

THE QUATERNARY GEOGRAPHY AND BIOGEOGRAPHY OF TIDAL SALTMARSHES

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Abstract. Climate change and sea-level change largely explain the changing distribution and structure of tidal saltmarshes over time, and these geographic attributes, in turn, are primarily responsible for the biogeography of tidal-saltmarsh organisms. This paper presents a general model of these relationships, and uses the San Francisco Bay-delta estuary (California) to demonstrate some of the model's implications and limitations. Throughout the Quaternary period, global cycles of glaciation and deglaciation have resulted in ca. 100-m variations in global mean sea level, which have been accompanied by large changes in the location of the intertidal coastal zone, and hence of potential sites for tidal marshes. Other climate-related variables (e.g., temperature and exposure to storms) have in turn substantially controlled both the location and size of marshes within the coastal zone and of specific physical environments (i.e., potential habitats) within marshes at any time. Since the most recent deglaciation resulted in a global rise in sea level of 100–130 m between about 21,000 and 7,000 yr BP, and a slower rise of about 10 m over the last 7,000 yr, modern tidal saltmarshes are relatively young geomorphic and ecological phenomena, and most continue to evolve in elevation and geomorphology. Therefore, the distribution of taxa between and within marshes reflects not only salinity and wetness at the time, the dominant controls on marsh zonation, but also antecedent conditions at present marsh sites and the extent and connectedness of habitat refugia during and since the glacial maximum. Unfortunately, direct stratigraphic evidence of paleommarsh extent and distribution is almost nonexistent for the Late Glacial-Early Holocene, and is incomplete for the late Holocene.

Key Words: biogeography, glacial-deglacial cycles, global climate change, Quaternary, San Francisco Bay, sea-level change, spatial patterns, tidal saltmarsh.

LA GEOGRAFÍA Y BIOGRAFÍA CUATERNARIA DE MARISMAS SALADAS DE MAREA

Resumen. Tanto el cambio climático como el cambio en el nivel del mar explican ampliamente el cambio en la distribución y la estructura de marismas saladas de marea en el transcurso del tiempo; y estos atributos geográficos a su vez, son los principales responsables de la biogeografía de los organismos de marismas saladas de marea. Este artículo presenta un modelo general de estas relaciones y utiliza el estuario Bahía-delta de San Francisco (California) para demostrar algunas de las implicaciones y limitaciones del modelo. A lo largo del período cuaternario, ciclos globales de glaciación y deglaciación han resultado en variaciones ca. 100-m en la media global del nivel del mar, lo cual ha sido acompañado por un gran número de cambios en la ubicación de la zona costera intermareal y por ende, de sitios potenciales para marismas de marea. Otras variables relacionadas al clima (ej. temperatura y exposición a tormentas) han hecho que se controle substancialmente tanto la ubicación, como el tamaño de marismas a lo largo de la zona costera así como de ambientes físicos (ej. habitats potenciales) entre los marismas en cualquier tiempo. A partir de la más reciente deglaciación que resultó en un incremento en el nivel del mar de 100–130 m entre 21,000 y 7,000 años AP, y un incremento más lento de cerca de 10 m en los últimos 7,000 años, las marismas saladas de marea modernas son un fenómeno relativamente joven morfológica y ecológicamente, que deberá seguir evolucionando en elevación y geomorfología. Es por esto que la distribución del taxa entre y dentro de los marismas no solo refleja salinidad y humedad en el tiempo, los controles dominantes de la zona de marisma, sino que también condiciones anteriores en sitios presentes de marisma y el alcance y conectividad del hábitat de refugio durante y a partir del máximo glacial. Desafortunadamente, es casi inexistente la evidencia directa estratigráfica del alcance y distribución del paleo marisma, para el Heleoceno Tardío Glacial-Temprano.

Two related but distinct phenomena—climate change and sea-level change—largely explain the changing distribution and structure of tidal saltmarshes over time, and this historical geography, in turn, is primarily responsible for the present biogeography of the organisms

that inhabit them. Marsh biogeography, the distribution of tidal-saltmarsh organisms at all spatial scales, has become a significant research question in recent years, and the conservation of these organisms a major priority for natural resource managers (Estuary Restoration Act

2000, Zedler 2001), but the limited extent of these ecosystems and the limited distribution of their fauna have made it difficult to formulate useful general conceptual models of marsh distribution, structure, and function (Daiber 1986, Goals Project 1999, Zedler 2001). This is reflected in the literature on marshes and marsh organisms, which has historically focused heavily on the attributes of specific sites (Zedler 1982, Stout 1984, Teal 1986, Goals Project 1999), and on generalities which emphasize the significance of local conditions as controls on marsh form and function (Chapman 1974, Adam 1990, Mitsch and Gosselink 2000).

One general principle widely recognized is that tidal saltmarshes are very young landscapes in geologic time and young ecosystems in evolutionary time, having existed in their present locations for no more than a few thousand years due to the transition from a glacially dominated global climate to warmer conditions with higher sea levels over the last 20,000 yr (Zedler 1982, Josselyn 1983, Teal 1986, Mitsch and Gosselink 2000). Although the youth of tidal saltmarshes can further serve to emphasize their uniqueness in time as well as in space, the primary aim of this paper is to explore how climate change and sea-level change can instead serve as organizing principles of a supplemental general conceptual model of tidal-saltmarsh geography and biogeography. We accomplish this by first articulating a standard model of tidal-saltmarsh geography and biogeography that is implicit in most of the literature, and then by proposing the supplemental model. Then to justify and expand the model, we present sections on the mechanisms, patterns, and consequences of global climate change; on the distribution of marshes and marsh types at multiple spatial scales; and on the distribution of taxa between and within marshes. Finally, although the underlying causes we review are essentially global, their local effects can vary dramatically, and the San Francisco Bay-delta estuary (California) is used to illustrate the complex interplay of global processes and local settings.

THE STANDARD MODEL OF TIDAL SALTMARSH GEOGRAPHY AND BIOGEOGRAPHY

Tidal saltmarshes, by definition, are coastal areas characterized by (1) tidal flooding and drying, (2) salinity in sufficient quantity to influence the biotic community, and (3) non-woody vascular vegetation (Mitsch and Gosselink 2000), although some authors have emphasized the role of tides (Daiber 1986, Zedler 2001), others of salt (Chapman 1974, Adam 1990), and

others of the specialized flora of these areas (Eleuterius 1990). Because climate change and other global-scale or long-term phenomena can influence water level and salinity patterns independently, it is important to carefully distinguish between marshes that are tidal, those that are salty, and those that are both.

In addition to their defining characteristics and their relative youth, tidal saltmarshes share relatively few attributes on a global scale, although some generalities have been noted. Tidal saltmarshes typically have high biotic productivity and food webs dominated by detritus rather than herbivory (Mitsch and Gosselink 2000). They frequently, although not inevitably, provide habitat for taxa that are only found in this type of environment, that are limited in geographic range, and/or that are rare (Zedler 2001). Tidal saltmarshes sometimes have high biodiversity at some taxonomic levels, but this varies considerably depending on the metric used, e.g., whether periodic visitors or only obligate residents are counted, marsh size and shape, the size and distribution of other marshes in the region, the elevation and distribution of landforms on the marsh, the degree of spatial variation in physical conditions within the marsh, the proximity and quality of adjacent refugia during high tides or other stressors, and the extent of anthropogenic disturbance. Although small, isolated, disturbed, and highly salty and/or highly tidal marshes can provide significant habitat for some taxa, they generally have low biodiversity at most taxonomic levels (Goals Project 1999, Zedler 2001).

Although the phrase is not commonly used, it is clear that a standard model of tidal-saltmarsh geography and biogeography (Malamud-Roam 2000) is implicit in the literature and is used to explain both the similarities and differences between marshlands (Daiber 1986, Adam 1990, Mitsch and Gosselink 2000, Goals Project 1999, Zedler 2001). This standard model includes several basic elements spanning a range of spatial and temporal scales: (1) distribution of marshes—tidal saltmarshes exist where favorable local conditions (protection from waves and storms, relatively gradual bedrock slope, and sediment accumulation faster than local coastal submergence) exist within latitudinal zones warm enough for vegetation but too cold for mangroves, (2) distribution of landforms—although geomorphic features of marshes are relatively stable, marshes are depositional environments and become higher and drier over time unless local sediment supplies are limiting, (3) distribution of marsh organisms between marshes—salinity gradients along estuaries dominate distribution of habitat types and hence

of taxa, and (4) distribution of marsh organisms within marshes—plants and animals are found in zones primarily reflecting elevation and hence wetness or hydroperiod. Local hydroperiod is modified by channel and pond configuration. As sediments accumulate, plants and animals adapted to drier conditions replace those more adapted to frequent or prolonged flooding.

In this standard model, long-term temporal changes in the distribution of marshes, marsh habitats, and marsh organisms are generally recognized to be consequences of climate change and, in particular, of deglaciation. Many authors recognize that modern tidal saltmarshes are young features, reflecting global sea-level rise during the late Pleistocene and early Holocene (ca. the last 21,000 yr), that this rise has been due to glacial melting and thermal expansion of ocean water, and that the rate of rise dropped dramatically about 7,000–5,000 yr BP (to 1–2 mm/yr), leading to relatively stable coastlines since that time (Chapman 1974, Mitsch and Gosselink 2000). Climate change, deglaciation, and global sea-level change are almost always presented as past phenomena, significant primarily for controlling the timing of marsh establishment and for setting in motion processes of landscape evolution and/or ecosystem succession (Zedler 1982, Josselyn 1983, Teal 1986, Mitsch and Gosselink 2000). Spatial differences in rates of relative sea-level rise, due to local crustal movements, have been described primarily where they have been large enough to result in marsh drowning (Atwater and Hemphill-Haley 1997) or dessication (Price and Woo 1988).

On shorter time scales—decades to centuries—the preferred explanations for changes in the distribution of marsh types and organisms have varied greatly, apparently reflecting trends in environmental sciences in general, as well as disciplinary differences and individual interests. Although relatively fixed successional pathways, emphasizing biotic, especially plant, roles in modifying the marsh environment, were commonly discussed in previous decades (Chapman 1974), explanations of progressive changes in marshes then shifted primarily to landscape evolution with an emphasis on geomorphic responses to local sediment supplies and coastal submergence rates (Josselyn 1983, Mitsch and Gosselink 2000). More recently, at least five trends are apparent in the literature: (1) a recognition that dynamic equilibrium can occur at relatively long time scales, and that change is rarely continuous in one direction for long (Mitsch and Gosselink 2000), (2) an increasing focus on the patterns and consequences of disturbance, and in particular human disturbance (Daiber

1986, Zedler 2001), (3) a shift in emphasis from fixed pathways to thresholds and bifurcation points between possible paths or trajectories of change (Zedler 2001, Williams and Orr 2002), (4) an explicit integration of geomorphic and biotic processes and interactions between them (American Geophysical Union 2004), and (5) a burgeoning concern that anthropogenic climate change might substantially increase the rate of sea-level change, with perhaps dramatic consequences for tidal saltmarshes (Keldsen 1997).

A HISTORICALLY FOCUSED SUPPLEMENTAL MODE

Although all of the elements and variations of the standard model are useful, they do not appear to adequately explain biodiversity, adaptive radiations, endemism, rarity, colonization-invasion patterns, historic marsh distribution, or many other qualities critical to conservation biology. Classical biogeography theory argues that these are most likely controlled by the historical distribution of habitats (e.g., islands, and refugia; MacArthur and Wilson 1967, Lomolino 2000, Walter 2004), and recent global-change research indicates that this historical geography has been largely controlled by large-scale climate dynamics. We therefore suggest that the standard model be supplemented by the conceptual model of tidal saltmarsh geography and biogeography shown in Fig. 1, which emphasizes climate change and sea-level change as organizing principles, and which sets local phenomena explicitly in the context of global and millennial scales of space and time than is typical.

The flow chart shown in Fig. 1 expands the standard model largely by emphasizing distinctions between related causes for observed phenomena. First, although global mean (eustatic) sea-level rise associated with the most recent deglaciation is still the primary causal factor in marsh history, climate change and sea-level change are distinct, with climate change influencing marsh form and function through many mechanisms. Second, climate and sea level determine not only the current locations and extent of marshes, but also their past distribution, extent, and connectedness; these antecedent conditions, especially the amount and location of habitat refugia, have probably strongly influenced the large-scale distribution of taxa. Third, the history of the coastal zone, which can be mapped with some precision, is distinct from the actual extent and distribution of marshes at any time, which has responded to many global and local variables, and which is, hence, much less definite. Fourth, the distribution of physical

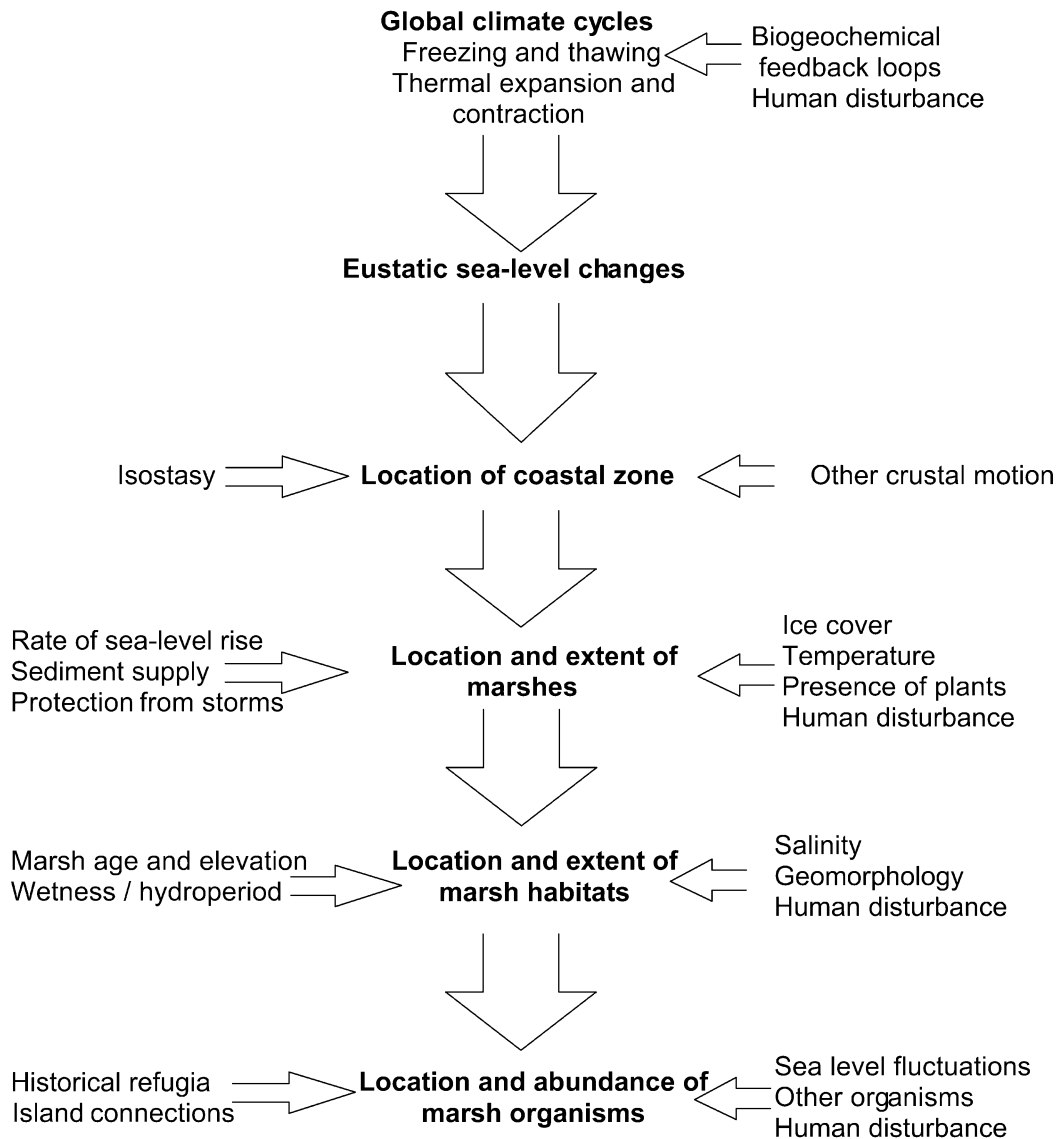


FIGURE 1. Conceptual model of historical geography and biogeography of tidal salt marshes. Major causal pathways are shown as large vertical arrows, and secondary causes are horizontal arrows. In the interest of simplicity and clarity, indirect or feedback influences are omitted from the figure, but discussed in the text.

environments within marshes, which is analogous to the distribution of potential habitats, is influenced both by external parameters and by antecedent internal feedback mechanisms. Fifth, climatic and oceanographic phenomena continue to cause fluctuations in both marsh elevation and sea level on many time scales, heavily influencing marsh hydrology, and thus the distribution of taxa within them. Details of and evidence for the model are discussed in the sections that follow.

Calibration of any historical geography model requires preserved evidence, generally buried in sediment, but the direct sedimentary evidence for past marshes is very limited (Goman 1996, Malamud-Roam 2002). Although tidal saltmarshes do provide good depositional environments for plant material, they represent a small proportion of the land surface at any time and their locations have changed significantly over time; therefore intertidal depositional environments will make

up only a small portion of sediment formations potentially spanning millions of years. In addition, the response of intertidal sediments to exposure or drowning ensures that preservation of the intertidal marsh sedimentary record is not good before the last few thousand years (Bradley 1985). As relative sea level drops, intertidal areas become exposed and the peat sediments can be lost to erosion and oxidation. Conversely, as relative sea-level rises, intertidal areas can become flooded if the change in sea level is greater than the ability of the marshes to accumulate sediments vertically. Thus former marshes can become buried both by the rising sea and by estuarine sediments (as in the case of the San Francisco Bay; Ruddiman 2001). These processes have resulted in the scarcity of marsh deposits from pre-Holocene periods. The best sedimentary records from tidal marshes cover no more than the past 5,000–10,000 yr, a period in which the deposits are both close to the surface and generally accessible beneath present tidal marshes. Although Holocene tidal-marsh deposits are especially valuable because they often contain abundant, well-preserved modern macro and microfossil assemblages that can be interpreted with regard to paleo-environmental conditions and because they can be dated very precisely using radiocarbon dating (Goman 1996, Malamud-Roam 2002), they do not provide direct records of the extent or locations of habitat during the last glacial maximum or during the years of rapid sea level rise that followed it.

QUATERNARY CLIMATE CHANGE AND SEA-LEVEL CHANGE

The primary causal factor in our model is spatio-temporal variation in climate, because climatic and oceanographic conditions of the world have varied dramatically over the last 2,000,000 yr, and in particular, because the world's coastlines were very different places just 21,000 yr ago. Understanding the present biogeography of tidal saltmarshes thus requires awareness of previous conditions when they were most different from the present; an understanding of how and when variables changed to their current states; and awareness of the terminology used to characterize these changes. In this section we first introduce the Quaternary period and its divisions to facilitate understanding of the climate literature. We then describe the world climate, and conditions along temperate coastlines in particular, during the peak of the most recent glacial maximum and during the years that followed. Changes in sea level are the primary mechanisms through which climate change

impacts coastal zones, and the next sub-sections address eustatic and relative local sea-level variation. We conclude the section with an introduction to other consequences of climate change, and in particular latitudinal shifts in temperature, that can influence tidal saltmarshes.

THE QUATERNARY, THE PLEISTOCENE, AND THE HOLOCENE

The global climate system of the last 2,000,000 yr or so has been characterized by large and relatively regular oscillations between glacial phases when large portions of the continental surfaces are covered by ice sheets, and when mean sea level is low, and interglacial phases when retreat of the ice sheets results in higher global sea levels (Hays et al. 1977, Ruddiman 2001). This time of alternating glacial and interglacial phases is known as the Quaternary Period, and its initiation is generally dated at about 1.8–2,600,000 yr BP, but various authors have focused on periods ranging from the last 3,000,000 yr (Ruddiman 2001) to the last 750,000 yr for which good paleoclimate records exist (Bradley 1985). Like all geological time periods, the Quaternary Period is formally delineated by rock strata, and the Quaternary was named in 1829 by the French geologist Jules Desnoyers to describe certain sedimentary and volcanic deposits in the Seine Basin in northern France which contained few fossils but were in positions above the previously described third or Tertiary series of rocks. The Scottish geologist Charles Lyell recognized that Quaternary deposits were primarily deposited by glaciers but that the most recent deposits did not appear of glacial origin. Thus, in 1839 he divided the Quaternary into an older Pleistocene Series, comprising the great majority of the deposits and popularly known as the time of Ice Ages, and a younger Recent Series which is now associated with the Holocene Epoch (Bradley 1985). Later, the Quaternary became popularly known as the Age of Man, but the paleontological and climatic records do not coincide well enough for this phrase to have any specific meaning (Bradley 1985). These terms are generally important for interpreting the climate change literature, and more specifically because the period of maximum difference from present coastal conditions—during the last glacial maximum (LGM; ca. 21,000 yr BP)—does not coincide with a transition between geological time periods; in fact glacial materials continued to be deposited for some 10,000 yr after the LGM while the glaciers retreated. Thus, the most recent low sea stand, which does coincide with LGM, occurred

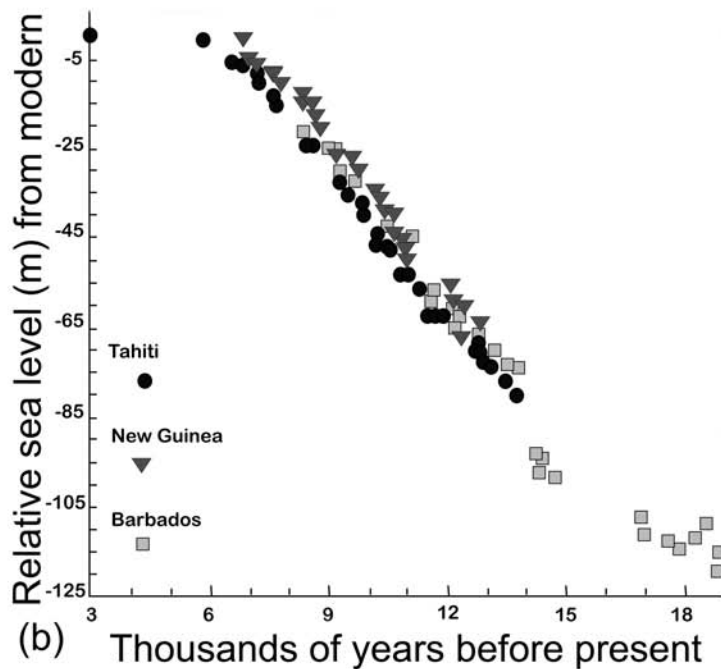
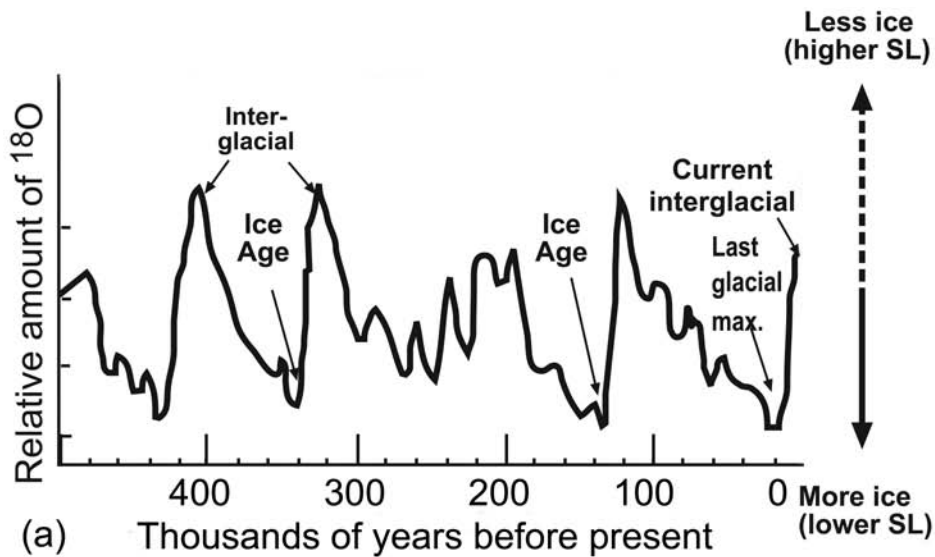


FIGURE 2. (a) Generalized oxygen isotope curve (after Bassinot et al. 1994) showing the cyclical changes in global climate. Negative oxygen isotope ratios indicate warmer climatic periods (less water stored as ice on land) and positive ratios indicate generally cooler conditions (more water as ice). (b) Sea-level curve since the Last Glacial Maximum. Adapted from Quinn (2000) with source data from Fairbanks (1989), Chappell and Polach (1991), Edwards et al. (1993), and Bard et al. (1996).

during the late Pleistocene and sea level has been rising through both the latest Pleistocene and throughout the Holocene (Ruddiman 2001).

During the Quaternary, glacial and interglacial conditions have oscillated on roughly 100,000 yr cycles, with periods of slow cooling

to glacial conditions over some 90,000 yr punctuated by relatively rapid warming to interglacial conditions lasting about 10,000 yr (Fig. 2a; Shackleton and Opdyke 1976, Bassinot et al. 1994). Periods when water was locked in glaciers are always associated with lowered sea

level and colder mean temperatures, and generally with dryer conditions, but regional climate patterns varied substantially (Ruddiman 2001). Although the changing climate patterns are clearly seen in numerous sediment cores and other climate proxy records, explanations for the large-scale oscillations are still controversial (Ruddiman 2001) and beyond the scope of this paper. It is important to remember during the following discussion on the recent glacial maximum and deglaciation that this is that this is only the latest of at least four such cycles (Fig. 2), which almost certainly had major impacts on the evolutionary and dispersal histories of coastal taxa.

Conditions during and since the LGM that could have impacted tidal marshes and other coastal ecosystems have been inferred from many proxy records (Bradley 1985, Kutzbach et al. 1998, Ruddiman 2001). The exact date of the LGM has been somewhat inconsistent in the literature, primarily because of measurement and dating problems (Ruddiman 2001), and also possibly because the ice reached its maximum extent at somewhat different times in different places (McCabe and Clark 1998), but it is clear that the global maximum extent of ice was about 21,000 yr BP (Fairbanks 1989, Kutzbach et al. 1998, Ruddiman 2001). At this time, sea level was 110–140 m lower, ice covered the coasts year-round in many areas now seasonally or permanently free of ice (McCabe and Clark 1998), the world ocean was colder by about 4 C, varying from 8 C colder in the North Atlantic (Kutzbach et al. 1998) to perhaps 2 C warmer in some tropical areas (CLIMAP 1981, etc. in Ruddiman 2001), atmospheric CO₂ was considerably lower than at present (Kutzbach et al. 1998), precipitation and runoff were lower world-wide although with potentially large regional variations (Kutzbach et al. 1998), fluvial supplies of sediment to the coastal zone were lower in some places than at present because of reduced runoff but were higher in others both because of the intense erosive impacts of glaciers and because of locally intense season runoff (Collier et al. 2000), and some coastal regions experienced more oceanic storms because they were not in the geological setting that now protects them.

GLACIAL DYNAMICS AND SEA-LEVEL CHANGE

The most significant aspects of Quaternary climate dynamics for tidal saltmarshes are: (1) the dramatic changes in local relative sea levels resulting from the advance and retreat of the world's ice sheets, (2) the dramatically varying rates of change during any period of rise or

fall, and (3) the repetition of these cycles. The total change in mean global eustatic sea level associated with glacial melting and thermal expansion of the oceans during the most recent deglaciation has traditionally been reported at between 110 m (Ruddiman 2001) and 120 m (Fairbanks 1989), as measured on relatively stable coasts, although more recent work (Issar 2003, Clark et al. 2004) now consistently report 130–140 m as more likely. These values are similar to those from earlier Quaternary cycles (Ruddiman 2001), although the previous high stand (the Sangamon) was higher than at present by 6 m (Chen et al. 1991) to about 16 m (Bradley 1985). Although the mean rate of rise has been about 5–7 mm/yr during the 21,000 yr since the LGM, the rate has varied substantially, and clearly has been much slower than the mean (ca. 1–2 mm/yr) during the most recent 5,000–7,000 yr (Atwater et al. 1979, Nikitina et al. 2000). However, the relatively rapid rise of the late Pleistocene and early Holocene was not uniform either, instead consisting of at least two melt water pulses characterized by rapid rise and a period of slow rise (ca. 14,000–12,000 yr BP) in between them, before the current period of slow average rise (Ruddiman 2001). Recent data by Clark et al. (2004) strongly support the idea that the first melt water pulse (at 19,119 ± 180 yr ago), was truly catastrophic, raising global sea levels by about 10 m over a period of time too short to be measured in dated sediments. A second period of rapid rise was described by Raban and Galili (1985, in Issar 2003) of 5.2 mm/yr rise between 8,000 and 6,000 yr BP. These same authors also used archaeological evidence to infer a high stand of almost a meter above present mean sea level in the Mediterranean Sea about 1,500 yr BP, despite evidence of local tectonic stability for the last 8,000 yr; although few other authors have claimed that eustatic, as opposed to local, sea levels have been higher earlier in the Holocene than at present, it appears that, given the magnitude of uncertainties in dating, surveying, and land stability (Atwater et al. 1979) previous Holocene eustatic high stands are possible.

Rates of sea-level rise are critical to understanding marsh history because marsh formation depends on sediment accumulation exceeding the rate of relative sea-level rise (Mitsch and Gosselink 2000), and only when the rate of rise slowed to about the modern rate (1–2 mm/yr) did modern marshes form in their current locations. However, when local sea level drops, marshes can rapidly experience loss of peat soils to oxidation and/or can be colonized by upland plants, losing their marsh character (Zedler 2001). In either case, it is

important to note that marshes do not respond directly to global influences such as eustatic sea-level changes, but instead to their local manifestations, and superimposed on the global eustatic patterns have been a range of local vertical crustal movements which have modified local relative sea-level curves. Thus, the rates of rise or fall in the sea relative to the land have differed substantially, especially during the late Holocene when the eustatic rate of change was relatively small (Nikitina et al. 2000).

A particularly significant form of local vertical land movement during this period is isostatic movements of the crust in response to its elastic response to the weight of the accumulated glacial ice. In high latitudes during glacial epochs, the accumulation of hundreds of meters of ice on the continents caused isostatic downwarping of the crust by hundreds of meters and to compensate for the crustal downwarping, adjacent areas were pushed up, creating a forebulge that was usually low and broad; in some settings the paired down-warp and uplift were of large amplitudes over a short distance (Peltier. 1994, Peltier et al. 2002). For example, the Pacific Northwest of North America was isostatically depressed by the weight of glacial ice on the continent to such a degree that relative sea level on the coast at British Columbia, Canada, was actually higher during the last glacial maximum than today (Barrie and Conway 2002, Clauge et al. 2002), and some sites in the British Isles experienced isostatic movements over 170 m during this time (Clark et al. 2004). On the Atlantic Coast of North America as well, isostatic rebound and simultaneous lowering of the forebulge land surfaces as the ice sheets receded have led to complex patterns of sea-level changes over time, including episodic reversals of sea-level change (Peltier 1994, Nikitina et al. 2000). These complex patterns result in part from isostatic adjustments of the crust lagging behind the ice retreat by differing amounts in different times and places (Barrie and Conway 2002), so that the crustal responses to glaciation and deglaciation have in many places modified the eustatic curve caused by glacial melting and thermal expansion long after the eustatic curve had flattened. This complex interaction of direct and indirect influences of climate on sea level have resulted both in coastlines with more modest (Mason and Jordan 2001) and/or more extreme (Barrie and Conway 2002) changes in height than predicted by eustatic changes alone. This has apparently been true throughout the period since the LGM, but would have had its greatest impacts on coastal processes during period of slow eustatic change, including the last 5,000-

7,000 yr, when the rate of crustal movements in many areas have been greater than eustatic changes in sea level.

Relative sea level has also been impacted by non-glacial factors. Along the western coastline of North America, relative sea level of local coastlines has been affected by tectonic movement of the lithospheric plates on which the continent and the ocean rest. The abrupt changes in land surface of marshes relative to sea level that can result from underlying active faults have been clearly shown along the Washington coast (Atwater and Hemphill-Haley 1997). In other tectonically active areas such as the San Francisco Bay region, it is likely that local relative sea level may also have been affected by vertical activity along the faults, though the evidence for this in marsh sediments is ambiguous (Goman 1996). Finally, many authors have expressed concerns about the potential impact on marshes of accelerated sea-level rise due to anthropogenic global warming (Keldsen 1997, Goals Project 1999). Although this is a very significant threat to marsh species, anthropogenic influences on sea level have been of such recent origin that they seem unlikely to have had a significant impact yet on marsh biogeography compared to natural variations in sea level and to other human disturbances (Daiber 1986, Zedler 2001).

OTHER ATTRIBUTES OF GLOBAL CLIMATE CHANGE

In addition to relative changes in sea level, global scale changes in climate during the late Quaternary had other major impacts on areas where marshes are currently located. First, and most dramatically, many areas along the shores of modern Canada and northern Europe were covered with thick ice, meaning that no vegetated ecosystem of any sort existed in these areas until the ice melted and retreated (McCabe and Clark 1998, Ruddiman 2001). Recolonization by all species after ice retreat must have occurred from outside the ice-covered areas. Second, the oceans were considerably colder, meaning that temperature-dependent organisms would have been displaced towards the equator, although the specific locations of tolerable water temperature would also have been influenced by changes in ocean currents (Ruddiman 2001). Third, the large quantity of water locked up in glaciers could have led to an increase in oceanic salinity, changing the distribution of marsh organisms, although ocean salinity at the glacial maximum probably did not exceed the tolerances of truly halophytic plants and animals, the distribution of more brackish species could have been influenced by this phenomenon.

In addition to these primarily marine changes, the global-scale changes associated with glacial expansion and retreat were primarily climatic, and even though oceanic influences would have buffered the effects of these on tidal saltmarshes, biotic communities throughout the temperate zones were influenced by dramatic changes in temperature and precipitation during the Quaternary. Both proxy records (Bradley 1985) and numerical models (CLIMAP 1981 and COHMAP 1998 in Ruddiman 2001 and Kutzbach et al. 1998) have been used to discern the climate and associated biotic changes since the LGM. Similar to relative sea-level changes, a global story exists with significant variations over time and space. In general, the most recent comprehensive review (Kutzbach et al. 1998) concludes that the global climate was both cold and dry, and that the period between 14,000 and 6,000 yr ago had relatively strong northern summer monsoons and warm mid-latitude continental interiors. The models are too coarse to show detailed latitudinal changes along coast lines, but clearly show large southward shifts in northern tundra and forest biomes at LGM, and contraction of subtropical deserts in mid-Holocene. Of particular interest to coastal researchers is the conclusion by Kutzbach et al. (1998) that the exposed continental shelves during the low sea stand would have been vegetated to the extent that they compensate for the areas covered with ice, resulting in the total area of vegetated land remaining nearly constant through time. How much of this vegetated shelf might have been marshlands is not discussed in Kutzbach et al. (1998).

At a finer scale, climate since the LGM includes a number of apparently global periods or events, although local variations could be extreme (Fletcher et al 1993, Diffenbaugh and Sloan 2004). An aridity maximum apparently lasted from around the LGM to about 13,000 yr BP, when conditions quickly became warmer and moister and similar to the present (Adams and Faure 1997), though with a strong cold dry event around 11,000 yr BP (the Younger Dryas). Early Holocene conditions seem to have been slightly warmer than at present, peaking around 8,000–5,000 yr ago, at least across central and northern Europe. Evidence for other strong cold events is seen about 8,200 and 2,600 yr ago (Adams and Faure 1997), and more recently, a medieval warm period occurred between about AD 1110 and 1250 (ca. 810–750 yrs ago), followed by the well-known Little Ice Age of ca. AD 1300–1700 (Bradley 1985, Ruddiman 2001). Although many of these global changes and their local manifestations would presumably have been moderated close to coasts, a detailed

review of their potential impacts on marshes and marsh organisms is beyond the scope of this paper.

DISTRIBUTION OF MARSHES, MARSH HABITATS, AND MARSH ORGANISMS

The extent and distribution of tidal marshes, and therefore the amount and connectedness of habitat for tidal marsh organisms, cannot be measured directly or even precisely estimated for the late Pleistocene or early Holocene, as rapid sea-level rise and coastal sediment accumulation have buried most, if not all, of these marshes from around the world (Bradley 1985, Malamud-Roam 2002). Therefore, fundamental parameters for interpreting tide-marsh biogeography, such as the number, size, and location of habitat areas must all be inferred indirectly for the period before, during, and after the LGM until about 5,000 yr ago. This is particularly challenging because this period includes not only the very different world of the glacial maximum, but also includes a time of slow cooling and dropping sea level before the LGM; at least two melt-water pulses, when the sea was rising very rapidly; a period of relative coastal stability between the melt water pulses; and the period after the rate of rise slowed, but before marshes were established enough to leave sedimentary records. Thus, the specific causes of specific biogeographic patterns in tidal marshes will inevitably remain somewhat ambiguous. However, the conceptual model in Fig. 1 allows for a structured approach to making these inferences, and for relating the possible or probable paleogeography of tidal marshes with the current distributions of specific marsh habitats and organisms.

The model shown in Fig. 1 is based on a series of strong causal relationships, primarily driven by global climate cycles leading to patterns of sea-level change, which determine the location of the intertidal coastal zone over time, which in turn sets the stage for the possibility of tidal marshes, habitat types, and specific organisms. Secondary influences on the location of the coastal zone, marshes within the coastal zone, marsh habitats, and taxa are shown as horizontal arrows. Indirect effects—global climate cycles causing glacially mediated isostatic rebound—and feedback loops—marshes require plants, just as many plants require marshes—are not shown with arrows in the interest of simplicity and clarity, but are discussed in the text that follows, and some can be inferred from the parameters in the side columns. One possible feedback mechanism that is unlikely to be significant is a role for tidal marsh extent or structure on global climate

cycles. Although the role of tidal marshes and other wetlands on global carbon cycles, and hence on climate, has been investigated (Bartlett et al. 1990), tidal marshes cover such a very small fraction of the land's surface area (Chapman 1974) that they probably have had little effect on global atmospheric and oceanographic phenomena. In contrast, the extent of marshes is essentially defined by the extent of marsh vegetation, which not only has a major role in defining the habitat value of a marsh for fauna (Adam 1990, Zedler 2001), but also in determining the distribution of sedimentation and other physical processes which help maintain the marsh surface (Zedler 2001, American Geophysical Union 2004). Thus, the lower three parameters in Fig. 1 for specific marshes result from constantly interacting physical and biotic processes (American Geophysical Union 2004), resulting in local spatial and temporal variation in these parameters that is even more pronounced than with climate or sea level. In this section, we use a global climate and sea-level change perspective to explore these variations, reviewing first the distribution of the intertidal coastal zone and of marshes within it, and then the distribution of marsh habitats, and finally the mechanisms governing the distribution of specific organisms.

GLOBAL CLIMATE CHANGE, THE COASTAL ZONE, AND POTENTIAL MARSH LOCATIONS

Rising sea levels since the LGM drowned the marshes that existed at that time, and forced their flora and fauna to migrate, to evolve, or to perish. Although the mean vertical rise of sea level, and hence of the entire intertidal zone, was globally around 110–140 m over the last 21,000 yr, with up to about 170 m of additional local crustal movement during this period (Clark et al. 2004), this has been accompanied by a much more variable pattern of horizontal movement of the coastal zone during this time. This horizontal movement is determined not only by the local rate of relative sea-level rise, but also by the slope of the underlying bedrock at a site, and by the abundance and character of the sediments. Even on very steep coastlines, the horizontal movement of the coastal zone associated with deglaciation, and the rate of movement, were far greater than the vertical change. For example, in areas with a mean surface slope of 1%, the late Pleistocene–early Holocene eustatic rise would have resulted in a horizontal movement of the shoreline of about 11 km, and along flatter areas this movement could have covered scores of kilometers. Atwater (1979) estimated that the intertidal coastal zone expanded into south San

Francisco Bay at a rate of about 30 m/yr horizontally during the early Holocene, a rate that could challenge the dispersal abilities of many marsh plants, especially those that reproduce primarily asexually, although it may be tolerable to most animals.

Changes in the location of the intertidal coastal zone control the potential distribution over time of tidal marshes, which can only occur along this narrow band, but the actual distribution of marshes at any time would have only reflected a subset of this potential distribution. Even at times and places where vegetation could migrate as fast as the shoreline was moving, a number of other factors preclude marsh formation in many coastal areas now (Chapman 1974, Adam 1990, Mitsch and Gosselink 2000), and presumably would have in the past. Thus, even if paleo-coastlines could be precisely mapped, these maps would not define the extent of marshlands along them.

THE DISTRIBUTION OF CONTEMPORARY AND PALEO-MARSHES

Tidal saltmarshes are found at sites along the fringes of most of the continents. Because of the lack of fossil or sedimentary evidence of late Pleistocene or early Holocene tidal marshes, the best guidance we have to their probable location within the paleo-coastal zone is their present distribution, which has been mapped by many authors on scales from local to global (Chapman 1974, Frey and Basan 1985, Daiber 1986, Adam 1990, Trenhaile 1997, Mitsch and Gosselink 2000). These authors and others consistently, if generally implicitly, attribute the distribution of marshes within the intertidal zone, on all spatial scales, to a common set of favorable regional and local conditions: (1) air and water temperatures warm enough for marsh plant growth and for freedom from permanent ice, but cool enough to preclude mangrove growth, (2) adequate protection from storms and destructive waves, (3) bedrock slope and sediment supply sufficient to allow net sediment accumulation (after resuspension and erosion) faster than local coastal submergence, (4) the presence of pioneer plants within dispersal distance of the incipient marsh, and (5) freedom from destructive human manipulation.

In addition, though this has been less frequently discussed, it is clear that some marsh and mudflat animals can significantly restrict marsh plant growth through herbivory and/or sediment disturbance, and must be considered potential constraints on marsh formation or stability (Collins and Resh 1989, Philippart 1994, Miller et al. 1996).

Traditionally, authors have used the existence of marshes as proof of where conditions are favorable, rather than to test theoretical models of potential marsh formation and stability against independently mapped physical attributes of sites. Although geomorphologists and ecologists have recently begun to rigorously model and quantify the needed inputs for marsh formation and maintenance (Temmerman et al. 2003), we know of no publications yet using these tools to estimate the extent of paleommarshes over any large areas or long time periods.

In comparison with sea-level changes, latitudinal temperature shifts associated with glaciation and deglaciation and their potential impacts on tidal marshes have received scant attention in the marsh literature, despite being a prominent feature of large-scale paleoclimate models (Kutzbach et al. 1998). In contrast to vertical fluctuations in sea level (110–140 m) and horizontal changes in the location of the coastal zone (ca. 10–40 km), zones of mean or extreme temperature and of major biomes can move toward the equator during glacial phases and toward the poles during interglacials by hundreds of kilometers. Although the extent of these shifts may have been smaller in the coastal zones than in the continental interiors because of a temperature-dampening effect of the sea, the extent of coastal mangroves was depressed during the full glacial, apparently due to the colder climate (Bhattacharyya and Chaudhary 1997, Wang et al. 1999), and shifts in the line between marshes and mangroves continues today, although perhaps due to other reasons (Saintilan and Williams 1999). The line of year-round ice, and hence the high-latitude limits of arctic-type tidal marshes, shifted by hundreds of kilometers toward the equator during the LGM (McCabe and Clark 1998), and the transition between arctic- and temperate-type tidal-marsh ecosystems also likely shifted towards the equator.

Another requirement of tidal marshes is protection from waves and storms above some critical threshold (Mitsch and Gosselink 2000, Zedler 2001); however, it is not clear what these thresholds are or how they vary between marsh types. One particular consequence of the horizontal movement of the coastal zone associated with sea-level changes is a perhaps substantial change in the degree of protection from storms and waves that can be provided by structural embayments. For example, the margins of both the San Francisco and Chesapeake bays are largely protected now from intense oceanic events, while at lower sea stands the intertidal zone would have been seaward of the structural

basins, and would not have had the bedrock protection. In light of the long gradual continental shelf off the Atlantic Coast of North America, it is likely that barrier islands or barrier spits could have protected Atlantic marshes as they do now over large areas without rocky natural breakwaters (Odum et al. 1995), but it is not clear that equivalent geomorphology would have developed on the California coast. Nor is it clear how extensive or how protective barrier island-marsh systems may have been off any coasts during and since the LGM, as climate change can influence both fluvial sediment supplies and river mouth form (Finkelstein and Hardaway 1988).

Protection from storm and wave energy is critical for tidal-marsh formation and persistence because the geomorphic dynamic basic to marshes is net sediment accumulation equal to or slightly greater than local relative sea-level change. Thus, a key element in all explanations and numerical models of tidal-marsh formation and stability is sediment supply, and change in the sediment budgets of marshes is another potentially significant impact of climate change. The literature on tidal saltmarsh sediment dynamics is extensive (Frey and Basan 1985, Stoddart et al. 1989, Pethick 1992, Trenhaile 1997), and a comprehensive review is beyond the scope of this paper, but some key processes have clear relationships to climate, sea level, and runoff. Patterns of sedimentation on tidal saltmarshes depend partly on factors extrinsic to the marsh itself but also heavily upon dynamics within the marsh (Frey and Basan 1985, Trenhaile 1997, Malamud-Roam 2000), which has made large-scale or long-term mapping difficult. Generally, tidal marshes are maintained over time by a null to slightly positive sediment balance, with the more frequently inundated parts of the marsh surface often accreting more rapidly than the areas of the marsh less frequently inundated (Trenhaile 1997). Significant changes in climate can alter these patterns by changing the availability of both mineral and organic sediment. For example, lake core and coastal records indicate that sediment supplies during the last glacial maximum were lower in some places than during the Holocene (Grosjean et al. 2001, Wanket, 2002), changes that may be attributed to shorter growing seasons and, in the higher latitudes, a reduction in land area exposed to erosion, although, as previously noted, these patterns vary substantially from place to place.

An exhaustive comparative review of saltmarsh development on different coasts is beyond the scope of this paper, but a brief comparison of the geologic setting and modern

distribution tidal saltmarshes along the Atlantic and Pacific coasts of the US helps explain differences between these regions and indicates possible causal relationships elsewhere. The Pacific and Atlantic coasts (and the Gulf of Mexico coast, although this region is not discussed here; see Stout 1984) of North America differ in their geomorphic and tectonic settings and this has probably had a significant impact on saltmarsh development. In contrast to the small and isolated tidal saltmarshes found along the Pacific coast, tidal marshes along the Atlantic Coast are presently larger and better connected (Josselyn 1983, Goals Project 1999, Zedler 2001). The effects of post-glacial isostasy has resulted in a complex north-south gradient in the relative rates of sea-level rise along the Atlantic Coast throughout the Holocene, and the rates of sea-level rise have changed over time (Fairbanks 1992; Peltier 1994, 1996). The two major estuaries on the U.S. Atlantic coast, the Delaware Bay and the Chesapeake Bay, are both subsiding, but at different rates. Tidal marshes surrounding these bay systems have been influenced by changing rates of relative sea level rise both between the two systems and within each system as they both have long north-south axes (Fletcher et al. 1990, Kearney 1996). The Chesapeake Bay system has had a slower rate of relative sea-level rise in the last 1,000 yr, and may have experienced a regression in sea level (Kearney 1996).

Marshes cannot form without the presence of pioneer marsh plants within dispersal range (Adam 1990, Malamud-Roam 2002). In addition, plants that can both colonize and tolerate wet and salty conditions are not only required for the establishment of tidal saltmarshes, but their presence is often critical to transformations of marsh type (Chapman 1974). Plant species do not generally disperse as well as many animal taxa, which initially implies that plant migration rates could be the major limiting factor on marsh establishment following deglaciation, but many of the plant species found in tidal marshes share a suite of evolutionary adaptations to the intertidal environment that may pre-adapt them to surviving during, and re-colonizing following, climate or sea-level changes. These adaptations include a high degree of phenotypic plasticity allowing the plants to respond quickly to rapidly changing conditions (Allison 1992, Duntun et al. 2001), asexual reproduction that can be an advantage for rapid establishment (Daehler 1998), increased chances of survivorship through clones (Pan and Price 2002), and specific physiological adaptations allowing exploitation of limited nutrients, tolerance of anoxia, absorption of water against osmotic

pressure, and excretion of excess salts (Adam 1990, Eleuterius 1990).

Finally, marshes cannot form or persist in the presence of excessive disturbance by humans or other animals. People have caused a significant decrease in tidal-marsh extent in recent centuries, and in some places an increase in extent and habitat values through intentional restoration activities (Daiber 1986, Goals Project 1999, Zedler 2001). These impacts have been well reviewed elsewhere, and will not be further discussed here. Although other animals do not have the same capacity for short-term impacts as humans with heavy equipment, it is clear that herbivory or faunal disturbance of the substrate can be sufficient to preclude marsh formation or to limit the extent of marsh plant spread (Collins and Resh 1989, Philippart 1994, Miller et al. 1996). We know of no published research on the potential impacts of animals on the extent or distribution of paleommarshes.

MACRO-SCALE BIOGEOGRAPHY — BIOTIC DISTRIBUTION BETWEEN REGIONS OR ESTUARIES

Distributional patterns of tidal-marsh organisms, as with other organisms, occurs on multiple scales, and a convenient delineation with coastal or estuarine species is macro-scale or between regions, meso-scale or within regions, and micro-scale or within specific sites. The primary controls on macroscale biogeography of all taxa are the sites of origin or adaptive radiation of taxa, the presence or absence of dispersal routes to other areas, and the presence and extent of refugia habitat during periods when conditions are stressful and populations have been vulnerable to extirpations (Arbogast and Kenagy 2001, Smith et al. 2001). In the case of tidal marshes, macro-scale biogeographic differences are seen between continents, between oceanic coasts, and along latitudinal gradients, and all of these patterns were significantly shaped by Quaternary climatic dynamics. In particular, the variables that control the distribution of marshes can also independently affect the global- to regional-scale distributions of the organisms that inhabit them.

Different authors have categorized tidal saltmarshes into different numbers of regional types on the basis of their dominant vegetation (Chapman 1974, Frey and Basan 1985), and these largely correlate with latitude (particularly arctic-semi-arctic versus temperate) and ocean basin, but a relatively small number of plant genera and species dominate most of the temperate tidal saltmarshes world-wide. Species

of marsh rosemary (*Limonium*), *Suaeda* spp., pickleweed (*Salicornia*) and fat hen (*Atriplex*), as well as arrowgrass (*Triglochin maritima*), saltgrass (*Distichlis spicata*), and jaumea (*Jaumea carnosa*) are common tidal-marsh species in the temperate latitudes, while cordgrass (*Spartina* spp.) is common both on mudflats and higher in the intertidal zone.

Modern high-latitude tidal saltmarshes are distinct in many ways from temperate saltmarshes (Earle and Kershaw 1989, Gray and Mogg 2001), and may indicate the probable structure of marshes near the LGM ice margin. Although some of the present differences may be due to seasonality of day length or other variables that are functions of latitude rather than ice proximity or temperature, other attributes apparently could have been translated farther from the poles. For example, the alkali grass (*Puccinellia phryganodes*) out-competes species of *Spartina* at low temperatures (Gray and Mogg 2001). These authors also suggested that greater generic diversity occurs in Arctic than in temperate saltmarshes because the high latitude coastal waters are relatively low in salinity; if this is generally true, then it could indicate a significant impact of climate change on marsh biogeography, because deglaciation led to dramatic changes in the distribution of near-shore salinity near rivers draining the melting glaciers (Ruddiman 2001).

Latitudinal shifts in temperature not only result in specific places becoming colder or warmer, but organisms adapted to specific temperature ranges may have had to survive in suitable refugia at a great distance from their present distribution, and potentially in areas without suitable settings for the formation of extensive marshlands. One example of an estuarine species apparently strongly influenced by glacial temperature shifts is the coho salmon (*Oncorhynchus kisutch*); genetic analysis of this species in estuaries in the northern hemisphere has shown increasing genetic diversity from north to south, indicating that previous glaciations eliminated coho salmon from the northern part of its range and led to adaptive radiation as it recolonized suitable habitats (Smith et al. 2001).

One particularly well-studied group of coastal-zone dwellers that apparently re-colonized temperate regions during the deglaciation are the varieties of the brown alga (*Fucus serratus*), which is potentially a good model of the biogeographic processes underlying Holocene re-colonization of coastlines impacted directly by ice cover or indirectly by cold climate in the previous glacial maximum. Coyer et al. (2003) hypothesize that brown alga originally evolved in the North

Atlantic and that present populations reflect re-colonization from a southern refugium since the LGM. The authors examined genetic structure across multiple spatial scales using micro-satellite loci in populations collected throughout the species' range. At the smallest scale (ca. 100 m) no evidence shows spatial clustering of alleles despite limited gamete dispersal (ca. 2 m from parent plants); instead, the minimal panmictic distance for this plant was estimated at between 0.5 and 2 km. At greater distances, even along contiguous coastlines, genetic isolation is significant, and population differentiation was strong within the Skagerrak-Kattegat-Baltic seas (SKB) region, even though the plant only (re)entered this area some 7,500 yr BP. On the largest scale, the genetic data suggest a central assemblage of populations with high allelic diversity on the Brittany Peninsula surrounded by four distinct clusters—SKB, the North Sea, and two from the northern Spanish coast—with lower diversity; plants from Iceland were most similar to those from northwest Sweden, and plants from Nova Scotia were most similar to those from Brittany. The authors were not sure if Brittany represents a refugium or a re-colonized area, but interpreted the low allelic diversity in the Spanish populations as evidence of present-day edge populations having undergone repeated bottlenecks as a consequence of thermally induced cycles of re-colonization and extinction.

In addition to re-colonization from extant areas of similar habitat, current occupants of tidal saltmarshes and other coastal areas may have evolved or found refuge in other types of environments and then colonized tidal saltmarsh habitats when they can come into contact with them. In addition to a number of specific marsh taxa which are discussed in other chapters in this volume, the possibility for broad groups of taxa is suggested by patterns of movement into the marine realm by previously terrestrial species not found on tidal marshes. For example, the non-halacarid marine mites apparently went through two distinct migration events in the past, based on their adaptive radiation (Proche and Marshall 2001). Another possibility is colonization from non-tidal freshwater marshes, such as those that have persisted continuously in the California inland delta for at least the last 35,000 yr, and which came into contact with oceanic tides and low levels of salt only about 4,000 yr BP (Atwater and Belknap 1980).

MESO- AND MICRO-SCALE BIOGEOGRAPHY — BIOTIC DISTRIBUTION WITHIN REGIONS AND MARSHES

As on the global scale, marsh types at smaller spatial scales are often distinguished

by their dominant vegetation (Chapman 1974), but increasingly classifications of marshes have focused more on the distribution of physical parameters such as salinity, wetness, elevation, and geomorphic pattern, and on the potential habitat values these provide (Goals Project 1999, Malamud-Roam 2000). In particular, high marsh and low marsh are very commonly used divisions (Chapman 1974, Teal 1986, Goals Project 1999), reflecting the significance of elevation as a control on wetness and hydroperiod (Malamud-Roam 2000). Following an old geomorphic convention, the apparent age of the marsh, primarily as inferred from its elevation and landforms, is often used as well as a descriptive tool (Goals Project 1999).

Bioregions are conventionally defined as areas with essentially similar species composition, although the actual presence or absence and abundance of specific taxa between sites within the region can vary dramatically (Goals Project 1999). Thus meso-scale biogeographic variability presumably reflects habitat suitability and local patterns of migration, extirpation, dispersal, and recolonization more than large-scale historical isolation or long-term barriers to migration (MacArthur and Wilson 1967). As noted in the description of the standard model, the most obvious region in which tidal marshes share potential species is specific estuaries, and the most significant cause for differences in biotic composition of marsh communities within estuaries is gradient in salinity (Josselyn 1983, Adam 1990, Goals Project 1999). In addition, marsh size and the distribution of marshes within estuaries have also been widely investigated as examples of landscape-level variables controlling biotic-community structure (Goals Project 1999), and these variables have occasionally been used to analyze tidal marshes as habitat islands in a theoretical biogeography sense (Bell et al. 1997, Lafferty et al. 1999, Micheli and Peterson 1999).

Finally, the distribution of specific marsh taxa or biotic communities within marshes is usually seen as a consequence of modern physical variables, with the frequency and duration of tidal flooding and drying given the most emphasis, and soil salinity and nutrient limitation also attracting research (Zedler 1982, Stout 1984, Teal 1986, Mitsch and Gosselink 2000, Zedler 2001). Elevational zonation is the conventional characterization of plant distribution with the explicit recognition that marsh plants do not directly respond to elevation, but instead to wetness and hydro period, for which elevation serves as a reasonably useful proxy (Frey and Basan 1985, Malamud-Roam 2000). Although animals also respond to physical parameters,

their distribution is also clearly influenced by the distribution of flora as well.

TIDAL SALT MARSHES OF THE SAN FRANCISCO BAY-DELTA ESTUARY

The tidal saltmarshes of the San Francisco Bay-delta estuary cover a large area, have many rare and endemic plant and animal taxa, have been intensively researched, and are the subject of intense current debate about how best to achieve protection and restoration of habitat values (Atwater et al. 1979, Josselyn 1983, Goals Project 1999; Malamud-Roam 2000, 2002). Therefore, these marshes are used to illustrate some the elements of the conceptual model, some significant site-specific patterns which may help explain the high rates of endemism found in the tidal saltmarshes there, and some associated conservation challenges. This estuary has been referred to in many ways in the literature (Malamud-Roam 2000), but hereafter will be referred to as the San Francisco estuary.

The basic configuration of the San Francisco estuary today is a series of bedrock basins linked by narrows or straits (Goals Project 1999, Malamud-Roam 2000). Inland of the Golden Gate, the only opening from the estuary to the Pacific Ocean, is Central Bay, followed in order upriver by San Pablo Bay, Carquinez Strait, Suisun Bay, and the delta of the Sacramento and San Joaquin rivers. An additional basin attached to Central Bay, known prosaically as South Bay, has little freshwater input, but the other basins form a classic estuarine gradient of decreasing salt and generally decreasing tidal character with distance upstream. Thus, although Central Bay has essentially oceanic salinity (~35 ppt) and tidal range (~2 m), the delta is a freshwater environment with tidal range ~1m, and Suisun Bay is an extensive brackish zone, the conditions of which vary substantially with the season and the year. All of the basins had extensive tidal marshes at the beginning of European contact with the site (ca. 1776), but some 90% or more of these have been diked, filled, or otherwise removed from the tides (Goals Project 1999).

In our model, we have treated the distribution of the intertidal coastal zone, the distribution of marshes, and the distribution of specific marsh habitats or communities as separate parameters; in practice, however, much of the evidence for each in the San Francisco estuary and elsewhere is provided by sediment cores collected at multiple sites (Bradley 1985, Malamud-Roam 2002). Dated sediments collected from below current marshes or estuaries can potentially provide evidence of sub-tidal estuarine and inter-tidal marsh history back to the LGM and

of riverine and non-tidal marsh settings even further back. In particular, the basic elements of the formation and evolution of tidal marshes within the San Francisco estuary, which had been articulated by Atwater and his colleagues (Atwater et al. 1977, Atwater 1979, Atwater and Belknap 1980), have been elaborated in recent years using a range of methodologies including stable isotopes (Malamud-Roam and Ingram 2001, 2004; Malamud-Roam 2006), fossil pollen (May 1999, Byrne et al. 2001, Watson 2002), fossil seeds and metals (Goman 1996, Goman 2001, Goman and Wells 2000), and diatoms (Starratt 2004). Although the site specificity of each core means that a complete paleo-mapping has not been completed, the history of some areas is well known, and sufficient information on causal variables has been collected that interpolations of areas between the cored sites are being developed. In addition, these studies have begun to show how the physical environment and biotic communities of these sites have responded to changes in inputs such as runoff or sea level. Information on LGM refugial intertidal habitats outside the Golden Gate, however, is not available, and inferences about these areas are tentative.

Paleo-shoreline maps can be developed not only from sediment cores, but also from current bathymetric maps where relative sea-level curves are known, although these maps will be imprecise if either sediment accumulation is significant or if regional crustal motions are non-uniform (Atwater 1979, Nikitina et al. 2000). Mapped former shorelines for the San Francisco Bay, based on calculated sea-level rise for the south San Francisco Bay, show that ocean waters entered through the Golden Gate approximately 10,000 yr BP (Atwater 1979). Although the Golden Gate is currently >100 m deep, the 50 m bathymetric contour lies some 30 km offshore now (NOAA 2003), and the current estuary was certainly non-tidal during the LGM and for thousands of years after (Atwater 1979, Atwater and Belknap 1980, Goman 1996, Malamud-Roam 2002). Therefore, to estimate the LGM shoreline as a first step in modeling late-glacial-phase marsh refugia, modern bathymetric maps of the California coast were used to produce an approximation for the shoreline which existed ca. 21,000 yr BP along the California coast (Fig. 3) and outside the Golden Gate (Fig. 4). This paleo-shoreline is based on a LGM sea level 120 m lower than today, and does not account for sediment accumulation or local variations in crustal stability.

The paleo-shoreline maps indicate potential tidal-marsh sites, but neither they nor the many sediment cores that have been collected in the

San Francisco estuary allow definitive maps of late Pleistocene or early Holocene tidal-marsh distribution; however, together with some observations of modern marshes, they do allow for some estimates and some conjectures. The San Francisco estuary clearly contains all the necessary conditions for tidal saltmarsh development and maintenance currently, and all of these can be estimated for at least some time into the past, although with varying degrees of precision. Evidence of ice or mangroves is lacking during the Quaternary in any of the environmental histories of the area (Goman 1996). Mineral sediments are supplied in large quantities by the Sacramento River and the San Joaquin River and smaller local rivers, which together drain a combined watershed region of ~40% of the state of California, and which have done so throughout the Quaternary (Goals Project 1999). Although tidal-marsh studies in the estuary reveal a pattern of incipient marsh formation and submergence in some sites until balance was achieved between sediment supply and sea-level rise (Malamud-Roam 2006), no clear evidence shows local crustal movement resulting in relative sea-level rise drowning marshes (Atwater et al. 1979, Atwater and Belknap 1980, Goman 1996). Plant and animal genetic material for the San Francisco estuary tidal marshes may have come from two sources: local invasions from adjacent uplands and fresh-water marshes, especially in the Sacramento-San Joaquin delta, and from small coastal saltmarshes that may have occupied the exposed coastline outside the Golden Gate. Finally, although human disturbance of the marshes has been substantial over the last 150 yr, no published evidence exists of extensive human disturbance prior to that time or of significant limitations on marsh formation by other animals (Goals Project 1999).

A major question is the extent to which the geological setting would have provided adequate protection from storms and wave energy for marsh establishment or persistence. The geologic constriction forming the Golden Gate now creates a buffer to the high-energy conditions that exist along the California coastline (NOAA 2003), but this would not have protected coastal environments during and for some 11,000 yr after the LGM (Atwater and Belknap 1980). Outside the Golden Gate, the principle feature that stands out in the paleo-shoreline maps (Figs. 3 and 4) is the absence of a large fully protected inlet or bay anywhere along the north and central coastline that could provide conditions similar to those inside the Golden Gate for extensive saltmarsh development during and shortly after the LGM, although a large (~5,000–10,000 km²)

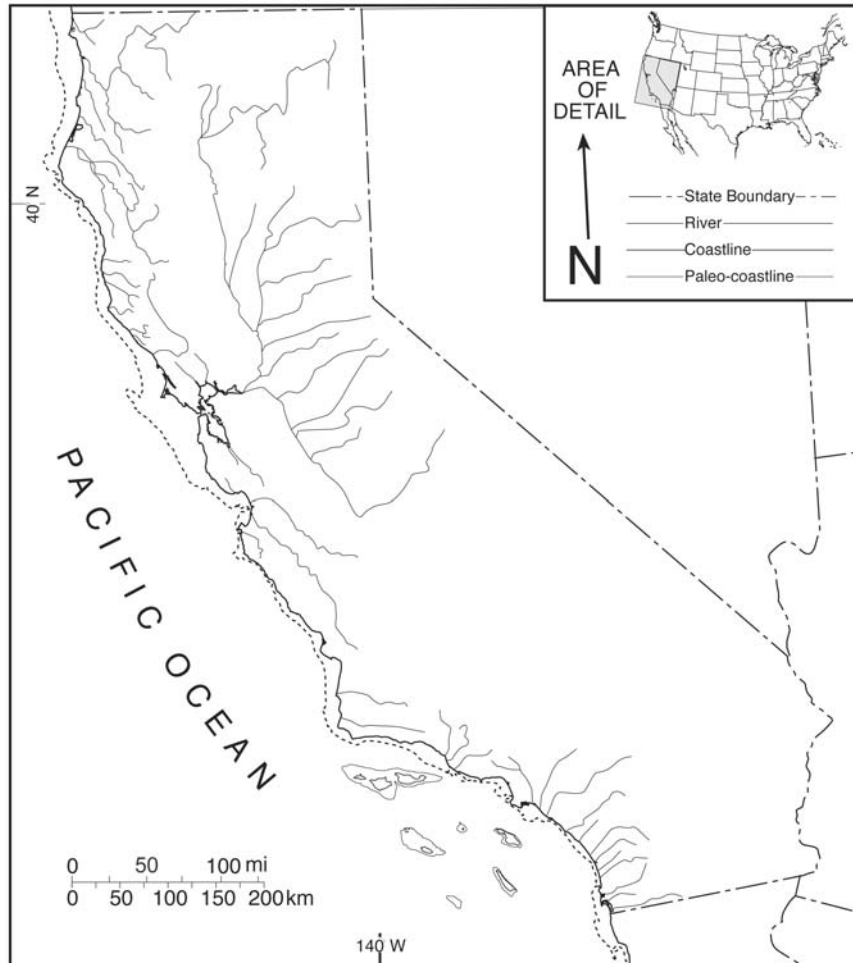


FIGURE 3. California shoreline and approximate shoreline present at 20,000 yr BP. This representation of paleo-shoreline assumes a drop of 120 m in sea level and does not account for local variations in geologic stability. This map was adapted from public domain bathymetric maps (U.S. Coast and Geodetic Survey 1967a, b, c, d; U.S. Coast and Geodetic Survey 1969, National Ocean Service 1974a, b.).

semi-enclosed basin—the Gulf of the Farallons and Cordell Bank—lies between the Farallon Ridge and the Golden Gate (NOAA 2003), and may have provided substantial protection for some of this period. Although Atlantic Coast marshes are extensive in many areas without bedrock protection, the lack of large marshlands along the central and northern California coastlines at present (NOAA 2003) and the structural-tectonic setting of this area, with steep bathymetry and a history of rapid vertical tectonic motion (Atwater and Hemphill-Haley 1997), suggests that LGM refugial tidal marshes outside the Golden Gate were very small and isolated, and may have been quite limited in size and possibly separated at times by large distances throughout the late Pleistocene and early Holocene.

Modern tidal marshes along the northern California coast outside the Golden Gate are currently associated primarily with river mouths (NOAA 2003), and several of these potential marsh sites can be seen in Figs. 3 and 4, such as at the mouth of the Eel River (Fig. 5), where a delta with seasonally variable sandy barrier spits and beaches currently creates some protected opportunities for salt-marsh development. In addition, sandy oceanic sediments have formed barriers and protected small marshes at Point Reyes and Tomales Bay, where structural barriers provide some protection to the sediments and marshes (NOAA 2003). Although direct evidence is lacking for tidal saltmarshes of the late glacial period in this region, it appears most likely that they also

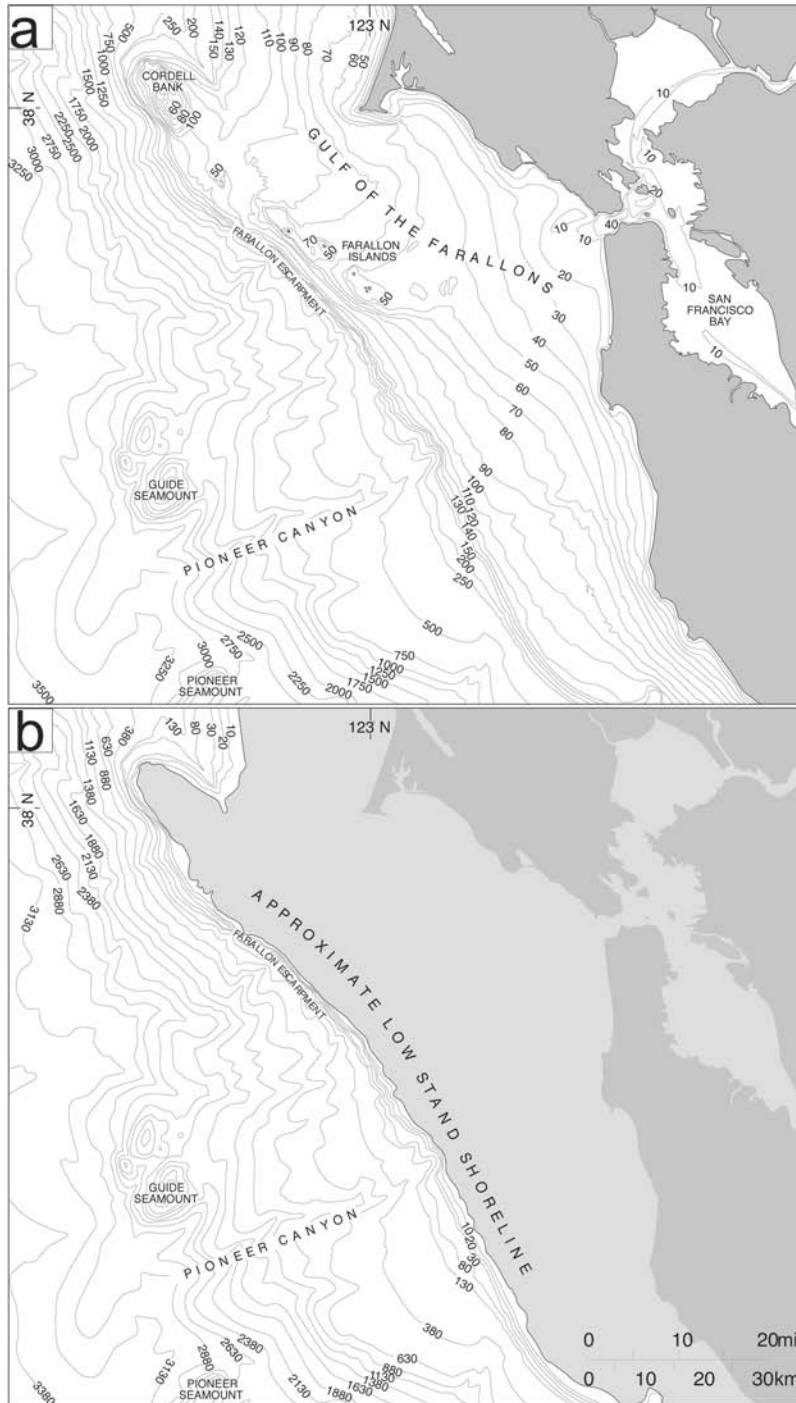


FIGURE 4. Near-shore bathymetry of north-central California during high and low stands of sea level. (a) During high stands, a large estuary is located east of the Golden Gate. (b) During low stands, shorelines are located east of the Farallon Islands. This representation of paleo-shoreline assumes a drop of approximately 120 m and does not account for changes in elevation as a result of tectonic uplift or subsidence. Bathymetry is in meters and reported relative to mean lower low water (MLLW). This map is adapted from a National Ocean Service (1974) bathymetric map.

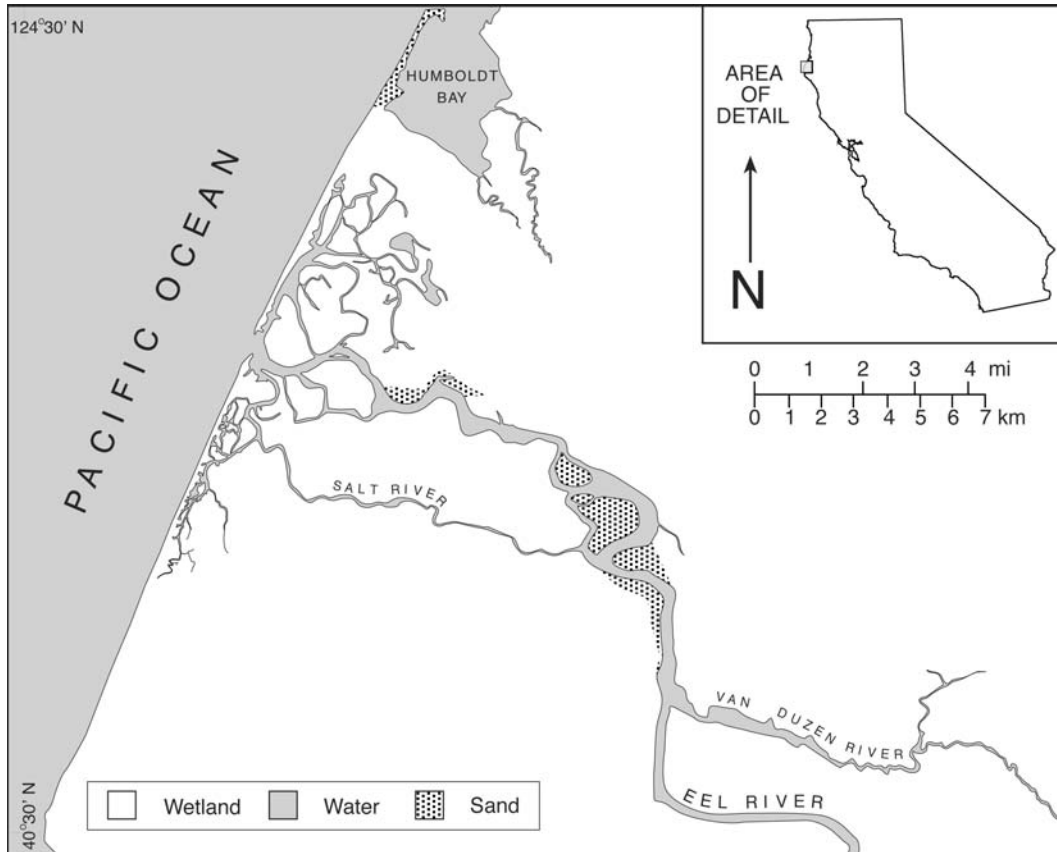


FIGURE 5. The Eel River delta before major coastal development occurred. This map was adapted from the U.S. Army Corps of Engineers (1916a, b).

developed as relatively small fringing coastal marshes where barrier spits and islands created by the build up of river-borne and coastal sediments provided some limited protection. Barrier features similar to those at the Eel River and Point Reyes may have existed throughout the glacial periods of the Quaternary where the Sacramento and San Joaquin rivers reached the paleo-shoreline, although the bathymetric maps indicate a significant drop in elevation just beyond the Farallon Islands, where the 21,000 yr BP shoreline would have been. At some point after the first melt-water pulse, the topographic ridge containing the Farallon Islands and the Cordel Bank west of Point Reyes (Fig. 4a) would have formed a semi-enclosed basin at the site of the current Gulf of the Farallons, which presumably provided some protection from storms during the latest Pleistocene and early Holocene. However, although some tidal marshes probably formed in the Gulf of the Farallons, the lack of evidence for extensive Atlantic or Gulf Coast marshes during this time

argues that rapidly rising sea level probably kept them small.

It is unclear when tidal marshes first formed inside the Golden Gate after the LGM. Evidence from other coasts as well as from the San Francisco estuary indicates that tidal marshes were able to colonize the mudflats in the bay only after the rate of sea level slowed to less than 2 mm/yr, roughly 6,000 yr BP (Atwater 1979, Fairbanks 1989), and numerous sediment cores in the lower and middle San Francisco estuary (east through Suisun Bay) have not found evidence for tidal marshes before about 4,000–5,500 yr BP (Atwater 1979, Atwater and Belknap 1980, Goman 1996, Goman and Wells 2000, Malamud-Roam 2002, Malamud-Roam and Ingram 2004). In salty parts of the estuary, the mudflats were often first colonized by the pioneer plant, California cordgrass (*Spartina foliosa*; Malamud-Roam 2002), a California endemic that can withstand prolonged periods of inundation. This grass does best in fresh conditions (Cuneo 1987), but can tolerate high

salinity and is therefore more commonly found in salt tidal marshes today. As the surface elevation of the mudflats rose, a result of the increased mineral and organic sediments accumulating due to the stands of California cordgrass, other marsh species became established, such as pickleweed (*Salicornia virginica*) and salt grass (*Distichlis spicata*), or sedge species (*Schoenoplectus californica* and *S. acutus*) in the case of the brackish marshes.

In contrast to tidal marshes, there is clear sedimentary evidence for continuous non-tidal freshwater marshlands in the delta of the Central Valley dating back over 30,000 yr, reflecting drainage impeded by tectonic-structural barriers at the transition from the Central Valley to Suisun Bay (Schlemon and Begg 1973, Atwater and Belknap 1980). Precisely when the delta marshes began to experience tidal influence has been controversial, and the complex geologic history of the Suisun Basin and the western delta has precluded precise estimates of tidal introduction to the delta based solely on bathymetry. Schlemon and Begg (1973) interpreted 12,000-yr-old sediments at Sherman Island, in the western delta, as intertidal, but this was disputed by Atwater et al. (1979) and Atwater and Belknap (1980), who believed that the site was non-tidal freshwater marshes until perhaps 7,600 yr ago. More recent sediment cores show clear evidence of perhaps 7,000 yr of fresh-water marshes and considerable taxonomic diversity at Browns Island (Goman and Wells 2000, May 1999, Malamud-Roam 2002) and a similar history at several sites that are now sub-tidal (Watson, Chin, and Orzech, unpubl. data) in Suisun Bay near the delta, but the degree of tidal action in these sites is ambiguous.

The occurrence of high endemism in tidal-marsh plants and animals in the San Francisco estuary (Greenberg and Maldonado, *this volume*) likely has many causes, and in addition to the rapid expansion of habitats over a physically diverse estuary spanning over 100 km, and dispersal and possibly adaptive radiation in an estuary that is largely isolated from other tidal-marsh gene pools, colonization or recolonization also apparently took place from multiple directions (tidal saltmarshes, non-tidal freshwater marshes, non-tidal salty or alkaline marsh, and uplands). Fresh-water marshes have occupied the area adjacent to the confluence of the Sacramento and San Joaquin rivers for approximately 7,000 yr (Goman, 1996). Animal species that may have stopped in the delta during their annual migrations may have taken advantage of the newly available niches provided by the development of

salty and freshwater tidal marshes in the San Francisco estuary. In addition to the delta, other wet and frequently salty or alkaline environments exist inland of the San Francisco Bay, including shallow seasonal lakes, pools and marshes. Resulting from the combination of California's mediterranean climate, soils which produce a subsurface hardpan and largely flat, but hummocky topography, vernal wetlands are common throughout the state of California, particularly in the Central Valley and along its adjacent coastal terraces and range from <1 ha to >20 ha in size (Holland and Jain 1977). Today vernal pools provide temporary habitats for many ducks, shorebirds, and passerines (Baker et al. 1992), and species richness is significantly correlated with the size of the vernal pool (Holland and Jain 1984). During the late Pleistocene and early Holocene, much of the Central Valley was covered by large vernal pools and lakes (Baskin 1994) and the marshy habitats that were associated with them may have provided some habitat for some of the vertebrate organisms occupying present day saltmarshes around the San Francisco Bay.

CONCLUSIONS AND IMPLICATIONS

The climate and sea-level variations seen since the last glacial maximum have had significant direct and indirect impacts on the location of the coastal zone, on the extent and distribution of saltmarshes worldwide, on the distribution of physical conditions and thus potential habitats within marshes, and ultimately on the biogeography at all spatial scales of the species associated with saltmarshes. The global-scale climate changes that led to rapid sea-level rise also influenced the distribution of marshes and their inhabitants through other, more subtle, mechanisms, including shifts in the distribution of sea-surface temperature, ice, rainfall and runoff, and sediments. Major consequences to tidal marshes of these global-scale changes and their local manifestations include frequent, periodic losses of habitat with associated consequences for population and genetic processes, sequential expansions from habitat refugia, and communities predisposed to invasion.

Some of the aspects of the historical geography and biogeography of tidal saltmarshes discussed in this paper are known conclusively while others, because of limitations in preserved data, are known only indirectly, inferentially, and/or imprecisely. There is no doubt that the global ocean rose everywhere relative to the land over the last 21,000 or so years, and that on a global scale the scale of this was about 110–140m, but there is incomplete knowledge

of the precise extent of rise relative to local land surfaces, because of complex local crustal movements due both to glacial rebound and other geologic processes. It is clear that the rate of rise varied dramatically during this period, and that the most recent 6,000 yr or so have been characterized by relatively slow rise on a global scale, but the precise rate and timing of phases of faster and slower rise is unclear both globally and locally. Tidal saltmarshes have no doubt existed in ephemeral settings, and their current locations and forms have existed for no more than a few thousand years, but there are significant challenges in mapping their extent and connectedness during the last glacial maximum and during the following 15,000 yr. It is almost certain that the extent and connectedness of marshlands along all coasts increased and decreased in several phases during the late Pleistocene and early Holocene, potentially allowing for phases of adaptive radiation and dispersal, but the precise distribution of antecedent tidal marshes is not known and probably never will be. It is certain that both the air and sea water were colder during and shortly after the LGM at all current tidal marsh sites, but it is not yet clear how far from the poles coastal biota were pushed by these temperature shifts and the associated expansion of year-round ice cover.

Some other general principles are certain—as sea level rises, aquatic environments invade the terrestrial realm, and tidal marshes persist either by accreting vertically, or by migrating landward. A result of the rise and fall of global sea level on glacial timescales is the burial and/or erasure of former saltmarsh sedimentary records. Glacial cycles have led to north-south gradients on all coasts because of isostasy, changes in ice cover, and other causes unrelated to current latitudinal variations in physical conditions. Glacial cycles may have contributed to cases, like in the San Francisco Bay, where tidal marshes have developed largely in isolation from other coastal saltmarshes, with a consequently high rate of endemism in tidal marsh plants and animals. As tidal marshes have developed in their current locations, their inhabitants have colonized them not only from refugial tidal marshes, but for some taxa at least, from other wetlands or upland areas with very different natural histories. Tidal saltmarshes and their flora and fauna have suffered significant losses due to human development and today face potentially serious threats related to invasive species and global.

Because direct stratigraphic evidence is missing, the specific underlying mechanisms leading to some modern biogeographic patterns are not completely clear, but are strongly suggested

both by the biotic distributions themselves and by the coastal environments implied from our model. For example, evidence is presented in Greenberg and Maldonado (*this volume*) that sparrows and other groups of the U.S. Atlantic Coast vary dramatically in the length of time that they have been genetically isolated from congeners, with a trend towards genetic longer isolation in the south than north. Although it is not possible to exactly map the low stand Atlantic coastline or its tidal marshes, it is clear that the sites of current northern marshes were under thick pack ice during the LGM and during earlier Pleistocene glacial advances, and that coasts near the ice front could have experienced significant storms associated with the pronounced temperature gradients. In contrast, more southern coasts, while kilometers east of their present location during low sea stands, would probably not have differed greatly in physical conditions from the present—gentle bedrock slope, sediment fluxes down the rivers and along the coasts, moderate tides, air and water temperatures within the current ranges of tidal marshes. Although droughts associated with glacial conditions would have reduced freshwater supplies and probably sediment fluxes, it seems likely that barrier islands and spits would have provided adequate protection from storms for significant marshes. Thus, the genetics of northern taxa may well represent recent colonization of tidal marshes and differentiation from upland types, while the southern taxa have had substantial time for specialization to tidal marsh conditions. This is in stark contrast to the California examples, where a lack of storm protection could have limited the extent of tidal marshlands along the length of the coast during low sea stands, with expansion and colonization of tidal marshes more determined by basin configuration and sea level than by latitude.

Some final questions remain unanswered despite the supplemental model:

1. Given the changing distribution of physical conditions in estuaries, especially in light of anthropogenic influences, where can marshes be effectively protected and restored for the long term?
2. Why are biodiversity, rarity, and endemism higher in some estuaries than in others?
3. In addition to maintaining marshes along salinity gradients, are other landscape-level attributes of patch size and distribution important for protection and restoration of rare, endemic, and/or native species?
4. How should restoration projects be planned to maximize the likelihood of producing desired taxa and minimize the abundance of pests?

5. What are the risk factors associated with invasive and/or non-native species in marshes?
6. Can marshes be designed to minimize invasion risk?
7. When temporal changes are noted in the distribution or abundance of marshes or marsh taxa, are these due to natural succession or landscape evolution, to natural periodicities in forcing functions, to unintentional human influences, and/or to intentional restoration activities? Although these questions have not been comprehensively answered in this review, it is hoped that the framework provided can suggest new interpretations and fruitful lines of research.

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