

ENVIRONMENTAL THREATS TO TIDAL-MARSH VERTEBRATES OF THE SAN FRANCISCO BAY ESTUARY

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Abstract. The San Francisco Bay and delta system comprises the largest estuary along the Pacific Coast of the Americas and the largest remaining area for tidal-marsh vertebrates, yet tidal marshes have been dramatically altered since the middle of the 19th century. Although recent efforts to restore ecological functions are notable, numerous threats to both endemic and widespread marsh organisms, including habitat loss, are still present. The historic extent of wetlands in the estuary included 2,200 km² of tidal marshes, of which only 21% remain, but these tidal marshes comprise >90% of all remaining tidal marshes in California. In this paper, we present the most prominent environmental threats to tidal-marsh vertebrates including habitat loss (fragmentation, reductions in available sediment, and sea-level rise), habitat deterioration (contaminants, water quality, and human disturbance), and competitive interactions (invasive species, predation, mosquito and other vector control, and disease). We discuss these threats in light of the hundreds of proposed and ongoing projects to restore wetlands in the estuary and suggest research needs to support future decisions on restoration planning.

Key Words: Contaminants, disease, fragmentation, San Francisco Bay, sea-level rise, sediment supply, threats, tidal marsh, water quality, wetlands.

AMENAZAS AMBIENTALES PARA VERTEBRADOS DE MARISMA DE MAREA DEL ESTUARIO DE LA BAHÍA DE SAN FRANCISCO

Resumen. La Bahía de San Francisco y el sistema delta abarcan el estuario más grande a lo largo de la Costa Pacífico de las Américas y el área más larga que aun queda para vertebrados de marisma de mar, a pesar de que los marismas de marea han sido dramáticamente alterados desde mediados del siglo 19. A pesar de que los esfuerzos recientes para restaurar las funciones ecológicas son notables, numerosas amenazas para ambos organismos de marea, endémicos y amplios, incluyendo pérdida del hábitat, están aun presentes. El alcance histórico de humedales en el estuario incluyeron 2,200 km² de marismas de marea, de los cuales solo el 21% permaneció, pero estos marismas de marea comprenden >90% de todos los marismas de marea que quedan en California. En este artículo, presentamos las amenazas ambientales más prominentes para los vertebrados de marisma de marea, incluyendo pérdida del hábitat (fragmentación, reducciones en el sedimento disponible, y aumento en el nivel del mar), deterioro del hábitat (contaminantes, calidad del agua, y disturbios humanos), e interacciones competitivas (especies invasoras, depredación, mosquitos y otro control vector, y enfermedades). Discutimos estas amenazas a luz de cientos de proyectos propuestos y llevados a cabo para restaurar humedales en el estuario, y las necesidades sugeridas por estudios para apoyar futuras decisiones en la planeación para la restauración.

Coastal and estuarine wetlands are resources of global importance to humans and wildlife, but they encompass <3% of the land surface in the Western Hemisphere and only 0.3% of the contiguous US (Tiner 1984). The most extensive regions of tidal marsh in the coterminous US are found along the Gulf Coast (9,880 km²), southern Atlantic Coast (2,750 km²), mid-Atlantic Coast (1,890 km²), and New England and Maritime Coast (360 km²; Greenberg and Maldonado, *this volume*). In contrast, much less tidal marsh is located on the West Coast, of which the largest extent is found in the San Francisco Bay and delta (SFBD; Fig. 1). SFBD is the largest estuary (4,140 km²) on the Pacific Coast of the Americas, encompassing <7% of the land surface, draining >40% (155,400 km²) of California (Nichols et

al. 1986), and supporting 162 km² of remaining tidal marshes.

Saltmarsh plant communities along the California coast often form mosaic patches and are dominated by common pickleweed (*Salicornia virginica*, syn. *Sarcocornia pacifica*) and Pacific cordgrass (*Spartina foliosa*). Common pickleweed occurs throughout the East and West coasts of the US (U.S. Department of Agriculture 2003), but Pacific cordgrass is traditionally found along the California coast from Bodega Bay (though it has been introduced to Del Norte County) in the north, to San Diego County in the south (Calflora 2003), extending into the Baja Peninsula of Mexico. In SFBD, relatively narrow strips (3–10 m) of Pacific cordgrass occur between mean tide level (MTL) and mean

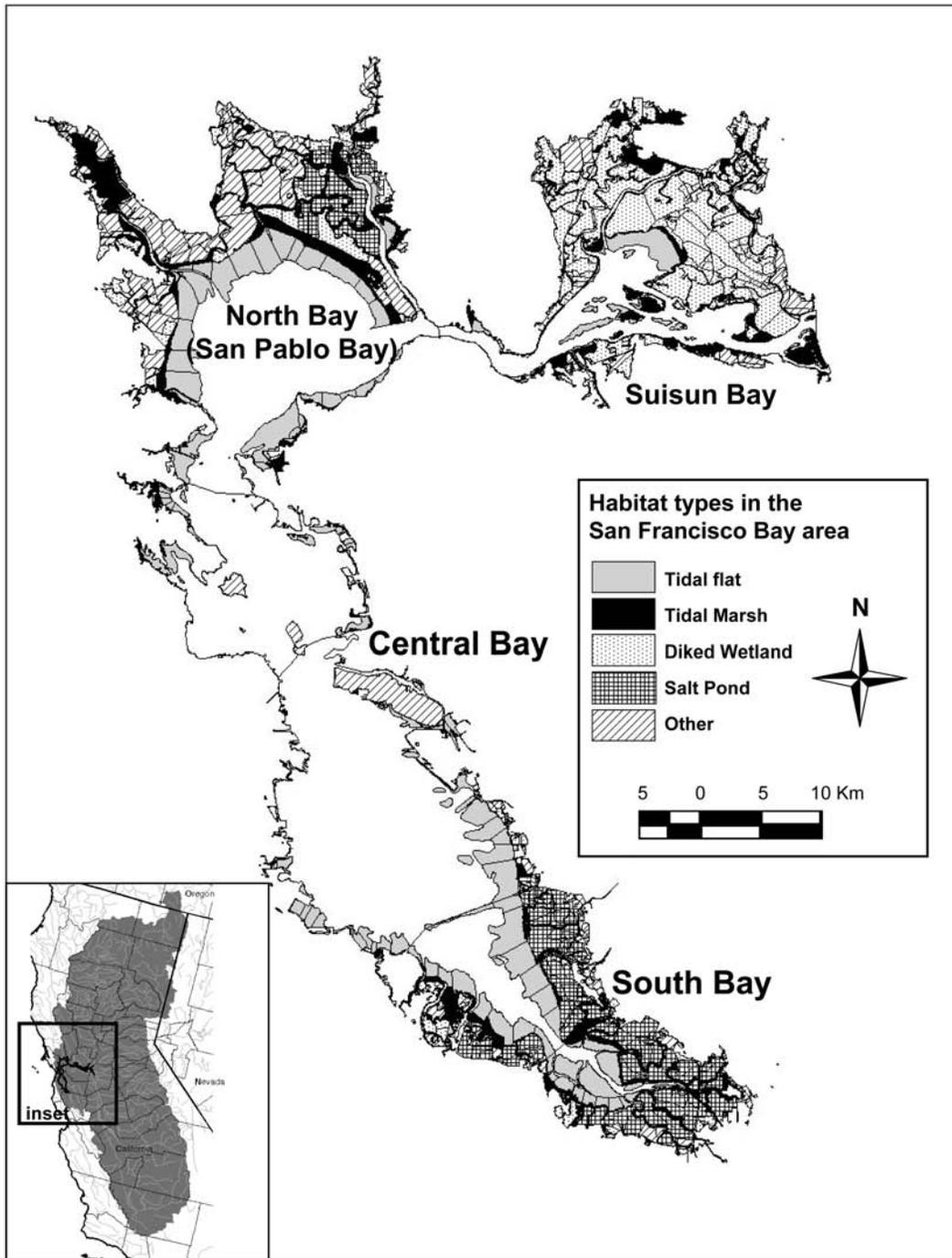


FIGURE 1. Area of California drained by the San Francisco Bay estuary and the Sacramento-San Joaquin River watershed (shaded), and distribution of tidal-marsh habitat within the estuary (San Francisco Estuary Institute 1998).

high water (MHW), and a wider band (up to a few kilometers) of common pickleweed ranges from mean high water (MHW) to mean higher high water (MHHW) (Josselyn 1983). In more brackish waters of the Sacramento and San Joaquin river delta, bulrushes (*Bolboschoenus* and *Schoenoplectus* spp.) are dominant. With the extensive losses of coastal wetlands in California, the SFBD now supports 90% of the remaining tidal wetlands (MacDonald 1977).

HUMAN DEVELOPMENT

The abundance of wildlife resources attracted the first humans to the estuary roughly 10,000 yr ago. Hunter-gatherer societies approached 25,000 inhabitants but likely posed little threat to most tidal-marsh wildlife (San Francisco Estuary Project 1991). In the last 200 yr, hunters and traders were attracted to the estuary by the abundant wildlife from as far away as Russia, causing the first notable decline of fur-bearing populations including sea otter (*Enhydra lutra*) and beaver (*Castor canadensis*) (San Francisco Estuary Project 1991). Spanish inhabitants set up missions and began grazing cattle and sheep in the 18th and 19th centuries. A rapid influx of humans occurred in 1848 when gold was discovered in the Sierra Nevada Mountains. Within 2 yr, the city of San Francisco grew from 400–25,000 individuals. Sierra Nevada

hillsides were scoured by hydraulic mining and mercury (Hg) was used to extract gold. Roughly 389,000,000 m³ of sediment, along with Hg-laden sediments, was transported downstream into the estuary from 1856–1983 (U.S. Geological Survey 2003).

The SFBD was home to over half of the state's population by 1860, and the population has steadily increased (Fig. 2). Population growth also stimulated rapid development and urbanization (Figs. 3, 4). Legislation for land reclamation (federal Arkansas Act of 1850, state Green Act of 1850) was enacted to encourage conversion of grasslands and wetlands to farmlands, and by the 1870s a network of levees had been constructed to protect low-lying fields. The deepwater harbor became a major shipping center, and by 1869, completion of the transcontinental railroad increased movement of food and goods from the region. Striped bass (*Morone saxatilis*) were intentionally introduced for a commercial fishery in 1879.

In the early 1900s, urban runoff polluted the bays, and thousands of hectares of wetlands were filled for development. Tidal wetlands in the South Bay were replaced by >5,000 ha of salt-evaporation ponds by the 1930s (Siegel and Bachand 2002). Dams and diversions on nearly every tributary prevented fish from spawning upstream, limited sediment transport downstream, and reduced freshwater

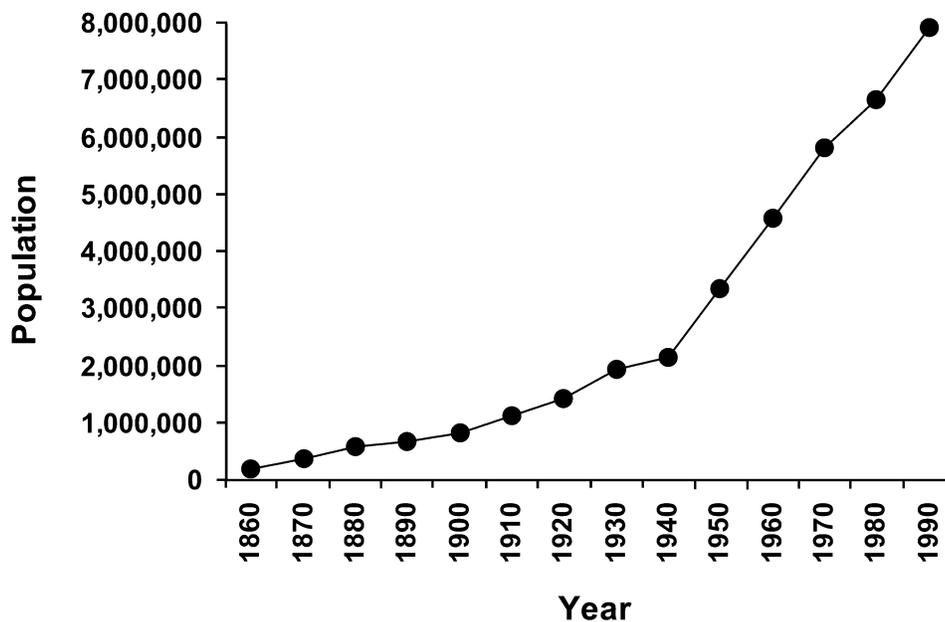


FIGURE 2. Increased human population in the San Francisco Bay estuary and delta from 1860–1990 (Bell et al. 1995).

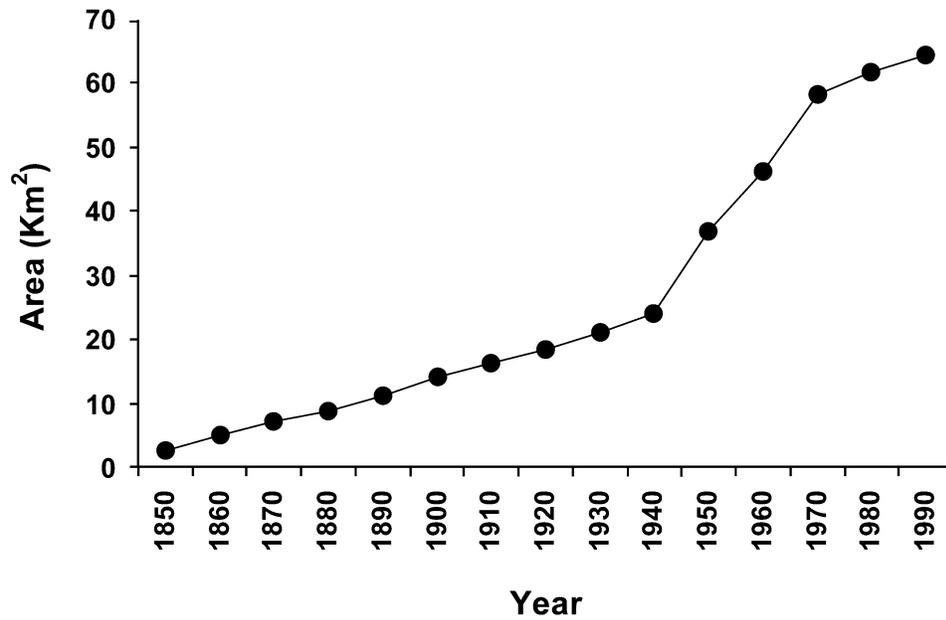


FIGURE 3. Expanding urban areas (in square kilometers) of the San Francisco Bay estuary and delta from 1850–1990 (Bell et al. 1995).

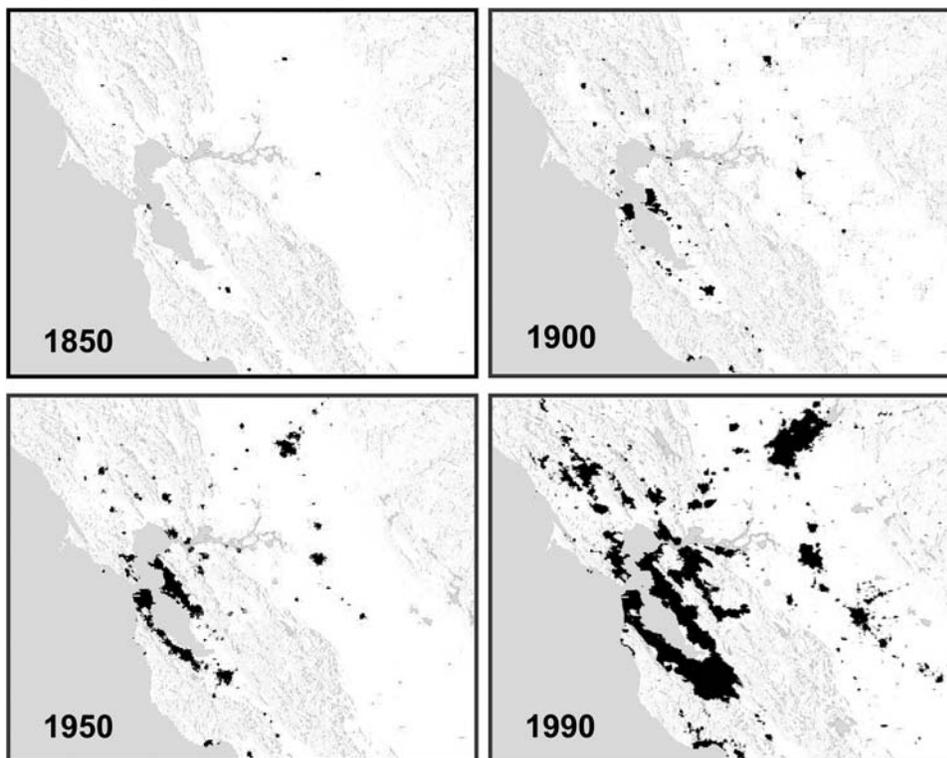


FIGURE 4. Distribution and changes in extent of development in the San Francisco Bay estuary from 1850, 1900, 1950, and 1990 (Pereira et al. 1999).

flows. The thousands of workers attracted to the area during World War II stimulated a housing and construction boom. Farmers became reliant on chemical practices increasing toxic runoff to estuary waters. The human population was nearly 6,500,000 in 1980, but it increased 34% to 8,700,000 by the end of the century (U.S. Census Bureau 2000). The historic (pre-1850) saltmarshes covered 2,200 km² or twice the extent of open water (Atwater et al. 1979), but the modern landscape has been altered by loss of 79% of the saltmarshes, 42% of the tidal flats, and construction of almost 14,000 ha of artificial salt-evaporation ponds (San Francisco Bay Area Wetlands Ecosystem Goals Project 1999).

THE MODERN ESTUARY

The diversity of the SFBD wetlands includes freshwater marshes in the eastern delta and upstream tributaries, brackish marshes in Suisun Bay and western delta, and saltmarshes (Fig. 1) in the South Bay, Central Bay, and San Pablo Bay (Harvey et al. 1992). That diversity supports 120 fishes, 255 birds, 81 mammals, 30 reptiles, and 14 amphibian species in the estuary, including 51 endangered plants and animals (Harvey et al. 1992). SFBD is a Western Hemisphere Shorebird Reserve Network site of hemispheric importance used by >1,000,000 shorebirds, supports >50% of wintering diving duck species counted on the Pacific flyway of the US during the midwinter, and is home to one of the largest wintering populations of Canvasbacks (*Aythya valisineria*) in North America (Accurso 1992).

Wetland conservation in the SFBD has evolved from slowing loss to preserving remnant wetlands to aggressively restoring areas. By 2002, 29 wetland restoration projects had been completed in the North Bay alone (S. Siegel, unpubl. data); however, these restoration projects were relatively small (≤ 12 ha). Large restoration projects, hundreds to thousands of hectares in size, have been proposed or initiated recently that will significantly change the regional landscape. Nearly 6,500 ha of salt ponds in the South Bay and 4,600 ha in the North Bay have been acquired (San Francisco Bay Area Wetlands Ecosystem Goals Project 1999, Steere and Schaefer 2001, Siegel and Bachand 2002). Some areas will be managed as ponds to provide habitat for thousands of shorebirds and waterfowl, but many areas are proposed for conversion to tidal marshes for the benefit of tidal-marsh species. Despite these wetland restoration efforts, tidal-marsh vertebrates still face many threats in the estuary.

In this paper, we summarize the major threats to tidal-marsh vertebrates including habitat loss (habitat fragmentation, sediment availability, and sea-level rise), deterioration (contaminants, water quality, and human disturbance), and competitive interactions (invasive species, predation, mosquito control, and disease). We describe how these threats affect tidal-marsh vertebrates, where proposed restoration projects may ameliorate their effects, and what studies would be helpful to support restoration planning.

HABITAT FRAGMENTATION

Habitat fragmentation results from changing large continuous areas to a pattern of smaller, more isolated patches of less total area within a matrix of altered habitats (Wilcove et al. 1986). Fragmentation usually also involves an increase in mean patch perimeter-to-area ratio and changes in patch configuration. Though habitat loss contributes directly to population decline, edge effects and habitat isolation may cause further reductions by an impact on dispersal and altering the ecological function within patches, especially near habitat edges (Andren 1994). These impacts may increase with time since isolation.

In the SFBD, loss of tidal-marsh habitat has resulted in many remnant marshes that are small and isolated from other marshes (San Francisco Bay Area Wetlands Ecosystem Goals Project 1999, San Francisco Estuary Institute 2000). Roads, levees, urban development, and non-native vegetation have replaced upland edges and transition zones (Table 1), much to the detriment of animals that rely on upland areas as high-tide refugia. Many modern wetlands are

TABLE 1. HISTORIC (PRE-1820) AND PRESENT DISTRIBUTION OF TIDAL-MARSH PATCHES IN THE SAN FRANCISCO BAY ESTUARY (DERIVED FROM THE SAN FRANCISCO BAY ECOATLAS 1998).

Patch size (hectares)	Number of tidal and muted marsh patches ^a	
	Historic habitat (pre-1800)	Present habitat (1990s)
<10	190	370
10-50	46	97
51-100	21	23
101-500	33	38
501-1,000	18	3
1,001-3,000	20	1
>3,000	4	0
Total area of tidal marsh	77,530	16,996

^a Patches derived by merging adjacent tidal (old and new) and muted marsh polygons. Muted marshes include wetlands without fully tidal flows.

patchy, linear or irregularly configured, confined to edges of large tidal creeks or sloughs, or on the bayside edges of levees where new marshes formed over sediments accreted during the 1850s. Levee networks, tide-control structures, and mosquito ditches not only fragmented wildlife habitat but also altered the hydrology and sediment dispersion patterns of outboard levee areas (Hood 2004). Although regulatory laws may prevent future losses of wetlands, increased urbanization and loss of native vegetation corridors may decrease the viability of populations (Andren 1994). Tidal-marsh species may be differentially affected depending on their level of habitat specialization (Andren 1994) and the scale of landscape heterogeneity to which they are sensitive (i.e., patch sensitivity, *sensu* Kotliar and Wiens 1990, Wiens 1994, Riitters et al. 1997, Haig et al. 1998).

Habitat fragmentation may act as an isolating mechanism resulting in higher extinction rates and lower colonization rates, lower species richness (MacArthur and Wilson 1963, 1967), higher nest-predation rates (Chalfoun et al. 2002), higher nest parasitization rates, and changes in ecological processes (Saunders et al. 1991). Numbers of avian marsh species in the prairie pothole region have been shown to vary with patch size and perimeter-to-area ratio as well as with vegetation and other local-scale factors (Brown and Dinsmore 1986, Fairbairn and Dinsmore 2001). The effects of fragmentation were also found to be variable, species-specific, and context-specific in a range of other habitat types (Bolger et al. 1997, Bergin et al. 2000, Chalfoun et al. 2002, Tewksbury et al. 2002).

Few studies have been done to assess the impact of fragmentation on tidal-marsh birds in the SFBD. Scollon (1993) mapped marsh patches and dispersal corridors for the Suisun Song Sparrow (*Melospiza melodia maxillaris*) based on theoretical estimates of dispersal distance and published population densities. Varying fragmentation effects on population size have also been predicted for San Pablo Song Sparrows (*M. m. samuelis*; Scollon 1993; Takekawa et al. chapter 16, *this volume*). The dispersal of San Pablo Song Sparrows from one fragmented marsh to another is thought to be rare since dispersal distance averages 180 m (Johnston 1956a). Thus, populations in smaller, more isolated fragments were more susceptible to local extinction. Recent empirical studies (Spautz et al., *this volume*; Point Reyes Bird Observatory, unpubl. data) have found that San Pablo, Suisun, and Alameda (*M. m. pusillula*) Song Sparrows, all California species of special concern, and California Black Rails (*Laterallus jamaicensis coturniculus*), a California state threatened

species, respond to marsh size, configuration, isolation, and other landscape-scale factors as well as to local-scale factors such as vegetation composition and structure. However, the underlying processes contributing to these patterns, along with dispersal patterns across the estuary, are not well understood.

RESTORATION CONCERNS

Several large-scale wetland restoration projects are underway, including the Napa-Sonoma Marsh on San Pablo Bay (4,050 ha) and the former Cargill salt ponds in the South Bay (6,475 ha; Siegel and Bachand 2002). These projects involve restoration of areas that were historically tidal, but were converted to salt-evaporation ponds. The goals of these restoration projects are to provide large areas of contiguous habitat, increasing marsh area with minimal fragmentation. Previous restoration projects in the estuary have been relatively small and opportunistic with limited study of restoration effects at the landscape scale.

One of the most important considerations in restoration is determining the optimum configuration and size of the project. A single large expanse of habitat may be preferable for some species rather than several smaller, isolated habitat patches (particularly for those species requiring large territories). However, a population in a single large patch may be more vulnerable to extinction because of demographic stochasticity or catastrophic events (such as fires and disease; Carroll 1992). Highly vagile species, including most birds, are generally better able to disperse between isolated habitat patches than small mammals, reptiles, and amphibians. However, radio-telemetry studies of the endangered California Clapper Rail (*Rallus longirostris obsoletus*) indicate low rates of movement between and within seasons (Albertson 1995) and habitat fragmentation is considered one of the main threats to the persistence of this subspecies (Albertson and Evens 2000).

REDUCTION IN SEDIMENT AVAILABILITY

Sediment deposition and tidal actions are the dynamic processes that sustain tidal-marsh wetlands. Rapid sediment accretion of tidal marshes in the SFBD extended for at least 20 yr after the start of hydraulic gold mining in the Sierra Nevada Mountains. San Pablo Bay received 300,000,000 m³ of sediment, and by 1887 created 64.74 km² of new mudflats (Jaffe et al. 1998). The concentration of suspended sediments in the delta declined 50% by the 1950s

with the cessation of hydraulic mining and the advent of dams on major tributaries from downstream reaches (Wright and Schoellhamer 2004). San Pablo Bay lost 7,000,000 m³ of sediment from 1951–1983 or an annual loss of 0.36 km² of mudflats (Jaffe et al. 1998).

Many wetland restoration project sites have subsided and require substantial sediment input to reach adequate levels for plant establishment. When sedimentation rates were studied in the south San Francisco Bay (Patrick and DeLaune 1990), one site (Alviso) was found to have subsided by >1 m based on records from 1934–1967 because of groundwater extraction (Patrick and DeLaune 1990). The large number of restoration projects occurring simultaneously may reduce predicted sediment availability (San Francisco Bay Area Wetlands Ecosystem Goals Project 1999). A shortage of sediment may result in a reduced turbidity, increased erosion, and a greater loss of mudflat and intertidal habitats (Jaffe et al. 1998).

Dredge material has been proposed for projects where natural sediment supply is inadequate. Annual yields from dredging operations produce an average of 6,120,000 m³ of sediment in the estuary (Gahagan and Bryant Associates et al. 1994). At current rates of sediment accretion, it would take 10–15 yr to raise elevations one meter in South Bay salt ponds (although actual rates will vary by pond) to a height appropriate for vegetation colonization (San Francisco Bay Area Wetlands Ecosystem Goals Project 1999). In recent years, regulatory agencies have included the potential use of dredge material for restoration to accelerate the process of restoration (U.S. Army Corps of Engineers 1987).

RESTORATION CONCERNS

Many contaminants such as Hg and PCBs are tightly bound to sediment particles. As a result, the transportation of contaminants is closely tied to the movement of sediments. Use of dredge material in restoration projects has the potential to transport and reintroduce buried contaminants to the soil surface where it may be biologically available (Schoellhamer et al. 2003). Another concern of dredge material use is the potential incompatibility with surrounding substrate conditions. Dredge material may not complement the fine particle size of naturally occurring tidal wetlands, and soils may not support vigorous plant growth (Zedler 2001). Dredge spoils may have coarser soils and less clay content (Lindau and Hossner 1981), and consequently less soil organic matter and microbial activity (Langis et al. 1991).

Coarser substrates may have a decreased ability to retain nutrients (Boyer and Zedler 1998) and may fail to support the vegetation structure and height required for target species (Zedler 1993). Despite the concerns of amending soils with dredge material, data in relation to its use in restorations are scarce. In the Sonoma Baylands restoration project, dredge materials were used to accelerate the restoration process. However, development of channels and vegetation has been slow, presumably because of limited tidal exchange. Additional studies would provide more detailed analyses of the benefits of dredge materials against the costs.

SEA-LEVEL RISE

Projections for future sea-level rise in the SFBD vary between 30 and 90 cm in the 21st century, depending upon which climate projection models are used (Dettinger et al. 2003). An estimated 10–20 cm of that rise is expected, regardless of anthropogenic global-warming effects based on the historic rate of 20 cm/100 yr seen during the course of the 20th century (Ryan et al. 1999). The remainder is due to the combined influence of thermal expansion as the ocean warms in response to global warming, and accelerated melting of glaciers and ice caps. Galbraith et al. (2002) predicted a conversion of 39% of the intertidal habitat in San Francisco Bay to subtidal habitat by 2100, as high as 70% in the South Bay. In addition to the projected long-term rise in global sea level, considerable short-term variability can be expected due to local factors including tides, increased storm surges and changes in upwelling along the coast of California, all of which act on a range of mechanisms and timescales (Table 2). The SFBD tidal marshes and their flora and fauna now face potentially severe threats associated with sea-level rise, because the magnitude of change and the accelerated rate of rise over the next few decades, and because human activities around the marshes have probably dramatically reduced the marshes' capacity for coping with sea-level changes.

POTENTIAL IMPACTS

Actual sea-level rise can be seen in the tidal data at the Golden Gate from 1897–1999 (Fig. 5), which have changed at different rates (Malamud-Roam 2000). For example, while mean sea level has increased by about 20 cm during the 20th century, the height of mean higher high water (MHHW) and the highest highs have increased by about 25 cm and 28 cm per century, respectively (Malamud-Roam

TABLE 2. MECHANISMS, VERTICAL RANGE, TEMPORAL PATTERNS, AND OVERALL EFFECTS OF VARIATION IN HYDRODYNAMICS ON SEA-LEVEL RISE IN THE SAN FRANCISCO BAY ESTUARY.

Mechanism	Vertical range	Temporal pattern	Effect
Wind waves, swash, and run-up	<1–60 cm	Oscillatory; frequency in seconds	Large waves may become more frequent if storms increase; Swash and run-up may increase where the shoreline is hardened.
Seiches	Few centimeters	Oscillatory; frequency in minutes	Increasing estuary depth may increase the frequency or amplitude; impact likely minor.
Tides	1–2 m	Oscillatory; dominant frequencies 12.5 and 25 hr	If tidal range continues to increase, the height of HW relative to MSL will increase, and the frequency and mean depth of over-marsh flooding will probably increase.
Storm surge	10s of centimeters	Episodic; winter	Frequency and amplitude will probably increase due to global warming.
Lunar modulation of the tides	Range ~ 120 cm; HW height ~ 60 cm; DHQ and DLQ ~ 30 cm	Dominant (spring/neap) = 14.6 d; Minor (lunar declination) = 13.6 d	Dredging can alter the fortnightly circulation patterns induced by lunar tidal modulation.
Annual cycles of solar radiation	Monthly MSL ~ 10 cm; Monthly MHHW ~ 20 cm	Annual cycle of rainfall and runoff (ppt high in winter, runoff high in spring, both low in fall)	Global warming could change amount and timing of precipitation and therefore runoff and water surface slope in the estuary.
Precession of lunar node	None	Daylight flooding occurs in winter and night flooding in the summer, varying slightly over a 18.6-yr period	Photosynthesis, predation, and dispersal may all respond to this pattern of flooding, temperature, and light.
Probably solar annual cycles, possibly beat frequencies	10–20 cm	MSL has annual cycle, low in April and high in September and MHHW has semi-annual cycle, high in January and July	Global warming induced changes in oceanic circulation may change seasonal tidal mean patterns, but it is not clear how.
El Nino/southern oscillation	15–30 cm rise	Episodic, occurring about every seventh year. Duration of rise in Estuary 6–12 mo	ENSO frequency apparently increasing. If this continues or accelerates, the frequency, duration, and height of extreme high water will increase.
Secular (multi-year) climatic cycles	100 m increase over Holocene, slowing about 7,000 yr ago.	Eustatic (absolute) rise ~ 1 mm/yr; relative (local) rise ~ 2 mm/yr	Global warming could increase the rate of relative rise in the bay to 3–9 mm/yr for the next 100 yr.

Note: The abbreviations include: DHQ = mean diurnal high water inequality (one-half the average difference between the two high waters of each tidal day observed over the National Tidal Datum Epoch); DLQ = mean diurnal low-water inequality; HW = high water; MSL = mean sea level; MHHW = mean higher high water; ENSO = El Niño southern oscillation.

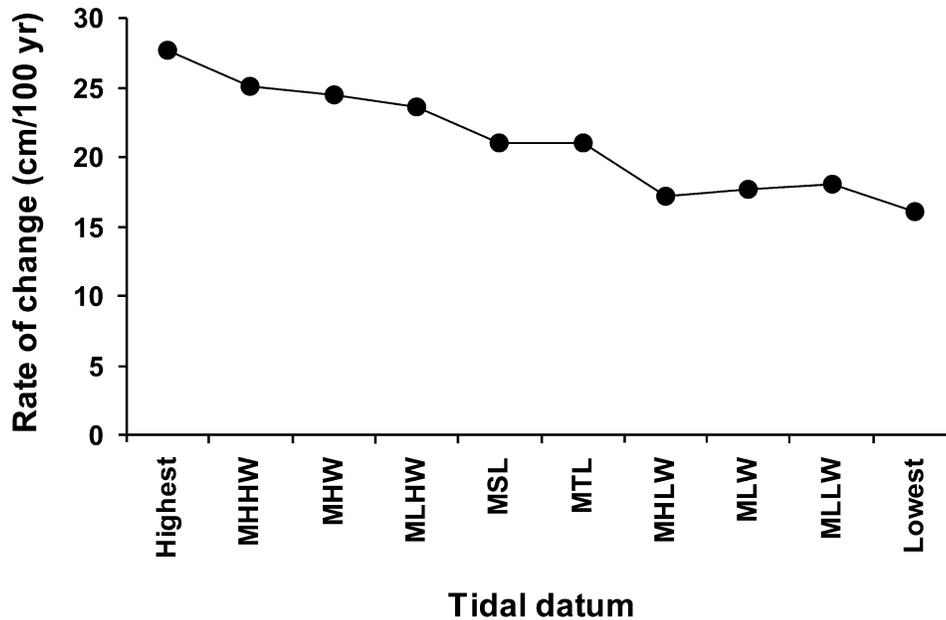


FIGURE 5. Rate of change in centimeters/100 yr in tidal data at the Golden Gate of the San Francisco Bay estuary from 1897-1999, including: MHHW = mean higher high water, MHW = mean high water, MLHW = mean lower high water, MSL = mean sea level, MTL = mean tide level, MHLW = mean higher low water, MLW = mean low water, MLLW = mean lower low water.

2000). Thus, for the animals living on the marsh surface, sea level has risen by an effective 25-28 cm in the last century. Should this pattern of a faster rate of change for the highest tides continue into the next century, projections of sea-level rise may underestimate the actual rise in sea level for the animals living in the tidal marshes. Furthermore, most global-warming scenarios for this region predict an increased frequency and severity of storm surges due to global warming (Cubasch and Meehl 2001).

Sea-level rise poses three major risks to wildlife that occupy the surrounding tidal marshes and mudflats.

1. Higher sea levels may drown the marshes and mudflats or increase storm surges causing greater shoreline erosion and habitat loss.
2. Increased frequency or duration of extreme high tides can lead to higher mortality of songbird eggs and young birds during extreme high-tide floods (Erwin et al., *this volume*; Point Reyes Bird Observatory, unpubl. data). In addition amplified high tides may increase the vulnerability of the salt marsh harvest mouse (*Reithrodontomys raviventris*), California Clapper Rails (*Rallus longirostris obsol-etus*), California Black Rails, and other

marsh inhabitants to predation as they seek refuge upland.

3. Increased salinity intrusion into inland areas of the estuary can change plant assemblages and alter habitat for wildlife, such as the Common Moorhen (*Gallinula chloropus*).

CHANGING SALINITY

As sea level rises at the Golden Gate, salinity can be expected to intrude further up-estuary. In terms of salinity, the effect of rising sea level can be analogous to a decrease in fresh-water inflow, as the depth of the bay has remained fairly constant throughout the Holocene (Ingram et al. 1996). Vegetation patterns in the marshes have changed significantly during the last century, reflecting a significant increase in salinity (May 1999, Byrne et al. 2001, Malamud-Roam 2002). For example, pollen cores from the Petaluma River have shown dramatic shifts from brackish waters (characterized by tules) around 1,800 yr ago to saline conditions (characterized by pickleweed) around 1,400-800 years ago, and back again to brackish conditions around 750 yr ago (Byrne et al. 2001). Climate explains only a part of the change in estuarine salinity; water diversion for agriculture and

human consumption explains the majority of the change (Peterson et al. 1995).

As sea level rises, the tidal-marsh habitats (fresh, brackish, and salt) can be expected to change as vegetation responds to higher salinity conditions. For some organisms, the changes may be favorable, with a greater area covered by saltmarsh habitat. Other organisms that rely on fresh water habitat, such as the Common Moorhen, may face significant loss of habitat, and a shift up-estuary in their range as the salt wedge approaches the delta. Strategies to compensate for the increase in marine influence due to sea-level rise could include increasing the area of marsh habitat within the delta or increased fresh water flows through the delta (requiring a decline in water diversion).

RESTORATION CONCERNS

A critical synergistic threat facing marsh inhabitants is the combined force of a sediment deficit and sea-level rise. The modern supply of sediments to the estuary has been significantly altered in historic times due to human modifications of the hydrologic system. However, future predictions based on historical rates of rise, and potential increases resulting from global warming, suggest significant losses of saltmarsh habitat in the South Bay and more significant losses of tidal mudflats, which are critical for shorebird species (Galbraith et al. 2002).

The North Bay, however, does not have a history of high subsidence as in the South Bay, though it is largely unknown whether the rates of sediment supply will be adequate to maintain marsh surface elevations in the future. Studies of long-term rates of sediment accretion in marshes in San Pablo Bay, the Carquinez Strait, and Suisun Bay indicate that for the last 3,000 yr the average rates of sediment accretion have matched sea-level rise (Goman and Wells 2000, Byrne et al. 2001, Malamud-Roam 2002). However, the long-term records also indicate that there were periods when sediment supply was clearly inadequate to maintain the marshes, resulting in a conversion of some areas to subtidal conditions (Goman and Wells 2000, Malamud-Roam 2002).

CONTAMINANTS

The SFBD has numerous sources of pollution, many of which are particle-bound, and their concentrations fluctuate with suspended sediment concentrations (Schoellhamer et al. 2003). Most restoration projects in the estuary are dependent on sediment inputs to elevate marsh plains; however, three sediment-

associated contaminants including mercury (Hg), selenium (Se), and polychlorinated biphenyls (PCBs) are listed as priority pollutants in SFBD under section 303(d) of the Clean Water Act. Sediment-bound contaminants or those re-suspended by dredging operations or changes in sedimentation dynamics pose a potential threat to tidal-marsh vertebrates when transported into wetlands. Although numerous other pollutants occur in the bay, we focus on those suspected to have direct bearing on tidal marsh health and food webs.

One of the most prevalent contaminants is Hg. Mercury extracted from the Coast Range was used to recover gold and silver in Sierra Range mining operations during the Gold Rush era (Alpers and Hunerlach 2000). Between 1955 and 1990, the SFBD received an average of 6,030,000 m³ of Hg-laden sediments annually (Krone 1996). Methylmercury (MeHg), a more toxic and readily bioaccumulated form (Marvin-DiPasquale et al. 2003), is magnified by passing through food webs with transformation initiated in phytoplankton. Acute toxicity in fish, birds, and mammals damages the central nervous system (Wolfe et al. 1998, Wiener et al. 2003), while lower-level exposure affects reproduction in vertebrates (Wiener and Spry 1996, Wolfe et al. 1998).

Human-health advisories for fish have been in effect since 1970, and Hg concentrations in striped bass have not changed significantly since that time (Fairey et al. 1997, Davis et al. 2002). Highest liver Hg concentrations for small mammals have been found in South Bay wetlands (Clark et al. 1992). A recent study documented that eggs of Forster's Tern (*Sterna forsteri*) and Caspian Tern (*Sterna caspia*) foraging in South Bay salt ponds and adjacent sloughs contained the highest concentrations (7.3 and 4.7 mg/kg total Hg) of any bird species in the estuary (Schwarzbach and Adelsbach 2002). Endangered California Clapper Rails exhibited depressed hatchability and embryo deformities with egg concentrations exceeding the lowest observed adverse effect concentration (LOAEC) of 0.5 µg/g (Schwarzbach et al. 2006; Novak et al., *this volume*).

Selenium (Se) is another persistent threat to tidal-wetland vertebrates. Se is substituted for sulfur in enzymes, resulting in reproductive failure and teratogenesis. Sources include oil refinery effluent and agricultural drainwater. Selenium loads from refineries have decreased (6.8 kg/d-1.4 kg/d) with recent regulation (San Francisco Bay Regional Water Quality Control Board 1992), but agricultural sources range between 20.4-53.2 kg/d (Luoma and Presser 2000). Dissolved Se concentrations are

consistently $<1 \mu\text{g/L}$ (Cutter and San Diego-McGlone 1990, San Francisco Estuary Institute 2003), below chronic criterion for aquatic life ($2 \mu\text{g/L}$). However, Se concentrations may be elevated because chemical speciation controls bioaccumulation (Luoma and Presser 2000). For example, Black-necked Stilts (*Himantopus mexicanus*) nesting at Chevron Marsh in Richmond, California, had eggs ($20\text{--}30 \mu\text{g/g dw}$) with similar concentrations found at Kesterson Reservoir ($25\text{--}37 \mu\text{g/g dw}$). Se in source water was 10% of the concentrations at Kesterson, but uptake was enhanced because the form of Se was selenite, the most bioavailable species.

Despite reduction in Se since 1998, concentrations in sturgeon and diving ducks remained elevated, possibly because of invasion of the Asian clam (*Potamocorbula amurensis*), a species that concentrates Se more than other clams (White et al. 1989, Linville et al. 2002, San Francisco Estuary Institute 2003). In a recent survey of wetland birds, Se concentrations in eggs ranged from $1.5 \mu\text{g/g dw}$ in Snowy Plover (*Charadrius alexandrinus*) eggs to $4.2 \mu\text{g/g dw}$ in Snowy Egret (*Egretta thula*) eggs, and $1.6 \mu\text{g/g dw}$ in failed California Clapper Rail eggs (Schwarzbach and Adelsbach 2002) compared with a threshold for reproductive problems of $6\text{--}10 \mu\text{g/g dw}$ (Heinz 1996). In birds, Hg and Se are toxicologically antagonistic, where exposure to one of these elements protects individuals from the toxic effects of the other (El-Begearmi et al. 1997); however, Heinz and Hoffman (1998) showed that the most environmentally realistic and most toxic forms of mercury (methylmercury) and selenium (selenomethionine) combined caused lower hatching success in Mallards (*Anas platyrhynchos*) than either contaminant alone.

Polychlorinated biphenyls (PCBs), synthetic chlorinated aromatic hydrocarbons with a wide variety of industrial uses, have been banned in the US since 1979. However, PCB concentrations in SFBD water remain high, and 83% of samples taken during 2001 by Regional Monitoring Program (San Francisco Estuary Institute 2003) exceeded water quality objectives. Sources to the estuary cannot be pinpointed, but are thought to be mainly historical. Runoff from creeks and tributaries has been identified as one significant source of PCBs (San Francisco Estuary Institute 2003).

PCBs are accumulated in fat and readily increase from trophic level to trophic level in estuarine food webs. Although PCB toxicity depends on the structure of individual congeners, general effects include thymic atrophy, immunotoxic effects, endocrine disruption, reproductive impairment, porphyria, and

liver damage (Hoffman et al. 1996). Failed California Clapper Rail eggs collected during 1992 in the South Bay had total PCB concentrations between $0.65\text{--}5.01 \mu\text{g g}^{-1}$ (Schwarzbach et al. 2001). Rail sensitivity to PCB congeners is not known, but the authors indicate such concentrations may cause reduced hatching success.

Section 303(d) of the Clean Water Act lists elements copper (Cu) and nickel (Ni), as well as organic contaminants DDT, chlordanes, dieldrin, dioxins, and furans as priority pollutants. In addition, sediment monitoring showed that arsenic (As) and chromium (Cr) consistently exceeded guidelines at several sites (San Francisco Estuary Institute 2003). Sediment toxicity could threaten tidal-marsh vertebrates by decreasing their invertebrate prey base (San Francisco Estuary Institute 2003). Polybrominated diphenyl ethers (PBDEs), used as flame retardants, have been increasing in sediment and biota, and Caspian Tern eggs from SFBD contain the highest concentrations found in any bird species (T. Adelsbach, USDI Fish and Wildlife Service, pers. comm.). Tributyl tin (TBT), an anti-fouling additive in paint, is an endocrine disrupter that may pose a threat to wetland organisms by increasing through wetland food webs (Pereira et al. 1999).

Oil spills remain a threat, because California is the fourth largest oil-producing state and the third largest crude-oil-refining state in the nation. Six oil refineries are located in the bay and comprise nearly 40% of the state's total oil production capacity (California Energy Commission 2003). More than a thousand tanker ships pass through the estuary each year, along with countless container ships, recreational boats, and other vessels. The tanker Puerto Rican spilled 5,678,118 l of oil in 1984, killing approximately 5,000 birds, while a Shell Oil storage tank spilled 1,589,873 l in 1988. Over an extended period of time (from at least 1992–2002, though likely for many years earlier), heavy fuel oil leaked out of the freighter S.S. Jacob Luckenbach that sank southwest of the Golden Gate Bridge in 1953 (Hampton et al. 2003). Roughly 378,541 l of oil were removed from the wreck, but over 18,000 bird mortalities were estimated in 1997 and 1998 from this one source (Hampton et al. 2003). In 2002, of 6,867 oil spills reported in California, 445 were in the SFBD (Office of Spill Prevention and Response 2003).

RESTORATION CONCERNS

Projects in the bay that re-expose, accrete, or use dredged Hg-laden sediments may pose

risks to fish and wildlife. This is especially true in tidal marshes where sulfate-reducing bacteria in anoxic sediments can transform inorganic Hg to MeHg. Boundary zones of oxic-anoxic areas in marshes have particularly high MeHg production. Site-specific parameters such as dissolved or organic carbon content, salinity, sulfate, and redox cycles also influence biotransformation rates and subsequent bioaccumulation in tidal wetland organisms (Barkay et al. 1997, Kelly et al. 1997, Gilmour et al. 1998).

WATER QUALITY

Water quality in the SFBDB has changed dramatically due to human activity during the past 150 yr, often to the detriment of estuarine ecosystems. The impact of water quality change on tidal-marsh terrestrial vertebrates is virtually unstudied but could be severe if left unmanaged. In this section, we discuss water-quality threats exclusive of toxic contaminant and sediment budget issues addressed earlier. Changes in water quality probably affect vertebrate populations indirectly via long-term changes in the vegetative and invertebrate communities that inhabit the marsh and short-term cascading trophic effects starting with aquatic organisms low in the food web.

The SFBDB is a highly variable environment commonly experiencing both wet and dry extremes within a year as well as wet and dry years. Humans have changed the timing and extent of these fluctuations as well as the chemistry of waters entering the estuary. Under current management regimes, river inflow and freshwater diversions can vary between years by as much as 25 times (Jassby et al. 1995). While native organisms are adapted to the seasonal fluctuations, recent and future extremes may tax their survival and reproductive capabilities.

SALINITY

Salinity, a key variable determining tidal-marsh vegetative and invertebrate community composition, has changed significantly in recent decades. A decrease in salinity can convert a saltmarsh to fresh-water marsh, as in the tidal wetlands near the San Jose and Santa Clara Water Pollution Control Plant, where up to 567,811,800 l of treated fresh wastewater empty into south San Francisco Bay every day. Despite fresh-water flows from treatment plants, overall salinity in the estuary has increased because of a reduction in fresh-water flows from the delta to 40% of historical levels,

due to water diversion for agriculture, municipal use, and local consumption (Nichols et al. 1986). Pollen and carbon isotope data from sediment cores from Rush Ranch in Suisun Bay clearly indicate a shift since 1930 in the dominance of marsh vegetation from freshwater to salt-tolerant plants as a response to increased salinity due to upstream storage and water diversion. This recent shift in the vegetative community was as extreme as the shift that occurred during the most severe drought of the past 3,000 yr (Byrne et al. 2001).

When freshwater flows are reduced, salt intrusion up-estuary can become a problem (Nichols et al. 1986), particularly in high-marsh areas that already become hyper-saline during certain times of the year. For example, historically large populations of the endangered San Francisco garter snake (*Thamnophis sirtalis tetrataenia*), have declined presumably due to the loss of several prey species from saltwater intrusion into less saline marsh habitats (San Francisco Bay Area Wetlands Ecosystem Goals Project 2000). Salt intrusion is a cause for concern particularly for tidal-marsh restoration projects in the Delta. When levees are breached, the total tidal prism increases, which allows saline waters to travel farther up-estuary during high tides. Change in salinity regimes may also facilitate the proliferation of invasive species. The Asian clam gained a foothold in Suisun Bay during a period of extreme salinity changes, with far-reaching consequences (Nichols et al. 1990).

Marsh vertebrates may be adapted to conditions that are specific to particular salinity ranges. For example, adaptations to kidney structures in the salt marsh harvest mouse may have allowed this species to use saline environments (MacMillen 1964). Zetterquist (1977) trapped the greatest numbers of salt marsh harvest mice in highly saline tidal marshes. Whether the high density of harvest mice in these marshes was due to an affinity for high salinity or lack of competitors is not known. In addition, Song Sparrow subspecies in San Pablo Bay saltmarshes and Suisun brackish marshes have different bill sizes and plumage colors that may reflect adaptation to local conditions (Marshall 1948). Because of the close association between vertebrate subspecies and tidal marshes of a specific salinity, long-term salinity changes could affect both the persistence and the evolution of endemic tidal-marsh vertebrates. Changes in salinity can affect the distribution of invertebrates as well, such as the winter salt marsh mosquito (*Aedes squamiger*), which is found not in freshwater, but in brackish and saline habitats.

PRODUCTIVITY

Water management can greatly affect primary productivity in the estuarine waters, which likely impacts marsh vertebrates that forage extensively on invertebrates and fish in the tidal channels. Phytoplankton forms the base of the food web that includes most of the wildlife in the estuary (Sobczak et al. 2002). Sometimes, productivity is low enough to affect fish growth and mortality, which may suggest that other vertebrates become food-limited as well (Jassby and Cloern 2000). Beneficial phytoplankton blooms occur when the null zone (the location where freshwater outflow balances saltwater inflow) is positioned across the broad shallows of Suisun Bay (Jassby et al. 1995). Management of delta inflows may alter the position of the null zone to facilitate optimal phytoplankton blooms and may be important for maintaining the food supply of vertebrates that forage in tidal channels.

EUTROPHICATION

Wastewater and runoff comprise a significant percentage of freshwater entering the estuary (Nichols et al. 1986). The main threat from these waters is toxic contaminants, but nutrient loading is also a concern. In past decades, summer die-offs due to eutrophication and ensuing oxygen depletion occurred in the South Bay. These events have not recurred following the institution of improved sewage treatment methods in 1979, although nitrogen concentrations remain high (Kockelman et al. 1982). Oxygen depletion continues to be a problem in areas of the delta when water retention times are long (B. Bergamaschi, U.S. Geological Survey, pers. comm.).

Eutrophication in the estuary is controlled by two factors. First, high turbidity causes algae to be light-limited, so nuisance blooms do not occur on the same scale as in other polluted bays (Jassby et al. 2002). Second, benthic bivalves consume much of the primary production and reduce the availability of nutrients in the water column (Cloern 1982). However, turbidity may decline in the near future due to retention of sediment behind dams and channel armoring (International Ecological Program 2003).

RESTORATION CONCERNS

Many agencies and hundreds of scientists are working to understand and manage water quality, although most of the focus is on open-water habitats rather than tidal wetlands. Delta inflow is currently managed to allow for movements of fish populations and keep summer primary

productivity at optimal levels in the Suisun Bay. The Environmental Protection Agency suggested guideline maximum salinity levels for sensitive areas of the estuary. Investigators at the U. S. Geological Survey, California Department of Water Resources, Interagency Ecological Program, and Stanford University continue to monitor and model water quality in the estuary as well as conduct original research experiments.

HUMAN DISTURBANCE

Residents and visitors are drawn to the waters, shorelines, and wetlands in this highly urbanized estuary for aesthetic and recreational opportunities. The needs of >8,000,000 people in the SFBD estuary encroach upon the many wildlife populations dependent on estuarine habitats. For example, wetlands attract large numbers of visitors (10,000/yr, >75% of surveyed sites) for recreational activities such as bird watching and jogging (Josselyn et al. 1989). Although natural disturbances may create areas used by birds (Brawn et al. 2001), anthropogenic disturbances that elicit a metabolic or behavior response (Morton 1995) generally reduce the value of habitats for birds (Josselyn et al. 1989).

TYPES OF HUMAN DISTURBANCE

People traverse marshes on vehicles, bicycles, and on foot—jogging or walking through the areas along roads or trails. Automobiles on established roads may not greatly affect the behavior of wildlife, but boats and aircraft may be highly disruptive by causing animals to flush, exposing them to predators. The activity or noise of boats and personal watercraft may cause avoidance or flight behavior (Burger 1998), especially near waterways, or result in trampled vegetation, while wakes from boats may erode bank habitats. Low-flying aircraft may create large disturbances in estuaries (Koolhaas et al. 1993), especially near small airports or in agricultural areas where aerial spraying is used. Longer and more extensive use of areas by campers, fishermen, hunters, and researchers may have greater individual short-term effects, while cumulative long-term effects of visitors on trails or boardwalks may effectively decrease the size of the marsh, provide pathways for predators, and degrade the value of edge habitats.

TYPES OF EFFECTS

Knight and Cole (1991) described hierarchical levels of disturbance on wildlife species from death or behavior change (altered behavior,

altered vigor, altered productivity, and death), to population change (abundance, distribution, and demographics), and finally community alteration (species composition, and interactions). In their studies of shorebirds in estuaries, Davidson and Rothwell (1993) described effects at local (movement) and estuary (emigration) levels, as well as impacts at estuary (mortality) and population (decline) scales. The adverse effects of human disturbance for waterbirds include loss of areas for feeding or roosting, elevated stress levels, and reduced reproduction including abandonment of nests or nestlings, as well as changes in behavior including avoidance of areas, reduction in foraging intensity, or feeding more at night (Pomerantz et al. 1988, Burger and Gochfeld 1991, Pfister et al. 1992, Burger 1993).

Human incursions into marshes may cause trampling of vegetation and soil compaction, reducing the quality of the habitats. Obligate saltmarsh species may be particularly sensitive to disturbance, especially because many are adapted to avoid predators by hiding within the vegetation and may avoid areas with repeated disturbance. Although habituation occurs for many species, birds displaced from coastal marshes were observed to fly to distant marshes rather than return to the same areas (Burger 1981), and disturbances displaced shorebirds from beaches (Pfister et al. 1992). Boats, especially small recreational boats, may be a particularly large disruption for waterbirds that flush at great distances (Dahlgren and Korschgen 1992).

DISTURBANCE LIMITS AND BUFFERS

Josselyn et al. (1989) found that long-legged waders in estuary marshes flushed when approached from 18–65 m, while waterfowl flushed from 5–35 m. Waterbirds avoided areas near paths where people traveled, and their behavioral responses were noted at distances of <50 m (Klein 1993). Green Heron (*Butorides striatus*) numbers were inversely proportional to the number of people at a site, and individuals that remained foraged less frequently (Kaiser and Fritzell 1984). Flushing distance was related to larger size and mixed-composition of flocks in waterfowl (Mori et al. 2001).

Stress responses are more difficult to detect. Hikers, joggers, and dogs, as well as avian predators, disturb the federally threatened Snowy Plover, prompting closure or fencing beach areas. Waterbirds avoided areas near paths where people traveled, and adverse behavioral responses were noted at distances of <50 m (Klein 1993). In addition, physiological

monitoring studies have found elevated heart-rate levels in breeding marine birds (Jungius and Hirsch 1979) and wintering geese (Ackerman et al. 2004) when approached (<50 m). In response to these findings, many government agencies support regulatory buffer distances of 31 m including the California Coastal Act buffer between developments and wetlands. Studies have shown that buffers are effective if they are large enough; 35% of buffers <15 m had direct human effects (Castelle et al. 1992), but larger buffers up to 100 m were found to be effective for waterbirds (Rodgers and Smith 1997).

RESTORATION CONCERNS

Most tidal marshes in the SFBD are adjacent to urban development or levees. Unfortunately, tidal marshes are often fragmented by levees that have a narrow and steep transition from high marsh to upland. The salt marsh harvest mouse may be found in upland areas up to 100 m from the wetland edge during high tides (Botti et al. 1986, Bias and Morrison 1999). Other marsh inhabitants, such as the California Clapper Rail and the California Black Rail, use upland transitional areas as refuge from high tides; however the narrow width of these zones makes rails more vulnerable to predation. During prolonged flooding from high tides, Suisun shrews (*Sorex ornatus sinuosus*) utilize upland habitats for cover and food (Hays and Lidicker 2000). Without consideration of adjacent habitats, tidal-marsh restoration may fail to support target species. In addition, many restoration projects include public access to the marshes. How and where such access is allowed may greatly influence the value of the tidal marshes for some species.

INVASIVE SPECIES

The SFBD is perhaps the most highly invaded estuary in the world (Cohen and Carlton 1998). Many of the plants now found in the tidal marshes, most of the invertebrates in the marsh channels and adjacent tidal flats, and several terrestrial animals that forage in tidal marshes are not native to the Pacific Coast. Here, we focus on the exotic species that are most likely to harm the native vertebrates in these tidal marshes. An exotic disease, the West Nile virus (WNV), which is expected to soon appear in estuary tidal marshes, is discussed below.

PLANT INVASIONS

Grossinger et al. (1998) recommended that monitoring, research, and control efforts focus

on the three exotic plants that have the widest distribution in tidal marshes: smooth cordgrass (*Spartina alterniflora*), dense-flowered cordgrass (*Spartina densiflora*) and broad-leaved peppergrass (*Lepidium latifolium*), and that four other exotic plants that as yet have a very limited distribution in these marshes be monitored: common cordgrass (*Spartina anglica*), salt-meadow cordgrass (*Spartina patens*), opposite leaf Russian thistle (*Salsola soda*), and oboe cane (*Arundo donax*). Of these species, smooth cordgrass and dense-flowered cordgrass are currently the most widespread and are likely to negatively impact native tidal-marsh vertebrates because they can become very abundant in the marsh plain (mid- to upper-marsh zones) (Ayres et al. 1999, Faber 2000). The marsh plain, which is naturally dominated by low-growing native cordgrass species provides key habitat for most of the resident tidal-marsh birds and mammals including the salt marsh harvest mouse (Shellhammer et al. 1982). Several native bird species including the federally endangered California Clapper Rail, the California Black Rail, and the three tidal-marsh Song Sparrow subspecies that are state species of special concern (Alameda, San Pablo, and Suisun), nest and forage in cordgrass (Johnston 1956a, b; San Francisco Bay Area Wetlands Ecosystem Goals Project 2000). Where smooth cordgrass and dense-flowered cordgrass become abundant, they can potentially alter marsh habitat by changing the vegetative structure (including canopy height, density, and complexity), sub-canopy physical conditions, root density and soil texture, sediment deposition and erosion rates, and perhaps ultimately marsh elevation, marsh topography, and channel morphology (Callaway and Josselyn 1992, Daehler and Strong 1996, Faber 2000). However, few data are available on how these changes would affect tidal-marsh vertebrates.

Most research on the impacts of exotic plants on tidal-marsh vertebrates in the SFBD has focused on smooth cordgrass. This Atlantic cordgrass was introduced in the early 1970s and over the next decade began to spread and hybridize with the native California cordgrass (*Spartina foliosa*; Ayres et al. 1999). This exotic cordgrass (*Spartina alterniflora*, *S. alterniflora* x *foliosa*, or both) is highly productive and now occurs in >2,000 ha of marsh and tidal-flat habitats (Ayres et al. 1999). The dramatic alteration of tidal-marsh habitat by the tall, thick, exotic cordgrass will likely affect resident species the most. Native vertebrate species do occupy invaded marshes; however, it is unclear whether these subpopulations are sustainable (Guntenspergen and Nordby, *this volume*). For

the California Clapper Rail, the biggest problem may be the loss of foraging habitat and food resources in invaded marsh channels where, during low tides, the rails do much of their foraging (Albertson and Evens 2000).

One ongoing study in the South Bay is investigating the impacts on Alameda Song Sparrows through changes in flooding regimes and interspecific interactions among native species. Preliminary analysis shows that Song Sparrow nests in exotic cordgrass are much more likely to flood than nests placed in native vegetation and so reproductive success may be lower in invaded marsh habitat (J. C. Nordby and A. N. Cohen, unpubl. data). The invasion may also be altering interactions among native species. Marsh Wrens (*Cistothorus palustris*), which are native to fresh- and brackish-water marshes, are now occupying invaded saltmarshes (J. C. Nordby and A. N. Cohen, unpubl. data). An increase in Marsh Wren density is potentially detrimental for Song Sparrows and other salt-marsh birds because Marsh Wrens are highly aggressive and are known to break the eggs of other species occupying adjacent nesting territories (Picman 1977, 1980). The addition of interference competition from Marsh Wrens could reduce the reproductive success and overall distribution of other saltmarsh-nesting bird species.

INVERTEBRATE INVASIONS

Exotic benthic invertebrates far outnumber natives in the marsh channels and mudflats, comprising >90% of the number of individuals and benthic biomass over most of the estuary (Cohen and Carlton 1995). Marsh birds and shorebirds must commonly feed on exotic invertebrates including clams, mussels, snails, and worms, and probably also ostracods, amphipods, and crabs (Carlton 1979). Moffitt (1941) found the Atlantic mussel (*Geukensia demissa*) abundant (57% of food by volume) and the Atlantic snail (*Ilyanassa obsoleta*) uncommon (2% of food) in the stomachs of 18 California Clapper Rails from South Bay. Williams (1929) observed California Clapper Rails feeding heavily on the western Atlantic clam (*Macoma petalum*), while ignoring the Atlantic snail. Overall, though, little specific information exists on what the tidal-marsh birds eat. Nor is it known what effect, if any, the replacement of native prey items by exotics has had on these birds—whether more or less food is available, whether it is more or less nutritious, or whether it is more or less contaminated by toxic pollutants than native prey.

De Groot (1927) reported in detail one impact of the Atlantic mussel. This mussel was first found in the SFBD in 1894, probably introduced in oyster shipments (Cohen and Carlton 1995). It quickly became abundant along channel banks and in the outer portions of cordgrass marshes where it typically lies partly buried so that the posterior margin of its shell protrudes just above the mud with the two valves slightly open. De Groot (1927) reported that the toes or probing beaks of rails were frequently caught and clamped between these valves. He estimated that at least 75% of adult rails had lost toes, others starved from having their beaks clamped shut or injured, and one-two nestlings per brood were caught by mussels and drowned by the incoming tide. Whether or not these injury and mortality estimates were valid, more recent observations confirm that California Clapper Rails in the SFBD are frequently missing one or more toes (Moffitt 1941, Josselyn 1983, Takekawa 1993), and Takekawa (1993) reported that a rail captured with a mussel clamped onto its bill subsequently lost part of its bill.

Exotic invertebrates may also have an indirect impact on tidal-marsh vertebrates by altering habitat. The southwestern Pacific isopod (*Sphaeroma quoyanum*) was first collected in the SFBD in 1893. It burrows abundantly in mud and clay banks along the channels and outer edges of saltmarshes, and has been credited with eroding substantial areas of marsh, though no direct studies or measurements have been made (Cohen and Carlton 1995). Two recently arrived crabs, the European green crab (*Carcinus maenas*, first seen in the estuary in 1989–1990) and the Chinese mitten crab (*Eriocheir sinensis*, first collected in the estuary in 1992), are also known to be common burrowers in saltmarshes or tidal channels (Cohen et al. 1995, Cohen and Carlton 1997). If these organisms do in fact contribute to the erosion and loss of marsh habitat, this would clearly have an impact on marsh vertebrates. The impacts could be greatest near marsh channels, since the slightly elevated areas alongside these channels are better drained and support taller vegetation, providing better nesting sites and habitat for saltmarsh Song Sparrows, and possibly for California Clapper Rails, and the salt marsh harvest mouse (Marshall 1948; Johnston 1956a, b; Shellhammer et al. 1982, Collins and Resh 1985, Albertson and Evens 2000).

VERTEBRATE INVASIONS

Red foxes (*Vulpes vulpes*) from Iowa or Minnesota were introduced into California in

the last half of the 19th century either released by hunters or escaped from commercial fox farms. A wild population became established in the Sacramento Valley, and from this and other centers, red foxes spread to the East Bay region by the early 1970s. They were observed in the San Francisco Bay National Wildlife Refuge (SFBNWR) in the South Bay by 1986 and have continued to expand their range (Foerster and Takekawa 1991, Harvey et al. 1992, Cohen and Carlton 1995). Dens have been found in tidal saltmarshes and in adjacent levee banks. Red foxes prey on resident California Clapper Rails, Black-necked Stilts, American Avocets (*Recurvirostra americana*), and Snowy Egrets and on various other marsh and aquatic birds and mammals, including endangered endemic species (Foerster and Takekawa 1991, Harvey et al. 1992, Albertson 1995).

The SFBNWR began a program of trapping and killing red foxes in 1991 (Foerster and Takekawa 1991, Cohen and Carlton 1995). Recent surveys show a strong recovery in local populations of California Clapper Rail following implementation of the red fox removal (Albertson and Evens 2000). In the early 1980s California Clapper Rail numbers in the South Bay were estimated at 400–500. The local population crashed to roughly 50–60 in 1991–1992 surveys, roughly 5 yr after the first detection of red foxes at the SFBNWR. In 1997–1998 winter surveys, rail numbers increased to 330. Because California Clapper Rails are year-long residents and have strong site tenacity, the variation between survey years is not thought to be from dispersal or migration.

Brown rats (*Rattus norvegicus*) became established in many parts of California by the 1880s. In the SFBD, brown rats are common in riparian areas, in fresh, brackish and saltwater tidal marshes, and in diked marshes (Josselyn 1983, Cohen and Carlton 1995). De Groot (1927) considered the brown rat to be the third most important factor in the decline of California Clapper Rail, after habitat destruction and hunting. More recent authorities (Harvey 1988, Foerster et al. 1990, Foerster and Takekawa 1991, Cohen and Carlton 1995) have also found substantial predation on California Clapper Rail eggs and chicks, with some estimating that brown rats take as many as a third of the California Clapper Rail eggs laid in the South Bay (Harvey 1988). Rats also prey on other marsh-nesting birds and their nest contents. Because brown rats are more likely in areas that abut urban development, habitat buffers might reduce their abundance in tidal marsh.

House cats (*Felis domesticus*) are widespread in California both as house pets and

feral individuals. In the SFBD, house cats have frequently been seen foraging in saltmarshes, along salt-pond levees, and wading at the edge of tidal sloughs (Foerster and Takekawa 1991). House cats are known to have killed adult Light-footed Clapper Rails (*Rallus longirostris levipes*) in southern California (Foerster and Takekawa 1991) and at least one California Clapper Rail in the SFBD (Takekawa 1993), and presumably also prey on other marsh birds and mammals. The SFBNWR began a program of removing feral cats in 1991.

RESTORATION CONCERNS

Exotic cordgrass colonization is a threat for most South Bay tidal-marsh restoration projects due to its gross alteration of vegetative structure, sub-canopy physical conditions and root density, and potential alteration of soil texture, sediment deposition and erosion rates, marsh elevation, marsh topography and channel morphology, which could in turn affect native plant and invertebrate populations, as well as vertebrate populations. Although a regional exotic cordgrass control program began in 2004, complete control may take many years to achieve. It is likely to remain a significant issue in most restoration of this subregion and an imminent threat to the North Bay. In contrast, few areas are invaded by exotic cordgrass in the North Bay; thus, vigilant monitoring and removal of hybrid populations would be highly beneficial, and restoration of tidal marshes with native cordgrass may be more successful in this subregion. Control of nonnative predators will likely be an essential part of most tidal-marsh restoration projects to maintain native fauna. Nonnative predators will be of most concern in restoration areas adjacent to urban development.

PREDATION

Increased rates of predation on tidal-marsh vertebrates can result from three types of human-induced changes: (1) introduction of non-native predators, (2) changes in the distribution or abundance of native predators, and (3) alterations of habitat that influence predation effectiveness or avoidance. For birds and other vertebrates in tidal saltmarshes of the SFBD, as in most other ecosystems, predation is generally the dominant cause of adult and juvenile mortality and nest failure (Point Reyes Bird Observatory, unpubl. data). Although the primary cause of significant declines in populations of tidal-marsh vertebrates is habitat loss and degradation, other factors may be contributing to further population declines through

increased predation: habitat fragmentation (Schneider 2001, Chalfoun et al. 2002), loss of vegetated upland edges for use as refugia from predators during high tides, establishment of boardwalks and power lines across marshes (the latter are used as perches by raptors), changes in marsh vegetation structure and the spread of urban-tolerant native predators (e.g., American Crow [*Corvus brachyrhynchos*] Common Raven [*Corvus corax*], raccoon [*Procyon lotor*], and striped skunk [*Mephitis mephitis*]), feral animals (house cats) and other non-native predators (especially red fox), many of whom are human subsidized in urban and suburban areas (USDI Fish and Wildlife Service 1992). Sanitary landfills and riprap shorelines are also sources of predators (USDI Fish and Wildlife Service 1992).

In the SFBD, tidal-marsh fragmentation has resulted in an increased mean perimeter to edge ratio, and thus more edge per unit area. Predators are hypothesized to be more active at habitat edges. Current studies of the relationship between edge habitat and predation indicate that nest predators vary in activity and impact depending on the taxon and the surrounding land use (Chalfoun et al. 2002). Studies in estuarine marshes indicate that patterns of predation vary between sites (PRBO Conservation Science, unpubl. data). This variation is probably due to differences in the suite of predators, which itself may be dependent on variation in land use on adjacent uplands and vegetation type, and on variation in tidal flooding, channel and levee configuration, marsh vegetation structure and human disturbance patterns. Some changes in vegetation involving increases in vegetation density, such as that associated with the spread of invasive smooth cordgrass may actually result in decreased nest predation, but with ecological trade-offs (Guntenspergen and Nordby et al., *this volume*).

Several predators have been documented to depredate tidal-marsh birds, bird nests, reptiles, and mammals. They include upland mammal species that forage in marshes such as: raccoon, red fox, coyote (*Canis latrans*), striped skunk, house cat, domestic dog (*Canis familiaris*), house mouse (*Mus musculus*), brown rat, and black rat (*Rattus rattus*); wetland mammals such as the river otter (*Lutra canadensis*); snakes such as gopher snake (*Pituophis melanoleucus*) and garter snake (*Thamnophis* spp.) which have been observed swallowing nest contents (Point Reyes Bird Observatory, unpubl. data); and numerous wetland birds including Great Blue Heron (*Ardea herodias*), Great Egret (*Casmerodius albus*), Snowy Egret, Black-crowned Night Heron (*Nycticorax nycticorax*), and gull species (USDI Fish and

Wildlife Service 1992, Albertson and Evens 2000; Point Reyes Bird Observatory, unpubl. data). Raptors, especially Northern Harrier (*Circus cyaneus*), White-tailed Kite (*Elanus leucurus*), and Red-tailed Hawk (*Buteo jamaicensis*) are also documented predators as are the Common Raven and American Crow. And finally, the nest parasite and egg predator, the Brown-headed Cowbird (*Moluthrus ater*) has been documented in SFBD tidal marshes, although rates of parasitism vary greatly among marshes (Greenberg et al., *this volume*). Some of these species, such as the Northern Harrier, nest in or near marshes and have probably always been part of the tidal-marsh food web. Other species, such as Common Ravens, American Crows, and raccoons, have adapted well to urban areas, and their large populations have resulted in increased predation in adjacent natural areas.

RESTORATION CONCERNS

Control of red foxes and other non-native predators in the south San Francisco Bay has contributed to a rebound in California Clapper Rail numbers. However, predator control is not a viable option in all parts of the estuary, and other measures to reduce predation, e.g., by modifying habitat, may have better long-term results (Schneider 2001). More studies are necessary to identify the primary predators of tidal-marsh birds and mammals in various parts of the estuary so that managers can decide which control measures, if any, are necessary.

MOSQUITOS AND OTHER VECTORS

Although wetlands, including tidal marshes, support high densities of many desirable species, they can also produce copious mosquitoes and potentially other disease vectors. These disease-carrying organisms can pose threats to tidal-marsh ecosystems because they can sicken and kill marsh animals as well as people, and because mosquito-control measures can have an adverse impact on marsh processes. Fortunately, neither traditional endemic vector-borne diseases nor current mosquito-control activities pose an imminent threat to existing marshlands; however, new diseases may have dramatic impacts on wildlife, particularly birds. The need to protect wildlife, as well as the public from diseases may pose serious challenges for wetland restoration proposals.

MARSH MOSQUITOES AND MOSQUITO-BORNE DISEASES

Because some mosquito species transmit widespread and serious diseases to humans

and other animals, they have been extensively studied over the last century (Durso 1996) and have been the subject of control programs in many areas, including SFBD. Mosquitoes are a diverse group of insects that share a common life history (egg, aquatic larvae, aquatic pupae, and flying adult), and a requirement for blood feeding by the adult females to produce eggs, with rare exceptions. In addition, all juvenile mosquitoes are weak swimmers and require habitats free from strong waves or currents or abundant predators. Thus, all mosquito species require shallow, still aquatic habitats for at least a few consecutive days.

Despite these similarities, mosquitoes vary considerably in their specific habitat requirements (several species may often coexist in close proximity) and in their potential for transmitting pathogens (public health significance of some species is higher than others). Mosquitoes are often distinguished by their specialized juvenile habitats, adult behavior, and vector status (Table 3 modified from Durso 1996, Maffei 2000). For example, *Culiseta incidens* is found in shaded, cool, clear fresh water, while *Aedes melanimon* prefers sunny, warm fresh water with dense grasses.

Some generalities are possible in this diverse assemblage. Larval habitat falls primarily along temperature (seasonal) and salinity (spatial) gradients, with only two truly salt-adapted mosquito species (*Aedes squamiger* and *A. dorsalis*) common in SFBD. Unlike freshwater genera that lay eggs in stagnant water, saltwater mosquitoes (*Aedes*), require an egg-conditioning period of at least a few days in which eggs cannot tolerate inundation. Thus, mosquito production is low in saltmarshes where dry periods are too short for egg conditioning (i.e., few impediments to drainage; Kramer et al. 1995). High flooding frequency is also beneficial for mosquito control because it is associated with currents sufficient to flush the larvae to unfavorable sites. Large populations of mosquitoes are almost invariably found where drainage is poor, whether the impounded water is saline (spring high tides that do not drain) or fresh (rain or seeps).

Although mosquito threats to human and animal health include disturbance, allergies, and infection secondary to scratching (Durso 1996), the most significant problems are the infectious pathogens carried between animals by mosquito blood feeding. West Nile virus (WNV) has killed hundreds of people, hundreds of thousands of birds (in almost all taxonomic groups), and smaller numbers of other vertebrate taxa, in the US over the last 4 yr (Center for Disease Control 2001, United States Geological Survey

TABLE 3. REPRODUCTIVE CONDITIONS, ADULT BEHAVIOR, AND VECTOR STATUS OF COMMON MOSQUITO SPECIES IN SAN FRANCISCO BAY ESTUARY MARSHES.

Common name	Scientific name	Eggs, larvae, and pupae	Adult behavior and vector status. ^a
Winter salt marsh mosquito (Maffei 2000)	<i>Ochlerotatus squamiger</i> (<i>Aedes squamiger</i>)	Egg conditioning on moist soil and plants. Simultaneous hatch following flooding. Highly salt tolerant. Cold water.	Flies 16–32 km. Bites humans day and dusk. Localized pest. May transmit CE-like virus.
Summer salt marsh mosquito (Maffei 2000)	<i>Ochlerotatus dorsalis</i> (<i>Aedes dorsalis</i>)	Egg conditioning on moist soil and plants. Simultaneous hatch following flooding. Highly salt tolerant. Warm to hot water.	Flies up to 16 km. Bites humans and other large mammals day and night. Localized pest. Secondary vector of CE and WEE.
Winter Marsh mosquito (Maffei 2000)	<i>Culiseta inornata</i>	Eggs laid directly on cold standing water. Low salt tolerance.	Flies up to 8 km. Bites humans and other large mammals at night. Localized pest.
Washino's mosquito (Maffei 2000)	<i>Ochlerotatus washinoi</i> (<i>Aedes washinoi</i>)	Egg conditioning on moist soil and plants. Simultaneous hatch following flooding. Cool to cold water. Low salt tolerance.	Flies up to 1.6 km. Bites humans and other large mammals day and dusk. Localized pest. May transmit CE-like virus.
Western encephalitis mosquito (Durso 1996)	<i>Culex tarsalis</i>	Eggs laid directly on warm to hot standing water. Low to moderate salt tolerance.	Flies 16–24 km. Bites birds, and humans and other mammals at night. Primary vector of WEE, SLE. High vector competence for WNV in the lab.

^aCE = California encephalitis; WEE = western equine encephalitis; SLE = St. Louis encephalitis; WNV = West Nile virus.

2003). WNV is the greatest immediate disease threat both to wetland organisms and humans. Lab research has demonstrated that it can infect *Culex tarsalis*, *Culex erythrothorax*, *Aedes dorsalis*, *A. melanimon*, *A. vexans*, and *Culiseta inornata*, and that all of these species can transmit the virus at some level, although the two *Culex* species were the most efficient vectors (Goddard et al. 2002). Field observations in states where *Culex tarsalis* occurs confirms that this species will probably pose the greatest threat in areas that have shallow fresh-water ponds (<5 ppt) that last until eggs, larvae, and pupae develop (5 d in the summer), but that become dry periodically to eliminate aquatic predators (Maffei 2000). While *Culex tarsalis* and its particular habitat types are the chief problems, other mosquito species and poorly drained marshes have been implicated in diseases in the past (Reisen et al. 1995, Durso 1996) and may also contribute to the establishment and spread of future pathogens (Center for Disease Control 1998, 2001).

RESTORATION CONCERNS

Because marsh mosquitoes have historically been recognized as a potential threat to animal health and human health and comfort, government agencies have acted to control marsh mosquito populations through a variety of activities, traditionally divided into physical control (habitat manipulation), biological control (stocking living predators or parasites), and chemical control (applications of biotic or chemical pesticides) (Durso 1996). Some of these strategies, such as widespread drainage of wetlands or extensive applications of DDT, clearly had substantial impacts on marshes and surrounding habitats in the past (Daiber 1986). Although these examples clearly indicate a need for continued monitoring and research, mosquito control activities have become more target-specific in recent decades and have not linked to significant adverse impacts on the marshes (Dale and Hulsman 1990; U.S. Environmental Protection Agency 1991, 1998, 2003; Dale et al. 1993, Contra Costa Mosquito and Vector Control District 1997, Center for Disease Control 2001).

In addition to mosquitoes, degraded tidal marshes can also provide habitat for brown and black rats (Breaux 2000), which are significant vectors of human disease, and for midges and other invertebrate pests (Maffei 2000). This combination of health threats and pests associated with marshes often has led to conflicts between wetland restoration proponents and neighbors, and the greatest threat to marshes associated with disease vectors may be the

continuing development of residential areas nearby. Reducing this conflict will depend on good working relationships between wetland restoration advocates and mosquito control and other public health personnel (San Francisco Bay Area Wetlands Ecosystem Goals Project 1999).

DISEASE

Avian species are faced with the greatest known, or anticipated, threats from disease among all wildlife populations in the estuary. The three diseases of greatest concern and demonstrated mortality in the SFBD are West Nile virus, avian cholera, and avian botulism. Infectious diseases are currently on the rise for two probable reasons—the earth's climactic changes (Colwell 2004) and imbalance in biological systems, probably because of degraded habitat quality and diminished habitat quantity (Friend 1992).

For example, increased temperatures can boost the survival and growth of infectious diseases such as *Pasteurella multocida*, the bacteria that causes avian cholera (Bredy and Botzler 1989). Degraded habitat quality can lead to changes in microbial populations, and subsequently disease outbreaks (Friend 1992). A decrease in habitat size often results in a greater density of birds, increasing exposure, transmission, and spread of the disease to other locations (Friend 1992).

WEST NILE VIRUS

WNV is the most recent of the serious disease threats, first identified in the US in 1999. Reports of bird infections began in the eastern part of North America and have rapidly spread west. The first cases of WNV in the country were reported in New York City, New Jersey, and Connecticut. By December 2003, WNV had been identified all states except Oregon, Alaska, and Hawaii with 12,850 cases of human infection and 490 deaths (U.S. Geological Survey 2003). As of December 2003, California had two cases of human infection of WNV in Riverside and Imperial counties, and WNV was detected in the SFBD in 2004. WNV is transmitted by a variety of mosquitoes, but two species in particular appear to be primary vectors, *Culex tarsalis* and *C. erythrothorax*. At least 138 species of wild birds have been infected, with the family Corvidae demonstrating the highest prevalence of the disease (National Wildlife Health Center 2003a). American Crow and Blue Jay (*Cyanocitta cristata*) have most often been infected; however,

this species composition may change as the virus moves westward. Coupled with the increasing number of corvids in the region, the threat to tidal-marsh birds is imminent. Other birds that inhabit wetlands of the estuary have been identified as hosts and vectors including cormorants, shorebirds, and Song Sparrows.

Transmission of WNV occurs when adult mosquitoes feed on the blood of an infected avian host followed by another vertebrate host. Mammals (humans and horses) do not appear to serve as intermediate hosts, though they can be infected (National Wildlife Health Center 2003a). The threat may be greatest for species of conservation concern, such as the three subspecies of Song Sparrows in the SFBD. The total estimated avian mortality due to the disease is over 100,000 individuals, though species breakdown is not available. Because the disease is so new, the mortality impacts, as well as the ecological interactions of the virus with its hosts, are virtually unknown (National Wildlife Health Center 2003a). Yet, if the Corvidae continues to be the principal group affected by the virus, WNV may have a beneficial impact on those bird species that compete with or are negatively affected by corvids.

AVIAN CHOLERA

AC is a highly infectious bacterial disease with the highest documented mortality rate of any disease for wetland birds in the estuary (USDI Fish and Wildlife Service 1992). Transmission is often direct and may involve surviving carrier birds; consequently, crowding is thought to increase incidence and mortality. California leads the nation in reported disease outbreaks, particularly in the delta. Waterfowl have been particularly affected, especially when concentrated on wintering areas or during spring migration. AC is of particular concern because roughly 50% of birds migrating along the Pacific flyway may pass through the SFBD. Outbreaks have occurred in a variety of habitats including freshwater wetlands, brackish marshes, and saltwater environments (National Wildlife Health Center 2003b). Since World War II, thousands of birds (mainly waterfowl) have been reported dead in each year. In one year, documented mortality was 70,000 birds for the state (USDI Fish and Wildlife Service 1992). The disease commonly affects more than 100 species of birds, though the Snow Goose (*Chen caerulescens*) has the greatest mortality (National Wildlife Health Center 2003b). Unlike botulism, AC often affects the same wetlands and the same avian populations year after year.

AVIAN BOTULISM

Avian botulism results from a neurotoxin produced by the bacterium, *Clostridium botulinum* type C (Friend 1987). The disease is caused by a bacterium that forms dormant spores in the presence of oxygen. The spores are resistant to heating and drying and can remain viable for years. Spores are widely distributed in wetland sediments and can also be found in the tissues of most wetland species, such as aquatic invertebrates and many vertebrates, including healthy birds. The botulism toxin is produced only when the bacterial spores germinate (Rocke and Friend 1999).

Although botulism is a more serious mortality causing factor than AC statewide, in the SFB, the reverse is the case. Outbreaks of botulism in waterbirds are sporadic and unpredictable, occurring annually in some wetlands, but not in adjacent ones. In the past, mortalities from botulism have ranged from 0–1,000 in south San Francisco Bay. Botulism outbreaks caused 950 and 565 mortalities in 1998 and 2000, respectively, mostly ducks and gulls (C. Strong, San Francisco Bay Bird Observatory, pers. comm.). Botulism has been documented in the South Bay in Ruddy Ducks (*Oxyura jamaicensis*), Mallards, and Northern Shovelers (*Anus clypeata*; USDI Fish and Wildlife Service 1992).

Ecological factors that are thought to play a critical role in determining outbreaks include conditions that favor spore germination, the presence of a suitable energy source or substrate for bacterial growth and replication, and a means of transfer of toxin to the birds, presumably through invertebrate prey. Botulism outbreaks appear to be associated with moderately high pH (sediment pH 7.0–8.0) and low to moderate salinity (≤ 5 ppt). Botulism outbreaks are not specifically associated with shallow water and low dissolved oxygen (Rocke and Friend 1999).

RESTORATION CONCERNS

Tidal-marsh restoration will require careful management to avoid disease outbreaks. Increased density of vertebrate species in new restoration sites may encourage concentrations that result in disease outbreaks. Restoration projects adjacent to urban development may introduce potential disease sources. Finally, degraded environmental conditions may increase the effects of disease, impairing the species targeted for recovery under restoration efforts.

DISCUSSION

We have summarized some of the key threats to tidal-marsh vertebrates and have identified specific issues that are major concerns in tidal-marsh restoration projects in the SFB. Unfortunately, it is difficult to compare the modern estuary to a historical period when the tidal marshes functioned naturally, because major changes to the system occurred before studies documented the importance of tidal marshes. For example, estuaries in SFB and the arid Southwest are driven by snow-pack conditions (Dettinger and Cayan 2003, Kruse et al. 2003), and water-user demands determine how closely the system follows the natural pattern of inflows. The climate results in two freshwater pulses—rainfall in the winter (November–February) and runoff in the spring (April–June). Most native vertebrate species are adapted to these wet periods, but changes in the environment have created a much different system than in the past. Flood protection and urbanization have resulted in a less dynamic estuary. The natural periodic, inter-annual, and annual flooding will be replaced by a static system that leaves little room for change. Under these conditions, the establishment and spread of exotic species may be facilitated. Exotic species continue to arrive in the SFB at a rapid rate (Cohen and Carlton 1998), and the mechanisms introducing these species remain poorly regulated (Cohen 1997, Cohen and Foster 2000). Many important effects of exotic species may be indirect or subtle, such as ways in which exotic plants alter habitat for vertebrates.

In the modern estuary, combined threats may have the most detrimental consequences for many tidal-marsh vertebrate populations. Decreased water quality and increased contaminant loads may exacerbate the effects of vertebrate diseases. Human disturbance, fragmentation, and predation by species such as the red fox may reduce the carrying capacity of native vertebrate populations in remnant marshes. The loss of downstream sediments may greatly alter the sediment balance and the rate of marsh plain accretion in the SFB. Dredge material may provide a beneficial solution to sediment deficits in some wetland restorations, but many estuarine contaminants are bound to sediments and the combined effects of dredging operations, dredge materials, and sediment-bound contaminants on vertebrates and their food webs are largely unknown.

In response to severe losses to wetland habitats, major efforts aim to regain and establish wetlands in SFB. The current wave of

restoration projects will alter the character of the estuary for the next century; however, with current rates of human development, the few remaining unprotected bay lands will no longer be restorable. Sea-level rise may eliminate tidal marshes squeezed between open water and urban development, rather than a mere relocation of marshes to higher elevations. Thus, identifying the critical environmental threats in advance may be the best way to guide restoration actions and management to ensure the conservation of tidal marshes into the future.

RESEARCH NEEDS

This paper represents the first step towards corrective action and management by identifying the major threats to tidal-marsh vertebrates in SFBFD. Further efforts to comprehend the mechanisms and processes at work are listed below as the next step in our understanding of tidal-marsh ecosystems. This list is not intended to be a complete compilation of research needs, but to highlight some key issues that require immediate attention.

1. Conceptual models and data validation of the combined interaction of threats (i. e., interaction between water quality, contaminants, and disease) to tidal-marsh vertebrates is needed to understand system-wide processes.
2. Information about the effects of fragmentation on tidal-marsh function and demographic and population-level processes (dispersal, gene flow, survivorship, and predation) would improve prediction of those species' responses to habitat restoration.
3. A greater understanding of the hydrology and transport of bay sediments is needed to help determine local effects of restorations (sediment sinks) and their effect on flow patterns and sediment movement.
4. Detailed studies on the dredge-ameliorated wetlands including vegetation and structure, contaminant load, and vertebrate food webs may help resolve sediment concerns in marsh restoration.
5. A sediment-supply model based on recent empirical data would allow for better assessment of sediment changes and effects of sea-level rise on marshes that have a sharp upland transition zone (i. e., levee fringe marshes).
6. Research that would greatly improve understanding of contaminant threats in tidal marshes includes: (a) factors that control contaminant abundance and bioavailability within the wetlands, (b) relationship between foraging ecology and bioaccumulation in tidal-marsh vertebrates, and (c) prediction of wetland restoration activities on the concentrations, distribution, and bioavailability of contaminants.
7. Future research also should document how changes in water quality (i.e., salinity) may affect vertebrate distribution through a bottom-up control of vertebrate food webs. Increased salinity and low primary productivity have the potential to change the distribution and abundance of vertebrate species, but the magnitude of these effects and the mechanisms by which they act on vertebrates (e.g., via the food web or changes in the vegetative community) are not well understood.
8. The effect of disturbance on secretive species of saltmarshes is very difficult to study, because their responses are not easily observed. However, documenting human activities near tidal marshes and studying marked populations, including bioenergetic studies, may better quantify costs of disturbance and lead to specific management plans.
9. Studies that detail the direct and indirect effects of invasive species, as well as the mechanisms of exotic species arrival, establishment, and spread may lead to better regulation of introductory pathways and control options.
10. Predation studies would help to clarify the relationship between mortality and tidal-marsh fragment size, number, and distribution, and the potential effect of exotics.
11. Finally, mortality caused by disease, as well as degraded conditions under which they have the greatest effect, should be estimated within the context of overall annual mortality.

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