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Global Climate Change and Sea Level Rise: Potential Losses of Intertidal Habitat for Shorebirds

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Abstract.—Global warming is expected to result in an acceleration in current rates of sea level rise, inundating many low-lying coastal and intertidal areas. This could have important implications for organisms that depend on these sites, including shorebirds that rely on them for feeding habitat during their migrations and in winter. We modeled the potential changes in the extent of intertidal foraging habitat for shorebirds at five sites in the United States that currently support internationally important numbers of migrating and wintering birds. Even assuming a conservative global warming scenario of 2°C within the next century (the most recent projections range between 1.4°C and 5.8°C), we project major intertidal habitat loss at four of the sites (Willapa Bay, Humboldt Bay, San Francisco Bay, and Delaware Bay). Projected losses range between 20% and 70% of current intertidal habitat. Such losses might jeopardize the ability of these sites to continue to support their current shorebird numbers. The most severe losses are likely to occur at sites where the coastline is unable to move inland because of steep topography or seawalls. The effects of sea level rise may be exacerbated by additional anthropogenic factors. In southern San Francisco Bay, for example, sea level rise may interact with land subsidence due to aquifer depletion, and the constraints imposed by existing seawalls on the landward migration of habitat, resulting in the greatest habitat loss. At the fifth site (Bolivar Flats) we project smaller losses as the intertidal habitats are unconstrained by sea walls and will be able to migrate inland in response to rising sea level. Installation of additional coastal protection barriers at this site and others is likely to exacerbate the rate and extent of intertidal habitat loss. *Received 20 June 2001, accepted 27 September 2001.*

Key words.—shorebirds, intertidal habitat, climate change, sea-level rise.

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During their migration and in winter, most shorebirds depend for their foraging habitat on intertidal sand and mud flats. The ability of a site to support large numbers of shorebirds is largely determined by the extent of these habitats, and by the density, availability, and seasonal predictability of their invertebrate prey: sites with greater densities of invertebrates typically support higher shorebird densities (Morrison 1983; Evans and Dugan 1984; Goss-Custard 1996). However, unlimited numbers of birds cannot simultaneously exploit a site, no matter how rich its food supply, since the availability of feeding habitat and prey will impose an upper limit on the number of birds that it can support. As the amount of feeding habitat at a site is reduced and densities of shorebirds increase, density-dependent interactions

(including competition between individuals for diminishing feeding areas, and interference between foraging birds) may be triggered. These may result in the exclusion of individuals from the site, increased mortality rates among the excluded birds, and, ultimately, in limitation of numbers (Goss-Custard 1977, 1980). Thus for some shorebird species, reductions in the availability of feeding habitat at a site may not be compensated by the birds simply crowding closer together, but may lower the number of birds that can be supported.

Data from localities at which changes in habitat availability and numbers of birds have been monitored confirm that reductions in foraging habitat area may lead to declines in shorebird numbers. In southern England, the conversion of mudflats to saltmarsh, through

colonization by the cordgrass (*Spartina anglica*) resulted in reductions in the numbers of Dunlin (*Calidris alpina*) using affected areas (Goss-Custard and Moser 1988). On the Tees estuary in England, large losses of mudflats led to reductions in shorebird numbers (Evans and Pienkowski 1983). Similarly, on the Oosterschelde estuary in The Netherlands, a 30% reduction in the area of intertidal feeding habitat resulted in a reduction in the numbers of European Oystercatchers, (*Haematopus ostralegus*) (Meire 1991). Thus, it seems probable that the availability and quality of feeding habitat during migration and winter may be major contributors to the limitation of numbers in some shorebird species.

During the 20th century, intertidal sand and mud flats have come under considerable pressure from human activities, particularly reclamation followed by agricultural, urban, or industrial development (Evans 1991, 1997), or the invasion of intertidal mud and sand flats by alien plants (Goss-Custard and Moser 1988). More recently, a new threat to shorebird staging and wintering sites has been recognized: sea level rise due to global climate change (Ens *et al.* 1995; Evans 1991, 1997; Myers and Lester 1992). Increasing global temperatures will result in increases in sea level due to the expansion of the oceanic water and to melting of glaciers and ice sheets. The most widely accepted projection is that over the next 100-years, sea level will rise globally by between 10 and 90 cm (IPCC 2001). However, local sea level rise may be much greater or smaller due to the confounding effects of crustal subsidence or uplift, respectively (U.S. EPA 1995). Inundation due to sea level rise could result in the conversion of intertidal to subtidal habitat and, therefore, reductions in the availability of the foraging habitats available to shorebirds. It seems logical to suggest that the greatest habitat changes will occur at sites where the tidal zone is not allowed to migrate inland either by topography or by seawalls.

In this study, we model the potential consequences of future sea level rise for shorebird intertidal foraging habitat at five important staging and wintering sites on the Atlantic, Gulf of Mexico, and Pacific coasts of

the United States, and the ability of these sites to continue supporting important numbers of shorebirds. Our model projects results to 2100 and assumes that existing seawalls will prevent inland encroachment of the coastline (until they are overwhelmed by rising sea levels), and evaluates how the installation of new structures might affect habitat change. While the focus of this study is on U.S. sites, sea level rise is a global phenomenon and it is likely that the patterns and consequences identified for the U.S. will be repeated at important shorebird sites elsewhere.

METHODS

This study has five main components: 1) selection of study sites on the east, west, and Gulf of Mexico coasts of the United States, 2) quantification of the current areas of intertidal feeding habitats for shorebirds at each of the study sites, 3) identification of probabilistic sea level change scenarios at each of the study sites, 4) projection of changes in the extents of intertidal feeding habitats in response to sea level change, and 5) evaluation of the likely effects of the predicted habitat changes on shorebird numbers at each of the study sites.

Study Site Selection

Study sites were selected based on five criteria: 1) they were categorized by the Ramsar Convention or by the Western Hemisphere Shorebird Reserve Network (WHSRN) as at least of hemispheric importance for migratory or wintering shorebirds, 2) shorebird census data were available, 3) probabilistic sea level rise scenarios were available, 4) digital information on the extents of intertidal habitats was available, and 5) digital elevation maps were available. Using these criteria, five study sites were selected (Fig. 1). These were Willapa Bay in southern Washington, Humboldt and San Francisco Bays in northern California, Bolivar Flats in northeast Texas, and Delaware Bay in New Jersey and Delaware.

Each of these sites is listed by the Ramsar Convention or the WHSRN as being of international or hemispheric importance for shorebirds. Count data from the Pacific Flyway Project and the International Shorebird Survey confirm that large numbers of shorebirds (tens to hundreds of thousands) use each of these sites during migration and, in the cases of San Francisco Bay and Humboldt Bay, in the winter (Page *et al.* 1999; Harrington *et al.* 1989).

Probabilistic sea level rise projections for each site are available in U.S. EPA (1995), and digital habitat data and Digital Elevation Model (DEM) maps were obtained from the U.S. Fish and Wildlife Service's National Wetlands Inventory (NWI) and the U.S. Geological Survey, respectively.

Current Extents of Intertidal Foraging Habitat at Study Sites

Although a small number of North American coastal shorebird species feed exclusively on rocky shores, and

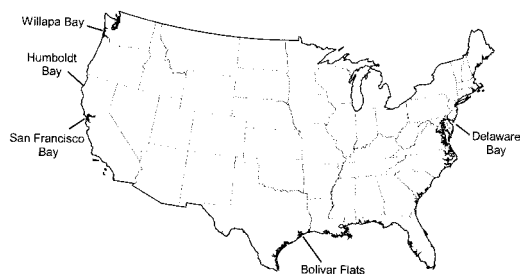


Figure 1. Locations of study sites.

other species may forage in artificial areas, such as flooded agricultural fields or saltpans, most coastal migrating and wintering shorebirds typically forage on intertidal flats (i.e., sand beaches or mudflats) (Hale 1980; Prater 1981; Cramp and Simmons 1983; Evans and Dugan 1984; Hayman *et al.* 1986). These are the habitats that we focus on in this study.

The current extents and distributions of intertidal sand and mudflat habitats at each of the study sites were obtained from the U.S. Fish and Wildlife Service's NWI maps. These maps, prepared from aerial photographs, delineate the major intertidal habitats at each of the sites. For this study, NWI intertidal habitat categories were combined, using a Geographic Information System, into four main habitat types: open water (i.e., below the extreme low water level), intertidal beaches and sand and mud flats (intertidal flats), saltmarsh, and upland (i.e., habitats above the extreme high tide level). The landward boundaries of the uplands at each site were the perimeters of the NWI and DEM quadrangles.

Sea Level Change Scenarios

The sea level change scenarios used in our analyses were obtained from Tables 9-1 and 9-2 in U.S. EPA (1995), supplemented, in southern San Francisco Bay, with data from local tide gauges. The tables in U.S. EPA (1995) allow the estimation of probabilistic sea level changes for specific sites and are partly based on historical rates of sea level change (obtained from tide gauges at or close to each of the sites) superimposed on projected 50% and 5% probability global sea level changes by 2100 of 34 cm and 77 cm, respectively. The 50% and 5% probability sea level change projections in U.S. EPA (1995) are based on assumed global temperature increases of 2°C (50% probability) and 4.7°C (5% probability), respectively. These temperature change estimates were developed by an expert panel (U.S. EPA 1995), and conform closely to the estimates in the most recent Intergovernmental Panel on Climate Change (IPCC) "best estimate" for 2100 (IPCC 2001).

Changes in sea level at specific sites will typically differ from global sea level change because of local and regional variability in land subsidence or uplift. At sites where the land is subsiding, the local rate of sea level rise will exceed the global. Conversely, at sites where land is rising (due, for example, to post-glacial uplift), the local rate of sea level rise may be less than the global. The use of historical rates of sea level change in the U.S. EPA (1995) study and in this study incorporates information on these local and regional influences in the estimation of likely future local sea level changes.

Modeling Habitat Change

Habitat change in response to sea level rise was modeled using the fourth version of the Sea Level Affecting Marshes Model (SLAMM 4). SLAMM is a discrete, algebraic model with time steps of 25 to 30 years. SLAMM 4 is the most recent version of this model. It uses a decision tree to convert the habitat type occurring in a 30-m cell to another for given changes in the inundation regime. The variables that are included in this process included elevation, habitat type, slope, sedimentation and accretion and erosion rates, substrate type (rock, sand, mud, etc.), overwash, the degree of exposure to the open ocean, salinity, the watertable in the affected area, and the extent to which the affected area is protected by sea walls. Thus SLAMM 4 includes considerations about the ability of sedimentation to preserve intertidal flats under rising sea levels, and the effects of topography and sea walls on marine encroachment and habitat change. In our modeling we initially assumed that only the currently existing sea walls would be in place. We then reran the model for Bolivar Flats assuming that all areas above the current extreme high water would be protected by new structures.

Additional details regarding SLAMM in general have been presented in Lee *et al.* (1992) and Park *et al.* (1993). Further details of the SLAMM 4 model and data pre-processing are given in Appendix 1.

RESULTS

Importance of the Study Sites for Shorebirds

More than 90% of the shorebirds counted at 66 Pacific coast sites during winter and autumn and spring migration by the Pacific Flyway Project comprise 13 species. Of these, between 40 and 90% of individuals counted are typically at the three Pacific coast sites considered in the study (Appendix 2), confirming their importance as staging sites for shorebirds. Similarly, 14 species comprise more than 80% of the shorebirds counted at between 50 and 100 Gulf of Mexico and Atlantic coast sites by the International Shorebird Survey during spring and autumn migration (Appendix 3). Of these 14 species, up to 46% of individuals counted occurred at the two sites considered in this study, confirming their importance as shorebird staging sites.

Rates and Extents of Sea Level Rise at the Study Sites

Figures 2 to 4 show the rates and extents of local sea level change predicted in U.S. EPA (1995) at each of the study sites. For each site three scenarios are shown: histori-

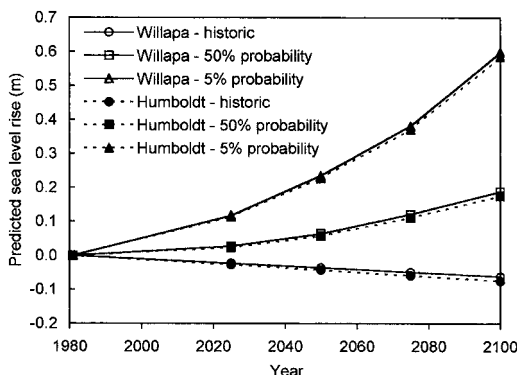


Figure 2. Predicted sea level change at Willapa Bay, Washington and Humboldt Bay, California. From data in U.S. EPA (1995).

cal (based on the historical rate of sea level rise that has actually been measured at one or more tide gauges at the site and excluding any future increase in this rate due to climate change); 50% probability [the median estimate of the likely rate of sea level change due to climate change from U.S. EPA (1995), superimposed on the historical rate]; 5% probability [the U.S. EPA (1995) estimate of the rate of sea level rise that has a 5% probability, superimposed on the historical rate]. For each of these scenarios, sea level change is predicted until 2100.

There is much variation in the predicted magnitudes of local sea level change. For example, on the Pacific coast, the predictions for Willapa Bay and Humboldt Bay are similar (Fig. 2). Historically, sea level has fallen slightly at both sites, perhaps due to tectonic

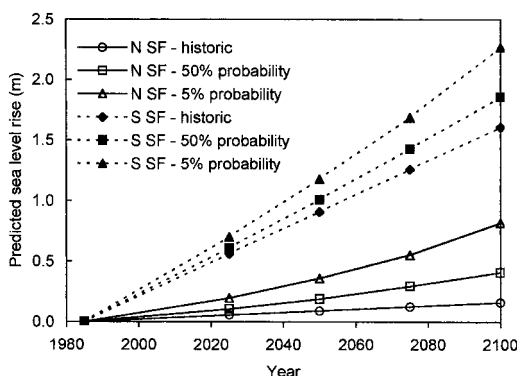


Figure 3. Predicted sea level change at north (N SF) and south San Francisco Bay (S SF), California. From data in U.S. EPA (1995).

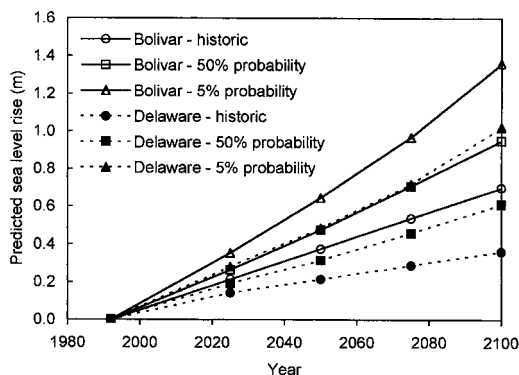


Figure 4. Predicted sea level change at Bolivar Flats, Texas and Delaware Bay, Delaware and New Jersey. From data in U.S. EPA (1995).

uplift of the land surface and/or post-glacial uplift. By 2100, U.S. EPA (1995) predicts that sea level at both these sites will have risen by about 0.25 m (50% probability). In contrast, sea level in San Francisco Bay has been rising historically, particularly in the southern bay. This could be due, in addition to global sea level rise, to tectonic movements resulting in land subsidence, and/or the depletion and compaction of subterranean aquifers (San Francisco Estuary Project 1992). When superimposed on the historical rates of sea level change, the predicted changes for the next two centuries are markedly different from those for either Humboldt or Willapa Bays. In northern San Francisco Bay, the 50% probability estimate from U.S. EPA (1995) is that sea level will rise by 0.3 m by 2100 (Fig. 3). The corresponding figure for southern San Francisco Bay is almost 2 m (Fig. 3). Even without considering any acceleration in the rate of sea level change due to climate change, the historical rate of change in southern San Francisco Bay could result in a 1.5 m rise by 2100 (Fig. 3).

At Bolivar Flats in the Gulf of Mexico, the historical rate of sea level change could result in a 0.6 m sea level rise by 2100 (Fig. 4). The 50% probability estimate is 0.8 m. At Delaware Bay, the historical rate of sea level change will result in a 0.3 m sea level rise by 2100 (Fig. 4). The 50% probability estimate is 0.6 m.

Figures 2 to 4 also show that the 5% probability sea level rise estimates are generally two to three times greater than the 50% estimates.

Sea Level Rise Effects on Intertidal Habitat

The changes in the extents of intertidal habitat projected by SLAMM 4 for each of the study sites are shown in Tables 1 to 3. These projections assume that no additional sea-walls will be installed at any of the study sites.

Tables 1-3 show that the degree of loss of intertidal feeding habitat for shorebirds (tidal flats) varies widely between sites, depending on the probability scenario used, current crustal movements, and on how far the change is projected into the future. Under the 50% probability scenario, Willapa Bay, Humboldt Bay, and northern San Francisco Bay show relatively little loss of habitat by 2050, whereas Bolivar Flats, southern San Francisco Bay, and Delaware Bay (three of the most important shorebird sites in North America) are projected to lose substantial areas of intertidal flats (approximately 38%, 24%, and 20%, respectively).

By 2100, substantial intertidal habitat loss is projected to begin to occur at the remaining sites under the 50% scenario, with approximately 18%, 29%, and 39% losses at Willapa, Humboldt, and northern San Francisco Bays, respectively, and 70%, 57% losses at southern San Francisco Bay and Delaware Bay, respectively.

In contrast, after showing initial habitat loss by 2050, the area of tidal flat habitat at Bolivar Flats is projected to slightly increase

by 2100. This is because at this site the coastline is able to migrate inland, converting up-land habitat to saltmarsh and intertidal flats. This is not possible at the other sites where the coastlines are constrained by either artificial protection structures (assumed to be effective in our modeling scenarios) or by topography.

The projections of the 5% probability scenario are similar to those of the 50% scenario, but generally more marked. By 2100, all sites except Bolivar Flats and Delaware Bay are projected to lose substantial areas of tidal flats. At Bolivar Flats, the tidal flats continue to extend in area at the expense of land habitat, while at Delaware Bay tidal flats are created as both saltmarsh and higher land are inundated.

In general, these projections indicate that, with the exception of Bolivar Flats, all of the study sites will lose tidal flat habitat but that the extent of loss will be site-specific. The habitat loss will be most marked at southern San Francisco Bay, and Delaware Bay. Substantial areas of tidal flats are projected to be lost at these sites even under the 50% scenario and as soon as 2050. In southern San Francisco Bay more than half of the current tidal flats may be lost by 2100 at the current rate of sea-level rise and without factoring in any future acceleration due to climate change. At Bolivar Flats, the tidal flat habitat loss is predicted to be almost com-

Table 1. Current extents (ha) and projected future percent change in intertidal and dry land habitat at Willapa and Humboldt Bays under three sea level rise scenarios.

Habitat	Historical rate of sea level change*			50% probability*		5% probability*	
	Current	2050	2100	2050	2100	2050	2100
Willapa Bay							
Tidal flats	21,157	-0.7	-0.7	-7.5	-18.1	-25.8	-61.5
Salt marsh	3,455	12.8	12.8	9.5	10.5	13.6	12.8
Dry land and other	62,389	-0.5	-0.5	-0.5	-0.7	-0.8	-1.3
Humboldt Bay							
Tidal flats	1,078	-0.1	-0.1	-13.0	-28.6	-42.4	-91.3
Salt marsh	40	72.6	72.6	88.9	175.6	229.2	1,886
Dry land and other	12,750	-0.2	-0.2	-0.3	-0.6	-0.7	-6.0

*The historical rate of sea level change projections are based on actual past sea level changes measured at the site.

The 50% probability projections represent future sea level change with an assumed 2°C warming (U.S. EPA's "best estimate" temperature scenario); 5% probability projections represent future sea level change with an assumed 4.7°C warming (U.S. EPA's 5% probability temperature scenario).

Table 2. Current extents (ha) and projected future percent changes in intertidal and dry land habitat at northern and southern San Francisco Bays under three sea level rise scenarios.

Habitat	Historical rate of sea level change*			50% probability*		5% probability*	
	Current	2050	2100	2050	2100	2050	2100
Northern							
Tidal flats	4,117	0.0	-4.0	-11.9	-39.4	-35.9	-80.7
Salt marsh	613	0.0	0.0	0.0	0.0	0.0	-18.1
Dry land and other	1,294	0.0	0.0	0.0	0.0	0.0	0.0
Southern							
Tidal flats	12,039	-12.9	-53.9	-24.0	-69.9	-42.9	-83.1
Salt marsh	3,534	0.8	-50.7	-2.2	-63.2	-11.6	-82.9
Dry land and other	75,694	0.0	-0.2	-0.1	-0.5	-0.2	-0.6

*The historical rate of sea level change projections are based on actual past sea level changes measured at the site. The 50% probability projections represent future sea level change with an assumed 2°C warming (U.S. EPA’s “best estimate” temperature scenario); 5% probability projections represent future sea level change with an assumed 4.7°C warming (U.S. EPA’s 5% probability temperature scenario).

plete (though temporary) by 2100 at the historical rate of sea level rise.

All of the above model predictions assume that no new coastal protection structures will be installed. However, it is likely that the local human populations at these sites will protect themselves and their property from the consequences of sea level rise. To evaluate preliminarily the likely influence of human responses, we considered one simple protection scenario for Bolivar Flats in which all current dry land areas will be protected with new sea walls. This model run resulted in reductions in the amount of higher land habitat predicted to be lost, but a 20%

increase in intertidal habitat loss by 2100 under the 50% scenario. Thus, the protection measures work in the sense that upland habitats are protected. However, this is at the expense of intertidal habitats where the rate of loss is exacerbated (or the rate of creation of intertidal habitat is reduced).

Habitat Loss Effects on Shorebird Numbers

It is difficult to predict the precise reduction in shorebird numbers likely to result from any estimated loss of habitat. This largely because the degree to which any site is saturated for any species is not known,

Table 3. Current extents (ha) and projected future percent changes in intertidal and upland habitat at Bolivar Flats and Delaware Bay under three sea level rise scenarios.

Habitat	Historical rate of sea level change*			50% probability*		5% probability*	
	Current	2050	2100	2050	2100	2050	2100
Bolivar Flats							
Tidal flats	398	-14.6	-93.8	-37.6	1.8	-80.6	1,073
Salt marsh	5,774	4.3	40.9	4.7	48.5	14.2	53.5
Dry land and other	18,275	-1.3	-12.9	-1.4	-17.6	-4.4	-53.1
Delaware Bay							
Tidal flats	2,665	-6.1	-23.0	-19.8	-57.4	-43.1	19.8
Salt marsh	13,766	6.4	9.3	9.0	12.2	11.3	-4.2
Dry land and other	20,538	-3.5	-5.5	-5.3	-7.5	-6.9	-11.3

*The historical rate of sea level change projections are based on actual past sea level changes measured at the site. The 50% probability projections represent future sea level change with an assumed 2°C warming (U.S. EPA’s “best estimate” temperature scenario); 5% probability projections represent future sea level change with an assumed 4.7°C warming (U.S. EPA’s 5% probability temperature scenario).

making predictions about changes in carrying capacity speculative. However, the scale of the habitat losses predicted in this study (even under the relatively conservative 50% probability scenario) leaves little room for doubt that major effects will likely occur to at least some shorebird species at some sites. Under the 50% scenario, southern San Francisco Bay and Delaware Bay are predicted to lose 60% or more of their intertidal feeding habitats by 2100. It is highly likely that this scale of habitat loss would be accompanied by major impairments in the ability of these sites to continue to support their current numbers of shorebirds. Conversely, the scale of habitat loss at Willapa Bay, Humboldt Bay, and north San Francisco Bay by 2100 (generally under 40% under the 50% probability scenario) may leave the shorebird carrying capacity of these sites less affected. Bolivar Flats (because of the ability of the sea at this site to encroach inland and convert upland habitat) is predicted to gain intertidal feeding habitat after initial losses up to 2050. In general, the scale of the intertidal habitat losses predicted for most of the sites cast serious doubts on their ability to continue supporting their current shorebird numbers.

DISCUSSION

This study provides evidence that future sea level rise due to climate change may adversely affect the ability of many coastal sites in the U.S. to continue to support large numbers of migratory and wintering shorebirds. Specifically, we predict that three of the five nationally and internationally important sites for shorebirds, San Francisco Bay, Delaware Bay and Humboldt Bay, may suffer severe habitat loss. The scale of these losses is likely to result in major reductions in shorebird numbers at these sites. Indeed, if our 50% probability predictions for south San Francisco Bay and Delaware Bay are realized, it is difficult to imagine how these sites could support shorebird numbers at fractions of their current sizes.

In general, our 5% probability scenarios result in even greater adverse effects. For example, almost twice as much habitat is pre-

dicted to be lost at Willapa Bay. However, at Delaware Bay, the 5% scenario results in a net gain of intertidal flats. This is due to the coastline migrating even farther inland at this site and converting dry land to intertidal habitat.

Our predictions for Bolivar Flats are very different from those at the other sites. Under our 50% probability scenario, our model predicts that, after initial loss of tidal flats, the coastline will move inland, converting existing saltmarsh to tidal flats. At the same time, the dry land edge of the saltmarsh will migrate inland, converting dry land habitat to saltmarsh. The reason for this difference between sites is because either existing coastal protection structures or topography constrain the abilities of the shorelines at the other sites to migrate inland. Our model also shows that installing seawalls at Bolivar Flats to prevent inundation of dry land would result in even greater loss of intertidal habitats.

This study also illustrates an important general point about the likely effects of climate change on ecological resources, which is that climate change does not happen in a vacuum; the impacts of climate change will interact with other already existing stress factors. For example, our modeling predicts that the extent of habitat loss at any one site will vary depending on local geomorphologic and anthropogenic factors. These include local land surface movements, human exploitation patterns (e.g., of aquifers) in the area, and human responses to the inland movement of the coastline. At sites where crustal movements exacerbate the rate of sea level rise, the loss of feeding habitat is likely to be accelerated. For example, we predict that by 2100 under the 50% scenario, southern San Francisco Bay will have lost about 70% of its intertidal feeding habitat. Comparison with the corresponding prediction for northern San Francisco Bay (a loss of about 39%) shows that much of the habitat loss in the southern bay is likely to be due to factors unrelated to, but exacerbating, the rise in sea level. In parts of southern San Francisco Bay, the land surface has historically been subsiding because of, at least in part, aquifer depletion and compaction (San Francisco Estuary

Project 1997). It is this crustal subsidence, superimposed on global sea level rise, which is responsible for the predicted large habitat loss. If current trends continue, by 2100 crustal subsidence alone is likely to have been responsible for about 1.5 m of the total 1.8 m sea level rise predicted by our 50% probability scenario. Thus, in this case, local human exploitation of natural resources greatly exacerbates the likely effects of global climate change. In contrast, we predict comparatively modest rates of habitat loss at Willapa Bay. At this site, global sea level rise is being mitigated by crustal elevation.

Furthermore, our modeling predicts that, if local human populations at coastal sites install new coastal protection structures such as seawalls, it may also result in the exacerbation of the rate of loss of shorebird habitat, as is shown in our preliminary analysis for Bolivar Flats.

Four important questions are raised by our study. The first concerns the likely interdependence of migration staging sites. If as our model predicts, Delaware Bay loses intertidal feeding habitat but Bolivar Flats shows gains, what will the overall effect be on the flyway? Similarly, what will the loss of San Francisco Bay, but the smaller effect on Willapa Bay, mean for shorebirds on the Pacific coast? The research that we have performed thus far raises, but cannot answer, these important questions.

Second, what is the likelihood that suitable new sites may be created by sea level rise as the sites discussed above are inundated? Without a coast-wide analysis, this question cannot be answered. However, given the generally steeper coastlines on the Pacific coast from central California northwards, it is likely that the potential for the creation of new sites may be greater on the Atlantic and Gulf of Mexico coasts. However, if such new sites were to mitigate habitat loss at existing sites, they would have to be created before (or at least at the same time), as the habitats at existing sites are lost. Any lag in the creation of new sites might result in their failure to prevent or mitigate population losses. Thus, it cannot be confidently concluded that new habitat will arise to replace that which will be lost.

Third, we have not attempted to incorporate the potential effects of climate change-induced habitat loss for shorebirds in their wintering or breeding areas. The late winter months may comprise energetic bottlenecks for many shorebirds and failure to gain access to adequate food reserves can result in increased mortality rates (Davidson and Evans 1982). Loss of feeding habitat due to sea level change could result in reductions in the carrying capacities of wintering areas in Central and South America. Also, it is in the high-latitude areas where shorebirds breed that the greatest habitat impacts of climate change are expected to occur [recent studies show that climate-induced habitat changes may already be occurring in arctic and subarctic areas of North America (Chapin *et al.* 1995)]. The combined effects of habitat change on their breeding areas (Zockler and Lysenko 2000), and intertidal habitat loss at their wintering and migratory staging sites could, potentially, have even more severe effects than could be brought about by any one factor.

Lastly, for many migrating shorebirds the synchronicity of events is important. For example, the timing of the Horseshoe Crab spawning at Delaware Bay and the arctic snowmelt interact to determine the feasibility of many species' migration strategies. These strategies have evolved in response to these parameters over many thousands of years. The relatively rapid predicted changes in sea level (and other climate change consequences, such as ambient temperature increase) could have adverse implications for these strategies.

Future research into the likely impacts of climate change on shorebirds (and, indeed, of any migratory animals) should attempt to incorporate the issues raised above into a more comprehensive, "life-cycle" approach than has been accomplished to date.

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Appendix 1.

SLAMM Model and Data Pre-processing

The first version of the SLAMM model was originally developed, in the early 1980s. It was based on manually coded elevation and habitat type data from topographic maps, using a 1-km² grid (Park *et al.* 1986a, b; Armentano *et al.* 1988). For the U.S. EPA Report to Congress on Climate Change (Park *et al.* 1989a, b; Titus *et al.* 1991), a second version of the model (SLAMM 2) used remotely sensed data and more refined modeling procedures to obtain estimates of vulnerability for coastal wetlands and lowlands for 20% of the nation's contiguous coastline. Subsequent to that, case studies were conducted for Puget Sound and Florida using a third iteration of the model, SLAMM 3 (Lee *et al.* 1992; Park *et al.* 1993).

SLAMM 4 differs from previous versions in several important respects. Most important, SLAMM 4 uses data from the Internet. It uses Digital Elevation Model (DEM) map data (<http://edcwww.cr.usgs.gov/doc/edchome/ndcddb.html>) instead of manually coded elevation data, and digital National Wetland Inventory (NWI) data (<ftp://www.nwi.fws.gov/arcdata>) instead of laboriously classified Landsat cover class data. The digital data enable the model to represent cells 30 m by 30 m, in contrast to a minimum 125-m cell size in SLAMM 3. However, the cover classes are restricted to the NWI classes; in particular, high and low salt marshes are not differentiated in SLAMM 4. Another important difference is that the current version uses probabilistic estimates of sea level rise rather than curvilinear regression estimates. Finally, the model provides the results directly in a grid file format suitable for use in a Geographic Information System, in contrast to the older version, which required a two-step conversion.

To combine the NWI and DEM data sets for use in the model, some pre-processing was necessary. The DEM quadrangles for each site were converted to Arc/Info GRID (v. 7.2.1) format and joined. Any cells that were missing elevation values were filled using a 4 × 4 cell window that assigned the mean of the fifteen 30-m cells surrounding the unknown value cell. After importing the NWI digital data into Arc/Info, adjacent quadrangles were merged and any boundaries separating contiguous areas of the same habitat type were eliminated. The resulting NWI coverage was then interrogated for all unique combinations of NWI codes and the list was grouped into the five habitat types. The resulting delineations were then rasterized into an Arc/Info 30-m grid and aligned with the DEM data. Finally, each of the processed grids was split by individual topographic boundaries and converted to ascii files as input into the SLAMM model.

Appendix 2. Pacific Flyway Project average counts of 13 species of shorebirds during autumn, winter, and spring at all coastal sites surveyed on the U.S. Pacific coast. Figures in parentheses are the percentages of the species totals that were counted at the three study sites (Willapa, Humboldt, and San Francisco Bays).

Species	Autumn	Winter	Spring
Black-bellied Plover <i>Pluvialis squatarola</i>	69,958 (69)	74,800 (70)	51,552 (67)
Semipalmated Plover <i>Charadrius semipalmatus</i>	17,371 (60)	8,387 (56)	20,244 (55)
Black-necked Stilt <i>Himantopus mexicanus</i>	26,008 (78)	17,845 (90)	9,966 (57)
American Avocet <i>Recurvirostra americana</i>	57,596 (97)	81,543 (92)	29,372 (87)
Greater Yellowlegs <i>Tringa melanoleuca</i>	4,298 (49)	2,972 (55)	6,450 (40)
Willet <i>Catoptrophorus semipalmatus</i>	131,343 (73)	103,362 (69)	34,563 (60)
Long-billed Curlew <i>Numenius americanus</i>	12,007 (72)	11,110 (58)	3,759 (53)
Marbled Godwit <i>Limosa fedoa</i>	161,031 (73)	129,150 (67)	181,346 (77)
Red Knot <i>Calidris canutus</i>	7,981 (76)	4,813 (45)	9,035 (39)
Western Sandpiper <i>Calidris mauri</i>	1,140,397 (66)	625,577 (74)	5,004,640 (60)
Least Sandpiper <i>Calidris minutilla</i>	276,110 (70)	147,903 (52)	193,347 (75)
Dunlin <i>Calidris alpina</i>	1,006 (a)	1,094,644 (58)	1,252,102 (37)
Dowitcher sp. <i>Limnodromus</i> spp.	118,202 (75)	98,851 (68)	443,777 (72)
Total (13 spp.)	2,023,308	2,400,957	7,240,153
Total all species	2,168,876	2,452,111	7,307,762

a: no accurate data for Dunlin in autumn.

Appendix 3. International Shorebird Survey average counts of 14 species of shorebirds during autumn and spring on U.S. Atlantic and Gulf of Mexico coasts. Figures in parentheses are the percentages of the species totals that were counted at the two study sites (Bolivar Flats and Delaware Bay).

Species	Autumn	Spring
Black-bellied Plover <i>Pluvialis squatarola</i>	52,278 (1)	29,462 (10)
Semipalmated Plover <i>Charadrius semipalmatus</i>	51,432 (1)	22,905 (6)
American Avocet <i>Recurvirostra americana</i>	32,153 (7)	21,692 (46)
Greater Yellowlegs <i>Tringa melanoleuca</i>	15,948 (1)	9,082 (12)
Lesser Yellowlegs <i>Tringa flavipes</i>	120,967 (2)	38,573 (6)
Willet <i>Catoptrophorus semipalmatus</i>	10,696 (3)	13,159 (12)
Whimbrel <i>Numenius phaeopus</i>	2,487	1,371 (a)
Ruddy Turnstone <i>Arenaria interpres</i>	9,913 (2)	33,162 (25)
Red Knot <i>Calidris canutus</i>	42,783 (<1)	31,435 (15)
Sanderling <i>Calidris alba</i>	88,563 (<1)	36,201 (4)
Semipalmated Sandpiper <i>Calidris pusilla</i>	274,763 (4)	226,703 (8)
Least Sandpiper <i>Calidris minutilla</i>	101,653 (3)	60,748 (3)
Dunlin <i>Calidris alpina</i>	55,904 (8)	65,798 (15)
Dowitcher sp. <i>Limnodromus</i> spp.	161,138 (16)	143,357 (34)
Totals	1,020,678	733,648
Total all species	1,092,247	898,009

No accurate data available for total Whimbrel numbers.