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RESEARCH

Toward Salt Marsh Harvest Mouse Recovery: A Review

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ABSTRACT

The salt marsh harvest mouse (SMHM, *Reithrodontomys raviventris*) is an endangered species, endemic to the San Francisco Estuary. Despite being protected for almost half a century and being included in a large number of recovery, restoration, and management plans, significant data gaps hinder conservation and management of the species, a challenge further complicated by developing threats such as climate change. In this review, we present the current state of knowledge; highlight research gaps on habitat requirements and distribution, taxonomic status and genetic structure, physiology, reproduction

and demographics, population dynamics, and behavior and community interactions; and present an overview of threats to the species. Our review indicates that substantial data gaps exist; although some aspects of SMHM ecology, such as habitat use, have been addressed extensively, others, such as the effects of environmental contamination, are largely unaddressed. We suggest that conservation and restoration-planning processes consider experimental approaches within restoration designs to address these deficiencies. Continued investment in basic and applied SMHM ecology to collect baseline and long-term data will also be beneficial. Additionally, further coordination among managers and researchers can facilitate more effective responses to uncertainties and emerging threats, especially climate change, which threatens the SMHM and its habitat throughout its range.

KEY WORDS

Reithrodontomys raviventris, recovery, conservation, management, San Francisco Estuary, community, genetics, wetlands, rodent

INTRODUCTION

The salt marsh harvest mouse (SMHM, *Reithrodontomys raviventris*; [Figure 1](#)) is the only mammal species (and one of only five terrestrial



Figure 1 A northern salt marsh harvest mouse (*Reithrodontomys raviventris halicoetes*)



Figure 2 (A) A tidal wetland dominated by pickleweed. This habitat type was long considered necessary for persistence of salt marsh harvest mice. **(B)** A diked managed wetland, with a variety of vegetation types present. This habitat type was once thought to be detrimental to salt marsh harvest mice, but is now known to support healthy populations of salt marsh harvest mice.

vertebrates) known to be fully restricted to coastal marshes (see [Figure 2](#); Greenberg 2006). The SMHM is endemic to the San Francisco Estuary (the estuary; [Figure 3](#)), California (Fisler 1965), and comprises two sub-species: the northern *R. r. halicoetes* and the southern *R. r. raviventris*. Originally described as distinct species (Dixon 1908, 1909), these were subsequently shown to be conspecific on both morphological (Howell 1914) and genetic grounds (Statham et al. 2016). The northern sub-species is found in the brackish to saline marshes of San Pablo and Suisun bays at relatively high numbers (e.g.,

18–181 mice ha⁻¹; Bias 1994; Sustaita et al. 2011); the southern sub-species occurs in the salt marshes of central and south San Francisco Bay (south bay hereafter), where populations are much smaller (e.g., <1–3.6 mice ha⁻¹; Padgett-Flohr 1999; Kingma 2003; Basson 2009).

The SMHM is highly adapted to its marsh habitat (Fisler 1965), but reliance on the marshes of the estuary has made this species vulnerable. Since the mid-1800s, over 90% of tidal marshes in the estuary have been lost to filling and diking (Williams and



Figure 3 The San Francisco Bay Estuary with tidal wetlands highlighted in purple, diked and managed wetlands highlighted in orange, and the historical extent of tidal wetlands indicated by the solid white line. The *dashed white line* indicates the best current estimate of the division between the northern and southern subspecies of SMHM. Data sources: Esri, DigitalGlobe [accessed 2017 Feb 01]; CWMW, EcoAtlas [accessed 2017 Feb 01].

Faber 2001). Amplifying the effect of this spatial constraint is the increasing fragmentation of remaining SMHM habitat (Fisler 1961). These factors led the US Fish and Wildlife Service (USFWS) to list the SMHM as endangered (Federal Register 1970); the State of California followed soon thereafter (see Table 1; CCR 1971). Since being listed, SMHM management and recovery has been addressed in two Recovery Plans (USFWS 1984, 2013) and at least nine other restoration and management plans for the estuary. Most of these documents emphasize the importance of habitat protection, enhancement, acquisition, and restoration as the primary strategies for SMHM recovery (see Appendix A for further detail). Despite the large number of threats to SMHM, and its incorporation into many plans, general knowledge of

the species remains limited, and significant knowledge gaps hinder conservation efforts. Additionally, research foci have changed little throughout the years, resulting in some aspects of SMHM conservation being addressed extensively in the literature (e.g., habitat use: Johnson and Shellhammer 1988; Bias and Morrison 2006; Sustaita et al. 2011), while others have remained largely unexplored (e.g., effects of environmental contamination, but see Clark et al. 1992).

In this contribution, we distill current understanding of the biology and management of the SMHM. We begin by outlining the current state of knowledge, and highlight research gaps on habitat requirements and distribution, taxonomic status

Table 1 Major recommendations to support salt marsh harvest mouse recovery criteria in the 1984 and 2013 recovery plans

SALT MARSH HARVEST MOUSE RECOVERY PLANS

1984 ^a	2013 ^b
Research and Management Recommendations	
Protect select existing marshes, especially those that will create large, well connected habitat patches.	Protect existing, historic, and restorable tidal wetlands.
Restore diked wetlands to create pickleweed-dominated tidal marshes.	Manage, restore, and monitor tidal wetlands.
Restore upland and transition zone habitats to create high tide refugia and to accommodate sea level rise.	Conduct range-wide species surveys and monitoring.
Perform biological research on anthropogenic actions that may affect water salinity, marsh floristics, and habitat suitability. Perform studies on the effects of sea level rise, reduced sediment input, marsh erosion, and marsh accretion.	Conduct research necessary for conservation and recovery such as demographic analyses or techniques for habitat management and restoration.
Perform ongoing habitat management.	Improve coordination, participation, and outreach.
Recovery Criteria	
Down-list to Threatened Status	
Secure and manage 3,900 ha of occupied, publicly owned essential habitat.	Protect ~2,500 ha of habitat around the Central and south San Francisco Bay.
Secure and manage 3,200 ha of occupied, privately owned essential habitat and/or 7,000 ha of tidal and diked baylands.	Protect ~1,800 ha of habitat around San Pablo Bay.
	Protect ~1,800 ha of habitat around Suisun Bay.
	Achieve 3-5% catch per unit effort during annual population surveys in a defined proportion of designated viable habitat areas.
	Reduce and control invasive plants.
Down-list to Fully Recovered	
Achieve the above and restore or enhance ~3,000 ha of essential habitat and complete restoration efforts on the San Francisco National Wildlife Refuge.	Implement the Suisun Marsh Habitat Management, Preservation, and Restoration Plan and the South Bay Pond Restoration Plan; develop oil spill response plans.
	Preserve or create enough high marsh and upland habitat to accommodate sea level rise while meeting acreage criteria.

a. USFWS (1984).
 b. USFWS (2013).

and genetic structure, physiology, reproduction and demographics, population dynamics, and behavior and community interactions. We then present an overview of threats to the species, both historic and emerging. The primary recovery strategies for SMHM are habitat acquisition, enhancement, and protection (USFWS 2013). Via recovery and other planning efforts, managers are creating a habitat reservoir for SMHM intended to be functional now and into a future where sea-level rise is projected to inundate many US Pacific coastal wetlands, leading to substantial habitat loss (Thorne et al. 2018).

HABITAT AND DISTRIBUTION

The Gold Rush during the mid- to late-19th century led not only to increased settlement throughout the estuary as San Francisco became a major port city, but also to ecological changes to the estuary through practices such as hydraulic mining and agriculture (Arnold 1996; Moyle et al. 2014). Consequently, by the time the SMHM was described (Dixon 1908, 1909), significant changes to its habitat had already occurred (USFWS 2010), and it is important to note that SMHM currently occur in wetlands both “natural” (e.g., subject to tidal fluctuations) and managed (e.g., altered by land reclamation and subject to water level manipulations). The latter comprise a large proportion of remaining wetlands in the estuary (see Figure 3). The earliest description of the species lists the geographic distribution simply as “restricted to the salt marshes of the San Francisco Bay” (Dixon 1908:197), and for many decades managers generally settled on a simplified definition of SMHM habitat as tidal marshes dominated by pickleweed (*Salicornia pacifica*). Thus, the historical range of the SMHM has largely been inferred from maps of historic distribution of habitat types throughout the estuary, and, although habitat associations have been examined extensively, the only major study of modern SMHM distribution was restricted to the Suisun Marsh (USFWS 1981).

Habitat Requirements

Understanding of SMHM habitat use is continuously evolving, and will likely continue to do so, especially if relationships among salinity, inundation, and vegetation change. The combined effect of increased

inundation and salinity, as projected under most climate scenarios, can reduce plant height and the structure of the salt marsh-dominant pickleweed (Woo and Takekawa 2012), compromise the competitive ability of stress-sensitive plant species and communities (Schile et al. 2017), and lead to shifts in plant communities where salt-tolerant plants replace salt-intolerant plants at low elevations (Watson and Byrne 2012). Earlier research found that shorter vegetation and more extreme tidal ranges of marshes in the south bay may make these less suitable for SMHM (Schaub 1971; Cummings 1975; Gilroy and Shellhammer 1980; Figure 4). The use of non-tidal wetland habitat types (e.g., levee berms) was also investigated early (Rice 1974), and by the 1980s it was well accepted that tidal saline wetlands with tall, dense pickleweed mixed with other halophytic species—especially fat hen (*Atriplex prostrata*) and alkali heath (*Frankenia salina*)—were optimal for SMHM (Zetterquist 1977; Gilroy and Shellhammer 1980; Shellhammer et al. 1982; Takekawa et al. 2001).

On the other hand, early trapping efforts failed to find mice in brackish wetlands, even with high-density pickleweed cover (e.g., Figure 5A). Therefore, it was concluded that management of diked wetlands for waterfowl (e.g., as standing ponds during the hunting season) and vegetation management that included, but did not promote, dominance of pickleweed, would lead to the extirpation of SMHM (Shellhammer et al. 1982). However, when researchers began capturing SMHM outside of pickleweed stands in the mid-1980s, the habitat was still classified as “marginal” (Botti et al. 1986; Shellhammer et al. 1988), presumably reflecting an unrecognized bias from earlier understanding of favored habitat.

Habitat associations for SMHM vary both temporally and spatially. Captures of SMHM have been correlated with a range of tall-to-short and saline-to-less-saline pickleweed (Shellhammer et al. 1982, 1988; Kingma 2003; Padgett-Flohr and Isakson 2003), although in some cases there was no association at all (Basson 2009). Similarly, SMHM captures have been correlated with both high and mid-level water salinities (Zetterquist 1977; Shellhammer et al. 1982; Kingma 2003, Padgett-Flohr and Isakson 2003). To an unknown extent, these contradictory associations could be attributed



Figure 4 (A) A marsh on the San Leandro Shoreline exemplifies some characteristics of most South Bay marshes: the narrow distance from the marsh edge on the far top right to the hard edge on the top left, in this case a housing development; close proximity to industrial development, in this case a water treatment plant visible in the distance on the top middle right. (B) Vegetation in the saline South Bay marshes is typified by short pickleweed and medium height, non-thatch forming plants such as cordgrass, with little structural complexity.



Figure 5 (A) A marsh on San Pablo Bay near the Napa River. Visible in the distance are the hills of southern Napa and Sonoma counties. Virtually no significant development exists between the San Pablo Bay and the hills. **(B)** Vegetation in the brackish marshes of the San Pablo Bay are typified by vast expanses of short pickleweed mixed with a low diversity of other halophytes providing a moderate amount of structural complexity.

to differences between the sub-species, inaccurate species identification, local population dynamics, local competition, or short time-frame, highlighting the need for coordinated efforts and replication throughout the range as well as for long-term data sets. Regardless, they indicate that the habitat metrics that characterize “good” SMHM habitat are likely too complex to simplify to one or two parameters (e.g., pickleweed height, water salinity).

Recent trapping efforts have detected SMHM in significant numbers in brackish marshes and in marshes dominated by plants other than pickleweed, such as alkali bulrush (*Bolboschoenus maritimus*; Shellhammer et al. 2010) and tri-corner bulrush (*Schoenoplectus americanus*; Sustaita et al. 2011). As a result, managed wetlands are recognized as important habitat for the persistence of this species (Sustaita et al. 2011; Shellhammer 2012; Figure 2B, 6A). However, because there has been very little research addressing the relative value of wetland types for SMHM, tidal habitat remains regarded as superior to managed wetland habitat (USFWS 2013).

Current Distribution

Because SMHM is no longer thought to be restricted to pristine tidal marshes, delineating current distribution and estimating total acreage has become complex and challenging, and no range-wide census or distribution study of the SMHM has been conducted. Consequently, SMHM habitat is usually described in terms of how much tidal marsh area has been lost, rather than how much remains (e.g., Shellhammer et al. 1982, 2010; Bias and Morrison 1999). Estimates of habitat loss range from 70% to over 90%, but, although some of this has been permanently lost through development, an unknown portion has been altered to a different habitat type that may also support SMHM (Goals Project 1999).

The northern SMHM sub-species is believed to occur throughout San Pablo Bay and the interior portions of the estuary (e.g., Suisun Marsh and Contra Costa shoreline; USFWS 2013), whereas the southern sub-species occurs throughout the south bay, and north to the Marin Headlands near Point Richmond. However, no empirical investigation has been made regarding the subspecific status of populations near the presumed taxonomic border, either on the east

or west sides of the central bay (USFWS 2013). Three major areas of the estuary that can be considered strongholds for the SMHM are the marshes of the south bay, the marshes of north San Pablo Bay, and the Suisun Marsh. These three areas differ greatly in past land use and management, current state, and ownership, and these differences translate to differing suitability for supporting SMHM and priority actions for SMHM recovery.

South Bay

Marshes in the South Bay are the most highly altered of the remaining wetland habitat throughout the estuary (SFEI 1998). South bay marshes currently consist of ~2,000 ha of managed wetlands (all diked and managed marshes; SFEI 1998) and ~3,900 ha of tidal wetlands (all high-, mid- and low-elevation and muted tidal marshes; SFEI 1998; Figure 3). The 2013 Recovery Plan calls for a total of ~2,500 ha of protected SMHM habitat in the south and central bay (USFWS 2013). Beginning in 1860, large tracts of the south bay were diked for salt production, and by the 1930s almost half of the tidal marshes had been converted through land reclamation, rendering a large proportion of potential SMHM habitat in the south bay unsuitable (Goals Project 1999). The remaining marshes in this region have the highest salinity of the three estuary regions. These marshes are narrow and fragmented (Figure 4A), the vegetation is dominated by relatively short pickleweed and cordgrass (*Spartina* spp.; Figure 4B), and land ownership is split primarily among state agencies and federal agencies (Goals Project 1999). Large-scale habitat restoration is possible by the acquisition of over 15,100 acres of former commercial salt evaporation ponds, which will be adaptively managed, enhanced, and restored. The south bay is highly urbanized, and aside from the south bay Salt Pond Restoration Project (SBSRP)—a large-scale, multi-phase restoration program totaling 6,100+ ha (<http://www.southbayrestoration.org>)—virtually all wetland habitat is bounded by steep levees adjacent to development, and is, therefore, highly vulnerable to sea-level rise because there are very limited opportunities for marshes to migrate upland (Thorne et al. 2018). Although modeling suggests that significant accretion rates may partially offset sea-level rise (Takekawa et al. 2013), accretion is unlikely to fully compensate for habitat loss. Combined, these studies

suggest that there is less potential SMHM habitat in the south bay than in other areas of the estuary.

At the California Department of Fish and Wildlife (CDFW) Eden Landing Ecological Reserve restoration site (part of the SBSRP), initial surveys indicate that restored areas support some SMHM (Statham et al. 2016). Recovering SMHM in the south bay will require wetland conservation and preservation, along with significant habitat restoration, enhancement of existing habitat, or protection of habitat from sea-level rise, to provide habitat acreage and connectivity (USFWS 2013). If marshes are unable to accrete to compensate for sea-level rise (contra Takekawa et al. 2013), managers may need to consider novel options such as sediment augmentation to increase marsh resiliency, or managing marshes as partially- or fully-diked, muted tidal systems.

San Pablo Bay

Because of inflow from the Sacramento and San Joaquin rivers, San Pablo Bay is less saline than the south bay, and although about one-fifth of San Pablo Bay marshes were utilized historically for commercial salt production, the primary use was agriculture, especially grazing (Goals Project 1999). Diking for agriculture ceased in the 1930s, but a large proportion of land near San Pablo Bay still remains under cultivation (Goals Project 1999). The marshes of San Pablo Bay currently consist of ~3,200 ha of managed wetlands and ~6,500 ha of tidal wetlands (SFEI 1998; [Figure 5](#)); the 2013 Recovery Plan calls for a total of ~1,800 ha of protected SMHM habitat in San Pablo Bay (USFWS 2013). The marshes here are deep (shore to inland margin; [Figure 5A](#)), dominated by short pickleweed ([Figure 5B](#)), and provide a significant amount of upland habitat for marsh expansion with sea-level rise (Goals Project 1999). As in the south bay, large, multi-phase restoration projects have occurred and are underway, including the Cullinan Ranch Restoration Project in the San Pablo Bay National Wildlife Refuge (620+ ha; <https://www.epa.gov/sfbay-delta/cullinan-ranch-tidal-marsh-restoration-project>), and the former salt evaporation ponds in the CDFW Napa–Sonoma Marshes Wildlife Area Restoration (5,600+ ha; <https://www.wildlife.ca.gov/Lands/Planning/Napa-Sonoma-Marshes-WA>). As noted

above, SMHM population densities in San Pablo Bay are much higher than those in the south bay (USFWS 2013). Therefore, protection of existing habitat—along with a moderate amount of habitat restoration and enhancement of tidal marsh and upland transition zones—could greatly increase the probability of SMHM recovery in San Pablo Bay.

Suisun Marsh

Situated directly between the Sacramento–San Joaquin Delta and San Pablo Bay, Suisun Marsh is brackish, with salinities lower than other parts of the estuary. Beginning in 1859, Suisun Marsh was used primarily by market hunters who supplied ducks to the massive influx of migrants flooding to San Francisco during the Gold Rush (Arnold 1996; Moyle et al. 2014). Reclamation began in earnest on Grizzly Island in the late 1870s and 1880s for dairy grazing and agriculture (Arnold 1996). Grazing gave way to agriculture in the early 1900s, but by the 1920s increased salinity and subsidence in the eastern marsh led to the abandonment of farming and the formation of private duck-hunting clubs (Goals Project 1999). In 1974, the Suisun Marsh Preservation Act was enacted; it protected the marsh from urban development, established water-quality standards, and specifically led to additional efforts, including other plans and acts (most notably the Suisun Marsh Habitat Management, Preservation, and Restoration Plan; USDOJ et al. 2013) to protect the marsh from development (Arnold 1996). Suisun Marsh currently consists of ~20,000 ha of managed wetlands ([Figure 6A](#)) and ~5,500 ha of tidal wetlands (SFEI 1998; [Figure 6B](#)); the 2013 Recovery Plan requires a total of ~1,800 ha of *protected* SMHM habitat in Suisun Marsh (USFWS 2013). Duck hunting remains the primary land use in Suisun Marsh, and more than half the land is owned by private duck clubs (USFWS 2013). Unlike salt production, waterfowl management can provide suitable habitat for SMHM; thus, duck clubs have resulted in the protection of significant tracts of habitat in Suisun Marsh (Sustaita et al. 2011; Smith et al. 2014). However, the multitude of land-owners in Suisun (150+) makes acquisition of large tracts of land difficult, and planned restoration here has been largely opportunistic (e.g., Montezuma Wetlands Project, 690+ ha, <http://www.sfei.org/projects/montezuma-technical-review-team>; Tule



Figure 6 (A) A managed wetland in the Suisun Marsh. Visible in the distance are the Potrero Hills. Development from the outer marsh edge to the hills is restricted to sparsely distributed duck hunting clubs. (B) Due to relatively low salinity vegetation in the Suisun Marsh is highly diverse ranging from herbaceous ground cover to bulrushes that can reach greater than 3 meters in height. The tidal marsh pictured here has tall pickleweed mixed with alkali heath (*Frankenia salina*) and dodder (*Cuscuta salina*) in the background, tall tricorner bulrush (*Schoenoplectus americanus*) mixed with cattail (*Typha* spp.) and herbaceous flowers in the midground, and very tall bulrush (*Schoenoplectus* spp.) and reeds (*Phragmites australis*) on the slough edge in the foreground.

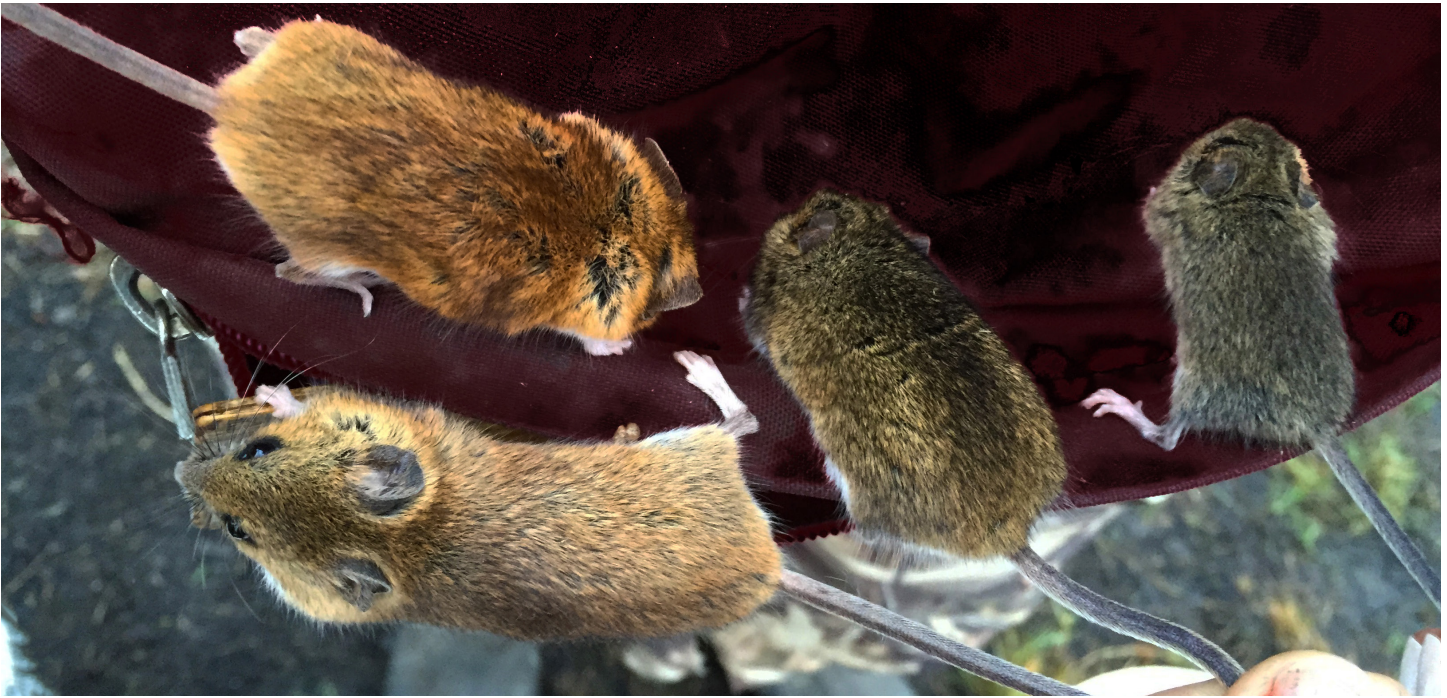


Figure 7 Due to high variation in color and significant overlap in morphology, salt marsh harvest mice (3 left) and western harvest mice (right) can be difficult to distinguish in the field.

Red Restoration Project, 140+ ha, <http://www.sfcwa.org/2013/03/27/tule-red-restoration-project>; Hill Slough Wildlife Area Restoration Project, 340+ ha, http://www.dfg.ca.gov/ERP/erp_proj_hill_slough.asp).

Marshes in this region are deep (Figure 6), with tall pickleweed intermixed with a variety of other halophytic plants such as bulrushes (*Bolboschoenus* spp. and *Schoenoplectus* spp.), fat hen, Baltic rush (*Juncus balticus*), and alkali heath (Goals Project 1999). Suisun Marsh has some of the largest remaining tracts of SMHM habitat, and it supports large populations of SMHM (Sustaita et al. 2011). Continued protection and maintenance of habitat in Suisun Marsh should increase the likelihood of SMHM recovery there, although much suitable habitat exists behind levees that may be vulnerable to several factors. Levee vulnerabilities include sea-level rise, earthquakes (Mount and Twiss 2005; Goals Project 2015), and shifts in vegetation (from brackish- to saline-associated species) as a result of water diversions in the Sacramento–San Joaquin Delta (Mall 1969), which are likely to worsen if additional water is diverted. Consequently, ongoing

and potentially intensive habitat management may be more vital here than in other parts of the estuary.

TAXONOMY AND GENETICS

The SMHM was originally thought to have descended from the western harvest mouse (WHM, *R. megalotis*; Hooper 1944; Fisler 1961), reflecting both their morphological similarity (Figure 7) and the geographic distribution of these taxa. The WHM ranges over much of the western US, completely encompassing the range of the SMHM. However, these two species are unable to produce viable offspring (Fisler 1965), and they have different chromosomal complements ($2n = 38$ and 44 , $FN = 72$ and 84 , for SMHM and WHM, respectively; Shellhammer 1967), which suggests more distant relatedness. Further work including additional *Reithrodontomys* species and analyzing karyotypes (Hood et al. 1984), allozymes (Nelson et al. 1984), and maternally- inherited mitochondrial DNA (mtDNA) sequence data (Bell et al 2001; Statham et al. 2016) clarified that the closest relative was the plains harvest mouse (*R. montanus*), which occurs in the Great Plains and northern Chihuahuan Desert.

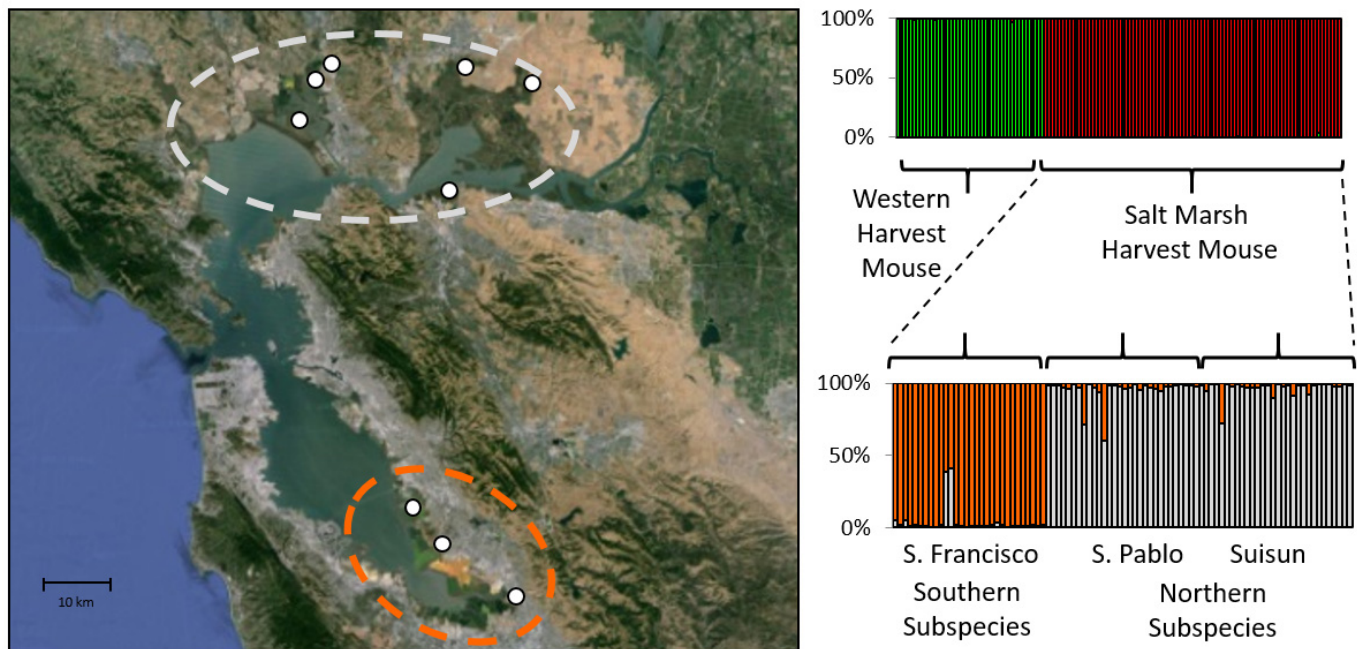


Figure 8 Genetic analyses support the separation of SMHM and WHM, as well as the northern and southern SMHM subspecies (Statham et al. 2016). Harvest mice were sampled from three sites in each of three bays (*white circles*), but further sampling is needed to understand relationships of intervening populations, as well as to confirm the spatial extent of each subspecies.

The two species likely diverged over 3 million years ago (Bell et al 2001; Statham et al. 2016); the modern estuary is less than 10,000 years old (Goman et al. 2008).

One of the most basic needs for monitoring and conservation of any endangered species is correct field identification. Difficulty distinguishing SMHM from WHM (Figure 7) undermines ongoing monitoring and research efforts. Brown (2003) identified mice from Suisun Marsh with mtDNA, and developed dichotomous keys to differentiate SMHM and WHM based on external characters. Comprehensive extensions of Brown's (2003) work have resulted in more refined statistical models to use the most important characteristics to differentiate between species (Sustaita et al. 2018). Although promising, these models remain limited to the northern sub-species, and even there they are unable to classify young and small harvest mice. In the south bay, genetic analyses determined that current methods were insufficient to correctly identify SMHM (Statham et al. 2016). Recent work has begun to more rigorously investigate the utility of traditional measurements, and to consider additional

morphological characteristics to differentiate these species.

Given the unique regional challenges, it may be constructive to consider the conservation status and needs of the two sub-species separately. Shellhammer (1967:549) argued that karyotypes of the two sub-species were sufficiently distinct "to suggest that the two are in the terminal stages of speciation." This is broadly consistent with recent genetic analyses (nuclear and mtDNA) that identified deep genetic subdivision within the SMHM (Statham et al. 2016; Figure 8). Significantly, potential intergradation or reproductive isolation between the two sub-species has not been assessed, because most habitat along the border of these taxa has been greatly altered. In addition to the taxonomic implications, ongoing genetic work has begun to explore genetic diversity and connectivity among populations throughout the estuary, as well as potential meta-population dynamics and demographic isolation of the SMHM. Thus far, limited sampling indicates that northern (San Pablo Bay, Suisun Marsh) populations have greater genetic diversity than southern populations (likely reflecting the greater range and population size of the former), but that both sub-species possess

endemic mtDNA haplotypes and nuclear alleles (Statham et al. 2016). Very recent analyses extend this work using immunogenetic data, and show higher diversity in both the northern sub-species and in Suisun Marsh, while the southern sub-species (San Francisco Bay) has a reduced ability to respond to selection (Ennis 2018).

PHYSIOLOGY

Both Fisler (1963) and Haines (1964) studied the exceptional ability of SMHM to consume and survive on salt water. Physiological adaptations (e.g., increased kidney function) appear to be more strongly developed in the northern sub-species than in either the southern sub-species or the WHM (Fisler 1963). Both sub-species of SMHM lost weight when drinking only seawater at 0.57 M (~33–35‰ NaCl), but whereas the northern sub-species survived an average of just over 200 days (and some individuals survived over a year), the southern sub-species survived an average of only 12 days (maximum of 48 days; Fisler 1963). The northern SMHM can survive on even more saline water (700 mN, ~40‰ NaCl) without loss of body mass, and with only modest changes to blood plasma (“urea was slightly elevated”; Haines 1964:271). It is important to note that these studies were completed before many of the modern tools used to differentiate SMHM sub-species were developed, and are best interpreted with some caution. Nonetheless, the ability to consume water far too saline for most terrestrial mammals confers upon both SMHM sub-species a competitive advantage in coastal marshes.

REPRODUCTION AND DEMOGRAPHICS

Understanding reproduction and demographics is fundamental to population ecology and management, and has implications for conservation efforts. Almost 5 decades after SMHM was listed, assessments of demographics, distribution, and density throughout the estuary remain critical data gaps (USFWS 2013). Although SMHM are monitored annually for many sites, surveys are rarely coordinated or standardized (e.g., methodology), and they lack both clearly defined (and shared) goals and a shared data repository, which in some cases has resulted in redundant research and monitoring efforts. Further,

as a result of limited resources, most monitoring is temporally limited to a single 3- to 5-day sampling session, and considers SMHM in isolation relative to the broader ecosystem in which it occurs. Furthermore, monitoring reports are rarely published, limiting the ability of researchers or managers to capitalize on these numerous, but disparate, data sets. Similarly, no large-scale, long-term studies have been undertaken to address any key facets of SMHM demographics (e.g., fecundity, age and sex ratios, survival, and density; but see Sustaita et al. 2011). One brief effort (Basson 2009) underscores challenges associated with studying small, mobile species such as SMHM, with exceedingly low estimated survival and highly variable monthly population growth rate (see below). Understanding the drivers of SMHM populations, and the mechanisms behind population declines or colonization in restored habitats, could help guide conservation and management actions.

The reproductive biology of wild SMHM was identified as a research need in the 1984 Recovery Plan, and remains under-studied (USFWS 1984, 2013). Captive females may produce multiple litters throughout the year, and while early field studies suggested that they reproduce only once per year in the wild (Fisler 1961), females of the northern sub-species may reproduce at least three times per year (Sustaita et al. 2011). Whereas reproductive males can be found year-round, reproductive females were detected mostly between March (southern sub-species) or May (northern sub-species) and November (Fisler 1965), although Geissel et al. (1988) posited that in years with high vole (*Microtus californicus*) numbers, SMHM breeding may be delayed into late spring. Reproduction for the southern sub-species appears to peak in March and April (Wondolleck et al. 1976). Based on embryo counts *in utero* and litters born in captivity, Fisler (1965) concluded that the northern sub-species can produce just over four young per litter, while the southern sub-species averages just under four. Furthermore, different wetland types appear to differ in reproductive value for SMHM (e.g., they vary in the proportion of juveniles and reproductive females; Sustaita et al. 2011). Recent observations on radio-collared SMHM indicate that males may play a role in parental care, a behavior which could have important effects on population growth rates (Trombley and Smith 2017).

Sex ratios appear to range from male-biased (Fisler 1971; Basson 2009) to even (Wondolleck et al. 1976), with no consistent pattern. Captive populations present a 1:1 ratio in newborn litters, whereas live-trapping efforts have yielded female-dominated captures both of the youngest and oldest wild mice (Fisler 1971). Adults comprise the majority of the population (Wondolleck et al. 1976), but juveniles comprised about one-third of the population in Suisun Marsh, and the proportion of juveniles increased with population density, presumably reflecting seasonal recruitment (Sustaita et al. 2011). Fisler (1971) found that captive SMHM may live for 31 months, although most wild mice likely live for no more than 8 months (maximum likely 12 months).

POPULATION DYNAMICS

Although anthropogenic activities continue to fragment available SMHM habitat in some parts of its range, it is important to recognize that habitat occupied by SMHM is naturally fragmented, and the species likely persisted historically as a series of meta-populations distributed around the estuary. Individual SMHM populations were historically separated by large-scale barriers (e.g., the San Francisco Bay, the Golden Gate Strait, the Carquinez Strait) as well as barriers to localized movements (e.g., sloughs that bisect wetlands). Urbanization and habitat conversion have generally increased patch isolation and decreased suitability for SMHM. Additionally, much of the species' range includes habitat owned by diverse land-owners who practice varied habitat-enhancement and management techniques (USDOI et al. 2013), few with the primary goal of maintaining SMHM habitat, which may provide different values to SMHM. These factors can create demographic sinks: habitat patches where SMHM populations appear to be self-sustaining, but persist only as a result of immigration from nearby source populations (McDonald and Greenberg 2006). Encouragingly though, Sustaita et al. (2011) found higher densities of SMHM in managed wetlands (which have traditionally been regarded as inferior habitat sinks) than in the tidal wetlands of Suisun Marsh.

Despite the fact that many recovery actions for the SMHM recommend that habitat patches created via

restoration or enhancement activities be situated within dispersal distance of source populations, very little is known of the dispersal and colonization capabilities of the SMHM (USFWS 2010, 2013). Many potential habitat patches for SMHM are isolated (often as literal islands surrounded by water) and may not be readily accessible, precluding timely re-colonization after local extirpation or restoration of previously unsuitable habitat. Whereas some managers (USFWS 2010) have made inferences about colonization based on differential habitat use (Geissel et al. 1988; Bias and Morrison 1999), our review found no research that directly addressed the level of habitat connectivity needed for dispersal and colonization by SMHM. In the sole published study assessing SMHM survival and population growth (spanning just 3 months, May to August 2008), Basson (2009) reported an apparent monthly survival rate of 0.13, and monthly population growth rates (λ) of 4.4 (May to June), 0.79 (June to July), and 0.75 (July to August) at one 10-ha site.

BEHAVIOR AND COMMUNITY DYNAMICS

Understanding the behavior of small mammals in natural conditions is challenging, and SMHM behavior is no exception. This challenge has likely led to the veritable paucity of research and limited emphasis of this theme by both researchers and managers. Our review found that neither direct nor indirect interactions of SMHM with potential competitors, predators, parasites, or other animals have been explicitly investigated; the few published observations are anecdotal or based largely on inference. Whereas direct interactions are easy to envision (e.g., direct predation), indirect interactions such as apparent competition, trophic cascades, and competitor- or predator-mediated habitat selection are less obvious but no less important to understanding the role of SMHM within ecological communities—and therefore also to informing land and resource managers. The same is generally true of most aspects of SMHM interactions with their habitat, such as feeding ecology. During most annual SMHM surveys, few observations of other species are recorded, including other captured small mammals, with little associated vegetation data to quantitatively describe the habitat.

Interactions with Other Animals

Interactions between SMHM and sympatric rodents have been documented both in the laboratory (Catlett and Shellhammer 1962; Fisler 1965) and opportunistically in the field (Catlett and Shellhammer 1962; Geissel et al. 1988; Bias and Morrison 1999; McDonald and Greenberg 2006; Sustaita et al. 2011). However, no studies have targeted this research area with a specific management question. SMHM coexist harmoniously with house mice (*Mus musculus*) in the laboratory (Catlett and Shellhammer 1962), but in the wild these species evidently partition habitat, with house mice associated with more fragmented habitat patches (Bias and Morrison 2006). Geissel et al. (1988) suggested that the SMHM acts as a fugitive species (using poorer-quality pickleweed) when voles are abundant, but may be competitively superior in areas of high salinity, while Bias and Morrison (2006) reported evidence of niche partitioning, with voles preferring taller pickleweed than SMHM. These observations suggest that rising sea levels may indirectly alter competitive dynamics by altering vegetation assemblages or by increasing competition for limited resources (e.g., food or high-tide refugia).

Understanding the effects of predation on SMHM was identified as a key priority in the 1984 Recovery Plan (USFWS 1984). The updated plan (USFWS 2013) recognized that predation pressure may be elevated by anthropogenic changes to habitat, such as landfills subsidizing predators, or public trails and levees increasing access to interior habitat. Predation risk is also likely to increase as sea-level rise causes more extreme flooding in tidal wetlands that can force SMHM onto uplands where they are more vulnerable (USFWS 2010). Surprisingly, virtually no research has assessed predation on SMHM. The only data we are aware of come from analysis of short-eared owl (*Asio flammeus*) pellets (Johnston 1956). Although cranial material was reported from <10% of pellets analyzed, skulls of SMHM and WHM are indistinguishable, rendering any conclusions about predation on SMHM somewhat equivocal.

The presence or effects of parasites on SMHM has also received almost no attention. The only published study of ectoparasites identified one species of flea, *Orchopeas leucopus*, on SMHM in Suisun Marsh

(Clark et al. 2006). This flea species is widespread throughout the US and Canada where it is found on rodent hosts from many different genera (especially *Peromyscus*; Lewis 2000). Work on endoparasites is similarly limited; Forrester (1971) found a strain of the nematode *Heligmosomoides polygyrus* in one of 24 wild-caught SMHM in San Pablo Bay, but determined they were not susceptible to two other strains of the same nematode in the lab. High parasitic loads may cause increased mortality from physical stress or disease transmission (Clark et al. 2006). Whether parasite loads are particularly high in SMHM is not clear, although many researchers report observing fleas, ticks, and mites on SMHM and other species during annual monitoring (K. Smith, unpublished data, see “Notes”). Stressed individuals are more susceptible to disease (Lafferty and Holt 2003), but the effects of disease—as well as the compounding effects of potential contaminants and environmental stressors associated with climate change (e.g., prolonged drought that results in changes in vegetation types, and wetland habitat loss via sea-level rise)—on SMHM populations are completely unknown.

In addition to the negative effects of interactions discussed thus far, SMHM may play other roles in wetland communities. Waterfowl in Suisun Marsh exhibit higher nest success where small mammals (primarily SMHM) are more abundant (Ackerman 2002). Understanding whether the SMHM may similarly receive a reciprocal benefit from the presence or actions of other species could better inform management efforts. For example, large populations of other rodents or nesting waterfowl may alleviate predation pressure on SMHM; alternatively, they may elevate competitive pressures or attract predators, leading to elevated risk to SMHM.

Interactions with Their Habitat

Substantial effort has gone into characterizing habitats where SMHM are captured, but little research has addressed how the species actually interacts with its habitat. One aspect of SMHM behavior that has been investigated is the use of refugia during high tides, a research need identified in the 2013 Recovery Plan (USFWS 2013). Since SMHM often reside in

the intertidal zone, they may require refuge during high tides. Some early studies concluded, based on trapping data or visual observations, that animals move out of tidal wetlands and into upland areas or onto levees to escape rising waters (Johnston 1957; Hadaway and Newman 1971); others concluded that SMHM remain in tall, dense vegetation over water, where they can easily move about in the dense thatch layer (Fisler 1965; Hulst et al. 2001). Recent work using radio transmitters demonstrated that mice remain in tall vegetation (e.g., bulrushes) throughout the cycle of tidal inundation when such vegetation is available (Smith et al. 2014). Unfortunately, this study was restricted to adult male SMHM in the Suisun Marsh, and further work is needed to confirm the generality of these observations (e.g., in other parts of the range) and extend this to other sub-populations (females, younger animals).

Feeding ecology and the effects of salinity on diet were identified early as important research needs, but no comprehensive assessments have been conducted (USFWS 1984; Shellhammer 2012). Stomach contents of wild-caught animals indicate that SMHM consume more stem and leaf matter than WHM, and that the diet of WHM is relatively constant throughout the year while that of SMHM appears to vary seasonally (Fisler 1965). When presented with two halophytic plant species (pickleweed and salt grass [*Distichlis spicata*]), captive WHM refused to eat either plant, to the point of starvation, whereas SMHM readily consume seeds, leaves, and stems of both species (Fisler 1965). Finally, when presented with insect prey, WHM ate the soft parts of the bodies while SMHM showed no apparent interest (Fisler 1965). Beyond these limited observations, essentially nothing is known of SMHM diet in the wild, and diet is not addressed in depth in the 2013 Recovery Plan or status review, although it is presumed to be dominated by pickleweed (USFWS 2010, 2013). Impacts associated with climate change, such as sea-level rise and increased salinity, could alter vegetative assemblages throughout the range of the species (Watson and Byrne 2012; Schile et al. 2017) and result in substantial habitat loss (Thorne et al. 2018). Without a baseline understanding of SMHM diet, managers lack the information needed to protect habitat that provides a rich food base, or to design

habitat enhancements and restorations for food production that are resilient to these sorts of impacts.

THREATS

Threats identified in both recovery plans that address SMHM all pertain to loss or degradation of habitat, and few are new to the system (USFWS 1984, 2013). Takekawa et al. (2006) also highlighted habitat loss and deterioration, but emphasized the importance of biotic interactions (including competition, predation, invasive species, and disease) as potential threats to tidal marsh vertebrates in the estuary. Ensuring SMHM persistence requires understanding and assessing the causes of these threats and the interactions among them, as well as taking actions to ameliorate the most pressing ones.

The effect of habitat loss in the estuary is extensive: virtually every hectare of historical SMHM habitat has been altered, either through direct action such as wetland filling or salt production, or indirectly through shifts in vegetation that result from water diversions (which change water availability, salinity, and sedimentation) as well as the introduction of invasive plants (Kimmerer 2002; Takekawa et al. 2006; Goman et al. 2008). Remaining habitat patches are fewer, smaller, and degraded when compared to pre-historical patches (Takekawa et al. 2006), likely leading both to direct reduction in the number and size—and an increase in the fragmentation of—SMHM populations. Small, fragmented populations are more prone to deleterious genetic effects and extinction, and small mammals may be especially susceptible because of their relatively low mobility in the face of what may be minor geographic barriers for large or volant animals (Soulé et al. 1992; Lowe et al. 2017).

Management of wetlands for extractive use has been considered a threat to SMHM (Shellhammer 2012). However, Native Americans were present in the area, managing habitat for resource extraction for thousands of years (ca. 10,000–15,000 years ago; Lewis 1993; Erlandson et al. 2007) before the modern estuary and its associated marshes formed (ca. 6,000 years ago; Goman et al. 2008). Today, many remaining wetlands are managed moderately to intensely, and the effects of habitat management on SMHM are poorly understood. In the Suisun Marsh, for example, most marshes are diked, and many of

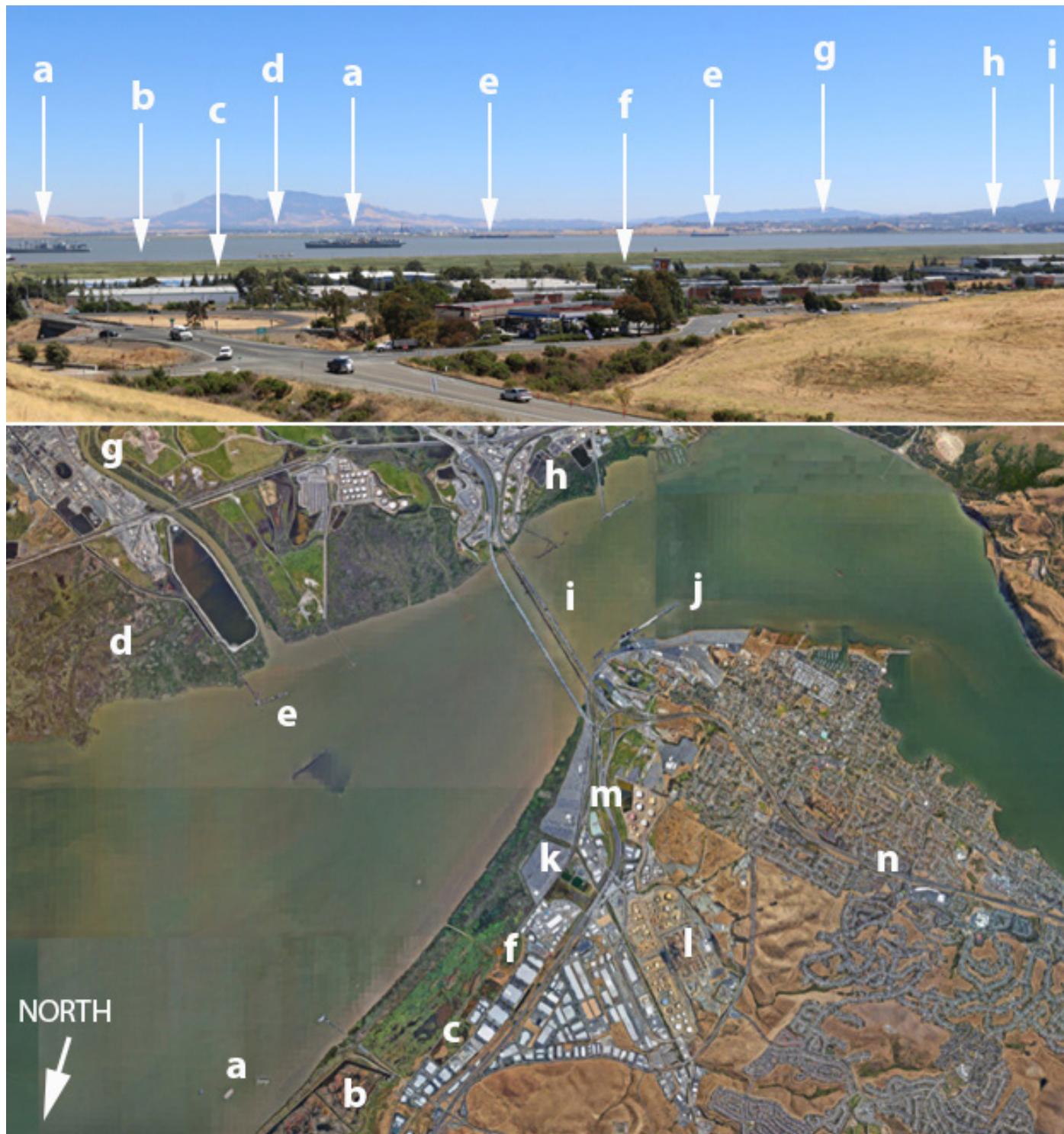


Figure 9 Many marshes in the San Francisco Estuary, such as the marshes of Suisun Bay pictured here, occur in close proximity to sources of chronic contamination and sources of potential acute catastrophic contamination. Labels: **(a)** Suisun Bay Reserve Fleet, **(b)** Goodyear Slough marshes which support some of the highest recorded densities of SMHM, **(c)** Industrial complex, **(d)** Point Edith Wildlife Area, **(e)** Petroleum tanker, **(f)** Southern Pacific Railroad, **(g)** Tesoro Golden Eagle Refinery, **(h)** Shell Martinez Refinery, **(i)** Benicia–Martinez vehicle and rail bridges, **(j)** Cargo docks, **(k)** Imported vehicle cargo storage, **(l)** Valero Benicia Refinery, **(m)** Highway 680, and **(n)** Highway 780.

these are managed to regulate hydrology, salinity, and vegetation to provide habitat for resident and migrating waterfowl (which provides habitat for other wildlife as well). Hence, estuary marshes have been under anthropogenic influence since their initial development, and the SMHM, while much older than the marshes themselves (see “Taxonomy and Genetics”), has likely never existed in the estuary’s modern marshes without human influence.

A number of invasive species likely affect the SMHM. Terrestrial vertebrates, such as feral cats (*Felis catus*) and house mice, affect the species through predation and competition, respectively. Invasive plants are a large concern (USFWS 2013); species such as smooth cordgrass (*Spartina alterniflora*), common reed (*Phragmites australis*), and perennial pepperweed (*Lepidium latifolium*) alter habitat structure and may displace native flora and fauna (Takekawa et al. 2006; Estrella and Kneitel 2011; Wigginton et al. 2014). Aquatic invasive plants can alter flows and displace native species in the estuary, which affects SMHM habitat (Moyle et al. 2010).

The effect of environmental contamination such as heavy metals, organochlorines, PCBs, or oil spills on SMHM (USFWS 2013) is an important research gap. Clark et al. (1992) tested house mice, deer mice (*P. maniculatus*), and California voles throughout the estuary for a number of contaminants. Although SMHM were not tested, this species was absent from all areas where house mouse livers contained elevated ($>0.19 \mu\text{g g}^{-1}$ dry weight) mercury and PCB concentrations ($0.06 \mu\text{g g}^{-1}$ wet weight). Because SMHM occur in habitats bordered in most parts of its range by dense urban and suburban habitats on one side, and busy maritime shipping routes on the other, they are subject to a steady barrage of environmental contamination (Phillips 1987; Clark et al. 1992; Figure 9) such as petroleum products, pesticides, and detergents that may negatively affect them (USFWS 2010). Beyond the threat of chronic environmental contamination, SMHM may be at risk from catastrophic chemical disturbance, such as oil spills from refineries, pipelines, or ships, which could rapidly affect a large proportion of remaining SMHM populations (USFWS 1984); to our knowledge, no contingency plans exist to protect SMHM from this risk.

Climate change and associated sea-level rise and saltwater intrusion in the Delta may be the greatest threat to tidal marshes and SMHM persistence in the future (USFWS 2010; Thorne et al. 2012). Where marshes lack area to migrate upland, and either enough time and sediment input for accretion in response to rising sea level, studies project a net loss of SMHM habitat as some areas of mid- and high-marsh become low- or mid-marsh, and some low-marsh converts to mud flat (Takekawa et al. 2006, 2013; Thorne et al. 2012). Projections using a modest estimate of 1.24-m sea-level rise indicate the loss of most low- and mid-marsh areas by 2050 and the loss of almost 100% of low-marsh areas by 2100 (Takekawa et al. 2013). More recent analyses project sea-level rise to exceed 1.66-2 m (Oppenheimer and Alley 2016), indicating that losses may be much more severe than previously estimated (Thorne et al. 2018). Using predictions of sea-level rise combined with wetland-specific accretion rates, Thorne et al. (2018) calculated that in California, 59% of coastal marshes will be lost if space is available for upland migration, and 99% will be lost if such space is not available. Seawater intrusion into brackish areas and decreased outflow will also alter vegetation structure and assemblages (Woo and Takekawa 2012). In addition, the multiple effects of climate change such as increased temperatures, reduced snowpack, more frequent and extreme weather events (prolonged drought, extreme storms, and king tides) in combination with sea-level rise effects on saltwater intrusion further into the estuary could have cascading impacts on the whole ecological system (Dettinger et al. 2016). While projections of changes in precipitation have high uncertainty, storms are likely to be more extreme and more frequent (Cloern et al. 2011; Dettinger et al. 2016). This extreme and unpredictable weather may further stress SMHM through processes such as exposure to extreme temperatures and precipitation events, which can reduce adult and pup survival (e.g., by soaking or inundating nests), or through reduced food availability as a result of prolonged drought (USFWS 2013).

CONCLUSIONS

The USFWS (2010, p. 27) has determined that the SMHM continues to need protection throughout its range from historical threats as well as from climate

change, which “likely imperils the salt marsh harvest mouse and the resources necessary for its survival.” Habitat threats, research needs (see Smith et al., this issue), funding support, and management approaches to restoration or enhancement opportunities can vary by project, region, and stake-holder needs. Regular communication and coordination between managers and researchers can help target research needs to support management actions and lead to innovative approaches (Smith et al. this issue).

Our review indicates that substantial data gaps exist, and that conservation and restoration planning processes could consider experimental approaches within restoration designs to address these deficiencies. This, in turn, could maximize wildlife functions (for SMHM and other tidal-marsh inhabitants) via adaptive strategies to confront sea-level rise and other climate change-related threats. Science-based decision-making as well as addressing uncertainties through adaptive learning can make restoration and conservation efforts more effective (Zedler 2017). Indeed, innovative approaches and experiments can incorporate wildlife needs within restoration designs for sea-level rise adaptation (Parker and Boyer 2017). Close coordination and sustained efforts can facilitate more nimble responses to uncertainties and emerging threats. Strategies based on a keen understanding of the species ecology, life-history traits, and habitat are likely to be more effective, suggesting that continued investment in basic and applied SMHM ecology to collect baseline and long-term data is beneficial. This summary of the current knowledge and complexities related to the species and ongoing management efforts informs the identification of data gaps and development of research priorities (see Smith et al. this issue) within a coordinated approach to support science-based decision-making for the recovery of SMHM.

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