marsh, with uneven, patchy zones of *Carex praegracilis*, *Juncus balticus*, *Potentilla anserina*, and *Typha latifolia*. Back Ranch Meadows Marsh. April 2011.

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low grove at the limit of tidal flooding below N. San Pedro Road. Tule–bulrush marsh zones are otherwise now found only in northern San Pablo Bay, primarily in upstream reaches of Napa Marsh, and very locally in upper Petaluma Marsh. *B. maritimus* also occurs along the landward edge of the tidal marsh plain where freshwater seepage from hillslopes or roadsides appears to cause local brackish gradients (Figure 9) that borders the terrestrial ecotone.

Terrestrial Ecotones of Tidal Marsh

The brackish tidal marshes of China Camp are formed by terrestrial freshwater discharge gradients between freshwater wetlands with tidal salt marsh, and represent the broadest terrestrial wetland ecotones of China Camp Marsh. Where other local terrestrial vegetation types (valley grassland, oak woodland, mixed

evergreen forest, riparian woodland, and freshwater marsh; Howell and others 2007) contact or intergrade with tidal salt marsh, they also form narrower zones of terrestrial–tidal marsh ecotones on original soils, some of which support distinctive and regionally uncommon plant assemblages. Dikes, ditches, and agricultural conversion have intensively altered or completely destroyed former terrestrial ecotones that were prevalent in most of the San Francisco Estuary’s tidal marshes, leaving a small number of prehistoric tidal marsh ecotones in the San Pablo Bay and Suisun Marsh, and extremely few in San Francisco Bay (Baye and others 2000; Boyer and Thornton 2012). China Camp retains some of the most intact and diverse, distinctive examples of terrestrial ecotones of tidal marsh in the estuary, although they cannot be assumed to represent the historic range of terrestrial ecotone variability in the North Bay.



Figure 8 Tidal marsh pans at China Camp. (A, B) Small channel pans (relict cut-off segments of tidal channels) in fully tidal salt marsh lack *Ruppia*. (C) Brackish marsh pan with choked tidal hydrology supports continuous cover by *Ruppia* across the bed in spring 2008.



Figure 9 Brackish high tidal marsh vegetation at China Camp east of North San Pedro Road with unconfined tidal flooding. **(A)** Tule–bulrush–cattail (*Schoenoplectus acutus*, *Bolboschoenus maritimus*, *Typha latifolia*) brackish tidal marsh between tidal pickleweed salt marsh and willow grove, south end of China Camp Marsh, in association with seasonal stream drainage and perennial groundwater discharge. **(B)** Aerial view of brackish tidal marsh shown in (A), Google Earth image October 17, 2012. **(C)** Narrow zone of *Bolboschoenus maritimus* bordering N. San Pedro Road north of Back Ranch Meadows Marsh, appearing to track hillslope seepage under the roadbed.

Multiple types of tidal marsh vegetation ecotones with terrestrial grassland, riparian scrub, and freshwater marsh occur at China Camp,

***Elymus triticoides* and *Juncus balticus* Ecotones.** A distinct vegetation zone occurs in the terrestrial ecotone along high tidal marsh, composed of co-dominant perennial, rhizomatous, dense sod-forming native rush and grass species *Elymus triticoides* (syn. *Leymus triticoides*) and *Juncus balticus*. The abrupt, conspicuous *Elymus*–*Juncus* zone between the upland hillslope bunchgrass/annual forb grassland and the tidal marsh is usually less than 2 to 3 m wide at China Camp (depending on slope; Figure 10). Since neither dominant species occurs in the adjacent ter-

restrial or tidal vegetation beyond this zone at China Camp, the status of this assemblage as an “ecotone” is ambiguous; it may properly be regarded as a distinct tidal marsh edge vegetation type rather than a vegetation transition zone. *Distichlis spicata* from the tidal salt marsh does extend locally into the *Elymus*–*Juncus* zone, but it is not generally dominant there. The *E. triticoides* zone, either single-species dominant or in association with *Juncus balticus*, recurs as a characteristic local remnant feature at many other prehistoric tidal marsh terrestrial ecotones formed on alluvial fans or clay loam hillslopes in the San Francisco Estuary (e.g., upper Newark Slough, San Francisco Bay; Whittell and Giant marshes, Point



Figure 10 High salt marsh ecotone with valley grassland of south-facing hillslopes is typically dominated by (A) co-dominant *Elymus triticoides* and *Juncus balticus*. (B). *Grindelia* abundance is typically confined to tidal creek banks rather than natural upland edges, but can locally dominate the lower edge of the high marsh zone. June 2008.

Pinole; Petaluma Marsh; Rush Ranch; Suisun Marsh). *E. triticoides* ecotones appear to have expanded at China Camp in the last two decades, as at Rush Ranch. The relative abundance of *Juncus balticus* in hillslope edges of tidal marsh increases in the vicinity of hillside seeps and road culverts, and on north-facing slopes (Figure 11); *E. triticoides* tends to dominate the assemblage otherwise. Both clonal perennial graminoid species exhibit relatively low salt tolerance compared with adjacent salt marsh halophytes, but they extend into the upper zone of *Sarcocornia*–

Distichlis salt marsh, possibly aided by clonal integration (Evans and Whitney 1992). Neither extends deep into the tidal marsh plain, and neither colonizes creek bank high marsh zones at China Camp tidal salt marshes. In contrast, *J. balticus* is common or locally dominant in brackish marsh plains of Suisun Marsh. The *Juncus*–*Elymus* zone is notably poor in typical invasive non-native species widespread in tidal marsh levees of other Marin baylands. *Grindelia* is generally infrequent or absent in the dense sod formed by rhizomatous *Elymus*–*Juncus* ecotone, but it locally occurs at the lower edge, particularly near indicators of freshwater seeps.

Riparian Vegetation Ecotones. The perennial *Asteraceae* component of the historical “willow-composite” riparian–high salt marsh ecotone species assemblage of San Francisco Bay, reconstructed by Cooper (1926), is not represented at China Camp Marsh. *Baccharis glutinosa* (syn. *B. douglasii*) *Euthamia occidentalis*, and *Symphotrichum chilense* (syn. *Aster chilensis*) occur locally in terrestrial ecotones of high brackish marsh in San Pablo Bay and Suisun Marsh, but they apparently do not occur at China Camp. The only clonal perennial *Asteraceae* species in China Camp terrestrial ecotones is the *Ambrosia psilostachya*, a moderately salt-tolerant forb (Salzman and Parker 1985), which occurs locally at the south-facing toe of Jake’s Island slopes, and at China Camp beach. This species also has an element of terrestrial ecotones at the Rush Ranch tidal marshes that borders Suisun Slough (Whitcraft and others 2011).

In contrast, mesic woody riparian scrub elements, including *Umbellularia californica*, *Toxicodendron diversilobum*, *Sambucus mexicana*, *Scrophularia californica*, *Rubus ursinus*, *Rosa californica*, *Carex barbarae*, and *Baccharis pilularis*, have either persisted or regenerated spontaneously in multiple local patches along tidal marsh–terrestrial ecotones at China Camp, particularly at the southwest end and north of Back Ranch Meadows along N. San Pedro Road. These relatively salt-sensitive species are rooted immediately above or even within the storm high-tide line, marked by old drift-lines of estuarine plant litter. On the dry north-facing slopes of Turtle Back Hill, oak woodland canopies replace riparian scrub, and overhangs or contacts tidal salt marsh, creat-



Figure 11 *Juncus balticus* locally dominates the high salt marsh ecotone and intergrades with *Distichlis*-dominated salt marsh along the northwest slope of Turtle Back Hill



Figure 12 Riparian woodland and brackish to fresh Cyperaceae-dominated marsh (*Juncus balticus*, *Carex praegracilis*, *Eleocharis macrostachya*) border tidally choked brackish *Sarcocornia*–*Distichlis* marsh west of San Pedro Road

ing dense shade and litter-dominated tidal marsh edges. *Quercus agrifolia*, *Heteromeles arbutifolia*, *Baccharis pilularis*, *Toxicodendron diversilobum*, and *Umbellularia californica* rooted above the tide line extend branches up to 2 m or more into tidal salt marsh at some locations where they dominate surface cover.

Freshwater–Brackish Wetland Terrestrial Ecotones.

Willow scrub, wetland sedge meadow, and oligohaline emergent (freshwater) marsh form terrestrial ecotones with brackish tidal marsh in the low-gradient alluvial valley of Back Ranch Meadows, landward of N. San Pedro Road (Figures 9 and 12). These form a patchy, irregularly zoned ecotone that fluctuates in position and composition during drought and high rainfall cycles (Figure 13). Willow thickets (*Salix lasiolepis*) with ground layers dominated by shade-tolerant and slightly salt-tolerant *Carex praegracilis* intergrade with fresh–brackish high marsh assemblages, rush–sedge meadows, and emergent freshwater marsh, including *Typha latifolia*, *Carex praegracilis*, *Eleocharis macrostachya*, *Isolepis cernuus*, *Juncus balticus* and *J. mexicanus*, *J. effusus*, *J. phaeocephalus*, and *Potentilla anserina*. These sedge–rush assemblages intergrade or overlap in patches with a brackish marsh plain dominated by *Sarcocornia*, *Distichlis*, and *Jaumea* (Figure 7). This brackish–fresh wetland gradient is flooded with estuarine waters during extreme high winter tides. During drought years, the *Typha* stands in the freshwater–oligohaline–brackish high tidal-marsh ecotone below the willow thicket at Back Ranch Meadows die back, and are invaded rapidly by *Distichlis* and *Sarcocornia* (Figure 13). *Carex praegracilis* also expands in the willow ground layer when the canopy thins during droughts, and light increasingly penetrates to the ground layer. Sedge–rush meadow dominated by *C. praegracilis* in the brackish ecotone, in contrast, appears to resist rapid displacement during droughts. Brackish marsh ecotypes of *Achillea millefolium* and *Scrophularia californica*, widespread in Petaluma, Napa–Sonoma, and Suisun brackish tidal marshes, are apparently absent at China Camp.

Groundwater seeps from upland and alluvial slopes are evident in local patches or zones of brackish marsh ecotone vegetation along some hillslope and roadside locations in years of high rainfall. These are indicated by atypical high marsh zones with locally abundant *Bolboschoenus maritimus* (Figure 9).

Uncommon Native Tidal Marsh Plants

China Camp Marsh supports only two plants currently considered to be rare or special-status taxa.



Figure 13 Senescent, moribund stands of *Typha latifolia* during drought years are rapidly invaded by *Distichlis* (A) and *Sarcocornia* (B) in the fluctuating fresh-brackish marsh ecotone

Populations of *Chloropyron maritimum* var. *palustre* (syn. *Cordylanthus maritimus* ssp. *palustris*; northern salt marsh bird's-beak, an annual halophytic hemiparasitic forb) have been reported from Bucks Landing, immediately north of China Camp, but this regionally rare plant has not spread into China Camp marshes. In San Francisco Bay, this historically widespread species is restricted to Marin County bay-shores, with the exception of one recently reported population at Newark, in Alameda County (Reder 2011). The annual forb *Polygonum marinense* occurs locally in high brackish marsh edges of the north side of Miwok Meadows Marsh, and at scattered locations at the southern shorelines of China Camp salt marshes (see Appendix A). This putative native “rare” salt marsh annual is now widespread in San Pablo Bay, and may be a cryptic, non-native introduced plant (Howell and others 2007; Costea 2012, in Baldwin and others 2012).

Rare tidal marsh ecotypes of *Castilleja ambigua*, another annual hemiparasitic forb, historically known from Mill Valley, Corte Madera, and Novato tidal marshes (now extirpated; Baye and others 2000; Howell 1970), have not been detected in remnant prehistoric tidal marsh at China Camp. Other native salt marsh annuals that were historically common in or near the terrestrial ecotones of tidal marshes, such as *Lasthenia glabrata*, are also absent at China

Camp, despite the presence of suitable habitat. In contrast, *L. glabrata* has persisted at other prehistoric tidal marsh remnants in the North Bay and Suisun Marsh (Petaluma Marsh at Lakeville, Rush Ranch, and Whittell Marsh).

Glaucous-leaved salt marsh ecotypes of *Festuca rubra* are common in Drakes Bay and Tomales Bay tidal marshes, but in the San Francisco Estuary they are unique to China Camp, where they occur locally in the high salt marsh on the northeastern shore of Turtle Back Hill. Non-glaucous terrestrial ecotypes of this species are otherwise locally common on dry grassland of hillslopes above salt marshes from San Rafael (Marin Islands) to Richardson Bay. The north shore of Turtle Back Hill also supports two other species seldom reported from high tidal marsh edges of San Pablo Bay: *Lotus purshianus* (growing extensively among *Distichlis* and *Salicornia*) and a very small high tidal marsh population of *Toxicoscordion fremontii* (syn. *Zigadenus fremontii*) that may be a vestige of the Marin halophytic population still recognized taxonomically as *Z. fremontii* var. *salsus* (originally described by W. L. Jepson, and reported by Howell as “rare along the edge of salt marshes, as ... near San Antonio Creek where it grows with *Distichlis* and *Salicornia*” [Howell 1970; Howell and others 2007]). No other populations of this variety are currently known from San Pablo Bay or Suisun

Marsh tidal marsh edges. *Zeltnera trichantha* (syn. *Centaurium trichantha*), a slender annual forb, occurs locally at several locations in the high tidal or brackish marsh zone of China Camp near Turtle Back Hill and Back Ranch Meadows, bordering hillslopes and road fills. This is the only known current salt marsh location remaining in San Pablo and San Francisco Bays for this species, which was historically present in their tidal marsh edges (Baye and others 2000).

Exotic and Invasive Tidal Marsh Plants

Compared with most San Pablo Bay tidal marshes, China Camp has escaped—to date—the brunt of regional invasions by exotic salt marsh species, mostly from Europe and Asia. In recent years, for example, perennial pepperweed (*Lepidium latifolium*), Mediterranean tarplant (*Dittrichia graveolens*) and Australian or Pacific bentgrass (*Agrostis avenacea*) have rapidly invaded disturbed levees and high tidal marsh edges in San Pablo Bay. *L. latifolium* is limited to local disturbed brackish marsh edges at the north and south end of China Camp, above and below N. San Pedro Road. The scarcity of *L. latifolium* and other ubiquitous upland ruderal forbs of North Bay levees (e.g., *Raphanus sativus*, *Brassica nigra*, and *Conium maculatum*) in the terrestrial ecotones of China Camp Marsh likely results from the marsh's lack of bay mud levees (deposition of artificially drained estuarine clay-silt sediments on steep slopes above tidal elevations) and the periodic levee maintenance disturbance by capping with anoxic, sulfidic bay mud (Baye 2000).

The annual forb *Dittrichia graveolens* has to date (2012) remained very infrequent in the roadside tidal marsh edges of China Camp. A non-native Algerian sea-lavender (*Limonium ramosissimum*) has recently invaded Richardson Bay, but has not yet spread to suitable habitat at China Camp. *Juncus gerardii*, an invasive clonal rush in brackish marshes in eastern San Pablo Bay and western Carquinez Straits (Point Pinole), has not yet been detected in China Camp or elsewhere in western San Pablo Bay, but may be expected if it is not eradicated (Brenda J. Grewell, U.C. Davis and USDA-ARS, pers. comm., 2011; personal observation).

Hybrid smooth cordgrass (*Spartina foliosa* × *alterniflora*), arguably the greatest invasive non-native plant threat to the estuary's tidal marshes, has established at least once in China Camp (Matthew Ferner, National Estuarine Research Reserve, pers. comm., 2012), with identification from selected molecular genetic markers tested by the Invasive *Spartina* Project, but the full abundance and distribution of the population is difficult to determine because of the inherent uncertainties of identifying morphologically cryptic introgressant (hybrid backcross) genotypes. Morphologically atypical *S. foliosa* phenotypes (see Appendix A) with intermediate hybrid traits (possibly multiple-generation backcrosses of *S. foliosa* and hybrids that lack markers), have been detected at multiple locations at China Camp Marsh (pers. obs.) This invasive and often cryptic hybrid/introgressant swarm is subject to ongoing eradication efforts by the Invasive *Spartina* Project of the California Coastal Conservancy. The spread of introgressant *S. foliosa* with greater wave tolerance, sediment-stabilizing ability, growth rates, and physiological tolerance to salinity and waterlogging (regardless of hybrid plant size) may significantly alter the erosion and progradation patterns of China Camp Marsh's fringing marsh/mudflat zone, as well as its prehistoric tidal channel networks.

Many non-native wetland and upland weeds occur in or near the drift-lines of the uppermost marsh edges, especially in the vicinity of road culverts and disturbed roadside fill. These species seldom become abundant or highly invasive in China Camp tidal marsh vegetation; they include *Atriplex prostrata*, *Bromus hordeaceus*, *Cotula coronopifolia*, *Hordeum gussoneanum*, *Festuca perenne*, *Lotus corniculatus*, *Lythrum hyssopifolium*, *Mentha pulegium*, *Polypogon monspeliensis*, *Parapholis incurva*, *Sonchus oleraceus*, and *Spergularia rubra*.

CONCLUSIONS

China Camp's tidal marshes conserve regionally rare and exceptionally well-preserved examples of salt marsh vegetation within a relatively intact late-Holocene tidal marsh platform, including multiple types of tidal marsh-terrestrial ecotones with distinctive

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native plant species assemblages. China Camp's remnant tidal marsh plant assemblages have some significant similarities with other prehistoric tidal marshes in the San Francisco Estuary. Most other prehistoric tidal marsh remnants in the Estuary, however, have strongly altered or agriculturally reclaimed (diked) terrestrial edges that are dominated by mostly non-native vegetation. China Camp's tidal marsh vegetation, in contrast, has retained some complex terrestrial ecotones with predominantly native terrestrial vegetation, and lacks a history of intensive agricultural modification. The complex vegetation structure of China Camp's prehistoric tidal marsh contrasts with the relatively homogenous, broadly zoned salt marsh vegetation of the historic, prograded, outer high salt marsh terrace, which was formed with relatively simple topography and drainage patterns. China Camp Marsh has suffered relatively little from regional invasions by non-native tidal marsh plants, even in recently formed (post-reclamation era) portions of its tidal marshes. China Camp Marsh provides outstanding opportunities for research on mature, diverse tidal marsh vegetation, and is important as a regional reference site for tidal marsh management and restoration planning.

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REFERENCES

- Albertson JD, Evens JG. 2000. California clapper rail. In: Olofson PR, editor. 2000. Goals Project. 2000. Baylands ecosystem species and community profiles: life histories and environmental requirements of key plants, fish, and wildlife. San Francisco Bay area wetlands ecosystem goals project. Oakland (CA): San Francisco Bay Regional Water Quality Control Board. p 332–341.
- Allen JRL. 1989. Evolution of salt-marsh cliffs in muddy and sandy systems: a qualitative comparison of British west-coast estuaries. *Earth Surface Processes and Landforms* 14:85–92.
- Allen JRL. 2000. Morphodynamics of Holocene salt marshes: a review sketch from the Atlantic and southern North Sea coasts of Europe. *Quaternary Science Reviews* 19:1155–1231.
- Atwater BF, Conard SG, Dowden JN, Hedel CM, MacDonald RL, Savage W. 1979. History, landforms and vegetation of the estuary's tidal marshes. In: Conomos TJ, editor. *San Francisco Bay: The Urbanized Estuary*. San Francisco (CA): Pacific Division of the American Association for the Advancement of Science. p 347–385.
- Baldwin BG, Goldman DH, Keil DJ, Patterson R, Rosatti TJ, Wilken DH. editors. 2012. *The Jepson manual: vascular plants of California*, 2nd edition. Berkeley (CA): University of California Press. 1568 p.
- Baye PR. 2000. Plants and environments of diked baylands. In: Goals Project. 2000. Baylands ecosystem species and community profiles: life histories and environmental requirements of key plants, fish, and wildlife. San Francisco Bay area wetlands ecosystem goals project. Oakland (CA): San Francisco Bay Regional Water Quality Control Board. p 33–48.
- Baye PR, Faber PM, Grewell B. 2000. Tidal marsh plants of the San Francisco estuary. In: Olofson PR, editor. Goals Project. 2000. Baylands ecosystem species and community profiles: life histories and environmental requirements of key plants, fish, and wildlife. San Francisco Bay area wetlands ecosystem goals project. Oakland (CA): San Francisco Bay Regional Water Quality Control Board. p 9–32.
- Boyer KE, Thornton WJ. 2012. Natural and restored tidal marsh communities. In: Palaima A, editor. *Ecology, conservation, and restoration of tidal marshes: the San Francisco Estuary*. Berkeley (CA): University of California Press. 288 p.
- Callaway RM, Pennings SC. 1998. Impact of a parasitic plant on the zonation of two salt marsh perennials. *Oecologia* 114:100–105.

- Cooper WS. 1926. Vegetation development of alluvial fans in the vicinity of Palo Alto, California. *Ecology* 7:1–30.
- Doane SN. 1999. Shoreline changes in San Pablo Bay, California. [Master's thesis]. Nashville (TN): Vanderbilt University.
- Evans JP, Whitney S. 1992. Clonal integration across a salt gradient by a nonhalophyte, *Hydrocotyle bonariensis* (Apiaceae). *American Journal of Botany* 79:1344–1347.
- Fagherazzi S, Gabet EJ, Furbish DJ. 2004. The effect of bidirectional flow on tidal channel landforms. *Earth Surface Processes and Landforms* 29:295–309.
- Gabet EJ. 1998. Lateral migration and bank erosion in a saltmarsh tidal channel in San Francisco Bay, California. *Estuaries* 4B:745–753.
- Goman M. 2001. Statistical analysis of modern seed assemblages from the San Francisco Bay: applications for the reconstruction of paleo-salinity and paleo-tidal inundation. *Journal of Paleolimnology* 24:393–409.
- Goman M. 2005. Discrimination of estuarine marsh subenvironments (San Francisco Bay, California, USA) using a multivariate statistical calibration of abiotic sediment properties. *Journal of Sedimentary Research* 75:398–408.
- Goman M, Malamud–Roam F, Ingram BL. 2008. Holocene environmental history and evolution of a tidal salt marsh in San Francisco Bay, California. *Journal of Coastal Research* 24:1126–1137.
- Grewell BJ. 2008. Parasite facilitates species coexistence in a coastal wetland. *Ecology* 89:1481–1488.
- Grewell, BJ, JC Callaway, Ferren Jr WR. 2007. Estuarine wetlands. In: Barbour MG, Keeler–Wolf T, Schoenherr AA, editors. *Terrestrial vegetation of California*, 3rd edition. Berkeley (CA): University of California Press. p 124–154.
- Grossinger R. 1995. Historical evidence of freshwater effects on the plan form of tidal marshlands in the Golden Gate Estuary. [Master's thesis]. Santa Cruz (CA): University of California, Santa Cruz.
- Hopkins DR, Parker VT. 1984. A study of the seed bank of a salt marsh in northern San Francisco Bay. *American Journal of Botany* 71:348–355.
- Howell JT. 1970. *Marin flora – Manual of the flowering plants and ferns of Marin County, California*. 2nd edition, with supplement. Berkeley (CA): University of California Press. 366 p.
- Howell JT, Almeda F, Follette W, Best C. 2007. *Marin flora, an illustrated manual of the flowering plants, ferns and conifers of Marin County, California*. San Francisco (CA): California Academy of Sciences and California Native Plant Society. 510 p.
- Jaffe BE, Smith RE, Torresan LZ. 1998. Sedimentation and bathymetric change in San Pablo Bay: 1856–1983. U.S. Geol. Survey Open–File Report 98–759.
- Kantrud HA. 1996. The alkali (*Scirpus maritimus* L.) and saltmarsh (*S. robustus* Pursh) bulrushes: a literature review. U.S. Department of the Interior, National Biological Service Information and Technology Report 6. U.S. Government Printing Office. Available from: <http://www.npwrc.usgs.gov/resource/plants/bulrush/>.
- Li L, Ustin SL, Lay M. 2005. Application of multiple endmember spectral mixture analysis (MESMA) to AVIRIS imagery for coastal salt marsh mapping: a case study in China Camp, CA, USA. *International Journal of Remote Sensing* 23: 5193–5207.
- MacDonald KB. 1977. Coastal salt marsh. In: Barbour MG, Major J. editors. *Terrestrial vegetation of California*. Davis (CA): University of California Press. p 263–294.
- Malamud–Roam F, Ingram BL. 2004. Late Holocene $\delta^{13}C$ and pollen records of paleosalinity from tidal marshes in the San Francisco Bay Estuary, California. *Quaternary Research* 62:134–145.
- Malamud–Roam F, Dettinger M, Ingram BL, Hughes MK, Florsheim JL. 2007. Holocene climates and connections between the San Francisco Bay Estuary and its watershed: a review. *San Francisco Estuary and Watershed Science* 5(1) [Internet]. Available from: <http://escholarship.org/uc/item/61j1j0tw>.

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- Möller I, Spencer T. 2002. Wave dissipation over macro-tidal saltmarshes: Effects of marsh edge typology and vegetation change. *Journal of Coastal Research* SI 36:506–521.
- Moreira MESA. 1992. Recent saltmarsh changes and sedimentation rates in the Sado Estuary, Portugal. *Journal of Coastal Research* 8:63–640.
- Pearcy RW, Ustin SL. 1984. Effects of salinity on growth and photosynthesis of three California tidal marsh species. *Oecologia* 62:28–73.
- Peinado M, Alcaraz F, Delgadillo J, De La Cruz M, Alvarez J, Aguirre JL. 1994. The coastal salt marshes of California and Baja California: phytosociological typology and zonation. *Vegetatio* 110:55–66.
- Pestrong R. 1965. The development of drainage patterns of tidal marshes. *Stanford University Publications in Geological Sciences* 10:1–87.
- Pestrong R. 1972. Tidal sedimentation at Cooley Landing, southwest San Francisco Bay. *Sedimentary Geology* 8:251–288.
- Pringle AW. 1995. Erosion of a cyclic saltmarsh, Morecambe Bay, North–West England. *Earth Surface Processes and Landforms* 20:387–405.
- Reder E. 2011. A happy return for bird's-beak. *Bay Nature*, April–June. Available from: <http://baynature.org/articles/apr-jun-2011/a-happy-return-for-birds-beak>.
- Ryan AB. 2009. Nitrogen and salinity interactions in *Sarcocornia pacifica*-dominated salt marshes. [Master's thesis]. San Francisco (CA): San Francisco State University.
- Ryan AB, Boyer KE. 2012 [in press]. Nitrogen further promotes a dominant salt marsh plant in an increasingly saline environment. *Journal of Plant Ecology* [Internet]. Available from: <http://jpe.oxfordjournals.org/content/early/2012/02/21/jpe.rts001.full>.
- Salzman AG, Parker MA. 1985. Neighbors ameliorate local salinity stress for a rhizomatous plant in a heterogeneous environment. *Oecologia* 65:273–277.
- Shellhammer HS. 2000. Salt marsh harvest mouse. In: Olofson PR, editor. 2000. Goals Project. 2000. Baylands ecosystem species and community profiles: life histories and environmental requirements of key plants, fish, and wildlife. San Francisco Bay area wetlands ecosystem goals project. Oakland (CA): San Francisco Bay Regional Water Quality Control Board. p 9–32.
- Schwimmer RA. 2001. Rates and processes of marsh shoreline erosion in Rehoboth Bay, Delaware, U.S.A. *Journal of Coastal Research* 17:672–683.
- Whitcraft CW, Grewell BJ, Baye PR. 2011. Estuarine vegetation at Rush Ranch Open Space Preserve, San Francisco Bay National Estuarine Research Reserve, California. *San Francisco Estuary and Watershed Science* 9(3) [Internet]. Available from: <http://escholarship.org/uc/item/6j89531r>.
- Yang SL, Shi BW, Bouma TJ, Ysebaert T, Luo XX. 2012. Wave attenuation at a salt marsh margin: a case study of an exposed coast on the Yangtze Estuary. *Estuaries and Coasts* 35:169–182.
- Zhang M, Ustin SL, Rejmankova E, Sanderson EW. 1997. Monitoring Pacific Coast salt marshes using remote sensing. *Ecological Applications* 7(3):1039–1053.