Estuaries Vol. 28, No. 2, p. 173–189 April 2005

Historical Ecology of a Central California Estuary: 150 Years of Habitat Change

ERIC VAN DYKE* and KERSTIN WASSON

Elkhorn Slough National Estuarine Research Reserve, 1700 Elkhorn Road, Watsonville, California 95076

ABSTRACT: We investigated the historical ecology of Elkhorn Slough, a 1,200 ha tidal wetland system in central California. The goal of this study was to identify patterns of change in the extent and distribution of wetland habitats during a 150-yr period and to investigate the causes of these changes. Using a geographic information system (GIS), we interpreted historic maps, charts, and aerial photographs. We created a series of summary maps to illustrate and quantify changes in tidal flow and habitat types at six representative historical periods. With the aid of custom software tools, we performed semi-automated spatial analysis of historic aerial photographs to quantify changes in marsh cover at fixed quadrats and tidal creek width at fixed cross sections. Our multiscale analysis documents dramatic shifts in the distribution of habitat types resulting from anthropogenic modifications to the hydrology of the slough. More than half of the marshlands were diked, and more than two thirds have either degraded or been converted to other habitat types. The construction of an artificial mouth abruptly transformed the wetland system from depositional to highly erosional, enlarging channels, widening creeks, and converting marsh to intertidal mudflat or open water. Increased tidal amplitude and velocity are the likely causes. In recent decades, levee failure and intentional breaching have restored the acreage under tidal influence to nearly historic levels, but recolonization of former wetlands by salt marsh vegetation has been minimal. Degraded former marshland and unvegetated mudflat are now the dominant habitat types at Elkhorn Slough. The rate of habitat change remains high, suggesting that a new equilibrium may not be reached for many decades. This study can help tidal wetland managers identify patterns and mechanisms of habitat change and set appropriate conservation and restoration goals.

Introduction

TIDAL WETLANDS AND HABITAT CHANGE

Estuaries and coastal lagoons are among the Earth's most biologically productive ecosystems and provide essential habitats for birds, fish, crustaceans, and many other species (Little 2000). Tidal wetlands are also some of our most highly altered landscapes, and their conservation lags behind that of other terrestrial and marine systems (Edgar et al. 2000). Rates of coastal wetland loss in the United States resulting from human activities exceeded 8,000 ha yr^{-1} in recent decades and are currently estimated to be 400 ha yr^{-1} (NOAA 1990; Dahl 2000).

Tidal wetlands are dynamic, responding to many types of environmental changes, including human activities. Apart from direct losses due to construction and reclamation, the principal anthropogenic forces driving tidal wetland habitat change at the local scale include diking, ditching, dredging, and similar activities that alter tidal flooding regimes and modify sediment input and marsh accretion rates (Kennish 2001). On a regional scale, important causes of estuarine habitat change are change in tidal energy due to hydrologic manipulations, increase in relative sea level due to land subsidence, and altered sediment input levels due to changing land use practices (Adam 2002). On a global scale, eustatic sea-level rise, accelerated by global climate change, can result in long-term estuarine habitat change (Scavia et al. 2002).

The ecological history of most of the world's tidal wetlands has not been studied. At those estuaries that have been investigated, habitat changes have often been dramatic. A widely reported example is the rapid erosion of salt marsh at Venice Lagoon in northeast Italy (Day et al. 1998). The redirection of rivers that historically supplied sediments to the estuary, in combination with eustatic sea level rise, subsidence resulting from groundwater withdrawal, and increasing tidal energy due to an enlarged tidal prism, have caused the marsh edge to retreat as much as 2 m yr^{-1} (Day et al. 1998). The loss of coastal wetland along the Louisiana Gulf Coast, a region that includes a significant percentage of U.S. salt marsh acreage, is another highly visible example. Reduced sediment input due to levees along the Mississippi River, the construction of extensive networks of canals, and subsidence rates as high as 1.5 cm yr^{-1} have contributed to a reported 100 km^2 yr^{-1} loss of tidal wetlands, although the

* Corresponding author; tele: 831/728-2822; fax: 831/728-1056; e-mail: vandyke@elkhornslough.org

relative importance of each factor remains controversial (Boesch et al. 1994; Turner 1997; Day et al. 2000). At Chesapeake Bay, the largest estuary in the U.S., significant coastal wetland losses are attributed to a combination of subsidence and sediment deficit (Stevenson et al. 1985; Kearney et al. 1988).

Habitat Change at California Estuaries

Wetlands are relatively small and infrequent along California's topographically complex and seismically active coastline, occurring mainly within occasional protected estuaries and lagoons (Emmett et al. 2000). While decreased riverine sediment inputs and relative sea level rise are major drivers of estuarine habitat change elsewhere, these factors are likely less important in California where drainage basins are relatively small and uplift typically outpaces sea level rise (Patrick and DeLaune 1990; Emmett et al. 2000). Subsidence resulting from groundwater extraction has been a significant factor at some sites, particularly in the San Francisco Bay area (Patrick and DeLaune 1990). Subsidence events resulting from seismic activity may also be regionally important along the tectonically active California coast, as they are in the Pacific Northwest (Atwater et al. 1977; Atwater 1987). The predominant cause of tidal wetland habitat change in California has been direct human alteration (Larson 2001).

As much as 91% of California's coastal wetlands (2 million ha) were lost during the 150 yr following statehood and settlement by European Americans, and nearly all that remain are altered or degraded (Larson 2001). Diking, draining, dredging, and filling for residential, commercial, and agricultural development have eliminated about 85% of tidal wetlands in the San Diego region (Zedler 1996a) and at least 78% in the San Francisco Bay area (Nichols et al. 1986; Goals Project 1999).

Because conversion of tideland to agriculture or salt evaporation ponds typically does not involve filling and is potentially reversible, these former wetlands provide important candidate sites for habitat restoration (Goals Project 1999). Tidal flow has recently been restored through either accidental or intentional breaching of levees at several of California's drained former wetlands (Zedler 1996b; Williams and Faber 2001; Williams and Orr 2002) and additional projects are planned (Steere and Schaefer 2001).

Historical Ecology and Habitat Change Analysis

The purpose of this study was to document earlier habitat conditions and to quantify trends of wetland change at a central California estuary during the past 150 yr, a period of major modifications to the landscape. Historical ecology is a relatively new branch of the environmental sciences that integrates historic sources to analyze and characterize past changes in natural communities (Swetnam et al. 1999). Development of a historical perspective is fundamental to efforts toward conservation and restoration of estuarine ecosystems (Goals Project 1999). Although predicting future conditions through simple extrapolation of past trends can be risky, knowledge of past conditions may suggest hypotheses that can be tested with contemporary data and can supply the parameters for retroactive testing of predictive models (Swetnam et al. 1999). Although it may not be meaningful to define ideal reference conditions based on one fixed point in time, historical ecological studies can identify the spatial and temporal range of variability in naturally dynamic systems and assist in setting ecologically justifiable, achievable, and sustainable management and restoration goals (Swetnam et al. 1999). Problems associated with analyzing the historical record include the fragmentary nature of individual source materials as well as the subjectivity inherent in the interpretation process (Swetnam et al. 1999; Grossinger 2000). Historical materials have been applied to ecological analyses at several West Coast estuaries (e.g., Berquist 1978; Niemi and Hall 1996; Goals Project 1999; Borde et al. 2003; Foxgrover et al. 2004).

A key goal of this project was to develop accurate, repeatable methods and tools for performing habitat classification and long-term change analysis from historic maps and aerial photographs. We employed a dual approach, combining broadscale manual interpretation of the entire wetland system with higher resolution, semi-automated analysis of replicated fixed quadrats and cross sections. The former method resulted in estuary-wide habitat classification maps for several representative periods that were subjected to quantitative analysis. The latter yielded detailed habitat data comparable to that obtained from long-term field studies of monitoring plots and transects. These two geospatial techniques complemented each other and provided independent evidence for the observed trends. Our rigorous, multiscale approach to identifying and quantifying estuarine habitat change is applicable to historical ecological studies of other threatened ecosystems.

Methods

Study Site

Elkhorn Slough is a 1,200 ha tidal wetland system adjoining Monterey Bay in central California (Fig. 1). The climate is mediterranean, with mean

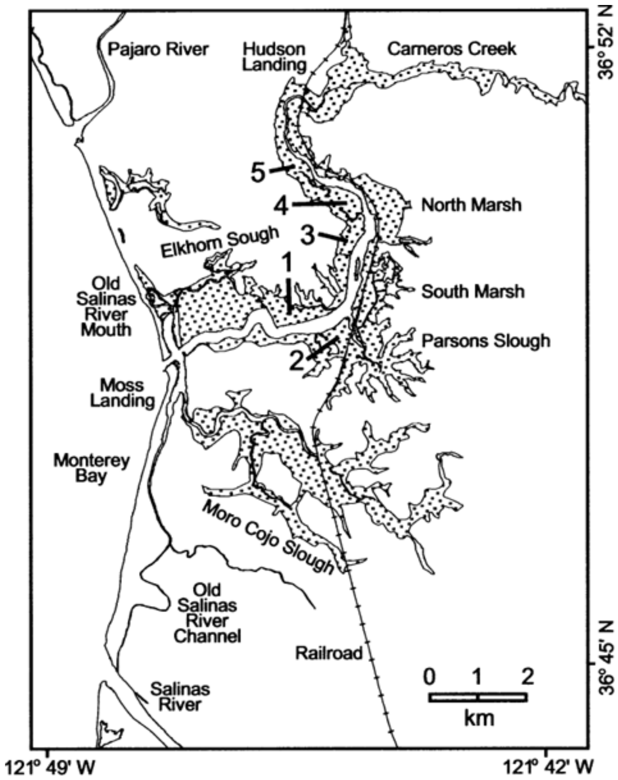


Fig. 1. Location of Elkhorn Slough and the Salinas River system adjoining Monterey Bay in central California. Numbers refer to marsh quadrat and tidal creek cross section regions (regions 1 and 2 comprise the lower slough, region 3 the mid slough, and regions 4 and 5 the upper slough).

monthly temperatures ranging from 11.1°C in the winter to 15.4°C in the summer and mean annual rainfall of 55.2 cm falling mainly in the winter months (Caffrey 2002). Tides are semidiurnal with a mean diurnal range of 1.7 m (Caffrey and Broenkow 2002).

The dominant vegetation in Elkhorn Slough's marshlands is *Salicornia virginica,* which almost exclusively dominates the intertidal zone between approximately 0.4 and 1.2 m above mean sea level (Atwater and Hedel 1976; MacDonald 1988). Several additional species, including *Distichlis spicata, Jaumea carnosa, Frankenia salina,* and *Atriplex* spp., are also present at the upper intertidal or infratidal zones. *Scirpus* and *Typha* species are common in brackishwater locations. *Spartina foliosa,* which dominates the lower intertidal zone at most California salt marshes, is conspicuously absent from Elkhorn Slough and nearby marshes, as are nonnative congeners (Zimmerman and Caffrey 2002). Introduced terrestrial plants, including *Conium maculatum* and *Carpobrotus edulis,* are locally abundant and invading the marsh from adjacent uplands (Wasson unpublished data).

Elkhorn Slough's extensive intertidal mudflats are inhabited by a diversity of invertebrates and are heavily used by birds for foraging and breeding (Harvey and Connors 2002; Wasson et al. 2002). The slough's deeper channels serve as nurseries for numerous species of fish and as feeding or refuge areas for two marine mammal species (Yoklavich et al. 1991; Barry et al. 1996).

Nearly 700 ha of Elkhorn Slough's wetlands are managed for wildlife and conservation purposes by the California Department of Fish and Game. Elkhorn Slough National Estuarine Research Reserve encompasses 567 ha of the slough's wetlands and adjacent uplands. Other land uses in the vicinity of Elkhorn Slough include cultivation of strawberries and other crops as well as rural residential and industrial development (Silberstein et al. 2002).

Elkhorn Slough Environmental History

Rising sea levels drowned a coastal valley approximately 10,000 years ago, converting it to a tidal embayment. Initially a high-energy marine system, several thousand years of sediment deposition and marsh accretion gradually transformed Elkhorn Slough into a low-energy estuary. Broad expanses of *Salicornia* developed, flanking a network of tidal channels (Schwartz et al. 1986). The slough remained largely a saltwater system due to the absence of major riverine inputs, although sediment cores record intervals of localized freshwater dominance (Hornberger 1991; Jones 2002), likely corresponding to episodes of increased flow or changes in the course of the nearby Salinas River system. Many areas of transitional brackish, freshwater, and riparian habitat developed near occasional seeps and springs and at the slough's upper reaches.

Native Americans lived in the vicinity of the slough for perhaps 10,000 yr (Dietz et al. 1988; Jones and Jones 1992). Reports from early explorations indicate that intentional burning occurred during this time, yet sediment cores do not suggest that this practice resulted in significant erosion (Gordon 1996). Before the mid 19th century, the predominant land use by European immigrants in north Monterey County was cattle grazing, which also apparently had a minimal effect on the slough (King 1981; Gordon 1996). The era of major anthropogenic wetland changes began shortly after the Gold Rush and California's statehood. The earliest maps included in this study were produced during this period.

With the arrival of Americans during the latter half of the nineteenth century, large areas of woodland and scrub were cleared for fuel wood and for the cultivation of hay and barley (Gordon 1996). On the upland sandhills adjacent to Elkhorn Slough, the thin topsoil eroded, depositing large

TABLE 1. Historic maps and charts.

Date	Description	Origin
1853	General Map of Explorations and Surveys in California	U.S. War Department/Pacific Railroad Surveys
1854	Part of the Coast of Cal. from Pajaro River Southward topographic sheet (T473)	U.S. Coast Survey
1855	Map of the Vicinity of Monterey Bay	W. P. Blake/U.S. Coast Survey
1857	Monterey Bay hydrographic chart (H5498)	U.S. Coast Survey
1859	Rancho Bolsa de San Cayetano plat	U.S. Surveyor General
1859	Rancho Carneros plat	U.S. Surveyor General
1867	Township 13 Range 2E plat	U.S. Surveyor General
1872	Rancho Bolsa Nueva y Moro Cojo plat	U.S. Surveyor General
1872	Southern Pacific Railroad Pajaro Branch/Elkhorn Slough	Southern Pacific Railroad
1873	Map of Turnpike Road from Castroville to "Ware House" on the Elkhorn Slough	unknown
1873	Topographical Map of Central California Together with a Part of Nevada	California Geological Survey
1877	Map of the County of Monterey	St. John Cox
1885	Map of Moss, Salinas, and Watsonville Landings Belonging to the Pacific Coast Steamship Company	J. H. Garber, surveyor
1885	Map of Watsonville Landing Belonging to the Pacific Coast Steamship Company	J. H. Garber, surveyor
1893	Point Buchon to Point Pinos hydrographic chart (H5400)	U.S. Coast and Geodetic Survey
1898	Official Map of Monterey County	Lou G. Hare, Monterey County surveyor
1901	Lower Salinas Valley soil survey	U.S. Department of Agriculture
1908	Map of Monterey County	Lou G. Hare, Monterey County surveyor
1909	Moss Landing and its Vicinity Contiguous to Monterey Bay	Lou G. Hare, Monterey County surveyor
1910	Monterey Bay, Pajaro River Southward topographic sheet (T473a)	U.S. Coast and Geodetic Survey
1911	Monterey Bay hydrographic chart (H5403)	U.S. Coast and Geodetic Survey
1913	Lands of the Empire Gun Club	Arnold M. Baldwin, licensed surveyor
1913	Turnpike Road Between Hudson Landing Bridge and J. Henry Meyer Gate	Lou G. Hare, Monterey County surveyor
1914	Capitola topographic quadrangle	U.S. Geological Survey
1917	San Juan Bautista topographic quadrangle	U.S. Geological Survey
1925	Salinas Area soil survey	U.S. Department of Agriculture

amounts of sediment into the wetlands (King 1981; Silberstein et al. 2002). Maps from the 19th century show a broad, deepwater basin at the mouth of the slough between Moss Landing and the old Salinas River mouth. Steamboats provided regular service all the way to Hudson Landing (Fabing and Hamman 1985), and maps show the broad main channel continuing for another 4 km, well beyond the present head of the slough. By the 1880s, sediment deposition had made the channel too shallow to permit navigation by steamers (Van Dyke unpublished data). Intertidal mudflats and shoals in the lower slough likely first appeared during this period. The channel above Hudson Landing rapidly filled and converted to marsh (Van Dyke unpublished data). By the time the first aerial photographs used in this study were taken in the early 1930s, Elkhorn Slough was a sluggish lagoon with limited tidal exchange for much of the year due to a persistent sandbar at its mouth (MacGinitie 1935). Episodes of increased sediment deposition during the same period at other coastal California locations have also been attributed to anthropogenic disturbance (e.g., Berquist 1978; Nichols et al. 1986; Niemi and Hall 1996; Cole and Wahl 2000).

Historic Maps and Aerial Photographs

Because of Elkhorn Slough's coastal location near the historic city of Monterey, a wealth of materials was available for analysis. We obtained, converted to digital format, georectified, mosaiced, and interpreted 26 historic maps and charts dating from 1853 to 1925, and 13 aerial photograph flights taken between 1931 and 2003 comprising more than 300 individual photos. Table 1 lists the historic maps and Table 2 lists the aerial photographs used in this study.

We scanned aerial photographs at resolutions selected to yield pixels of approximately 0.6 m after rectification. Mosaics were assembled by extracting only the least-distorted effective area from the overlapping photographs of each flight. Effective areas were identified using the proximity function of the ArcView Geographic Information System (GIS) Spatial Analyst extension (ESRI, Redlands, California). To minimize distortion, individual photographs were resampled using the plane pro-

TABLE 2. Historic aerial photographs.

Date	Type	Count	Scale	Origin
May 1931	panchromatic	24	1:19,500 0.63 m pixel^{-1}	Western Gulf Oil Co./Fairchild Aerial Surveys, Inc.
November 1937	panchromatic	17	1:20,800 0.66 m pixel^{-1}	U.S. Department of Agriculture/Fairchild Aerial Surveys, Inc.
August 1949	panchromatic	16	1:21,100 0.66 m pixel^{-1}	U.S. Department of Agriculture/Park Aerial Surveys, Inc.
May–June 1956	panchromatic	14	1:24,300 0.6 m pixel^{-1}	U.S. Department of Agriculture/Aero Service Corp.
May–July 1966	panchromatic	15	1:20,800 0.67 m pixel^{-1}	U.S. Department of Agriculture/Cartwright Aerial Surveys, Inc.
May 1971	panchromatic	14	1:24,300 0.67 m pixel^{-1}	U.S. Department of Agriculture/Western Aerial Contractors
April 1976	panchromatic	28	1:9600 0.4 m pixel^{-1}	California Department of Transportation
April 1980	color infrared	28	1:12,400 0.52 m pixel^{-1}	California Coastal Commission/Western Aerial Photographs, Inc.
April 1987	color infrared	21	1:12,100 0.51 m pixel^{-1}	Moss Landing Marine Labs./Western Aerial Photographs, Inc.
May 1989	true color	40	0.4 m pixel^{-1}	California Department of Fish and Game Air Services
May 1992	color infrared	19	1:12,400 0.53 m pixel^{-1}	Elkhorn Slough Foundation/Aerial Data Systems
December 1999	panchromatic digital ortho	6	0.6 m pixel^{-1}	County of Monterey/HJW GeoSpatial, Inc.
April 2000	true color digital	40	0.43 m pixel^{-1}	California Department of Fish and Game Air Services
May 2001	color infrared digital ortho	6	0.6 m pixel^{-1}	County of Monterey/HJW GeoSpatial, Inc.
April 2003	true color digital	40	0.5 m pixel^{-1}	California Department of Fish and Game Air Services

jective model to ground control points selected near the perimeter of each identified effective area. Ground control points were obtained from recent 0.6 m pixel^{-1} digital orthophotographs. Rectification and resampling was performed using TNT Mips (MicroImages, Lincoln, Nebraska). Mosaics were then assembled from a cut-line template using TNT Mips.

A variety of factors may have contributed error to our digitally processed aerial photograph mosaics. Aircraft tilt, terrain relief, and camera geometry are potential sources of distortion on the original photography, and contact printing and scanning introduce additional distortion (Moore 2000). The process of matching ground control points during rectification is also a source of error. We performed a spatial accuracy assessment by randomly selecting 20 points within the study area and then locating identifiable features near each point on each photo mosaic. These locations were compared with their corresponding locations on the digital orthophotos. Although residuals reported during rectification were consistently less than twice the resampled pixel size, our accuracy assessment identified a mean error of 4.8 m for the 13 aerial photo mosaics. Positional error on the base orthophotos, which would not be identified in this error assessment, was presumed to be minor.

Historic maps and charts were scanned at various resolutions according to the quality of the image and then georectified to ground control points selected from digital U.S. Geological Survey (USGS) topographic quadrangles using a first-order polynomial model. Rectification and resampling was performed in ArcView with the Image Analysis extension. Because the reliability of historic maps varies and is generally unknown, we overlaid all available maps from each time period to produce a composite interpretation (Grossinger 2000). We assumed a level of spatial and representational accuracy for each source according to our understanding of the map's intended purpose. For example, early USGS maps were presumed to be highly accurate for representing topography, but less reliable for distinguishing wetland habitat types.

Habitat and Tidal Flow Mapping

We interpreted historic maps and aerial photographs and produced a spatially accurate chronology of six representative years (1870, 1913, 1931, 1956, 1980, 2000) to characterize the overall sequence of wetland changes at Elkhorn Slough. The study area was limited to Elkhorn Slough; tributary wetlands at Carneros Creek to the east and Moro Cojo Slough and the old Salinas River channel to

TABLE 3. Habitat classification system.

Habitat type	Habitat class	Tidal flow
Saltwater channel	saltwater	unrestricted
Seagrass bed	saltwater	unrestricted
Restricted saltwater channel	saltwater	restricted
Mud or degraded salt marsh (<25% vegetation cover)	mud	unrestricted
Restricted mud or degraded salt marsh (<25% vegetation cover)	mud	restricted
Diked mud or degraded salt marsh (<25% vegetation cover)	mud	nontidal
Degraded salt marsh or mud (25–75% vegetation cover)	salt marsh	unrestricted
Restricted degraded salt marsh or mud (25–75% vegetation cover)	salt marsh	restricted
Diked degraded salt marsh or mud (25–75% vegetation cover)	salt marsh	nontidal
Salt marsh (>75% vegetation cover)	salt marsh	unrestricted
Restricted salt marsh (>75% vegetation cover)	salt marsh	restricted
Diked salt marsh (>75% vegetation cover)	salt marsh	nontidal
Reclaimed former tidal wetland	reclaimed	nontidal
Brackish-fresh marsh or channel	fresh marsh	nontidal
Restricted brackish-fresh marsh or channel (behind tidegate)	fresh marsh	nontidal
Impounded brackish-fresh marsh or channel (behind levee)	fresh marsh	nontidal
Riparian woodland	riparian	nontidal

the south were excluded. Interpretation for the first two periods was based on maps and is less detailed than the four subsequent periods where aerial photographs were used. We developed a pair of GIS layers for each time period: habitats (digitized polygons delineating generalized land use and land cover classes) and tidal flow (digitized polygons delineating areas with either unrestricted, restricted, or excluded tidal flow). The complete classification scheme is listed in Table 3. A consistent scale of 1:1,200 was maintained during digitizing for consistency. Digitizing was performed using ArcView GIS.

For the habitats layers, we selected a set of land use and land cover classes based on what was indicated on historic maps or clearly distinctive on the oldest panchromatic aerial photographs. Marsh habitat indicated on maps was assumed to represent areas with vegetation cover > 75%. With aerial photographs, marsh habitat was classified by estimating the percentage of vegetation cover within a 100 m square grid at our standard 1:1,200 scale. No distinction was made between sparsely vegetated marsh (<25% cover) and unvegetated panne or mudflat because they are visually indistinguishable at this scale. Brackish-freshwater marsh was distinguished from salt marsh by its greater textural variance (*Salicornia* marsh is uniformly gray on panchromatic aerial photographs) and an absence of tidal channels. No attempt was made to differentiate subtidal from intertidal areas as tidal heights varied between aerial photograph series. The main channel boundary was determined either by the water line (maps and photographs at higher tides) or by a visible line on the mudflats at approximately mean high water (photographs at lower tides).

For the tidal flow layers, we began by digitizing lines representing either intact or breached levees. Levees were interpreted as breached if an aerial photograph showed evidence of tidal channels flowing through or around the levee. We also located road and railroad embankments and tidegates. We then digitized polygons to delimit areas with unrestricted tidal exchange (e.g., undiked), areas with restricted tidal flow (e.g., behind breached levees and tidegates), and nontidal areas (e.g., behind intact levees). Areas with brackish-freshwater habitat behind intact levees or gates were classified as impounded; areas without wetland vegetation behind intact levees or gates were interpreted as reclaimed.

To assess the accuracy of our interpretation of habitats and tidal flow from aerial photographs, we visited the 20 locations that we randomly selected for spatial accuracy assessment and compared ground truth observations with our interpretation of the 2000 aerials. In all but one case, field observation and photo interpretation matched exactly. The single disagreement involved percent cover in an area of deteriorating marsh, and may represent a change between the 2000 photo date and the 2004 field visit. In any case, because we could not perform similar accuracy assessment with earlier aerial photographs and maps, we did not modify our interpretation as a result of this ground truthing.

Marsh and Tidal Creek Time Series

We performed detailed quantitative analysis of fixed quadrats using aerial photographs taken at 12 different dates between 1931 and 2003, and of tidal creek cross sections using aerials taken at 13 dates between 1931 and 2003. Five regions of Elkhorn Slough's tidal wetlands were studied, encompassing all areas that have remained undiked throughout the 72-yr study period (Fig. 1).

To quantify changes in vegetated marsh cover, we divided the study area into 196 100×100 m quadrats. Within each quadrat (and each date), we determined the proportion of salt marsh vegetation versus unvegetated habitat (mud and water). We developed a custom, interactive ArcView Spatial Analyst application to perform semi-automated image interpretation. This tool allowed us to rapidly determine the precise grayscale value that would trace isoline boundaries between vegetated and unvegetated portions of each quadrat and automatically produce the corresponding set of polygons in an ArcView shapefile. Grayscale values were adjusted for every quadrat to account for contrast variations within and between photographs. For interpretation consistency, all analysis was performed on grayscale imagery; for years where color or color infrared imagery was available, we performed red-green-blue to hue-saturation-intensity conversion (Jensen 1996) and interpreted only the intensity component.

Tidal creek changes were quantified by measuring the width of 196 cross sections within the marsh drainage network. These sampling locations were chosen to include every major segment of every creek that was visible on the 1931 photographs. Cross section width was defined as the distance between vegetated creek banks and was measured at each point (and each date) with the aid of a custom, interactive ArcView GIS script. In some areas, marshland has completely converted to unvegetated mudflat in recent years. In these cases, cross section width was defined as the distance to the nearest remaining recognizable fragment of marsh vegetation in the most recent photograph where such remnants were still visible.

To determine the significance of changes in salt marsh cover, we performed repeated measures analysis of variance (ANOVA) on mean percentage of vegetated area within the quadrats with year as within-sample factor and region as between-sample factor. Cover percentages were arcsin transformed to meet the assumptions of ANOVA (Sokal and Rohlf 1995). To test the significance of changes in tidal creek cross section widths, we performed repeated measures ANOVA on log transformed creek width with year as within-sample factor and region as between-sample factor. To determine the significance of changes between pairs of years, we performed Fisher's protected least significant difference (PLSD) post-hoc comparison ($p < 0.05$). Statistical analysis was performed with StatView software (SAS Institute Inc., Cary, North Carolina).

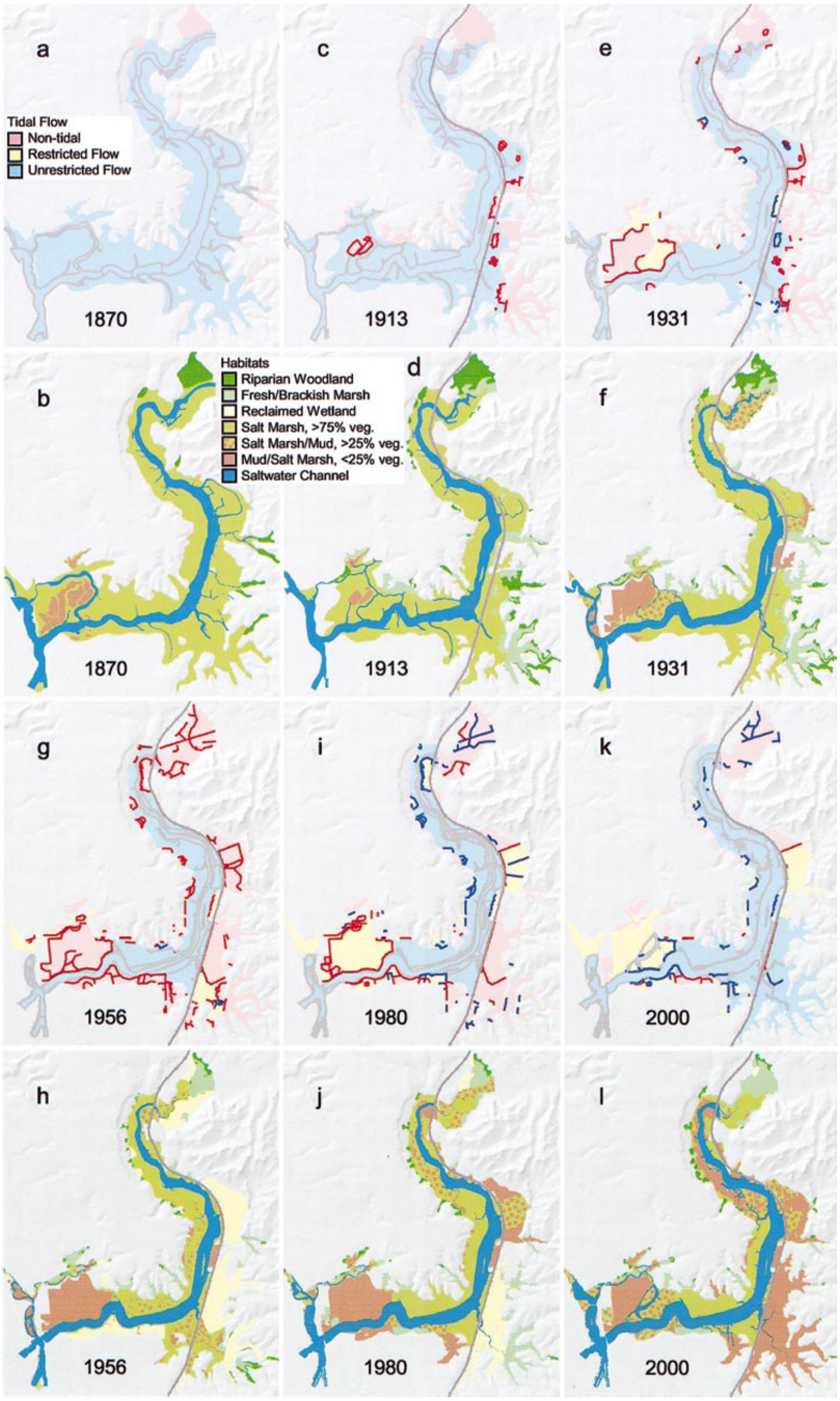
Results

Habitat and Tidal Flow Mapping

Elkhorn Slough has undergone dramatic changes in the extent and distribution of wetland habitat types during the past 150 yr. These changes are illustrated by six pairs of thematic maps (Fig. 2) and summarized by a corresponding pair of charts (Fig. 3). Two major trends are apparent: an initial decrease and subsequent recovery of total acreage under tidal influence and a continuing decrease of salt marsh acreage. Since 1870, more than two thirds of the slough's salt marsh has either degraded or converted to other habitat types. The majority of this loss occurred during the middle third of the study period, concurrent with a period of extensive diking that either restricted or completely excluded tidal exchange from more than half of the slough's wetlands. Marsh loss has slowed somewhat during the final decades of the study, concurrent with an era of breaching levees and restoration of tidal flow to former wetlands, although the extent of degraded former marsh and unvegetated mudflat continues to increase. The total wetland area decreased slightly through the study period due to the conversion of marsh to upland vegetation.

During the period between 1870 and 1956, more than 60 km of levees and embankments were constructed, reducing the range of unobstructed tidal influence by 59%. During the same period, the extent of intact salt marsh habitat (vegetation cover $> 75\%$) decreased by 66%. Within this era of extensive diking and salt marsh loss, the acreage of four habitat types increased. Between about 1900 and 1913, more than 90 ha of salt marsh was converted to fresh and brackish habitats through the impoundment of freshwater within created ponds and marshes, although the extent of these habitat types eventually decreased after many of the levees were abandoned. Between about 1900 and 1956, 97 ha of the slough's salt marsh converted to unvegetated mudflat (vegetation cover $< 25\%$), primarily within a complex of diked salt evaporation ponds, and another 95 ha converted to degraded marsh (vegetation cover $< 75\%$). Between 1931 and 1956, 275 ha, more than 30% of Elkhorn Slough's remaining salt marsh, were drained and reclaimed for agricultural use.

After 1956, the pattern of tidal restriction abruptly reversed as a result of accidental and intentional levee breaches. As little as 4 km of levees remained intact by 2000, and the acreage under tidal influence (with either unrestricted or partially restricted flow behind culverts, tidegates, or breached levees) slightly exceeded what it had been in 1913. Despite this reversal, salt marsh con-


a
Tidal Flow
Non-tidal
Restricted Flow
Unrestricted Flow
1870
c
1913
e
1931
b
1870
Habitats
Riparian Woodland
Fresh/Brackish Marsh
Reclaimed Wetland
Salt Marsh, >75% veg.
Salt Marsh/Mud, >25% veg.
Mud/Salt Marsh, <25% veg.
Saltwater Channel
d
1913
f
1931
g
1956
i
1980
k
2000
h
1956
j
1980
l
2000

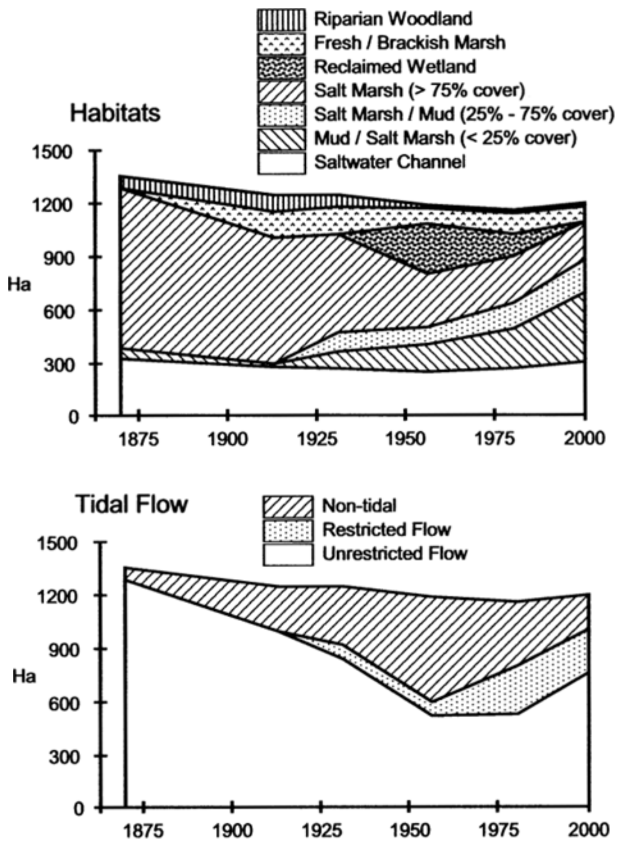


Fig. 3. Habitat and tidal flow change summary, 1870–2000.

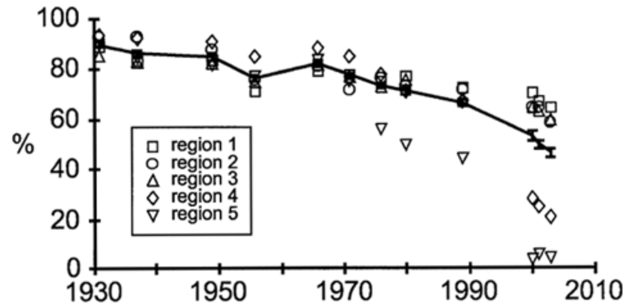


Fig. 4. Mean percentage of salt marsh vegetation cover within 196 quadrats in 5 regions, 1931–2003. Line is mean for all regions. Error bars represent 1 standard error.

tinued to deteriorate. During the period between 1980 and 2000, 45 ha of formerly vegetated marsh converted to mudflat and shallow water at the slough's upper east side, a region that never experienced extensive diking. By 2000, 36% of Elkhorn Slough's tidal wetlands had converted to unvegetated mudflat and an additional 21% converted to degraded marsh, a habitat category that was not present prior to 1913. The extent of high-quality salt marsh in 2000 was 207 ha, 23% of what it was a century earlier.

Marsh and Tidal Creek Time Series

Vegetation cover across Elkhorn Slough's marshes has decreased dramatically since 1931, and this trend accelerated during the final decades of our study. Clear differences are apparent between the lower and mid slough (regions 1, 2, and 3) and the upper slough (regions 4 and 5). Much of the upper slough, which was once densely vegetated, is now completely unvegetated. Tidal creek width has also increased since 1931 and exhibits a similar rate of acceleration. In the upper slough, many former creeks and pannes have completely degenerated into open mudflat. These results confirm the trend of salt marsh degradation and loss that was apparent from our broadscale habitat mapping.

The mean percentage of salt marsh vegetation within 196 quadrats in five regions distributed throughout Elkhorn Slough's undiked marshlands decreased from 89.6% in 1931 to 46.4% in 2003 (Fig. 4). Differences in vegetation cover were significant between the five regions (repeated measures ANOVA, $F = 9.2$, $p = 0.0001$), between the 12 yr ($F = 469.9$, $p = 0.0001$), and for the interaction between regions and years ($F = 42.4$, $p = 0.0001$). Vegetation cover changes were significant between all pairs of years except those immediately surrounding a temporary period of recovery (1956–1976, 1956–1989, and 1976–1980). The magnitude of marsh loss increased with increasing distance from Monterey Bay. Mean vegetation cover for regions 1, 2, and 3 in the lower and mid slough was 89.6% in 1931, decreasing to 60.8% by 2003. The rate of marsh loss in the lower slough was relatively gradual. Mean cover for regions 4

←

Fig. 2. Tidal flow and habitat mapping. 1870 (a,b): Unrestricted tidal flow; extensive salt marsh; natural salt pannes present at lower slough. 1917 (c,d): Levees have been constructed at lower slough for salt production and east of the railroad to create fresh or brackish ponds and marsh within artificial impoundments. 1931 (e,f): Tides have been restricted or excluded from expanded salt production ponds and reclaimed salt marsh; marsh has started to degrade at areas with restricted or excluded tides. 1956 (g,h): More than 60 km of levees exclude tides from 59% of wetlands; salt ponds and reclamation have reduced salt marsh acreage by 66%; large areas of marsh degrading at undiked regions of lower and mid slough. 1980 (i,j): Breaching of levees returning flow to diked or reclaimed former wetlands; undiked areas of lower and mid slough show noticeable salt marsh recovery; degraded marsh expanding at upper slough. 2000 (k,l): Less than 4 km of intact levees remain; tidal flow returned to most former wetlands; 77% of original salt marsh degraded or converted to mudflat; losses greatest at eastern and upper slough (Red lines represent intact levees, blue lines breached levees).

and 5 in the upper slough was 89.9% in 1931, but decreased to 21.1% at region 4 and 4.1% at region 5 by 2003. The rate of marsh loss in the upper slough accelerated in the 1970s, slowed somewhat in the 1980s, and then accelerated rapidly through the 1990s. All regions exhibited a period of marked deterioration in the 1950s followed by a period of recovery in the 1960s; this trend was somewhat more pronounced in the lower slough. Figure 5 illustrates this loss and recovery within region 1.

A more complex pattern emerges when changes in vegetation cover are depicted geospatially. Figure 6a,c,e illustrates the annualized change at each quadrat during the intervals 1931–1956 (25 yr), 1956–1980 (24 yr), and 1980–2003 (23 yr), respectively. During the first third of the study period, the rate of marsh loss was generally high (>0.5% yr^{-1}) to very high (>1.0% yr^{-1}) in the lower slough (regions 1 and 2) and moderate (>0.25% yr^{-1}) in the mid and upper slough (regions 3, 4, and 5). For much of this first interval, the overall rate of change was low, but accelerated rapidly after 1949. About one third of the quadrats in the upper slough did not follow this trend; these quadrats, which were typically adjacent to large tidal channels, experienced minimal change before the 1960s. During the middle third of the study period, differences between the lower and upper slough became even more striking. The majority of quadrats in the lower slough, the mid slough, and the eastern third of the upper slough showed either little change or an increase in vegetation cover. About half of the lower slough quadrats experienced moderate to rapid recovery (>0.25% yr^{-1}). In contrast, every quadrat in the western portion of the upper slough experienced high or very high rates of marsh loss during this second interval. By the final third of the study period, moderate to high rates of marsh loss had returned to the lower slough and losses in the upper slough were uniformly very high.

The mean cross section width of 196 tidal creeks in undiked areas increased from 2.5 m in 1931 to 12.4 m in 2003 (Fig. 7). Differences in creek width were significant between the 13 yr (repeated measures ANOVA, $F = 257.3$, $p = 0.0001$) and for the interaction between regions and years ($F = 3.1$, $p = 0.0001$), although not significant between regions ($F = 0.7$, $p = 0.6$). Creek width changes were significant between all pairs of years except immediately successive pairs (1937–1949, 1956–1966, 1978–1980, 1987–1992, and 2000–2001). Increasing tidal creek width was related to distance from Monterey Bay. In the 1930s, mean creek width was between 2 and 2.5 m within all five regions. By 2003, mean creek width in all four regions of the lower and mid slough (1, 2, 3, and 4) was between 9 and 11 m. At the far upper slough (region 5), mean width had increased to 17 m. At a number of sampling points in region 5, vegetated banks were no longer present after 2000. Fig. 8 illustrates

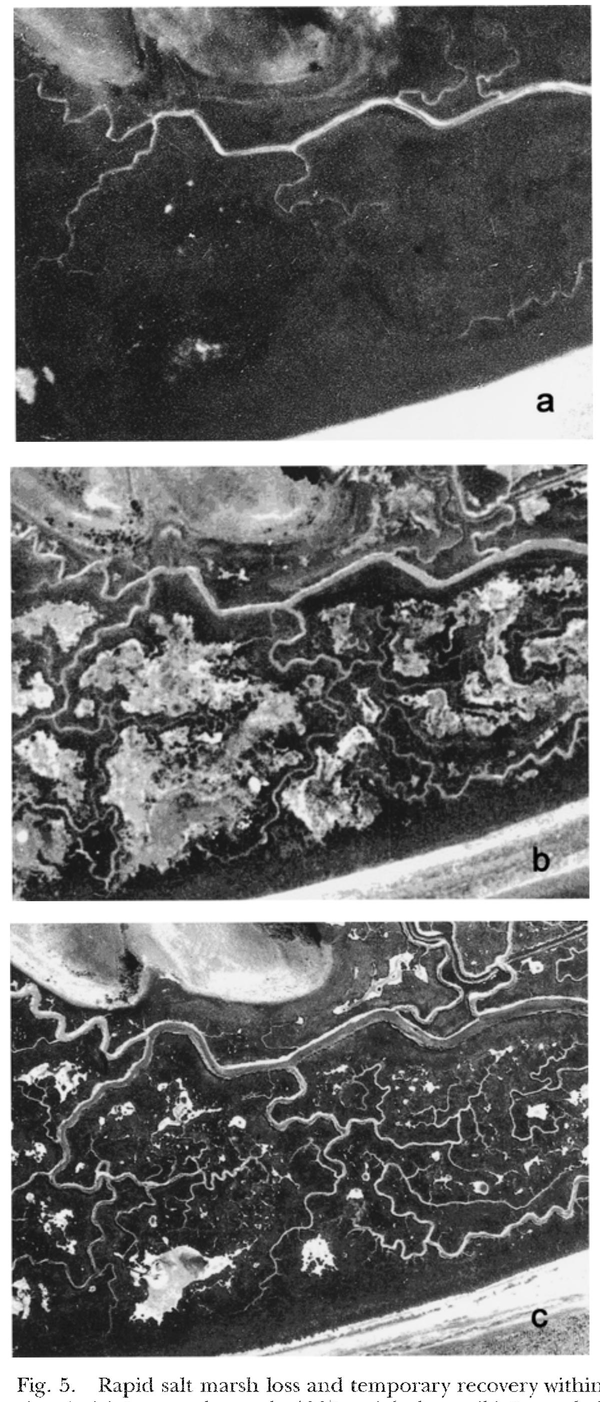


Fig. 5. Rapid salt marsh loss and temporary recovery within region 1. (a) Intact salt marsh, 1937 aerial photo. (b) Degraded vegetation in marsh interior, 1956 aerial photo. (c) Temporary vegetation recovery, 1980 aerial photo.

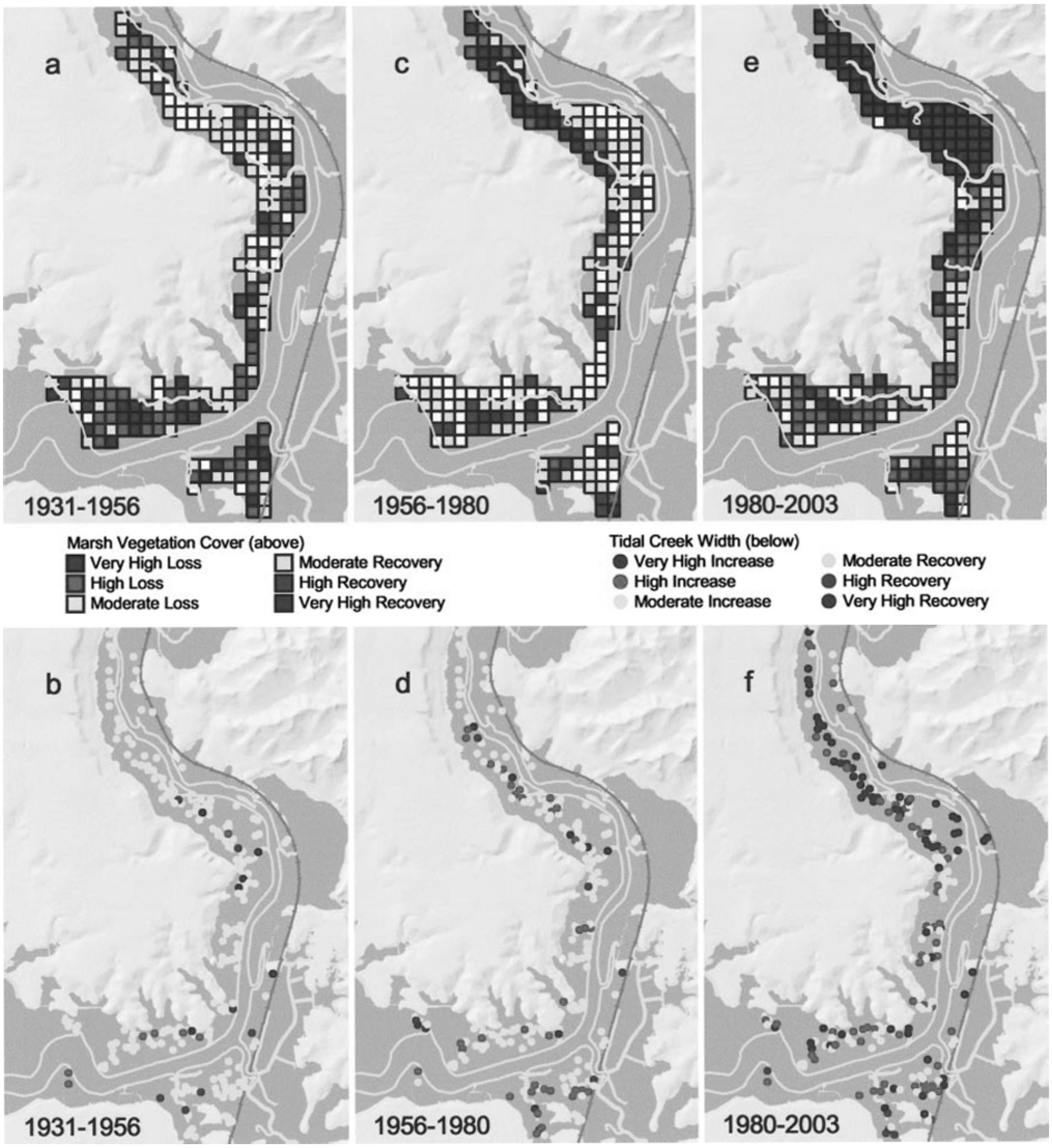


Fig. 6. Annualized change, vegetation cover and tidal creek width. 1931–1956: (a) High to very high marsh loss at lower slough; moderate loss at mid and upper slough. (b) Low to moderate overall tidal creek width increase. 1956–1980: (c) Little change or marsh recovery at lower and mid slough; very high loss at upper slough. (d) High to very high creek width increase at upper slough and southern part of lower slough; low to moderate increase elsewhere. 1980–2003: (e) Moderate to high marsh loss at lower and mid slough; very high loss at upper slough. (f) Moderate to very high creek width increase at lower and mid slough; very high increase at upper slough.

this evolution from a network of tidal creeks to open mudflat within region 5. No period of significant recovery was evident in any of the regions.

A geospatial depiction of annualized changes in creek width during the intervals 1931–1956, 1956–1980, and 1980–2003 is shown in Fig. 6b,d,f. The rate of creek widening was generally low to moderate (<0.1 m yr^{-1}) during the first third of the study period, with a somewhat lower overall rate in the upper slough. A small number of creek cross

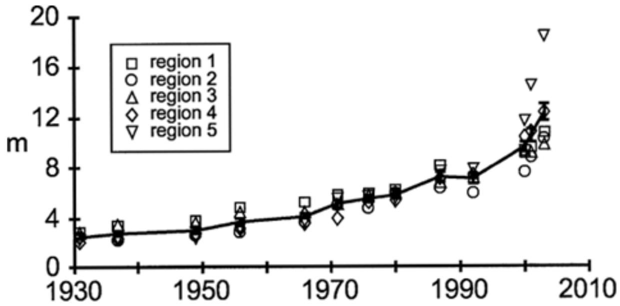


Fig. 7. Mean cross section width of 196 tidal creeks in undiked areas, 1931–2003. Line is mean for all regions. Error bars represent 1 standard error.

sections experienced high (>0.1 m yr^{-1}) or very high (>0.25 m yr^{-1}) rates of change during this initial interval; these large increases occurred along several of the slough's widest channels. During the middle third of the study period, differences between the lower, mid, and upper regions of the slough became increasingly apparent. Although the rate of change remained low to moderate throughout most of the study area, a number of creeks in the southern portion of the lower slough (region 2) and the western portion of the upper slough (regions 5 and much of region 4) widened at high to very high rates. By the final third of the study period, rates of tidal creek widening were uniformly moderate to very high across the lower and mid slough and predominately very high in the upper slough.

Discussion

Causes of Tidal Wetland Habitat Change

We have documented dramatic shifts in the extent and distribution of wetland habitat types at Elkhorn Slough during the past 150 yr. These changes can largely be attributed to contrasting anthropogenic influences on the slough's hydrology: restrictions to the range of tidal flow that occurred earlier in the study period and expansion of tidal range, amplitude, and velocity that have occurred more recently.

Tidal wetlands adjust to a dynamic equilibrium of erosional and depositional processes through a uniform distribution of channel bed shear stress and a balancing of mouth cross-sectional area to tidal volume (Allen 2000). Reduction of tidal prism volume due to restricted tidal flow (e.g., diking) can result in channel shoaling and mouth closure, while an enlarged tidal prism due to expanded tidal flow (e.g., levee breaching) drives channel erosion (O'Brien 1931; Williams et al. 2002).

Restrictions to Tidal Flow

Diking and draining of wetlands was the key driver of estuarine habitat change during the initial 100 yr of the study period. In 1872, a raised embankment for the Southern Pacific Railroad was constructed through marshlands on the east side of Elkhorn Slough (Fabing and Hamman 1985). This linear feature separated more than one third of the slough's wetlands from the main channel. Despite their physical separation, these wetlands remained largely intact for several decades, likely due to the construction of bridges and culverts that permitted continued tidal flow under the railroad.

In the early 20th century, landowners began to isolate wetlands east of the railroad embankment from tidal flow by blocking culverts and creeks under bridges. During the same period, tidal exchange was excluded from additional wetland acreage as levees were constructed for various purposes (Silberstein et al. 2002). Beginning around 1900, sportsmen purchased tracts of tideland and managed about 120 ha as waterfowl habitat by impounding freshwater behind dams across inlets and levees around artificial ponds (Grinnell et al. 1918). In the following decades, an additional 120 ha of marsh were diked and removed from tidal influence to create salt evaporation ponds for the Monterey Bay Salt Works (Ver Planck 1958). Between the 1920s and 1940s, approximately 600 ha of former tidal wetland were converted to agricultural uses, particularly pastureland for dairy operations (King 1981). Several additional wetland areas on the periphery of the slough were isolated from tidal flow by the construction of roads. By 1956, these projects had resulted in a 45% decrease in tidal range and a 60% loss of salt marsh acreage.

Expansion of Tidal Flow

Prior to 1947, Elkhorn Slough was a depositional system with reduced tidal volume, the result of extensive diking and reclamation of tidelands and the clearing of adjacent uplands. Tidal energy was muted due to shoaling in the lower channel and a persistent sand bar at the natural mouth into Monterey Bay, 0.5 km north of the slough on the Salinas River (Gordon 1996).

In 1947, the U.S. Army Corps of Engineers constructed an artificial channel to accommodate vessel traffic into a newly created harbor at Moss Landing (Silberstein et al. 2002). This deeper, wider mouth is directly in line with the slough's main channel, and is kept clear with jetties and periodic dredging. The result was an immediate increase in the velocity and amplitude of tidal exchange within the slough (Wong 1989). Stronger tidal flow, greater tidal reach, and a mismatch between the larger opening and the estuary's shallow, meandering channels and creeks abruptly transformed the slough into a highly erosional system. In the years since 1947, the main channel has rapidly increased in both width and depth, resulting in an increase in volume of over 200% (Crampton 1994; Malzone 1999). Field measurements record bank erosion rates averaging 0.5 m yr^{-1} between 2000 and 2004 (Wasson unpublished data).

Greater tidal energy, increased tidal amplitude, and extended periods of marsh inundation resulting from the 1947 opening are almost certainly the principal causes of marsh degradation and tidal creek widening during the most recent five decades of the study period. Our marsh quadrat and tidal creek analyses show that conversion of salt marsh habitat to mudflat and the widening of tidal creeks accelerated to significant levels only after 1949, timing that coincides with the artificial channel opening.

During the final two decades of our study, intentional and unintentional breaching of levees allowed tidal flow to return to many of the slough's diked former wetlands. Habitat restoration returned full flow to about 120 ha at Elkhorn Slough National Estuarine Research Reserve's South Marsh in 1983, followed by the return of partial flow (through tidegates) to an additional 40 ha at North Marsh in 1985. During the same period, levees at Parsons Slough and the abandoned salt works failed, as did numerous smaller levees. In less than a decade, Elkhorn Slough's tidal prism expanded by about 30% (Malzone 1999). The result was significantly higher tidal velocities (Wong 1989), accelerating the rate of tidal erosion in channels and creeks. Expanding channels and creek networks drive a positive feedback loop by further enlarging the tidal prism and by extending the reach of tidal flow deeper into the marsh.

Patterns of marsh degradation and tidal creek widening varied by region and by period (Fig. 6). In the decade following the 1947 opening, the rate of vegetation loss was greatest in regions nearest the new artificial mouth. During the subsequent 24 yr, losses were extremely high in regions farthest from the new mouth, while the lower and mid slough experienced minimal marsh loss and, in many cases, significant recovery. This period of renewed accretion in the lower slough probably resulted from the onset of high erosion rates farther up the slough, as large volumes of sediment began to be dislodged and transported. In any case, the recovery was short-lived. During the final 23 yr of the study, high rates of marsh loss and tidal creek widening returned to the lower slough. At the same time, rates of loss have accelerated to uniformly very high levels throughout the upper slough.

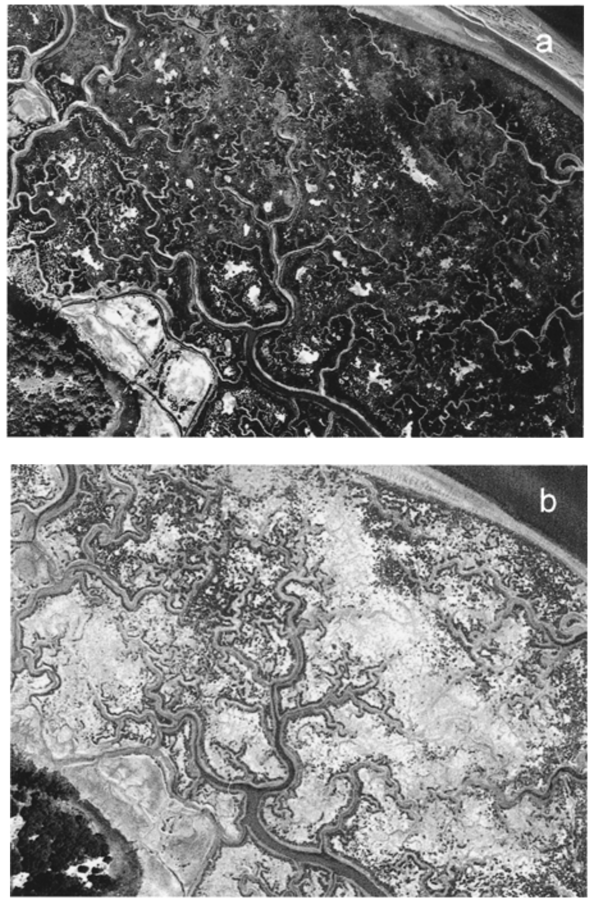


Fig. 8. Evolution of salt marsh to mudflat within region 5. Dark areas are salt marsh, light areas unvegetated. (a) Tidal creek network and growing interior pannes, 1980 aerial photo. (b) Deteriorated marsh largely converted to open mudflat, 2001 aerial photo.

The exact mechanism by which increased tidal amplitude, velocity, and volume have caused marsh vegetation to degrade is unclear. Surface erosion may be reducing elevations to beneath the level where *Salicornia* can survive, although current velocities within the marsh are typically too low to erode the substrate (Lowe 1999). Stronger currents may result in decreased sediment deposition, gradually lowering the marsh plain (Orr et al. 2003). Vegetation thinning appears to progress from the interior of the marsh, initiating the formation of growing mud pannes (Fig. 8). In time, only a fringe of vegetation remains along the banks of channels and creeks; eventually these banks deteriorate as well, leaving an expanse of mudflat. The pattern is consistent with other reports of marsh degradation resulting from relative lowering of the marsh plain and an accompanying increase in the frequency and duration of inundation (Phillips 1986; Kearney et al. 1988; DeLaune et al. 1994; Downs et al. 1994; Hartig et al. 2002).

Additional Possible Causes of Change

Although we attribute the changes we have documented largely to diking, channel construction, levee breaching, and other anthropogenic modifications to tidal flow, several additional factors might contribute to wetland habitat change at Elkhorn Slough.

Before 1909, the Salinas River shared a common mouth with Elkhorn Slough. Redirection of the river directly into Monterey Bay in 1909 eliminated this seasonal source of freshwater and sediment (Gordon 1996). Decreased sediment input is reported to be a principal cause of salt marsh loss at some locations, and redirection of the Salinas River likely reduced the supply of sediment to Elkhorn Slough's tidal wetlands, although highly erodible soils, steep slopes, and extensive agricultural and residential development adjacent to the slough continue to provide large quantities of sediment (Dickert and Tuttle 1985).

Relative sea level increase is a cause of wetland habitat change in many regions, although the rate of eustatic sea level rise on the central California coast is relatively low and not likely to outpace the rate of marsh accretion (Atwater et al. 1977). If a change in relative sea level is contributing to wetland loss at Elkhorn Slough, it is more likely the result of land subsidence (Patrick and DeLaune 1990). Lowe (1999) suggests that rapid salt marsh loss in the upper slough may have been due to a drop in the marsh plain following the 1989 Loma Prieta earthquake, although our results reveal not a single episode, but a trend of marsh loss that began decades before the 1989 event. Subsidence of the marsh plain might also result from groundwater overdraft. Groundwater levels in the Elkhorn Slough area have been falling since the 1950s, although the magnitude of associated land subsidence is unknown (Fugro West 1995).

Biotic factors such as disease and herbivory are also potential causes of wetland habitat change (e.g., Miller et al. 1996). Marsh degradation is occurring rapidly in undiked areas at Elkhorn Slough while areas with extremely limited tidal flow are relatively unaffected. It is unclear how disease or herbivory might be linked to these hydrological conditions.

Effects of Habitat Change on Biological Communities

The consequences to Elkhorn Slough's plant and animal communities from 150 yr of hydrologic alteration and habitat change are poorly understood. Additional studies aimed at understanding the effects of a dramatic decrease in salt marsh acreage, corresponding increases in intertidal mudflats and pannes, and enlarged subtidal channels and creeks will be fundamental to future conservation planning.

Only about 3% of conterminous U.S. salt marsh acreage occurs along the Pacific Coast (Field et al. 1991), so the degradation or loss of more than two thirds of Elkhorn Slough's salt marsh is extremely significant. In addition to providing a variety of key ecosystem services, such as trapping sediments and filtering nutrients from upland runoff, California's tidal marshes provide food or habitat for a variety of organisms including shore crabs (*Hemigrapsus oregonensis*) and song sparrows (*Melospiza melodia*), as well as supporting various threatened animals, including the California clapper rail (*Rallus longirostris obsoletus*) and California brackishwater snail (*Tryonia imitator*) (Zedler 1996b; Wasson et al. 2002). As Elkhorn Slough's marshlands have degraded or converted to other habitat types during the past century, salt marsh associated faunal communities have undoubtedly declined in abundance and distribution.

A less apparent consequence of Elkhorn Slough's history of hydrologic modifications has been the loss of transitional vegetation communities. Before dikes were constructed to segregate tidal from nontidal habitat types, wetlands at the margins of the slough were subjected to extreme variations of salinity and inundation regimes as a result of periodic cycles as well as occasional, episodic events. During the decades since the 1940s, numerous surface streams, springs, and seeps in the vicinity of Elkhorn Slough have disappeared, presumably due to lowered groundwater levels resulting from agricultural and domestic pumping (Van Dyke unpublished data). Although our habitat maps delineate the slough's vegetated wetlands as uniformly salt marsh during the earliest periods, a variety of small patches of freshwater-influenced vegetation undoubtedly existed in the vicinity of freshwater features (Hayward 1931). Vegetation types adapted to extreme salinity fluctuations are now very uncommon within Elkhorn Slough's modified tidal wetlands. Because these brackish and transitional wetland habitat types are increasingly uncommon, species associated with these conditions (e.g., the tidewater goby, *Eucyclogobius newberryi*), which were likely once relatively common at Elkhorn Slough, are now very rare (Yoklavich et al. 2002).

As Elkhorn Slough's intertidal habitats have undergone changes, adjacent subtidal communities have been affected by the slough's altered hydrology as well. Physical parameters, such as water movement, salinity, and sediment size, are known to influence estuarine faunal communities (Edgar et al. 2000; Little 2000). Extensive eelgrass (*Zostera marina*) beds were present along much of the slough's lower main channel in the 1920s; only a few small patches remain today (MacGinitie 1935; Zimmerman and Caffrey 2002). Increased turbidity and channel depth resulting from higher tidal energy are likely causes. This decline is a significant conservation concern because eelgrass is a major contributor to productivity in California estuaries and provides important habitat for many invertebrates and fish species (Ricketts et al. 1985; Yoklavich et al. 2002). The widening and deepening of Elkhorn Slough's main channel and tidal creeks has also enabled the slough to be colonized by large marine fish and mammals. Several species that would only have been present near the mouth a century ago, such as leopard sharks (*Triakis semifasciata*), bat rays (*Myliobatis californica*), harbor seals (*Phoca vitulina*), and sea otters (*Enhydra lutris*), are now abundant throughout much of the estuary (Harvey and Connors 2002; Yoklavich et al. 2002).

Tidal Wetland Conservation and Habitat Change

Conservation and restoration of estuarine ecosystems have emerged as major environmental concerns in recent decades (Kennish 2002). As our study demonstrates, Elkhorn Slough's tidal wetlands have undergone more than a century of habitat change. The majority of these wetlands are now owned and managed for conservation purposes, and anthropogenic modification of the slough's hydrology has largely ceased. Yet rates of conversion from salt marsh to mudflat or open water and expansion of tidal channels and creeks remain high and may be accelerating, suggesting that a new equilibrium may not be reached for many decades. Conservation planning is difficult within this context of uncertainty and rapid change.

Wetland managers face a dual challenge of developing and implementing strategies that not only slow the rate of change to protect existing intact habitats, but also restore and enhance degraded wetlands in order to maintain an appropriate diversity of habitat types. Restoration of estuarine habitats frequently fails to meet desired goals (Zedler 1996a; Zedler and Callaway 1999). More than 200 ha of diked and drained former salt marsh at Elkhorn Slough National Estuarine Research Reserve were returned to tidal influence through restoration projects undertaken during the 1980s. These newly created tidelands support rich communities of birds, fish, and invertebrates within tidal lagoons and mudflats, yet restoration to the former landscape of salt marsh, pannes, and tidal creek networks has not succeeded.

The likelihood of restoration success is increased when plans imitate the complex structure of natural tidal wetlands and maintain connectivity with intact wetland habitats as well as with adjoining subtidal and upland habitats (Williams and Zedler 1999; Desmond et al. 2000). The currently rapid rate of habitat change at Elkhorn Slough is the result of a long history of deliberate tidal alteration and habitat isolation through the construction of levees, channels, and tide gates. Ironically, slowing the rate of habitat change may require these same tools—the construction and maintenance of levees, channels, and gates—to mute tidal energy, reduce erosion, and enhance marsh accretion. Wetland managers must balance the need to mitigate for the effects of historic alterations (e.g., mute tidal flow by building new dikes and gates) with the need to reintroduce natural tidal flushing, salinity and inundation variability, and habitat connectivity (e.g., by removing existing dikes and gates).

Conservation planning at other West Coast estuaries has been strengthened by studies that document past habitat conditions and historic patterns of change (e.g., Zedler 1996b; Goals Project 1999; Borde et al. 2003). We believe that our analysis of 150 yr of habitat change can similarly inform conservation and restoration efforts at Elkhorn Slough. Historical ecology may not supply easy answers to Elkhorn Slough's complex habitat conservation questions, but a thoughtful analysis of the historical record can help guide the development of feasible and sustainable restoration goals.

Acknowledgments

Pioneering studies by John Oliver and colleagues at Moss Landing Marine Laboratories and by Rikk Kvitek and colleagues at the California State University, Monterey Bay Seafloor Mapping Lab inspired this project. Andrea Woolfolk, Robin Grossinger, and Mark Silberstein provided early direction, and Andrea's continued collaboration has strengthened this work. Thanks to Kristin Byrd, John Callaway, Josh Collins, Mike Foster, John Oliver, Barb Peichel, Doug Smith, and two anonymous reviewers for thoughtful discussions or comments on the manuscript. Thanks to the University of California, Santa Cruz Map Room, Monterey County Surveyors Inc., and many other archives that provided access to important historic maps and images. We are grateful to the Estuarine Reserves Division of the National Oceanic and Atmospheric Administration for funding and to the California Department of Fish and Game and the Elkhorn Slough Foundation for ongoing support of historical ecology studies at Elkhorn Slough National Estuarine Research Reserve.

Literature Cited

Adam, P. 2002. Saltmarshes in a time of change. *Environmental Conservation* 29:39–61.

Allen, J. R. L. 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, B. F. 1987. Evidence for great Holocene earthquakes along the outer coast of Washington State. *Science* 236:942–944.

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. U.S. Geological Survey Open-File Report 76-389. Menlo Park, California.

Atwater, B. F., C. W. Hedel, and E. J. Helley. 1977. Late quaternary depositional, Holocene sea-level changes, and vertical crustal movement, southern San Francisco Bay, California. U.S. Geological Survey Professional Paper 1014. Washington, D.C.

Barry, J. P., M. M. Yoklavich, G. M. Cailliet, D. A. Ambrose, and B. S. Antrim. 1996. Trophic ecology of the dominant fishes in Elkhorn Slough, California, 1974–1980. *Estuaries* 19: 115–138.

Berquist, J. R. 1978. Depositional history and fault-related studies, Bolinas Lagoon, California. U.S. Geological Survey Open-File Report 78-802. Washington, D.C.

Boesch, D. F., M. Josselyn, A. Mehta, J. Morris, W. Nuttle, C. Simenstad, and D. Swift. 1994. Scientific assessment of coastal wetland loss, restoration, and management in Louisiana. *Journal of Coastal Research* 20:1–103.

Borde, A. B., R. M. Thom, S. Rumrill, and L. M. Miller. 2003. Geospatial habitat change analysis in Pacific Northwest coastal estuaries. *Estuaries* 26:1104–1116.

Caffrey, J. 2002. Climate, p. 25–28. *In* J. Caffrey, M. Brown, W. B. Tyler, and M. Silberstein (eds.), Changes in a California Estuary: A Profile of Elkhorn Slough. Elkhorn Slough Foundation, Moss Landing, California.

Caffrey, J. and W. Broenkow. 2002. Hydrography, p. 29–42. *In* J. Caffrey, M. Brown, W. B. Tyler, and M. Silberstein (eds.), Changes in a California Estuary: A Profile of Elkhorn Slough. Elkhorn Slough Foundation, Moss Landing, California.

Cole, K. L. and E. Wahl. 2000. A late Holocene record from Torrey Pines State Reserve, California. *Quaternary Research* 53: 341–351.

Crampton, T. A. 1994. Long Term Effects of Moss Landing Harbor on the Wetlands of Elkhorn Slough. M.S. Thesis, University of California, Santa Cruz, California.

Dahl, T. E. 2000. Status and trends of wetlands in the conterminous United States 1986 to 1997. Fish and Wildlife Service, U.S. Department of the Interior, Washington, D.C.

Day, Jr., J. W., G. P. Shaffer, L. D. Britsch, D. J. Reed, S. R. Hawes, and D. Cahoon. 2000. Pattern and process of land loss in the Mississippi delta: A spatial and temporal analysis of wetland habitat change. *Estuaries* 23:425–438.

Day, Jr., J. W., F. Scarton, A. Rismondo, and D. Are. 1998. Rapid deterioration of a salt marsh in Venice Lagoon, Italy. *Journal of Coastal Research* 14:583–590.

DeLaune, R. D., J. A. Nyman, and W. H. Patrick. 1994. Peat collapse, ponding and wetland loss in a rapidly submerging coastal marsh. *Journal of Coastal Research* 10:1021–1030.

Desmond, J. S., G. D. Williams, and J. B. Zedler. 2000. Improving the design of fish habitat mitigation projects in southern California, p. 245–251. *In* J. E. Keeley, M. Baer-Keeley, and C. J. Fotheringham (eds.), 2nd Interface Between Ecology and Land Development in California. U.S. Geological Survey Open-File Report 00-62. Sacramento, California.

Dickert, T. G. and A. E. Tuttle. 1985. Cumulative impact assessment in environmental planning: A coastal wetland watershed example. *Environmental Impact Assessment Review* 5:37–64.

Dietz, S. A., W. Hildebrandt, and T. Jones. 1988. Archaeological investigations at Elkhorn Slough: CA-MNT-229, a middle period site on the central California coast. *Papers in Northern California Anthropology* 3.

Downs, L. L., R. J. Nicholls, S. P. Leatherman, and J. Hautzenroder. 1994. Historic evolution of a marsh island: Bloodsworth Island, Maryland. *Journal of Coastal Research* 10:1031–1044.

Edgar, G. J., N. S. Barrett, D. J. Graddon, and P. R. Last. 2000. The conservation significance of estuaries: A classification of Tasmanian estuaries using ecological, physical and demographic attributes as a case study. *Biological Conservation* 92: 383–397.

Emmett, R., R. Llanso, J. Newton, R. Thom, M. Hornberger, C. Morgan, C. Levings, A. Copping, and P. Fishman. 2000. Geographic signatures of North American West Coast estuaries. *Estuaries* 23:765–792.

Fabing, H. W. and R. Hamman. 1985. Steinbeck Country Narrow Gauge, 1st edition. Pruett Publishing, Boulder, Colorado.

Field, D. W., A. J. Reyer, P. V. Genovese, and B. D. Shearer. 1991. Coastal wetlands of the United States: An accounting of a valuable national resource. Office of Oceanography and Marine Assessment, National Ocean Service, National Oceanic and Atmospheric Administration, Rockville, Maryland.

Foxgrover, A. C., S. A. Higgins, M. K. Ingraca, B. E. Jaffe, and R. E. Smith. 2004. Deposition, erosion, and bathymetric change in south San Francisco Bay: 1858–1983. U.S. Geological Survey Open-File Report 2004-1192. Reston, Virginia.

Fugro West. 1995. North Monterey County Hydrogeologic Study, Volume 1. Water Resources, Prepared for Monterey County Water Resources Agency. Fugro West, Inc., Monterey, California.

Goals Project. 1999. Baylands Ecosystem Habitat Goals. U.S. Environmental Protection Agency, San Francisco, California and San Francisco Regional Water Quality Control Board, Oakland, California.

Gordon, B. L. 1996. Monterey Bay Area: Natural History and Cultural Imprints, 3rd edition. Boxwood Press, Pacific Grove, California.

Grinnell, J., H. C. Bryant, and T. I. Storer. 1918. The Game Birds of California, 1st edition. University of California Press, Berkeley, California.

Grossinger, R. 2000. Documenting local landscape change: The San Francisco Bay area historical ecology project, p. 425–441. *In* D. Egan and E. A. Howell (eds.), The Historical Ecology Handbook, 1st edition. Island Press, Washington, D.C.

Hartig, E. K., V. Gornitz, A. Kolker, F. Mushacke, and D. Fallon. 2002. Anthropogenic and climate-change impacts on salt marshes of Jamaica Bay, New York City. *Wetlands* 22:71–89.

Harvey, J. T. and S. Connors. 2002. Birds and mammals, p. 187–214. *In* J. Caffrey, M. Brown, W. B. Tyler, and M. Silberstein (eds.), Changes in a California Estuary: A Profile of Elkhorn Slough. Elkhorn Slough Foundation, Moss Landing, California.

Hayward, I. 1931. The Marsh and Aquatic Plants of the Pajaro Valley. M.A. Thesis, Stanford University, Stanford, California.

Hornberger, M. I. 1991. Paleoenvironment of Elkhorn Slough and Surrounding Wetland Habitats: A Geological Study Using an Ecological Approach. M.S. Thesis, San Jose State University Moss Landing Marine Laboratories, Moss Landing, California.

Jensen, J. R. 1996. Introductory Digital Image Processing: A Remote Sensing Perspective, 2nd edition. Prentice Hall, Upper Saddle River, New Jersey.

Jones, T. L. 2002. Archaeology and prehistory, p. 53–91. *In* J. Caffrey, M. Brown, W. B. Tyler, and M. Silberstein (eds.), Changes in a California Estuary: A Profile of Elkhorn Slough. Elkhorn Slough Foundation, Moss Landing, California.

Jones, T. L. and D. A. Jones. 1992. Elkhorn Slough revisited: Reassessing the chronology of CA-MNT-229. *Journal of California and Great Basin Anthropology* 10:163–186.

Kearney, M. S., R. E. Grace, and J. C. Stevenson. 1988. Marsh

loss in Nanticoke estuary, Chesapeake Bay. *Geographical Review* 78:205–220.
KENNISH, M. J. 2001. Coastal salt marsh systems in the U.S.: A review of anthropogenic impacts. *Journal of Coastal Research* 17: 731–748.
KENNISH, M. J. 2002. Environmental threats and environmental future of estuaries. *Environmental Conservation* 29:78–107.
KING, J. M. 1981. Estero Grande: Cultural Ecology and the Evolution of a Coastal Ecosystem. M.S. Thesis, University of California, Davis, California.
LARSON, E. J. 2001. Coastal wetlands-emergent marshes, p. 483–486. *In* W. S. Leet, C. M. Dewees, R. Klingbeil, and E. J. Larson (eds.), California's Living Marine Resources: A Status Report. California and California Department of Fish and Game, Sacramento, California.
LITTLE, C. 2000. The Biology of Soft Shores and Estuaries, 1st edition. Oxford University Press, Oxford, U.K.
LOWE, P. B. 1999. Marsh Loss in Elkhorn Slough, California: Patterns, Mechanisms, and Impact on Shorebirds. M.S. Thesis, San Jose State University Moss Landing Marine Laboratories, Moss Landing, California.
MACDONALD, K. 1988. Coastal salt marsh, p. 262–294. *In* M. G. Barbour and J. Major (eds.), Terrestrial Vegetation of California, 2nd edition. California Native Plant Society Special Publication No. 9. Sacramento, California.
MACGINITIE, G. E. 1935. Ecological aspects of a California marine estuary. *American Midland Naturalist* 16:629–765.
MALZONE, C. M. 1999. Tidal Scour and its Relation to Erosion and Sediment Transport in Elkhorn Slough. M.S. Thesis, San Jose State University Moss Landing Marine Laboratories, Moss Landing, California.
MILLER, D. L., F. E. SMEINS, AND J. W. WEBB. 1996. Mid-Texas coastal marsh change (1939–1991) as influenced by lesser snow goose herbivory. *Journal of Coastal Research* 12:462–476.
MOORE, L. J. 2000. Shoreline mapping techniques. *Journal of Coastal Research* 16:111–124.
National Oceanic and Atmospheric Administration (NOAA). 1990. Estuaries of the United States: Vital Statistics of a National Resource Base. Office of Oceanography and Marine Assessment, National Ocean Service, National Oceanic and Atmospheric Administration, Rockville, Maryland.
NICHOLS, F. H., J. E. CLOERN, S. N. LUOMA, AND D. H. PETERSON. 1986. The modification of an estuary. *Science* 231:567–573.
NIEMI, T. M. AND N. T. HALL. 1996. Historical changes in the tidal marsh of Tomales Bay and Olema Creek, Marin County, California. *Journal of Coastal Research* 12:90–102.
O'BRIEN, M. P. 1931. Estuary tidal prisms related to entrance areas. *Civil Engineering* 1:738–739.
ORR, M., S. CROOKS, AND P. B. WILLIAMS. 2003. Will restored tidal marshes be sustainable? *San Francisco Estuary and Watershed Science* 1:1–33.
PATRICK, W. H. AND R. D. DELAUNE. 1990. Subsidence, accretion, and sea level rise in south San Francisco Bay marshes. *Limnology and Oceanography* 35:1389–1395.
PHILLIPS, J. D. 1986. Coastal submergence and marsh fringe erosion. *Journal of Coastal Research* 2:427–436.
RICKETTS, E. F., J. CALVIN, J. W. HEDGPETH, AND D. W. PHILLIPS. 1985. Between Pacific Tides, 5th edition. Stanford University Press, Stanford, California.
SCAVIA, D., J. C. FIELD, D. F. BOESCH, R. W. BUDDEMEIER, V. BURKETT, D. R. CAYAN, M. FOGARTY, M. A. HARWELL, R. W. HOWARTH, C. MASON, D. J. REED, T. C. ROYER, A. H. SALLENGER, AND J. G. TITUS. 2002. Climate change impacts on U.S. coastal and marine ecosystems. *Estuaries* 25:149–164.
SCHWARTZ, D. L., H. T. MULLINS, AND D. F. BELKNAP. 1986. Holocene geologic history of a transform margin estuary: Elkhorn Slough, central California. *Estuarine Coastal and Shelf Science* 22:285–302.
SILBERSTEIN, M., C. ZABIN, L. NEWBERRY, D. MOUNTJOY, L. STRNAD, AND J. CAFFREY. 2002. History of land use, p. 93–116. *In* J. Caffrey, M. Brown, W. B. Tyler, and M. Silberstein (eds.), Changes in a California Estuary: A Profile of Elkhorn Slough. Elkhorn Slough Foundation, Moss Landing, California.
SOKAL, R. R. AND F. J. ROHLF. 1995. Biometry: The Principles and Practice of Statistics in Biological Research, 3rd edition. W. H. Freeman and Company, New York.
STEERE, J. T. AND N. SCHAEFER. 2001. Restoring the Estuary: Implementation Strategy of the San Francisco Bay Joint Venture. San Francisco Bay Joint Venture, Oakland, California.
STEVENSON, J. C., M. S. KEARNEY, AND E. C. PENDLETON. 1985. Sedimentation and erosion in a Chesapeake Bay brackish marsh system. *Marine Geology* 67:213–235.
SWETNAM, T. W., C. D. ALLEN, AND J. L. BETANCOURT. 1999. Applied historical ecology: Using the past to manage for the future. *Ecological Applications* 9:1189–1206.
TURNER, R. E. 1997. Wetland loss in the northern Gulf of Mexico: Multiple working hypotheses. *Estuaries* 20:1–13.
VER PLANCK, W. E. 1958. Salt in California. California Division of Mines Bulletin 175. California Division of Mines, San Francisco, California.
WASSON, K., J. NYBAKKEN, R. KVITEK, C. BRABY, AND M. SILBERSTEIN. 2002. Invertebrates, p. 135–161. *In* J. Caffrey, M. Brown, W. B. Tyler, and M. Silberstein (eds.), Changes in a California Estuary: A Profile of Elkhorn Slough. Elkhorn Slough Foundation, Moss Landing, California.
WILLIAMS, G. D. AND J. B. ZEDLER. 1999. Fish assemblage composition in constructed and natural tidal marshes of San Diego Bay: Relative influence of channel morphology and restoration history. *Estuaries* 22:702–716.
WILLIAMS, P. B. AND P. M. FABER. 2001. Salt marsh restoration experience in the San Francisco Bay estuary. *Journal of Coastal Research* Special Issue 27:203–211.
WILLIAMS, P. B. AND M. K. ORR. 2002. Physical evolution of restored breached levee salt marshes in the San Francisco Bay estuary. *Restoration Ecology* 10:527–542.
WILLIAMS, P. B., M. K. ORR, AND N. J. GARRITY. 2002. Hydraulic geometry: A geomorphic design tool for tidal marsh channel evolution in wetland restoration projects. *Restoration Ecology* 10:577–590.
WONG, C. R. 1989. Observations of Tides and Tidal Currents in Elkhorn Slough. M.S. Thesis, San Jose State University Moss Landing Marine Laboratories, Moss Landing, California.
YOKLAVICH, M. M., G. M. CAILLET, J. P. BARRY, D. A. AMBROSE, AND B. S. ANTRIM. 1991. Temporal and spatial patterns in abundance and diversity of fish assemblages in Elkhorn Slough, California. *Estuaries* 14:465–480.
YOKLAVICH, M. M., G. M. CAILLET, D. S. OXMAN, J. P. BARRY, AND D. C. LINDQUIST. 2002. Fishes, p. 163–185. *In* J. Caffrey, M. Brown, W. B. Tyler, and M. Silberstein (eds.), Changes in a California Estuary: A Profile of Elkhorn Slough. Elkhorn Slough Foundation, Moss Landing, California.
ZEDLER, J. B. 1996a. Coastal mitigation in southern California: The need for a regional restoration strategy. *Ecological Applications* 6:84–93.
ZEDLER, J. B. 1996b. Tidal wetland restoration: A scientific perspective and southern California focus. California Sea Grant College System Publication T-038, University of California, La Jolla, California.
ZEDLER, J. B. AND J. C. CALLAWAY. 1999. Tracking wetland restoration: Do mitigation sites follow desired trajectories? *Restoration Ecology* 7:69–73.
ZIMMERMAN, R. C. AND J. CAFFREY. 2002. Primary producers, p. 117–133. *In* J. Caffrey, M. Brown, W. B. Tyler, and M. Silberstein (eds.), Changes in a California Estuary: A Profile of Elkhorn Slough. Elkhorn Slough Foundation, Moss Landing, California.

Received, August 18, 2004
Accepted, October 28, 2004