TERRESTRIAL VERTEBRATES OF TIDAL MARSHES: EVOLUTION, ECOLOGY, AND CONSERVATION

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THE IMPACT OF INVASIVE PLANTS ON TIDAL-MARSH VERTEBRATE SPECIES: COMMON REED (*PHRAGMITES AUSTRALIS*) AND SMOOTH CORDGRASS (*SPARTINA ALTERNIFLORA*) AS CASE STUDIES

GLENN R. GUNTENSPERGEN AND J. CULLY NORDBY

Abstract. Large areas of tidal marsh in the contiguous US and the Maritime Provinces of Canada are threatened by invasive plant species. Our understanding of the impact these invasions have on tidal-marsh vertebrates is sparse. In this paper, we focus on two successful invasive plant taxa that have spread outside their native range—common reed (*Phragmites australis*) and smooth cordgrass (*Spartina alterniflora*). A cryptic haplotype of common reed has expanded its range in Atlantic Coast tidal marshes and smooth cordgrass, a native dominant plant of Atlantic Coast low-marsh habitat, has expanded its range and invaded intertidal-marsh habitats of the Pacific Coast. The invasions of common reed in Atlantic Coast tidal marshes and smooth cordgrass in Pacific Coast tidal marshes appear to have similar impacts. The structure and composition of these habitats has been altered and invasion and dominance by these two taxa can lead to profound changes in geomorphological processes, altering the vertical relief and potentially affecting invertebrate communities and the entire trophic structure of these systems. Few studies have documented impacts of invasive plant taxa on tidal-marsh vertebrate species in North America. However, habitat specialists that are already considered threatened or endangered are most likely to be affected. Extensive experimental studies are needed to examine the direct impact of invasive plant species on native vertebrate species. Careful monitoring of sites during the initial stages of plant invasion and tracking ecosystem changes through time are essential. Since tidal marshes are the foci for invasion by numerous species, we also need to understand the indirect impacts of invasion of these habitats on the vertebrate community. We also suggest the initiation of studies to determine if vertebrate species can compensate behaviorally for alterations in their habitat caused by invasive plant species, as well as the potential for adaptation via rapid evolution. Finally, we urge natural-resource managers to consider the impact various invasive plant control strategies will have on native vertebrate communities.

Key Words: food webs, geomorphology, invasive plants, marsh birds, North America, *Phragmites*, *Spartina alterniflora*, saltmarsh, vertebrates.

EL IMPACTO DE PLANTAS INVASORAS EN ESPECIES DE VERTEBRADOS EN MARISMA DE MAREA: EL CARRIZO (*PHRAGMITES AUSTRALIS*) Y EL PASTO (*SPARTINA ALTERNIFLORA*) COMO CASOS DE ESTUDIO

Resumen. Grandes áreas de marisma de marea a lo largo EU así como y en las Provincias de Marisma de Canadá, se encuentran amenazadas por especies de plantas invasoras. Nuestro entendimiento acerca del impacto que estas especies tienen en los vertebrados de marismas de marea es escaso. En este artículo nos enfocamos en dos taxa de especies de plantas exitosas que se han dispersado fuera de su rango nativo—el carrizo (*Phragmites australis*) y el pasto (*Spartina alterniflora*). Un haplotipo críptico de carrizo ha expandido su rango en las marismas de marea en la Costa del Atlántico. El pasto (*Spartina alterniflora*), nativa y dominante del hábitat de marisma baja de la Costa del Atlántico, ha expandido su rango e invadido habitats de marisma intermareal en la Costa Pacífico. Las invasiones del carrizo en las marismas de marea de la Costa Atlántica y el pasto en marismas de marea de la Costa del Pacífico parece que tienen impactos similares. La estructura y composición de estos habitats ha sido alterada y la invasión y dominancia por estas dos taxa, pueden derivar en cambios profundos en los procesos geomorfológicos, alterando la mitigación vertical y pueden potencialmente afectar las comunidades de invertebrados y toda la estructura trófica de estos ecosistemas. Pocos estudios han documentado impactos de taxa de plantas invasoras en especies de vertebrados de marisma de marea en Norte América. Sin embargo, especialistas del hábitat, los cuales ya están considerados como en peligro, son los que están siendo más afectados. Se necesitan estudios extensivos experimentales para examinar el impacto directo de especies de plantas invasoras en especies nativas de vertebrados. El monitoreo cauteloso de los sitios durante los estados iniciales de la invasión de plantas y el rastreo de los cambios del ecosistema en el tiempo son esenciales. Debido a que las marismas de marea son el foci para la invasión por numerosas especies, también necesitamos los impactos indirectos de invasión de estos habitats en la comunidad de vertebrados. También sugerimos el inicio de estudios para determinar si especies de vertebrados pueden compensarse en términos de comportamiento por las alteraciones en su hábitat causado por especies de plantas invasoras, como también el potencial para la adaptación vía evolución rápida. Finalmente, recomendamos a los manejadores de recursos

naturales a que consideren el impacto que tendrán las estrategias de control de varias plantas invasoras en comunidades nativas de vertebrados.

Invasive plant taxa are profoundly changing North American saltmarshes, but this is not an isolated phenomenon. The introduction of non-indigenous plants in diverse habitats represents some of the most dramatic examples of biological invasions. Their impact on natural habitats, and the biodiversity of those habitats, is a pervasive threat and one of the most daunting ecological challenges facing twenty-first century natural-resource managers.

Considerable attention has been devoted to understanding the attributes of successful invaders and the characteristics of invaded regions and habitats, as well as to documenting the patterns and history of invasion (Mooney and Drake 1986, Drake et al. 1989, Cronk and Fuller 1995, Pysek et al. 1995). The consequences of invasive taxa on biological communities and ecosystem processes have been documented more recently (D'Antonio and Vitousek 1992, Mack et al. 2000). MacDonald et al. (1989) calculated that of the 941 vertebrate species thought to be in danger of extinction worldwide, 18.4% are threatened in some way by introduced species. In North America, they calculated that >13.3% of the native avifauna is threatened by invasive species. In another study focusing on threats to biodiversity in the US, Wilcove et al. (1998) found that 49% of all imperiled species (plants and animals) were threatened by invasive species.

The study of biological invasions has only recently focused on coastal and estuarine habitats (Grosholz 2002). Large numbers of non-indigenous species have been identified in U.S. coastal estuaries >200 non-indigenous species from San Francisco Bay alone (Cohen and Carlton 1998). Most research has concentrated on non-native aquatic invasive species including crustaceans, clams, crabs, and hydrozoans (Cordell and Morrison 1996, Crooks 1998, Bagley and Geller 2000, Byers 2000). In contrast, efforts to examine the ecological effects of non-native emergent wetland plant taxa in saltmarshes have lagged behind (except Weinstein et al. 2003). In this chapter, we focus on two of the more problematic invasive marsh-plant taxa in North American saltmarshes—common reed (*Phragmites australis*) and smooth cordgrass (*Spartina alterniflora*).

Atlantic and Pacific Tidal Saltmarshes

In the contiguous US and Maritime Provinces of Canada saltmarshes occur in three distinct regions: the Northeastern Atlantic Coast from the Hudson River north to the St. Lawrence estuary, the coastal plain of the United States from New Jersey south along the southeastern US Atlantic Coast to the northern Gulf of Mexico, and the western US along the Pacific coast (Dame et al. 2000, Emmett et al. 2000, Roman et al. 2000). In this chapter, we are interested in two areas—the Atlantic Coast, with an emphasis on the northeastern Atlantic region, and the Pacific Coast.

Northeast-coast saltmarshes are formed largely by reworked marine sediments and in situ peat formation. These marshes are largely limited to small, narrow fringing systems because the physiography of the region and broad expanses of rocky coast limit their areal extent (Nixon 1982). Farther south, more extensive saltmarshes occur in the drowned valley estuaries of Delaware Bay and Chesapeake Bay (Teal 1986). Pacific Coast saltmarshes occur in a geologically young region structured by tectonic and volcanic forces (Emmett et al. 2000). Because of the rocky and unfeatured wave-dominated shoreline along much of the Pacific Coast, extensive areas of saltmarsh are restricted to large estuaries such as those associated with the San Francisco Bay and the Columbia River or behind sheltering bay-mouth bars.

Strong physical gradients of salinity and tidal inundation contribute to the characteristic patterns of tidal-height zonation. The two main marsh zones include low marsh and high marsh. Low marsh is lower in elevation relative to mean low water and is regularly flooded by tides. High marsh occupies the higher elevations in the intertidal zone, and is less influenced by tidal forces.

The organization of tidal-marsh vegetation communities varies in the different regions. A short-statured grass, saltmeadow cordgrass (*Spartina patens*), dominates the high marsh along the northeast coast—often intermixed with the short form of smooth cordgrass and black needlerush (*Juncus gerardi*) at the upland border of the high marsh. Smooth cordgrass persists as a dominant species in low-marshes, in this region reaching heights as tall as 1.25–2 m (Teal 1986). Open tidal mudflats characterize the lower intertidal zone of Pacific Coast estuaries. The mid-intertidal zone is dominated by California cordgrass (*Spartina foliosa*), which forms a narrow band of vegetation along the outer edges of the native terrestrial vegetative zone and along tidal channels (Mahall and Park 1976, Ayers et al. 2003). California cordgrass's range extends from Baja California north to

Humboldt Bay (Josselyn 1983). California cordgrass, the only species of *Spartina* native to the Pacific Coast, grows sparsely and is relatively short (usually <1 m tall; Ayres et al. 2003). The Pacific Coast high marshes, with high salinity and saturated soils, are dominated by low-growing (<0.5 m) cordgrass species (Baye et al. 2000). A transition in vegetative composition of saline marshes occurs in the Pacific Northwest and these marshes are dominated by *Salicornia* spp. and beach salt grass (*Distichlis spicata*) in the high marsh and seaside arrowgrass (*Triglochin maritima*) in the low marsh (Seliskar and Gallagher 1983) but much of the intertidal area in the Pacific Northwest remains un-vegetated (Simenstad et al. 1997).

Over the last 200 yr, marsh and tidal flats have been lost to or degraded by human development activities including diking, draining, dredging, or filling for agriculture or urbanization, and conversion to salt-production ponds. A substantial portion of U.S. tidal wetlands has been destroyed (Tiner 1984) and unaltered coastal saltmarshes are rare (Roman et al. 2000). Over 80% of the saltmarshes that once occurred in New England have already been lost (Teal 1986). Originally, New England saltmarshes had networks of salt ponds, pannes, potholes, and channels in the high marsh where the water was semi-permanent. Roads and other obstacles have cut off or reduced tidal flow into these habitats (Roman et al. 1984, Burdick et al. 1997). Most saltmarshes along the Atlantic Coast have also been ditched to remove standing water and pools and prevent mosquito breeding, resulting in lowered water tables, vegetation changes, and associated trophic impacts on fish and waterbirds (Roman et al. 2000). Pacific Coast marshes have suffered the same fate as those along the Atlantic Coast. For example, a 70% loss of tidal wetlands has occurred in the Puget Sound estuary in Washington with localized loss being virtually complete in heavily urbanized areas (Washington Division of Natural Resources 1998). At the turn of the 19th century, the San Francisco Bay estuary included approximately 76,900 ha of tidal marshes and 20,400 ha of open tidal flat. Today, only about 16,300 ha (21%) of tidal marshes and 11,800 ha (58%) of tidal flats remain (Goals Project 1999).

Northeast coast saltmarsh vegetation patterns have changed dramatically over the past 50 yr. Surveys of southern New England saltmarshes suggest that increases in sea levels leading to increased waterlogging of upland marsh soils and plants has in turn led to the replacement of black needlerush in the upper high marsh by seaside arrowgrass and the replacement of saltmeadow cordgrass by the short form of smooth cordgrass (Niering and Warren 1980, Warren and Niering 1993). Cultural eutrophication leading to higher loadings of nitrogen to northeast tidal marshes is also hypothesized to have resulted in changes in tidal-marsh vegetation patterns (Bertness et al. 2002). Nitrogen fertilization experiments in nitrogen-limited New England tidal marshes resulted in increased abundance of smooth cordgrass in high-marsh plots while marsh hay decreased (Levine et al. 1998, Emery et al. 2001).

Invasive Tidal Saltmarsh Plant Species

Atlantic and Pacific coast tidal saltmarshes are characterized by a few dominant emergent plant species organized in characteristic zones resulting from both physical stress and competition, leading to distinct plant communities at specific elevations (Bertness and Ellison 1987). But, because of habitat degradation, they may be among the most susceptible to invasive plant species. Shoreline development, tidal restriction, and habitat destruction result in disturbed conditions including bare soil, high nutrient inputs, altered hydrology, and high light levels which are thought to be among the conditions that promote successful plant invasions. The colonization and spread of common reed in Atlantic Coast marshes and cordgrass in Pacific Coast marshes has been rapid and follows a pattern often typical of plant invasions. Windham (1999) describes the typical invasion sequence of reeds in Atlantic Coast saltmarshes initiated by the first appearance of isolated small patches, the continued initiation of numerous other isolated patches over time, the coalescence of these patches and eventual dominance of an area. She cited an average annual rate of spread >20% at a site in southern New Jersey from 1972–1991.

Common reed

Common reed is found worldwide. It tolerates a range of abiotic conditions and is found in both freshwater and coastal habitats, although its establishment and growth is limited by flooding duration and high salinity and sulfide levels (Chambers 1997). Reeds have been shown to form extensive stands in tidal marshes with salinities <15 ppt. Small, more recently established plants grow well at salinities from 0–5 ppt, exhibit some reduction in growth up to 35 ppt, and have difficulty persisting when salinities exceed 35 ppt (Chambers et al. 1999). In North America, the range of reeds has expanded dramatically since the late 19th century, and in

some areas reeds have formed extensive monocultures displacing native species (Chambers et al. 1999). Reeds now occupy many tidal habitats in Maritime Canada, New England, the mid-Atlantic, and the northern Gulf of Mexico. Reeds form dense monocultures following establishment (Meyerson et al. 2000) and are thought to be a robust competitor relative to other saltmarsh species. They grow to 3–5 m tall and can form solid stands with stem densities ranging from 50–125 shoots/m^2 (Meyerson et al. 2000).

Wrack accumulation, erosion, ice scour that promotes bare soil, ditching and other hydrologic disturbances, and nutrient enrichment associated with shoreline development provide reeds with opportunities to become established (Chambers et al. 1999). Dispersal and burial of large rhizome fragments into well-drained and low-salinity sites improve the chances of successful establishment (Bart and Hartman 2003). Once established, poorly drained areas and sites with high salinity and sulfide levels tend to be invaded by clonal spread (Chambers et al. 2003).

Many explanations have been invoked for the recent change in the relative abundance and distribution of reeds in North American tidal marshes (Chambers et al. 1999, Orson 1999). Recent advances in genomics, including the ability to examine nucleotide sequences in chloroplast DNA, have shed considerable light on this question. Comprehensive genetic analyses of herbarium specimens collected before and after 1910 reveal significant changes in the haplotype frequency of North American reed populations (Saltonstall 2002, 2003). Today one distinct haplotype derived from an introduced Eurasian lineage (Type M) is the dominant type found in the tidal marshes of the Northeast and mid-Atlantic Coast although populations of native haplotypes still persist in the region. Although native haplotypes still dominate along the Pacific coast, haplotype M has been identified in urban areas in the western US (Saltonstall 2003).

It is currently not known why haplotype M has become the dominant reed lineage and has increased its distribution throughout Atlantic Coast tidal habitats. Type M may be a superior competitor or environmental conditions may have changed and played a role in the expansion of its range (Silliman and Bertness 2004). New experiments evaluating the growth and persistence of native and invasive haplotypes along salinity and hydrologic gradients as well as competition experiments with other saltmarsh dominants are currently underway (Vasquez et al., 2005).

Smooth cordgrass

Among the invasive plants in Pacific Coast marshes, several cordgrass species have been particularly successful because they are among the most abundant and aggressive intertidal plants in North America (Adam 1990). For instance, four of the 12 non-native plant species identified as introduced species of concern in the San Francisco Bay estuary are cordgrass species—smooth cordgrass, saltmeadow cordgrass, dense-flowered cordgrass (*S. densiflora*) and common cordgrass (*S. anglica*) (Grossinger et al. 1998). The introduction and spread of smooth cordgrass, however, is arguably the most devastating of the tidal-marsh-plant invasions on the Pacific Coast. The dominant plant species of low marsh along the Atlantic Coast of the US, smooth cordgrass has become established in open tidal mudflats of the Pacific Coast and has extended its range up through the high-marsh zone as well.

Multiple intentional and accidental introductions of smooth cordgrass have occurred in Pacific estuaries. In Washington, smooth cordgrass was accidentally introduced to Willapa Bay sometime before 1911 (Scheffer 1945) and by 1988 it had spread to occupy >445 ha of tidal flat (Aberle 1993). More recently, the rate of spread appears to be accelerating. In 1997, the area solidly covered by smooth cordgrass was estimated at >1,315 ha, and by 2002 it was estimated at >2,500 ha equaling nearly 47% of the tidalflat habitat in Willapa Bay (Washington Division of Natural Resources 2000, Buchanan 2003). In the 1930s and 1940s, smooth cordgrass was intentionally introduced in four areas of Puget Sound for duck-habitat enhancement, but the spread there has been minor compared to that in Willapa Bay (Frenkel 1987). Smooth cordgrass was also introduced in the late 1970s into one area in Oregon, the Siuslaw estuary (Aberle 1993). In California, the Army Corps of Engineers brought smooth cordgrass plants into the South Bay of San Francisco Bay in 1973 for a marsh-restoration project and over the next decade it was transplanted to at least two other sites, and likely others, within the South Bay (Ayres et al. 2004, Grossinger et al. 1998). Over the next 10 yr, smooth cordgrass spread slowly to other areas and began to hybridize with the native California cordgrass. This hybrid (smooth cordgrass × California cordgrass) is highly productive, out competes both parental species, and is the form that is now aggressively spreading throughout San Francisco Bay (Daehler and Strong 1997, Ayres et al. 2004). The latest surveys show that smooth cordgrass/hybrid now occupies approximately 2,030 ha which

equals approximately 17% of the tidal flat and marsh habitat in south San Francisco Bay where the invasion is concentrated (Ayres et al. 2004). Ayres et al. (2003) predicted that, if unchecked, invasive smooth cordgrass has the potential to spread throughout the San Francisco Bay estuary and beyond such that it would cause the global extinction of the native California cordgrass. Indeed, recent surveys have confirmed the presence of smooth cordgrass in two other California estuaries north of San Francisco Bay (Bolinas Lagoon and Drakes Estero) indicating the potential for widespread colonization of other Pacific Coast estuaries (Ayres et al., 2003). Daehler and Strong (1996) estimate, that along the Pacific Coast of the US, the final distribution for smooth cordgrass will stretch from Puget Sound, Washington, south through the Tijuana River Estuary, California.

Effects of Invasive Reeds and Cordgrass on Tidal-marsh Habitat

The expansion of reeds into high-marsh areas along the Atlantic Coast of the US can result in important changes in plant community structure and potential declines in the vertebrate species dependent on these habitats. In New England marshes, the impacts of human development and cultural eutrophication are affecting the distribution of plant species (Bertness et al. 2002). Shoreline development and enhanced nitrogen supplies appear to be associated with the expansion of common reed populations into the high marsh. Rooth et al. (2003) documented increased rates of sediment accretion following invasion by reeds in oligohaline tidal marshes of the Chesapeake Bay. The high productivity of reeds and accumulation of litter on the marsh surface, coupled with high stem density and high inorganic sediment loading, appears to be the mechanism resulting in the higher rates of sediment accretion. The enhanced rates of sediment accumulation in reeds stands can alter the physical structure of tidal marshes by building up the marsh surface and filling in topographic depressions and first order tidal channels, resulting in a loss of microtopographic variation (Lathrop et al. 2003).

Similar habitat alteration occurs in Pacific Coast estuaries that have been invaded by non-native smooth cordgrass (and/or the hybrid form smooth cordgrass × California cordgrass). The non-native cordgrass often grows to heights of 2 m or more and the above- and below-ground biomass is much denser than any of the native plant species (Callaway and Josselyn 1992). Smooth cordgrass is able to occupy a much larger portion of the tidal gradient than any of the native marsh plants and has been dubbed an ecosystem engineer because of its ability to alter habitat through increased sediment accretion (Ayres et al. 1999). When invaded by smooth cordgrass, marshes can ultimately be transformed into solid non-native cordgrass meadows (Daehler and Strong 1996). In San Francisco Bay, this non-native cordgrass colonizes open intertidal mudflats and clogs tidal channels (growing as low as 73 cm above the lower limit of the intertidal zone), and grows throughout the marsh plain up to the high marsh (as high as 15 cm below the maximum elevation of tidal-marsh vegetation) where it appears to be displacing native plant species (Ayres et al 1999, Collins 2002). Based on estimates of smooth cordgrass tidal inundation toleration rates, current water levels, and tidal regimes, Stralberg et al. (2004) predicted that approximately 33% of intertidal mudflat habitat could be encroached upon by smooth cordgrass and its hybrids. In addition, the upward spread of smooth cordgrass could be accelerated by future sea-level rise (Donnelly and Bertness 2001).

Changes in habitat structure and composition that accompany the smooth cordgrass invasion on the Pacific Coast and the common reed invasion on the Atlantic Coast, lead to alterations in geomorphological processes in tidal marshes and have implications for many aspects of the tidal-marsh ecosystem including basic hydrologic function (e.g., altering flow regimes in marshes by clogging tidal channels). Thus the effects of the invasion and dominance of tidal wetlands by common reed and smooth cordgrass could cascade throughout the tidal-marsh system and alter the trophic structure of the marsh ecosystem as well, although little is currently known about these effects. For example, the increase in sediment accretion (e.g., 1–2 cm/yr in Willapa Bay [Sayce 1998]), coupled with the increase in mass and density of above-ground biomass of smooth cordgrass invasions in Pacific Coast estuaries, could potentially change the invertebrate community composition of intertidal zones, reducing benthic invertebrate densities (Capehart and Hackney 1989), while increasing insects and arachnids of the cordgrass canopy.

Potential Impacts on Tidal-marsh Vertebrates

The impact of the introduction and spread of non-native reeds and smooth cordgrass on tidal-marsh vertebrate populations remains largely unstudied. For instance, few data correlate the distribution of these invasive plant species with the distribution and abundance of native tidal-marsh bird or mammal species.

One of the most widely recognized values of saltmarshes is their support of migrant and resident avian species. Fundamental changes in habitat structure, shifts in primary productivity, and the potential modification of trophic pathways that accompany the invasion will likely have their biggest impacts on resident, non-migratory species that are dependant year-round on tidal marshes.

Potential Impacts of Common Reed

Several studies provide evidence that many species of vertebrates use marshes dominated by reeds (Kiviat et al., pers. comm.), which appears to be more important to wildlife as shelter than as food. Wildlife species tend to use the edges of stands, mixed-reed stands, and smaller patchy stands than the dense extensive interiors of larger stands. Interestingly, colonial-nesting long-legged wading birds may benefit from the proximity of reed stands. In certain sites in Delaware, reeds provide critical habitat for nesting colonial wading birds by offering substrate and material for nesting, and serves as a buffer from human disturbance (Parsons 2003).

Reed-dominated marshes support more species of coastal marsh-breeding birds than commonly believed (Kiviat et al., pers. comm.). Kiviat et al.'s literature review documented 24 species of birds that utilized reed stands located in either estuarine tidal marshes and creeks or saltmarsh habitat. Although dense populations of reeds appear to have little value for birds, stands interspersed with tidal creeks and open water and mixed stands or habitat on the edge of reed stands do support some bird species (Swift 1989, Brawley 1994, Holt and Buchsbaum 2000).

Holt and Buchsbaum (2000) suggested that factors other than the dominant plant species also have a major role in determining the distribution of bird species in tidal marshes. They found that the presence of reeds in northern Massachusetts's coastal marshes appeared to have little effect on the numbers of Red-winged Blackbirds (*Agelaius phoeniceus*), Marsh Wrens (*Cistothorus palustris*), Virginia Rails (*Rallus limicola*), or Saltmarsh Sharp-tailed Sparrows (*Ammodramus caudacutus*). Benoit and Askins (1999) conducted one of the few direct comparisons of bird use of reeds and unaltered saltmeadow cordgrass habitat in Atlantic Coast saltmarshes. They found significantly fewer species of birds in reed-dominated stands than in high-marsh saltmeadow cordgrass stands. The Seaside Sparrow (*Ammodramus maritima*), Saltmarsh Sharp-tailed Sparrow, and Willet (*Catoptrophorus semipalmatus*), three tidal-marsh specialists adapted to nesting in the short high-marsh vegetation, had low frequencies in stands dominated by reeds. The Marsh Wren, Swamp Sparrow (*Melospiza georgiana*), and Red-winged Blackbird (marsh generalists that prefer tall reedy vegetation) were found in sites dominated by reeds. Even within these examples of species that maintain populations in reeds, more detailed study is required. Olsen and R. Greenberg (pers. comm.) report that in Delaware, Swamp Sparrows require saltmeadow cordgrass for nest cover. Clumps of this vegetation can be found along the edge of reed beds, but not in the interior of large stands. Therefore, it is unlikely that Swamp Sparrows can maintain nesting populations in larger stands of reeds. In fact, Benoit and Askins (1999) also found that homogeneous stands of reeds did not provide sustainable habitat for many wetland bird species. Wading birds, shorebirds, and waterfowl were absent from surveyed reed stands. By contrast, the high-marsh stands dominated by short-stature grasses included a wide variety of generalists: waders, shorebirds, ducks, and aerial insectivores as well as high-marsh specialists. A phenomenon less well documented was the use of reed stands embedded in a larger more heterogeneous landscape. Benoit (1997) reported Virginia Rails and King Rails (*Rallus elegans*) using patches of reeds interspersed with areas of open brackish marsh.

In Atlantic Coast tidal marshes where reeds have recently established, the availability of prey resources (snails, amphipods, and isopods) to adult mummichogs (*Fundulus heteroclitus*) may be no different than in non-invaded tidal marshes (Fell et al. 1998). However, as the hydrology of these sites change and marsh surface heterogeneity and topographic depressions disappear, there is evidence that fish recruitment and utilization may change in reed-dominated stands (Weinstein and Balletto 1999, Osgood et al. 2003). A growing body of research suggests that mummichogs may exhibit reduced feeding and reproduction in response to the structural changes that occur as tidal-marsh sites naturally dominated by cordgrass species become dominated by common reed (Able et al. 2003, Raichel et al. 2003). This suggests that prey for larger wading birds may not be accessible within dense stands of reeds but these large wading birds may forage on the edges of reed stands intermixed with more typical low or high marsh.

Potential Impacts of Smooth Cordgrass

On the Pacific Coast, the smooth cordgrass invasion may have negative effects on native vertebrate species, but as yet few data are available.

The salt marsh harvest mouse (*Reithrodontomys raviventris*), a federally endangered species endemic to San Francisco Bay saltmarshes, prefers the mid- and upper-tidal areas that are largely dominated by pickleweed (*Salicornia virginica;* Shellhammer et al. 1982). Shellhammer et al. (1982) found very few mice in pure stands of salt-marsh bulrush (*Schoenoplectus maritimus*), a tall, reedy bulrush with structural characteristics more similar to the non-native smooth cordgrass than to the preferred *Salicornia* spp. Shellhammer et al. speculated that the value of pickleweed was higher for the saltmarsh harvest mouse than was bulrushes because pickleweed provides denser cover and more horizontal branching. While smooth cordgrass may provide fairly dense cover, it provides little horizontal structure. Other mammals that occur in San Francisco Bay tidal marshes that may be affected by habitat alteration associated with smooth cordgrass include the saltmarsh wandering shrew (*Sorex vagrans haliocoetes*), the Suisun shrew (*Sorex ornatus sinuosis*), and the California vole (*Microtus californicus*). All three of these species are known to occur in the middle and upper intertidal zones of salt or brackish marshes (Lidicker 2000, MacKay 2000, Shellhammer 2000).

Relatively few bird species are restricted year-round to tidal saltmarshes in San Francisco Bay. Resident bird species that breed in the tidal marshes include the federally endangered California Clapper Rail (*Rallus longirostris obsoletus*) and three subspecies of tidal-marsh Song Sparrow (*Melospiza melodia pusillula, M. m. samuelis, and M. m. maxillaris*) listed as California species of special concern because of habitat loss and because they have extremely restricted ranges and adaptations for nesting in Pacific Coast saltmarshes (Marshall 1948a, Johnston 1954). While California Black Rails (*Laterallus jamaicensis coturniculus*) and Salt Marsh Common Yellowthroats (*Geothlypis trichas sinuosa*), also species listed in California, typically breed in brackish or freshwater marshes, they do occur in saltmarshes during winter and so may also be affected by the smooth cordgrass invasion.

Although California Clapper Rails do occur and nest in areas that have been invaded by non-native smooth cordgrass (S. Bobzien, pers. comm.; J. C. Nordby, pers. obs.), it is unclear whether these sub-populations are sustainable. Clapper Rails forage mainly at low tide when the mud substrate in tidal channels and tidal flats is exposed and their preferred foods (clams, mussels, snails, and crabs) are more available (Williams 1929, Moffit 1941, Albertson and Evens 2000). By colonizing tidal flats and clogging tidal channels, smooth cordgrass may reduce the foraging habitat of rails as well as alter what food items are available. Also, Clapper Rails do occasionally nest in native California cordgrass (Zucca 1954) but no studies have yet examined the success of Clapper Rail nests placed in either exotic or native cordgrass.

Like the California Clapper Rail, the Alameda Song Sparrow (*Melospiza melodia pusillula*) does occupy marshes that have been invaded by smooth cordgrass (J. C. Nordby and A. N. Cohen, unpubl. data). In a native marsh, Song Sparrow breeding territories are typically arrayed in a tight linear fashion in the taller plants (gumweed [*Grindelia stricta*] and Virginia picklewood) that occur along tidal channels (Marshall 1948a, Johnston 1954). Preliminary analyses from an ongoing study of how saltmarsh Song Sparrows are responding behaviorally to the rapid alteration of habitat by smooth cordgrass have shown that Song Sparrows do include the non-native cordgrass habitat in their territories and use those areas for foraging as well as for nesting. However, no observed Song Sparrow territories have been composed entirely of smooth cordgrass, and nests that were placed in smooth cordgrass were somewhat less successful and much more likely to fail due to tidal flooding than were nests placed in native vegetation (J. C. Nordby and A. N. Cohen, unpubl. data). It is possible that the Song Sparrows are drawn to inappropriate nesting sites in smooth cordgrass that are too low in elevation relative to the tides. Whether smooth cordgrass is acting as an ecological trap for Song Sparrows, where overall reproductive success is reduced, remains to be tested

The impact of the smooth cordgrass invasion is not restricted to resident species because the open tidal flats of Pacific estuaries provide crucial habitat for migrating shorebirds. San Francisco Bay is designated as a Western Hemisphere Shorebird Reserve Network that provides breeding habitat or critical migratory stopover sites for >1,000,000 waterfowl and shorebirds each year (Kjelmyr et al. 1991), more than any other wetland along the Pacific Coast of the contiguous US (Page et al. 1999). Most of these bird species forage extensively on benthic organisms found in the vast tidal mudflats that rim the bay (Takekawa et al. 2000). In a study of the affect of the spread of common cordgrass (a close relative of smooth cordgrass) on shorebird populations in the British Isles, Goss-Custard and Moser (1988) found the largest reduction in Dunlin (*Calidris alpina*) in estuaries where the cordgrass had replaced much of the intertidal mudflat foraging habitat. Ayres et al. (2004)

predicted that in San Francisco Bay the loss of tidal mudflat habitat to smooth cordgrass colonization could be extensive if the invasion goes unchecked over the next two centuries. Stralberg et al. (2004) estimated that 33% of shorebird habitat value (range 9–80%) could be lost under realistic spread scenarios.

In Willapa Bay, Washington, where smooth cordgrass increased three-fold between 1994 and 2002 (Buchanan 2003), aerial surveys conducted in 2000–2001 suggest a reduction in shorebird numbers by approximately 60% and foraging time by as much as 50% in the southern portions of the bay as compared with data from the 1991–1995 surveys (Jaques 2002).

In addition to the direct alteration of habitat, invasive plants may be altering competitive interactions among native species as well. Pacific Coast Marsh Wrens (*Cistothorus palustris paludicola*), which normally nest in freshwater or brackish marshes and not in open saltmarshes (Verner 1965), have begun to establish breeding territories in the newly available smooth cordgrass habitat in San Francisco Bay as well as in other smooth cordgrass-invaded marshes such as those in Willapa Bay (Williamson 1994; J. C. Nordby and A. N. Cohen, unpubl. data). Marsh Wrens are highly territorial and will defend their nesting areas by breaking the eggs of other species that attempt to nest nearby (Picman 1977). They can control the distribution and alter the behavior and reproductive strategy of much larger and aggressive birds, such as Red-winged Blackbirds and Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*; Picman 1980, Picman and Isabelle 1995). Preliminary analyses of birds in smooth cordgrass-invaded marshes in San Francisco Bay have shown that Song Sparrows and Marsh Wrens have segregated territories with little overlap and that marsh wren territories are more highly correlated with the non-native cordgrass habitat than are Song Sparrow territories (J. C. Nordby and A. N. Cohen, unpubl. data). It is not yet known, however, whether Marsh Wrens are excluding Song Sparrows from the smooth cordgrass habitat or if song sparrows are selecting against those areas for other reasons (e.g., nesting habitat or food resources are limited).

Future Research Needs

It is clear that the replacement and dominance of tidal-marsh communities in North America by invasive non-native reeds and cordgrasses can have important and perhaps severe consequences. These taxa may alter geomorphological processes, hydrologic regimes, and habitat structure. It is presumed that invasion by these taxa can affect the trophic structure and vertebrate species composition of tidal marshes. However, we know of no experimental studies of vertebrate species that provide quantitative estimates of these effects. These studies are needed to examine the impact of habitat alteration by invasive plant species on the structure and function of tidal-marsh communities in settings that allow for rigorous comparisons with appropriate controls.

Additional studies are needed that determine the current distribution, abundance, and population trends of native vertebrate species and their correlation with the presence of different species of invasive plants, as well as the effects of invasive species on important demographic parameters such as reproductive success and survival. We also need to assess the landscape-scale consequences of plant invasions in tidal marshes and whether a relationship exists between vertebrate community structure and landscape patchiness. Small isolated stands characteristic of the early stages of invasion may not negatively impact native vertebrate populations and may even provide additional edge habitat for certain species. As patches coalesce, however, and a threshold is reached in the invasive cover of an area, we may only then see detrimental effects as dense interior areas occupy a greater share of the landscape and intact native habitat becomes increasingly rare. Because the spread of exotic species is an ongoing process, we often have unique opportunities to establish baseline data in areas that are not yet invaded and also to track changes over time in areas where invasions are actively spreading. The development of predictive theoretical and empirical models that incorporate metapopulation dynamics of vertebrate species would enhance our understanding of the potential future impacts of these invasions.

It is also important that we assess the behavioral and genetic responses of native species to the exotic-species invasions. Because the alteration of habitat can occur so rapidly, we need to understand whether, or to what extent, native species can alter their behavior to compensate for changes in their environment. A high level of behavioral plasticity would be beneficial as it could also buy species more time to evolve adaptations to their rapidly changing habitat.

Not only must we examine the direct impact of non-native, invasive species, we also need to expand our understanding of the indirect impact of habitat alteration that can be associated with invasions such as trophic cascades in which the entire food web is altered, facilitation of further exotic invasions as newly altered habitat attracts additional non-native species

or even alters interspecific interactions among native species. Only by examining both the direct and indirect effects of habitat alteration and the effects of other invasive species on tidal-marsh vertebrates will we be able to determine the full extent of the impacts of invasive plant species.

Millions of dollars are being spent on controlling the cordgrass and reed invasions and natural-resource managers have been making decisions about invasive-plant control measures without knowing the appropriateness of the different control programs currently in place. These control measures (e.g., large-scale glyphosate spraying, fire, mechanical removal, or tarps), as well as the seasonal timing of application, may well have unintended consequences for native species and should be balanced with careful monitoring of vertebrate communities. A mechanistic understanding of the impacts of invasive species on vertebrate communities is an essential step in determining if suitable alternative management strategies are needed.

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