The impact of sea-level rise on Snowy Plovers in Florida: integrating geomorphological, habitat, and metapopulation models

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Abstract

Sea-level rise (SLR) is a projected consequence of global climate change that will result in complex changes in coastal ecosystems. These changes will cause transitions among coastal habitat types, which will be compounded by human-made barriers to the gradual inland migration of these habitat types. The effect of these changes on the future viability of coastal species will depend on the habitat requirements and population dynamics of these species. Thus, realistic assessments of the impact of SLR require linking geomorphological models with habitat and population models. In this study, we implemented a framework that allows this linkage, and demonstrated its feasibility to assess the effect of SLR on the viability of the Snowy Plover population in Florida. The results indicate that SLR will cause a decline in suitable habitat and carrying capacity for this species, and an increase in the risk of its extinction and decline. The model projected that the population size will decline faster than the area of habitat or carrying capacity, demonstrating the necessity of incorporating population dynamics in assessing the impacts of SLR on coastal species. The results were most sensitive to uncertainties in survival rate and fecundity, and suggested that future studies on this species should focus on the average and variability of these demographic rates and their dependence on population density. The effect of SLR on this species' viability was qualitatively similar with most alternative models that used the extreme values of each uncertain parameter, indicating that the results are robust to uncertainties in the model.

Keywords: Charadrius alexandrinus, climate change, coastal land-cover, demographic modeling, MaxEnt, population viability analysis, RAMAS, SLAMM, species distribution modeling

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Introduction

One of the most uncertain aspects of future climate change is the projected rise in sea level. In addition to the uncertainties in predicting future changes in sea levels, complex interactions among climatic and biotic components of coastal systems (Scavia *et al.*, 2002) and human activities make it difficult to project the effects of sea-level rise (SLR) on species and ecosystems. Although many coastal land-cover types (or habitat types) such as tidal marshes, sandy beaches, intertidal areas, open water, and dry-lands change continuously as a result of geological processes, rising sea levels will likely cause substantial reductions in the area of these land-cover types. This problem will be compounded by

barriers to inland migration of coastal habitats, such as seawall and coastal developments (EPA, 2009).

A few previous studies have analyzed the effect of projected SLR on particular species (Daniels *et al.*, 1993; Shriver & Gibbs, 2004; LaFever *et al.*, 2007; Fuentes *et al.*, 2010; Peterson *et al.*, 2010; Traill *et al.*, 2010). However, these studies considered the future, higher sea level as a static condition; they did not consider the gradual changes in sea level and the possibility of transitions among land-cover types as result of SLR, which would lead to their gradual inland movement. Other studies have examined the effects of SLR in a more dynamic manner, by using geomorphological models to forecast land changes due to SLR, but generally focus on changes in habitat types, emphasizing impacts on habitats important for some species, but not focusing on the dynamics or persistence of particular species (Moorhead & Brinson, 1995; Galbraith *et al.*, 2002). In addition, at least one study examined the effects of SLR

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on flooding events and the subsequent impacts on fecundity for six shore-bird species in Europe and linked this model to a population viability analysis (PVA) for one species (van de Pol *et al.*, 2010). This study focused on the impacts of extreme events (i.e. flooding) on population viability, whereas our study focuses more generally on the impacts of changes to overall habitat suitability due to SLR on Snowy Plover population viability.

In addition to SLR, tropical cyclones are expected to change coastline profiles. Given projections of warming seas tropical cyclone frequency is expected to decrease; however, intensity is expected to increase (Elsner *et al.*, 2008). Complex interactions and feedbacks among species, tropical cyclones, and the coastal habitat exist (Convertino *et al.*, 2011) and are difficult to forecast without large uncertainties. At the species level, the changes in coastline and transitions among coastal land-cover types will cause changes in both the size and quality of habitat patches. Such changes can result in negative effects on species persistence. Examining SLR impacts as static changes after an elapsed time will neglect to account for the effects on population demographic processes during the transition period.

In this study, we implemented a framework that integrates three existing tools, a geomorphological model of SLR, a habitat model, and a metapopulation model, in a novel way to provide more realistic estimates of the effects of SLR on species viability. The geomorphological model predicts the gradual increase in sea level, and the transition among coastal land-cover types; the habitat model converts these into a time series of habitat maps for the focal species, and a time series of population structures; and the metapopulation model simulates the dynamics of populations to predict future population sizes, and risks of extinction and decline. We applied this integrated model to estimate the effect of SLR on the viability of Snowy Plover (*Charadrius alexandrinus*) populations along the Gulf Coast in Florida.

Materials and methods

We integrated a deterministic SLR model (Sea Level Affecting Marsh Models; SLAMM) (Clough *et al.*, 2010), a habitat suitability model (Maximum Entropy; MaxEnt) (Phillips & Dudik, 2008), and a demographic population model (RAMAS GIS) (Akçakaya, 2005) to assess the viability of the Snowy Plover populations along the Gulf Coast of Florida (Fig. 1). This framework provides a novel method for integrating SLR due to climate change effects into a PVA. In this application of the framework, we only considered climate change effects on available habitat as affected by projected SLR; we did not account for direct climate change effects on this species (e.g. possible change in survival rates due to increasing mean temperature).

Study species and study area

Snowy Plover (*C. alexandrinus*; known also as Kentish Plover) is a small shorebird species, with breeding habitat comprised of sparsely vegetated sandy ocean beaches, dry salt flats, high salinity drying salt ponds, dredged material islands, and gravel river bars (Colwell *et al.*, 2005; Page *et al.*, 2009). In most populations, male birds are the sole provider of parental care (i.e. chick rearing) and females frequently double-brood during the breeding season. Though not threatened globally, most North American populations are of conservation concern. The Florida Fish and Wildlife Conservation Commission classifies Florida Snowy Plover populations as Threatened (Gruver, 2010). In Florida, Snowy Plovers are restricted to beach areas
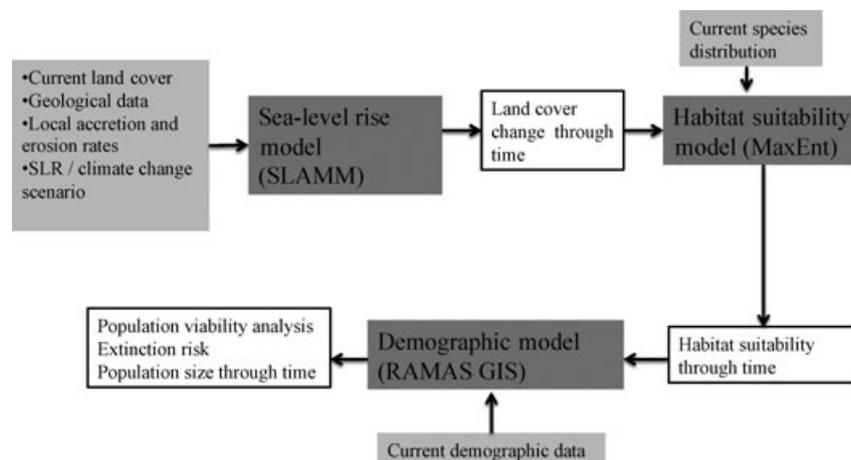
Fig. 1 The framework used in this study to analyze the effect of sea-level rise (SLR) on the viability of a species. The dark-shaded components are the three main models integrated in our framework. The light-shaded components are data inputs, and the clear rectangles list the primary outputs of these models.

along the Gulf Coast (Fig. 2), with ca. 80% of nesting pairs found in the Panhandle region, and the remainder found in the Peninsula region. Successful nesting primarily depends on extent of dune habitat, lack of beach development (e.g. road construction, beach hardening), and lack of human disturbance (e.g. recreational beach use) (Lamonte *et al.*, 2006). In addition, all nests in Florida are observed on beaches of <3° in slope (Page *et al.*, 2009) and >5 m wide, and frequently near tide pools (Himes *et al.*, 2006). These characteristics describe locations that are particularly vulnerable to landscape changes due to SLR.

Predicting SLR-induced land-cover changes

We used the Sea Level Affecting Marshes Model (SLAMM; Lee *et al.*, 1992; Clough *et al.*, 2010) to predict land-cover changes along the Gulf Coast of Florida under 1 and 2 m SLR scenarios. The SLAMM program is a deterministic model of the geomorphological processes resulting in coastal wetland conversions and shoreline modifications during long-term SLR (Clough *et al.*, 2010), and has been used to simulate changes due to SLR in numerous coastlines in the United States (Lee *et al.*, 1991, 1992; Park *et al.*, 1991, 1993; Galbraith *et al.*, 2002; Glick & Clough, 2006; Chu-Agor *et al.*, 2011). Beaches (estuarine and ocean) are among the land cover categories considered in SLAMM, and were the focus of Galbraith *et al.* (2002), who investigated the changes to shore-bird habitat (i.e. sand beaches and mud flats). The version used in this study, SLAMM 6, includes an empirical accretion model, which simulates changes in accretion rate as sea levels rise
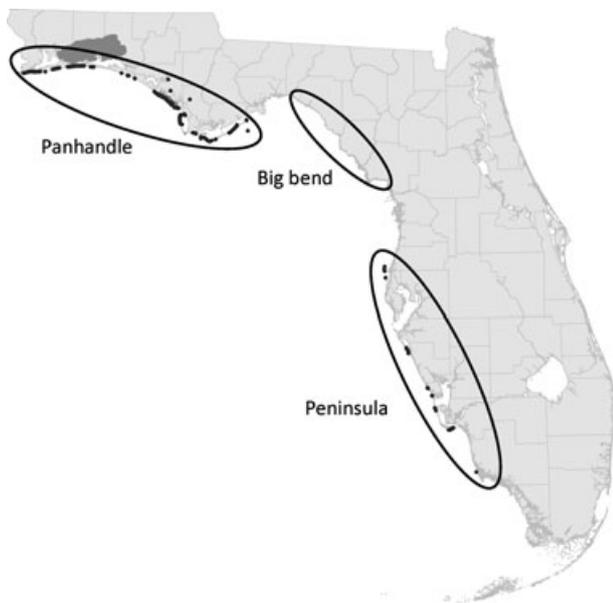
Fig. 2 Geographical extent of study area. Survey locations (●) for 2009 Snowy Plover census on the Gulf Coast of Florida. The metapopulation structure is depicted by three ellipses outlining approximate location of three distinct populations. Dark gray areas in Panhandle region denote Eglin and Tyndall Air Force Bases.

(Clough *et al.*, 2010). In brief, as sea level increases, inundation time and depth increase, allowing more time for sediment to settle and thus providing a greater source volume for suspended sediments.

The SLAMM operates using a GIS framework, where input data and output results are stored as map layers. The model divides a map layer of the study region into independent equally sized grid cells and calculates the conversion of each individual cell from one land-cover category to another primarily based on minimum elevation of the cell. Each land-cover category is associated with specific elevation boundaries based on the site specific input parameters (discussed below). Each cell is assigned to a land-cover category based on its minimum elevation in relation to these elevation boundaries. Changes to a cell's minimum elevation are calculated at each model time step (annual time steps in our study) based on the user selected SLR scenario, accounting for both global and local SLR trends. For each time step, conversion from one land-cover category to another for each cell is determined based on the new minimum elevation for the cell and a complex internal decision tree (Park *et al.*, 2003; Clough *et al.*, 2010).

The inputs to SLAMM include elevation, land-cover, site-specific information (e.g. erosion rate, accretion rate, storm frequency, tidal trends), and a forecast for future SLR based on a climate change scenario. We used tidal and current data collected from a publicly available dataset (NOAA, 2010) to estimate tidal ranges and local SLR trends, and estimated local accretion rates based on values found in published literature (parameter values are reported in Supporting Information – SLAMM Parameters). SLAMM 6 includes an option to delineate sub-sites within the whole modeled region, for which site-specific information can vary (e.g. accretion rate). In our model, we define seven sub-sites, providing sub-site specific information on accretion rates and tidal ranges for each. We used SLAMM default values (Clough *et al.*, 2010) for accretion and erosion rates for which we were unable to acquire site-specific data.

Many implementations of SLAMM use land-cover data provided by the National Wetlands Inventory (NWI) and the SLAMM documentation provides a conversion from NWI land-cover classification values to SLAMM land-cover classification values (Clough *et al.*, 2010). We used categorical land-cover data from the Coastal Change Analysis Program of the National Oceanic and Atmospheric Administration (C-CAP NOAA) that were converted to match the SLAMM land-cover categories (see Table S1 in Supporting Information for conversions applied). We used C-CAP data, rather than NWI data, because these data have been updated more recently for our study region (C-CAP data were collected in 2006 for this region), and based on visual inspection, more accurately represent important barrier island regions.

We used the USGS National Elevation Dataset (NED) at a spatial resolution of 1 arc second (ca. 30 × 30 m) (Gesch *et al.*, 2002; Gesch, 2007). This elevation dataset covers the conterminous United States with a vertical accuracy of ±4.75 m (95% confidence interval). The vertical accuracy of this dataset is spatially variable and is much higher for coastal areas (Gesch,

2007, 2009; Weiss *et al.*, 2011). Data sources for the NED are standard production USGS Digital Elevation Models (DEMs) and elevations datasets that are project-specific or agency-specific. Many, but not all, areas along the Florida Gulf Coast were developed using high-resolution LiDAR data (NED Metadata), which have been reported to have a vertical accuracy of approximately ±0.2 m (95% confidence interval) (Gesch, 2009). In our study, the $NED_{1\,Arc}$ was aggregated to a spatial resolution of 120 × 120 m. Investigations of the effects of SLR on near-shore habitats benefit from high-resolution, high accuracy elevation data such as LiDAR (Cahoon & Guntenspergen, 2010), and this is true for SLAMM (Clough *et al.*, 2010). However, SLAMM was developed prior to the availability of high-accuracy elevation data (e.g. LiDAR) and readily utilizes lower accuracy data (Clough *et al.*, 2010). The potential effects of vertical inaccuracy are addressed in the Discussion below (see also Table S5).

We parameterized SLAMM to model SLR of 1.0 and 2.0 m by 2100. These values are pre-calculated options in SLAMM and annual SLR increments are calculated by rescaling the SLR curves projected with the IPCC A1-B scenario (i.e. SLR determined by the IPCC A1-B was scaled such that SLR by 2100 is 1.0 and 2.0 m) (Clough *et al.*, 2010). The outputs of the SLAMM program are new land-cover map layers that reflect the changes due to SLR for the time period from 2010 to 2100 in annual time-steps. Overall, the IPCC (2007) scenarios predict SLR in the range of 0.18–0.59 m. However, these predictions exclude 'future rapid dynamical changes in ice flow' (IPCC, 2007), i.e. they exclude the possibility of increased rates of Greenland and Antarctic ice sheet flow in the future; 'therefore the upper values of the ranges are not to be considered upper bounds for sea level rise' (IPCC, 2007; *Summary for Policymakers*). More recent studies have predicted higher levels, including a rise of 0.8–2.0 m (Pfeffer *et al.*, 2008), and 0.9–1.3 m (Grinsted *et al.*, 2010) by the end of the century. Based on the temperature increases projected by the same IPCC scenarios and using a statistical, 'semiempirical' approach, Vermeer & Rahmstorf (2009) project a SLR ranging from 0.75 to 1.9 m. Thus, we used 1.0 and 2.0 m SLR as a plausible and realistic range of scenarios.

Projections of Snowy Plover habitat suitability

We used MaxEnt (Phillips & Dudik, 2008) to calculate the current and future distribution of Snowy Plover habitat. MaxEnt is a widely used species distribution model (SDM) and has been applied previously to shorebird species (Fuller *et al.*, 2008; Smith & Deppe, 2008). Species presence records and environmental variables are used as input data for MaxEnt. MaxEnt is a machine learning algorithm that attempts to determine the function that is the best fit of the environmental variables given the species presence records as response variables. For environmental layers, we used the C-CAP NOAA land-cover dataset converted to SLAMM land-cover categories (same layer as was used for first year of SLAMM simulations) and geological layers (Scott *et al.*, 2001). The SLAMM outputs provide information on the land cover type (i.e. estuarine beach, ocean beach, etc.), but the geology of a particular land

cover type may differ across sites. For example, Convertino *et al.* (2011) found that ocean beach areas of the Panhandle and Peninsula regions are characterized by alkaline medium fine white sand and silt, whereas ocean beach areas of the Big Bend region are characterized by sediments composed of limestone, limestone/dolomite, and dolomite. The geological layer (GEO) that we used represents the distribution of soils, rocks, and sediment types located within 3 m of land surface. The C-CAP data were last collected in 2006, thus we used data from the 2006 census of Florida Snowy Plover populations as our presence records. In total, there were 273 presences (Snowy Plover nest sightings) in 2006; 227 in the Panhandle region and 46 in the Peninsula region. To evaluate the fit of the MaxEnt model, 75% of the presence records were used to train the MaxEnt model, and the remaining 25% of presence records were used as test data to evaluate the model fit. The MaxEnt model run using only the output of SLAMM did not fit the testing data as well as the MaxEnt model run using both SLAMM output and GEO. While we cannot say with certainty why differences in geology lead to differences in habitat suitability, we may speculate that different soil compositions support different invertebrate communities (a major food source for Snowy Plovers) that are more desirable to Snowy Plovers. We used the projection functionality of MaxEnt to predict future habitat suitability for Snowy Plovers. MaxEnt projected the species distribution by substituting the current land-cover map with future land-cover maps (the results of the SLAMM analysis), and applying the presence-environment relationship estimated for 2006. This process resulted in a time series, from 2010 to 2100, of predicted habitat suitability. In using the geological layer, we were able to better fit the 2006 presence data, however, by including this layer for future habitat suitability projections, we are assuming that the geology of this area remains stable over the simulation period.

Demographic model

We developed a metapopulation model, with an age- and sex-structured, density-dependent, stochastic model for each population of the metapopulation. The details of the model development are given in the Appendix in the Supporting Information, including the estimation of most model parameters. To analyze the sensitivity of model parameters to data uncertainties, we estimated *Low*, *Medium*, and *High* values of each parameter (Table S2). We developed the model using RAMAS GIS (Akçakaya, 2005), which calculated the spatial structure of the metapopulation (the location and size of populations) for each time-step based on the habitat suitability maps calculated using the MaxEnt SDM. This analysis yielded a metapopulation structure consisting of three separate populations along the Florida Gulf Coast, here after referred to as the Panhandle, Big Bend, and Peninsula populations (Fig. 2; further details in the Appendix – Spatial structure of the metapopulation). For a no SLR scenario, we used the habitat suitability map calculated for 2010 and assumed no change in habitat suitability over the 90 year simulation run.

We calculated carrying capacity (K) and initial abundance of a population as functions of total patch habitat suitability

(THS), with functions scaled according to population size estimates from census data for 2009 (FSA, 2010; FWC, 2010). We used the 2009 data because they provide the most recent estimate of Snowy Plover population size and were collected by veteran surveyors, yielding improved surveyor abilities over past survey years. As upper and lower bounds (i.e. *Low* and *High* values) for both initial abundance and carrying capacity, we increased and decreased the scaling values by 20%, respectively (Table S2).

We based our demographic model on breeding season census data collected in both Florida (Sprandel *et al.*, 1997, 2000; Himes *et al.*, 2006; Lamonte *et al.*, 2006) and the Pacific Coast of the United States (i.e. Western Snowy Plover) (Colwell *et al.*, 2008; Knapp & Peterson, 2008; Lauten *et al.*, 2008; Page *et al.*, 2008) as well as on data presented in published studies from Pacific Coast US populations (Stenzel *et al.*, 1994, 2007; Colwell *et al.*, 2005, 2007; Page *et al.*, 2009). We constructed an age- and sex-structured matrix model with two age classes (juvenile and adult), parameterized according to a pre-reproductive census and polyandrous mating system (Table 1). We assumed a 1 : 1 initial sex ratio based on observations from several studies (Mullin, 2006; Stenzel *et al.*, 2007; Page *et al.*, 2009). Although the initial sex ratio is 1 : 1, the sex ratio can get skewed in small populations due to demographic stochasticity, which in turn may affect reproduction. To account for this effect, we included separate male and female stages in the model. We calculated variability in survival and fecundity due to environmental fluctuations by subtracting estimated demographic variance from total variance observed in long time series of these variables, using the methods of Akçakaya (2002) with data from (Colwell *et al.*, 2008; Lauten *et al.*, 2008; Page *et al.*, 2008; Stenzel *et al.* (2007).

Density dependent factors play a role in population dynamics for this species (Page *et al.*, 2009), and provide the link between the habitat model and the demographic rates. Density dependence is implemented by reducing demographic rates as a function of population size and carrying capacity (K) at each time step, with K determined from habitat maps projected by the SDM as described above. The available data were not sufficient to precisely quantify density dependence. Thus, we selected two types of density dependence: Ceiling, which assumes that the population grows according to the stage

matrix until it reaches the carrying capacity, and Contest, which requires specifying a maximum population growth rate, R_{max}, at low population sizes, and assumes Beverton–Holt type density effects on growth rate as the population approaches its carrying capacity.

Because of a lack of data for dispersal of Snowy Plover in Florida, we estimated dispersal rates based on data collected from populations on the Pacific Coast of the United States, where adult Snowy Plovers show high breeding site fidelity. There is substantial dispersal within and between breeding seasons (Page *et al.*, 2009), with larger distances covered between breeding seasons (Stenzel *et al.*, 1994). In addition, natal dispersal is common (Colwell *et al.*, 2007; Stenzel *et al.*, 2007). We parameterized a dispersal–distance function to fit the observed dispersal trends (see Appendix – Dispersal). We then adjusted dispersal rates for each population by scaling dispersal from larger populations to small populations by the ratio of carrying capacities as outlined in (Akçakaya & Raphael, 1998). This correction yields asymmetric dispersal rates (Table S3), such that the dispersal rate from larger populations to smaller populations is smaller than the reciprocal dispersal, decreasing the number of estimated dispersers from the large population. If such a correction is not applied, small populations may act as sink populations in the model simulation, resulting in pseudo-sink dynamics that inappropriately increase the risk of extinction for a species. Our dispersal rate estimates are consistent with the small amount of data collected on dispersal of Snowy Plover between the Panhandle and Peninsula populations in Florida (R. Pruner, personal communication).

Spatial correlation in the variability of vital rates arises from correlations in environmental conditions in different populations (e.g. partial synchrony of climatic variables across large distances), and can have substantial effects on metapopulation viability. We assumed that spatial correlation between Florida Snowy Plover populations is similar to observed spatial correlations among Western Snowy Plover populations, and fitted a correlation–distance function to data on fecundity (see Appendix – Correlation–distance function).

Simulations

Using the demographic parameters outlined above, we simulated the dynamics of the Florida Snowy Plover metapopulation for a 90 year interval. Simulations were run both with the *Medium* values of all parameters, and with the extreme values of each parameter discussed above, changed one at a time (i.e. all other parameters were set to their *Medium* value while one parameter of interest was varied to the *Low* or *High* value). Each simulation run consisted of 1000 replications. We summarize the predictions of the simulations by reporting risk of extinction, risk of decline to 20 individuals, and the expected minimum abundance (EMA). Risk of extinction is the proportion of replications that reach 0 individuals during the 90 year simulation interval; we used this measure because of its direct relevance to conservation. The risk of decline to 20 individuals is the proportion of replications in which the total number of birds in the metapopulation declines to 20 at least once during the 90 year simulation interval. We used this measure because

Table 1 Stage matrix for Snowy Plover demographic model

	Female – juvenile	Female – adult	Male – juvenile	Male – adult
Female – juvenile	0	0	$f_F S_J$	$f_M S_J$
Female – adult	$S_{A,F}$	$S_{A,F}$	0	0
Male – juvenile	0	0	$f_M S_J$	$f_M S_J$
Male – adult	0	0	$S_{A,M}$	$S_{A,M}$

The matrix is age-structured and sex-structured, including two age classes, juveniles and adults, and two sex classes. The matrix was parameterized according to a pre-reproductive census and polyandrous mating system. $S_{A,F}$ and $S_{A,M}$ are adult female and male survival rates, respectively, f_F and f_M are female and male fledglings per male, respectively, and S_J is juvenile survival rate.

decline to a threshold larger than zero (total extinction) is thought to give more reliable estimates of risk because of the uncertainty in the dynamics of very small populations due to various Allee effects. The EMA is the minimum metapopulation abundance during the 90 year period, averaged over the 1000 replicates. We used this measure because it provides a robust indication of the propensity for decline, especially when the risk of extinction is small (McCarthy & Thompson, 2001). There may be a substantial impact of SLR even if extinction risk is zero in both cases (with and without SLR); a population with very few individuals left at the end of a 90 year simulation is still not extinct, even if it has a very high risk of extinction beyond the simulated time period. EMA takes this into account by comparing the minimum population sizes within the 90 year period.

Results

The SLR model (SLAMM) predicted future changes in the composition of land-cover types in the coastal habitats within the range of the Snowy Plover, resulting in an overall decrease in 'dry' land-cover classes and an increase in the 'open ocean' class (Figure S1; for a subset of map layers, see Supporting Information Figure S2). The species distribution model MaxEnt indicated that SLAMM land categories 'Estuarine Beach' and 'Ocean Beach' (SLAMM class codes 10 and 12, respectively) were the most suitable categories for Snowy Plovers, with average suitability values of approximately 0.6 and 0.5, respectively (because of the GEO layer, a SLAMM category does not correspond to a single habitat suitability value). Habitat maps created by the SDM based on these predictions showed how changes in land-cover translate into changes in the dis-

tribution of potential Snowy Plover habitat (for a subset of map layers, see supporting information Figure S3). The time series of habitat maps were used to predict the future changes in the total area of habitat and total carrying capacity (K) of the populations (Fig. 3). Finally, the population simulations predicted the future change in average abundance (Fig. 3) and viability of the Snowy Plover populations. The proportional decrease in population abundance was larger than the decrease in habitat area or carrying capacity (Fig. 3).

The simulation results show that SLR will likely cause a decrease in the viability of the Florida Snowy Plover populations (Fig. 4). A metapopulation model that incorporates land-cover changes resulting from either a 1 or a 2 m, SLR scenario resulted in a decreased population viability of Florida Snowy Plovers, based on three viability measures examined in this paper: risk of extinction, risk of decline to a total metapopulation size of <20 birds, and the expected minimum total metapopulation abundance for the 90 year time period forecasted (Table 2, Variable Change – None). With 2 m SLR, the risk of extinction was 3.7% (0.037) more than the baseline risk of about 7%, risk of decline to 20 birds 7.6% (0.076) more, and EMA was 27.3 individuals less than without any SLR (Table 2), under the *Medium* values of all parameters. With 1 m SLR, the impacts were less: 1.9% increase in extinction risk, 6.3% increase in risk of decline, and 20.1 individuals decrease in EMA. We also calculated the increase in risks of extinction and decline, and the decrease in EMA caused by SLR under the assumption of *High* and *Low* values of each parameter. With this, the effect of SLR was a 0–4.9%
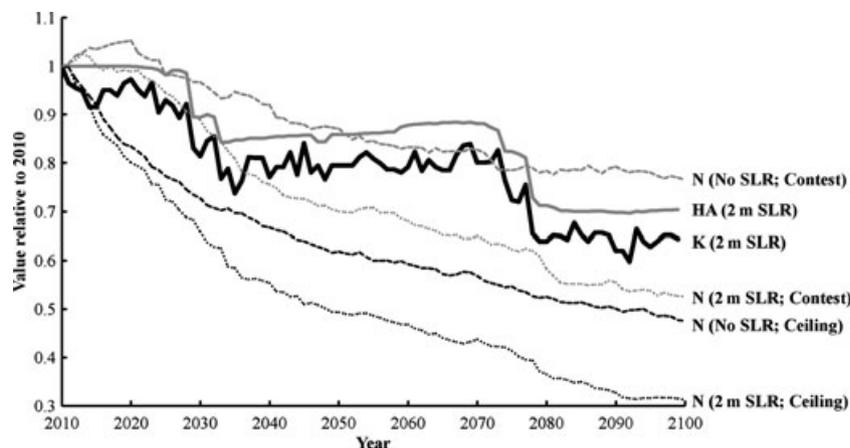
Fig. 3 Projected declines in: the total area of Snowy Plover habitat area predicted by the habitat model, based on the projections of the 2 m sea-level rise model (HA); the total carrying capacity of populations identified by RAMAS, based on the habitat model (K); and total metapopulation abundance (N), averaged over 1000 replications, with 2 m sea-level rise (2 m SLR) and without SLR (No SLR) considering ceiling and contest density dependence functions. Simulations considering 1 m SLR gave smaller declines but qualitatively similar results.
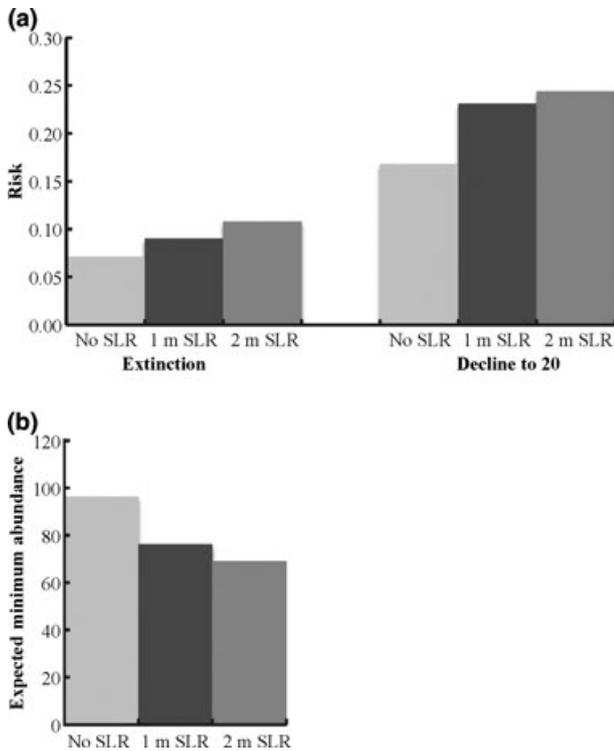
Fig. 4 Risks of extinction and decline to 20 birds (a) and expected minimum abundance (b) with No, 1 m and 2 m sea-level rise (SLR).

increase in extinction risk, 0–9.9% increase in decline risk, and 0.1–75.3 decrease in EMA.

Sensitivities of these results to uncertainties in model parameters were quantified by the difference in each viability measure (such as risk of extinction) with the *High* and *Low* values of the parameter, under 2 m SLR. The results were most sensitive to uncertainties in fecundity and survival rates, and moderately sensitive to R_{max}, and variability of survival rates and fecundity (Table 3). The results were similar under 1 m SLR.

Discussion

Our results suggest that the Florida Gulf Coast Snowy Plover populations face additional risk due to projected SLR. As a result of SLR, the risk of extinction in the next 90 years increases from about 7% to 9% for 1 m SLR, and or to 11% for 2 m SLR. It is important to emphasize that our model focuses only on one regional metapopulation of this species. Because this is a highly mobile species with a cosmopolitan distribution, and inland as well as coastal breeding populations, the effects of SLR on this metapopulation cannot be extrapolated to the global viability of the species.

Although we believe the range of SLR we assumed (1–2 m) is realistic, a smaller SLR (e.g. 0.5 m) can also

be considered plausible. We did not simulate this because the precision of the available DEM may not be high enough to simulate such a small increase in sea levels (Weiss *et al.*, 2011). If the SLR is indeed about 0.5 m, its effects on risks will likely be between the risks we predicted for 0 and 1 m SLR (Fig. 4). Related to this issue, vertical inaccuracies in elevation data may lead to uncertainty in our estimates of habitat suitability for Snowy Plover, and consequently our estimates of the population carrying capacities (K). However, we believe this uncertainty is accounted for in our analysis of model sensitivity to the estimated carrying capacity (K) for each population, because any vertical error should be normally distributed across map cells, and we estimate the effects of Snowy Plover habitat quality on demographic rates by combining information from hundreds to thousands of cells (see Appendix – Carrying capacity and initial abundance).

If effective conservation measures are taken (see below), the risks of extinction and decline of this metapopulation may be lower than predicted by our model. However, under current conditions, we believe our results may underestimate the risk due to climate change, because we modeled only habitat change resulting from SLR, and its effects on vital rates and population dynamics, through density dependence. There will likely be other effects of climate change, which may include shifting, fragmenting or shrinking habitat due to changes in temperature and precipitation regimes, or direct effects on survival and fecundity via changes in average values or the variability of temperature and rainfall. For example, an increase in the probability of heavy rainfall during the breeding season may increase the variance and decrease the mean of these demographic rates. In addition, there may be positive effects of climate change on this species; Snowy Plovers seem to prefer nesting in locations that recently experienced a hurricane (likely because hurricanes can create favorable Snowy Plover breeding habitat; Convertino *et al.*, 2011). However, a shift in the timing of hurricanes toward the breeding season can also result in reduced survival and fecundity and increased variance of these rates.

In principle, such effects can be incorporated into our framework, because the population model we used allows modeling catastrophic events or even gradual increase in variability of survival rates and fecundity. Previous applications with the same modeling platform have incorporated various types of climate effects (Keith *et al.*, 2008; Anderson *et al.*, 2009; Brook *et al.*, 2009; Lawson *et al.*, 2010). However, modeling these direct effects requires projections of the climatic extremes and knowledge of their impact on demographic rates. When data on these factors become

Table 2 The effect of 1 and 2 m sea-level rise (SLR) on the viability of Snowy Plover metapopulation in Florida, expressed as the difference in each measure (the risk of extinction, risk of decline to 20 birds, and expected minimum abundance) with and without SLR

			Effect of sea-level rise (SLR)					
			Extinction risk (RE)		Decline risk to 20 individuals (R20)		Expected minimum abundance (EMA)	
			$RE_{SLR}-RE_{NoChange}$		$R20_{SLR}-R20_{NoChange}$		$EMA_{SLR}-EMA_{NoChange}$	
Density dependence type	Variable changed	Estimate	1 m	2 m	1 m	2 m	1 m	2 m
Ceiling	None	Medium	0.019	0.037	0.063	0.076	−20.1	−27.3
	Adult survival	High	0.000	0.000	0.002	0.001	−44.2	−64.7
		Low	0.019	0.040	−0.007	0.008	0.1	−0.2
	Juvenile survival	High	−0.002	0.002	0.005	0.014	−31.5	−51.7
		Low	−0.030	0.003	0.014	0.030	−2.3	−2.7
	Fecundity	High	0.001	0.000	−0.001	0.002	−49.2	−75.3
		Low	0.016	0.016	0.005	0.012	−0.2	−0.7
	Dispersal	High	0.013	0.002	0.017	0.019	−15.9	−21.1
		Low	−0.014	0.023	0.022	0.033	−15.5	−24.2
	Initial abundance	High	0.004	0.008	0.026	0.043	−15.7	−26.9
		Low	−0.012	0.007	0.024	0.047	−16.7	−23.0
	Correlation	High	0.012	0.004	0.040	0.058	−19.3	−27.7
		Low	0.049	0.047	0.073	0.099	−21.5	−31.4
	Carrying capacity	High	0.027	0.025	0.036	0.036	−19.6	−27.3
		Low	−0.001	0.002	0.019	0.038	−13.4	−20.0
	Variability in adult survival rate (SD)	High	−0.012	0.046	0.024	0.082	−14.2	−22.5
		Low	0.005	0.009	0.022	0.019	−37.4	−50.2
	Variability in juvenile survival rate (SD)	High	0.009	0.005	0.041	0.052	−18.4	−21.3
		Low	0.006	0.006	0.039	0.047	−17.8	−25.3
	Variability in fecundity (SD)	High	0.032	0.026	0.050	0.019	−10.6	−11.9
		Low	−0.012	0.031	0.009	0.041	−17.6	−29.2
Contest	Maximum population growth rate (R_{max})	High	0.000	0.000	0.000	0.000	−39.0	−58.6
		Medium	0.003	0.007	0.014	0.021	−13.8	−31.2
		Low	−0.002	0.039	−0.001	0.042	−2.7	−9.6

A positive value indicates that the SLR causes an increase in that measure. The first row shows results with the best (*Medium*) values of all parameters. The other rows show results when each parameter is changed to its extreme *High* or *Low* value.

available, we will incorporate these types of directs effects in our model.

The proportional future decline in average population abundance (based on simulations with the demographic model) is predicted to be larger than declines in habitat area or total carrying capacity (Fig. 3). This is because fluctuations in population size due to demographic and environmental stochasticity lead to local (subpopulation) and regional (metapopulation) extinctions, even when growth rate is greater than 1, causing suitable habitat to become or remain unoccupied, and leading to a faster decline in population size than in habitat area or carrying capacity. Local extinctions that keep one or more subpopulations unoccupied also

explain why the average population size is predicted to decline even without SLR (albeit much more slowly than with SLR; Fig. 3). Thus, assessments based only on projected change in habitat area or carrying capacity may underestimate the future declines in populations of shoreline dependent species due to SLR.

The sensitivity analysis indicated that the model results are most sensitive to uncertainties in fecundity and survival rates, and moderately sensitive to maximum growth rate under Contest-type density dependence, and variability of survival rates and fecundity. The four most important parameters in terms of risk sensitivity were the same regardless of the amount of SLR. These results suggest that future studies and

Table 3 The sensitivity of risk of extinction, risk of decline to 20 birds, and expected minimum abundance to each model parameter

Parameter	Δ Risk of extinction	Δ Risk of decline to $N = 20$	Δ Expected minimum abundance
Fecundity	−0.890	−0.981	184.2
Survival, adult	−0.748	−0.904	183.1
Survival, juvenile	−0.605	−0.816	134.1
R_{max} – Contest Desn Dep.	−0.257	−0.452	98.8
Variability in adult survival (SD)	0.164	0.312	−86.9
Variability in fecundity (SD)	0.090	0.178	−41.0
Carrying capacity	−0.031	−0.084	32.7
Dispersal	−0.023	−0.008	4.2
Variability in juvenile survival (SD)	−0.009	−0.009	1.3
Correlation	−0.007	0.003	−2.6
Initial abundance	−0.007	−0.011	−2.4

The sensitivities are in terms of the difference in each of the three viability measures, with the *High* and *Low* values of the parameter, under 2 m SLR. A negative value indicates that the increase in parameter value causes a decrease in the viability measure. For example, increasing fecundity from the *Low* value to the *High* value causes a decrease in the risk of extinction of 89%. The parameters are sorted by the absolute value of the change in extinction risk. Results are similar for the 1 m SLR scenario.

conservation measures on the Florida populations of Snowy Plover should focus on the average and variability of demographic rates and density dependence. In particular, the negative effects of SLR may be mitigated by conservation measures that are designed to increase fecundity (e.g. nest success) and survival rates in these populations. In addition, density dependence is a crucial factor that provides a link between habitat and population dynamics. The projected impacts of SLR depend on the strength and type of density dependent effects. Thus, future studies should aim to reduce uncertainties regarding the nature and strength of density dependence. Our results were not very sensitive to uncertainties in sub-population carrying capacities. This indicates that vertical inaccuracies in the DEMs used in SLAMM, which would result in uncertainties in *K*, do not seem to have substantial effects on our model results.

Our sensitivity analysis is limited because it considers only one model parameter at a time, and thus ignores interactions among parameters. In a continuation of this study, we are going to employ global sensitivity and uncertainty analysis (GSA) to numerically measure the contribution of each uncertain model input as well as their interactions to output uncertainty. This will help identify critical regions in the space of inputs and establish priorities for research (Saltelli *et al.*, 2008; Chu-Agor *et al.*, 2011).

Although we incorporated uncertainties in a large number of model components, these uncertainties did not affect our main conclusion that the Florida Gulf Coast Snowy Plover populations face additional risk due to projected SLR. Despite the uncertainties in model parameters, the impact of SLR was consistent: the difference in each viability measure (such as risk of extinction) with and without SLR was always in the same direction under all assumptions. In other words, regardless of whether we used the *High* or the *Low* values of each parameter, the relative risks (additional risk due to SLR) were consistent. This indicates that our results are robust to uncertainties in model parameters.

These results also demonstrate the importance of using a variety of viability measures. Under some assumptions (e.g. *High* adult survival), the risk of extinction is not sensitive to SLR (because the risk is zero with or without SLR), but EMA is sensitive to SLR. Under other assumptions (e.g. *Low* adult survival), the EMA results are insensitive to SLR (because EMA is low with or without SLR), but the extinction risk is sensitive to SLR. By using a variety of different viability measures, we were able to demonstrate the impact of SLR despite uncertainties in model parameters.

As we approached the end of this study, a new major factor threatened the Snowy Plover populations we modeled: a failed well operated by British Petroleum in the Gulf of Mexico led to the largest accidental oil spill in history (Crone & Tolstoy, 2010). Needless to say, our results do not take into account potential impacts of this or future similar anthropogenic events. However, as data on the extent and effects of this catastrophe become available, they could be incorporated into our model. A major advantage of our approach is its ability to incorporate cumulative impacts and stresses. In fact, effects of a variety of toxicants have been incorporated into the demographic model we used for several species (e.g. see Akçakaya *et al.*, 2008). Developing a similar ecotoxicological component for the Snowy Plover would require data and models on exposure (e.g. a map of concentrations of organic compounds, such as PAH, that the Snowy Plover populations are exposed to) and the demographic response of the species (also called a dose–response model) to provide the necessary input for the population model.

In the meantime, the oil spill has several implications for our results. First, our results on the absolute value

of risks of decline are likely conservative, especially in the short term. The results on relative risks (i.e. the additional risk due to SLR) are likely not affected as much as the absolute results. Second, the oil spill may result in source-sink dynamics, because one of the two large populations (Panhandle) will likely be impacted by the spill much more than the other large population (Peninsula). Even if the oil spill does not result in source-sink dynamics, its uneven impact on the two main populations increases the long-term conservation importance of the Peninsula population. This is especially important because our model predicts that the carrying capacity of this population will be relatively stable for the next 20–30 years, but then decline in a matter of a few years to about one-third of its current value. Thus, habitat restoration and management actions focused on this population for the next 2–3 decades may result in improvement of the long-term viability of Snowy Plovers in Florida, and in the Gulf region in general.

This study demonstrated the feasibility of integrating a SLR model with a metapopulation model. The changes to habitats of coastal species as a result of SLR are the outcome of complex interactions and transitions among different geological factors, land cover types, and human-made obstacles. Predicting these requires a detailed mechanistic model. However, habitat change by itself is not sufficient to project the long-term persistence of these species, because various demographic and landscape-level factors interact to determine species viability. Thus, the ecological consequences on species of SLR in particular and climate change in general are most realistically predicted by integrating climatic, geomorphological models with ecological models.

Acknowledgements

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Details of the demographic model (RAMAS GIS).
Table S1. Conversion from C-CAPP NOAA land-cover classifications to SLAMM land-cover classifications (from Convertino *et al.*, 2011).
Table S2. *Low*, *Medium*, and *High* estimates of parameter values used in the Snowy Plover metapopulation model.
Table S3. Estimated dispersal rates.
Table S4. SLAMM parameterization.
Table S5. Area of land-cover categories used by Snowy Plovers on Santa Rosa Island, FL.
Figure S1. Area (ha) for each SLAMM land-cover classification for 2010 and 2100 resulting from (a) 1 m SLR and (b) 2 m SLR.
Figure S2. Predicted future land cover. SLAMM projections for 2010, 2050, and 2090.
Figure S3. Habitat suitability maps.

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