

Climate-Smart Conservation of Western Snowy Plovers

A Spatial-Analytic Approach



Final Technical Report
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EXECUTIVE SUMMARY

The Pacific coast population of the western snowy plover is highly vulnerable to climate change, primarily because rising sea levels are predicted to greatly alter coastal beaches over the next century. To maintain viable snowy plover populations, it is essential to determine how snowy plovers are likely to respond to predicted changes in sea level, habitat, and climate. In this study we used long-term plover and climate data sets within a GIS framework to analyze the relationship between snowy plover reproductive success (hatching and fledging success) at two major study areas (Point Reyes National Seashore and Monterey Bay), a single measure of beach habitat (distance of a plover nest from mean high water), and two climate variables (temperature, precipitation). We also considered whether nests were protected with nest exclosures, which reduce nest predation rates. We used these results to model significant relationships between snowy plover hatching and fledging success and these variables and to predict reproductive success across a range of future sea level rise scenarios using CoSMoS sea level rise models. We also used CoSMoS sea level rise models to estimate the total area of beach habitat that will be lost within each of the two major study areas due to sea level rise over the next century.

Hatching success did not vary significantly between the two major study areas but did show significant variation among the group locations (smaller subregions) within each major area. Clutch initiation date, distance to mean high water, and temperature also were significant predictors of hatching success. Hatching success increased with increasing distance to mean high water, and this effect did not differ between exclosed and non-exclosed nests. Hatching success also was strongly influenced by temperature; warmer minimum temperatures in October of the previous year and in May of the nesting year were both predictive of lower hatching success. This effect did vary for exclosed nests versus unexclosed nests for both October and May temperature variables; exclosed nests were unaffected by warmer temperatures, suggesting that the mechanism that is driving the temperature effect was related to predators. Probing this temperature effect further, for nests where the cause of nest failure was known, we examined the probability that nest failure was due to predation and found that as minimum October and May temperatures increased, nest failure rates increased, and among failed nests, the probability that failure was due to predation also increased. We also found that, even though the probability of hatching is greater at greater distances from mean high water, the probability that predation was the cause of nest failure also increases at greater distances from mean high water. These pieces of evidence, taken together, suggest that the climate and habitat relationships that are driving lower hatching success are related to predators.

Fledging success did not vary significantly between the two major study areas but did show significant variation among the group locations within each major area and like hatching success, was significantly influenced by clutch initiation date. In contrast to hatching success, fledging success was positively influenced by warmer temperatures, with increased maximum February temperature associated with greater fledging success for Monterey Bay only and increased maximum May temperature associated with increased fledging success for both areas.

In Monterey Bay, we found a contrasting spatial pattern between predicted probabilities of hatching and fledging success. Predicted hatching success was consistently higher in the southern half of Monterey Bay, with some minor variation related to nest initiation date, whereas fledging success was consistently higher in the northern half of Monterey Bay, irrespective of nest initiation date. In Point Reyes, spatial patterns of predicted hatching success were consistent across group locations, with later nest initiation date generating the highest hatching success across all group locations, but fledging success was strongly tied to group location, Kehoe and a large portion of the Restoration Area consistently had the highest predicted probability of fledging success.

We project that sea level rise will cause significant declines in the amount of available sandy beach habitat to high tide inundation with 200 cm of sea level rise at both study areas. In general, Point Reyes (32% loss of habitat) is projected to be more resilient to sea level rise than Monterey Bay (52% loss) and at Point Reyes, all group locations will retain more than 14 ha of habitat compared to only two sites at Monterey Bay. Spatial projections of future hatching success across the remaining extent of habitat were very sensitive to the use of nest exclosures. Not using exclosures resulted in significant declines, with declines occurring earlier in Monterey Bay; however, widespread use of exclosures could substantially increase future hatching success at both study areas. Spatial predictions of fledging success across the remaining extent of habitat varied between the two major study areas. For all Monterey segments and all segments at Point Reyes except the Restoration Area and Kehoe, we find that warming temperatures will lead to improved fledging success.

The results of this study suggest that a warming climate will result in countervailing forces on the two reproductive rates that we examined, with hatching rates decreasing and fledging rates increasing. It also highlights the potential causal mechanism of increased risk of nest predation caused by warming and the potential gains in hatching success from using exclosures that could help to offset warming effects. However, we did not consider the increased risk of mortality that is caused by exclosures so these results related to increased hatching success should be viewed with caution since we did not analyze the effect of increased mortality on population viability. Nor did we account for an increased level of human use on beaches that may occur due to warming and could likely have negative impacts on both reproductive rates. Finally, and most importantly, losses in overall sandy beach habitat could obviate any gains in fledging success that occur due to warming, unless habitats are allowed to migrate inland. Future management approaches will likely need to be adapted to changing predator and environmental conditions and future research should focus on elucidating the relationship between reproductive success, predators, and environmental conditions.



Adult male western snowy plover, Point Blue Conservation Science photo

INTRODUCTION

Coastal beaches and dunes are highly vulnerable to the impacts of climate change and associated changes in sea level (Schlacher et al. 2008, Defeo et al. 2009, NRC 2012) and the physical characteristics of sandy beach habitats are likely to be heavily altered by climate change. For example, models project that 31% - 67% of southern California beaches could become totally eroded with 0.93 - 2.0 m of sea level rise (Vitousek et al. 2017). On the coast of California, physical characteristics of sandy beaches directly influence patterns of shorebird occurrence and the selection of nest sites by the federally threatened western snowy plover (*Charadrius nivosus nivosus*) (Neuman et al. 2008, Patrick and Colwell 2014). Specifically, wider, flatter beaches, and beaches with greater habitat availability are favored by shorebirds (Hubbard and Dugan 2003, Neuman et al. 2008, Nielson et al. 2013). Under most projected climate change scenarios, sea level rise is expected to reduce the total amount of available habitat and increase the temporal variability in habitat availability, unless beaches are allowed to migrate inland. However, with most of California's beaches backed by agricultural and human infrastructure, few beaches have the capacity to migrate inland in response to sea level rise. For snowy plovers, narrower beaches may result in increased conflicts with beach recreation (Faillace and Smith 2016) and greater exposure of plover nests and chicks to predators. Other effects of climate change, such as increased storm amplitude and frequency, are anticipated to result in cumulative effects when combined with higher sea levels, causing greater loss of coastal shorebird nests to direct wave exposure, peak tides, and flooding during the breeding season (van de Pol 2010, Neuman et al. 2020). Reductions in overall productivity resulting from habitat loss or specific climate-linked factors like flooding may increase the extinction probability of climate-vulnerable, coastally dependent plover species (Aiello-Lammens et al. 2011, Galbraith et al. 2014).

Research on other coastally dependent species has demonstrated that determining best future management plans using only "current conditions" for guidance is not a robust approach due to ongoing environmental change (Veloz et al. 2013). A range of future climate change scenarios should be examined (e.g., minimum and maximum predicted sea level rise) and management plans should be adapted to address the forecasted scenarios. To do this, it is critical to understand how the changing climate will influence snowy plover productivity in the future to determine which management actions can mitigate climate change threats and provide the time necessary for species to adapt. Snowy plovers are considered highly climate vulnerable (Gardali et al. 2012, Galbraith et al. 2014, Hutto et al. 2015); yet to date there has been no attempt to combine spatially explicit information on plover productivity with climate predictions. In this study, we analyze the effects of habitat and climate drivers on snowy plover productivity with respect to two key demographic parameters: hatching success of clutches and fledging success for clutches that hatch. We then use these results to predict the effects of expected changes in climate and increases in sea level rise on future productivity and nesting habitat for two central California snowy plover breeding populations.

METHODS

Study Area and Snowy Plover Nest Monitoring

We used long-term data on snowy plover reproductive success (see for example Neuman et al. 2019 and Lau 2020) from the two key breeding areas within Recovery Unit 4 (RU4; Figure 1), Point Reyes National Seashore (2003-2019) and Monterey Bay (2003-2019), that together account for >95% of the RU4 breeding population (USFWS 2007, [USFWS unpubl. data](#)). Point Reyes consists of 5 variable-length beach segments that were combined into 4 group locations and Monterey Bay consists of 27 variable-length segments that were combined into 8 group locations (Table 1, Appendix A).



Figure 1. Study area showing location of Point Reyes National Seashore and Monterey Bay snowy plover breeding populations.

Table 1. Group locations and beach segments for Point Reyes National Seashore (PRNS) and Monterey Bay (MOBA).

Area	Group Locations	Beach Segments	Descriptors
PRNS	Kehoe	KH	Kehoe Beach
	Limantour	LI	Limantour Beach
	North Beaches	NB, NP	North Beaches, North of Parking Area
	Restoration Area	RA	Restoration Area
MOBA	North Beaches	ME, MO, NO, NM, NT, PN, PH	Manresa State Beach, private North Sunset Beaches, Sunset State Beach
	Pajaro River	PS, ZB	Pajaro Spit, Zmudowski State Beach
	Central North Beaches	ZS, JR	South Zmudowski, Moss Landing State Beach
	Central South Beaches	MP, MD	Salinas River State Beach
	Salinas River	SN, SX	South Salinas River State Beach, Salinas River National Wildlife Refuge
	North Marina Dunes	SG, MN, MA, MX	Martin and Cemex dunes
	Fort Ord Dunes	RR, RO, FO	Marina State Beach and Fort Ord Dunes State Park
	Monterey Beaches	NC, HI	Sand City, Monterey State Beach

These data were produced by intensive monitoring programs where the goal was to locate and monitor the fate of every plover nest and, for hatched nests, the survival of chicks to fledging age (28 days). Nest fate was categorized as hatch, fail, or unknown fate; only nests with known fates were analyzed here. Causes of nest loss included environmental (i.e., tide, flooding, rain, wind), mammalian predator, avian predator, nest abandonment, human, infertility, and unknown cause. Across the study period, individual nest enclosures were used on some nests at each area. The use of nest enclosures is more prevalent at Point Reyes than at Monterey Bay. To determine fledge rates, most Monterey Bay chicks were banded with individual color-combinations at hatch; at Point Reyes, some but not all chicks were banded because the relatively small size and low nesting density of this population has allowed for determination of chick survival to fledge age without banding. However, since a new banding program was initiated in 2015, the Park Service has attempted to band all chicks. Fledge status for each nesting attempt was categorized as fledge or no fledge. All nests were mapped using hand-held GPS units and data on reproductive success was linked with the spatial locations of each individual nest. For detailed information on field monitoring methods and protocols, see Adams et al. 2014 (Point Reyes) and Neuman et al. 2021 (Monterey Bay).

Climate Covariates

We characterized the climatic conditions during each snowy plover nest attempt and the preceding non-breeding season using the nest initiation date, nest location and spatial data layers that were developed for the Basin Characterization Model (BCM; Flint et al. 2014; https://ca.water.usgs.gov/projects/reg_hydro/basin-characterization-model.html). Flint et al. (2014) downscaled climate data from PRISM (Parameter elevation Regression on Independent Slopes Model) and calculated a spatially explicit estimate of climate covariates for all locations within California using observations from nearby stationary climate recorders; PRISM uses a weighted regression schematic to extrapolate climate observations while accounting for orography, rain shadows, temperature inversions, slope aspect, coastal proximity, and other factors. Climate data layers were developed at a 270-m spatial resolution.

For our models, we used separate data layers for three climate metrics that have the potential to affect snowy plover reproductive success: monthly average maximum daily temperature (°C), monthly average minimum daily temperature (°C), and monthly total precipitation (mm). We used data layers from 2003-2019 that corresponded to the month and year of the nest initiation date for each nest.

We attributed monthly climate data to individual breeding attempts by averaging estimates within a fixed distance of the nest site. We created a 500m buffer around each nest site and averaged estimates within the buffer separately for each monthly data layer. Climate metrics were calculated at two temporal scales: for each calendar month and for three-month running averages, centered on the individual month. For each breeding season, the months analyzed spanned the period from the previous October to the September following the breeding season.

For future projections of each climate variable, we used 30 year averages (2010 - 2039, 2040 - 2069, 2070 - 2099) made available through the California Climate Commons ([2014 California BCM \(Basin Characterization Model\) Downscaled Climate and Hydrology - 30-year Summaries](#)). We used the CCSM4 RCP 8.5 general circulation model and emissions scenario as this combination is close to an ensemble average of temperature and precipitation projections that have been analyzed in California. We used Program R (R Core Team 2020) and the package “raster” (Hijmans 2020) to extract all climate data.

Beach Measurements

We characterized the location of each snowy plover nest site in relation to key features of the sandy beach ecosystem using the nest site coordinates, a digital elevation map (DEM) from remotely sensed Light Detection and Ranging (LiDAR) data, and aerial imagery of the study area. For each nest site, we measured the beach width, which was defined as the Euclidean distance from the mean high water (MHW) line and the back beach feature (e.g., the base of the cliff or dune), and the distances between the nest site and the MHW line or back beach. We also created covariates that categorized the type of back beach feature (base of the cliff, dune, estuary, or revetment) and location of the nest relative to the back beach (inland or oceanside).

We identified the MHW line using a DEM created by the California Coastal Conservancy Coastal LiDAR Project from 2009-2011 (NOAA Office for Coastal Management; <https://www.fisheries.noaa.gov/inport/item/48166>). LiDAR data for our study sites were collected during 2010 at a resolution of 1 m. We delineated the MHW line as cells with an elevation of 0 m and transformed those cells into a line that was smoothed to better represent an ecological gradient. We manually created a line representing the back beach feature using a partially transparent version of the DEM overlaid on an aerial image of the study sites from 2010; we modified the DEM using the Hillshade function (hillshade angle = 270°) to illuminate variation in the slope of the sandy beach and thus the location of the seaward edge of the back beach feature.

All physical beach measurements were conducted using GIS software (ArcGIS Desktop 10.5.1; Environmental Systems Research Institute, Redlands, CA, USA) and an add-in created by the U.S Geological Survey (Digital Shoreline Analysis System, version 5.0; Himmelstoss et al. 2018)

Statistical Analysis

Analysis of Hatching and Fledging Success

For the purposes of developing projections to the future, we first analyzed the historic data to identify variables (spatial and temporal) that influence (1) the probability that a clutch, once initiated produces one or more hatched young, which we refer to as “hatching success,” and (2) the probability that a clutch that hatched at least 1 chick produces one or more fledged young, which we refer to as “fledging success.” Each parameter was scored as 0 (fail) or 1 (success). We conducted separate analyses of hatching success and fledging success using logistic regression, an example of a Generalized Linear Model, analyzing success or failure for the individual nesting attempt (Hosmer et al. 2013). We analyzed these two parameters separately to better identify and characterize processes that may affect each of the two parameters. Statistical analyses were conducted using Stata 16 (StataCorp. 2020), unless otherwise noted. All clutches and broods with known fates were included in the statistical analyses, except for a very few with incomplete data (35 out of 6085 clutches, i.e., 0.6%).

Our objective was to identify a statistical model for each parameter (hatching success and fledging success) that best predicted current patterns of hatching/fledging success and that could also be used to project to future scenarios. For each response (hatching or fledging success) we took a four-stage approach to identifying the final, preferred statistical model. We first investigated clutch initiation date (CID) and variation among breeding locations (Table 1). We considered linear and higher-order terms with respect to CID, which was scored as 1 for 1 March, 32 for 1 April, etc., up to fourth-order. We also analyzed locations, grouped as described above (Table 1). This was done for both hatching success and fledging success; in addition, for hatching success we also included whether the nest had a predator exclosure (scored as 1) or not (scored as 0). Nest exclosure was not applicable for consideration of fledging success.

In the second stage, we considered 41 candidate variables with respect to habitat and climate. Habitat variables included: distance to mean high water (MHW), distance to backshore, beach width, back beach feature (as factor), and nest location (inland or oceanside). There were 36 candidate climate variables initially considered: minimum temperature, maximum temperature, and precipitation for each of the 12 months.

We then used a stepwise, forward-selection process to select the habitat variable(s) and climate variable(s) that best predicted hatching success or fledging success. At this stage, variables identified in Stage 1 were retained (as described above), and habitat/climate variables were added to the statistical model, one at a time, provided that they met the criterion of $P < 0.05$ for that variable, given the other variables already in the model. This provided us with an interim statistical model for each response.

In the third stage, we evaluated whether specific statistical interactions should be included in our interim model. Here we evaluated specifically an interaction between predictor variables (as identified above) and area (Monterey Bay or Point Reyes), as well as an interaction between predictor variables and nest exclosure, that is whether the effect of a predictor variable differed for exclosed and non-excused nests. Statistical interactions were included at this stage if they met the criterion of $P < 0.05$.

In the fourth stage, we considered whether any additional terms should be added or dropped, based on the criterion of $P < 0.05$, given those identified at the third stage of the modeling. We also considered whether a 3-month running average provided better predictive values than the previously identified monthly values. This stage of modeling was necessary to ensure that the final statistical models for hatching success and fledging success, included only significant variables and that there were no additional variables that could be added which met the criterion of $P < 0.05$. Through this process we arrived at the best predictive models for hatching success and fledging success for the historical data.

All final models were assessed for goodness of fit, using the Hosmer-Lemeshow GOF test (Hosmer et al. 2013). We illustrate statistical model results for each covariate of interest, while adjusting for the effects of all other variables in the model using the margins and marginsplot procedures (Stata 16).

Analysis of Cause of Nest Failure

The predominant cause of nest failure is predation of the clutch, which has long been identified as a high concern for the Pacific coast snowy plover population. Therefore, we analyzed the cause of nest failure for clutches that failed, with respect to whether predation was identified as the cause of failure (scored as 1) or whether some other cause (e.g., adverse weather, flooding, human disturbance) was identified (scored as 0). Unsuccessful clutches with no identified cause of failure were not included in this analysis.

For this analysis, we started with the final model identified for hatching success, evaluated those variables, and retained significant variables. However, the number of depredated, exclosed nests were too few to adequately analyze the interaction of exclosure and other predictor variables of interest. We analyzed cause of nest failure in two ways: First, for all nests, exclosed or not, controlling for the effect of exclosures; and second, repeating the analysis but only considering non-excused nests. Results for the predictor variables examined were very similar; hence, we only present results of the latter analysis. This analysis was only for failure of clutches to hatch; no cause of fledging failure was attributed in the dataset.

Spatial Projections

We used the equations from the models for hatching success and fledging success to project results spatially across all beach habitat in the Point Reyes and Monterey Bay study areas. We created 1 m x 1 m rasters of each of the model covariates. We decided to make spatial predictions using the 5th, median and 95th percentile of nest initiation dates from all nests in the dataset for hatching success (29, 75, and 124 days from March 1) and for all nests that hatched for fledging success (28, 84 and 125 days since March 1). In each case a raster was created with the nest initiation date value (i.e., 29) applied across the whole study area. Similarly, we made spatial projections for whether predator exclosures were used across the whole study area or not. The climate data were missing values along parts of the shoreline, so we converted the original climate rasters to points and then spatially interpolated values into the no data cells using the IDW tool in the Spatial Analyst Interpolation toolbox in ArcGIS 10.8.1.

We used projections of sea level rise developed in the Coastal Storm Modeling System (CoSMoS) to estimate future distance to mean high water (MHW). We used projected flood exposure shapefiles for Point Reyes using CoSMoS version 2.0 (Barnard et al. 2019) and for Monterey Bay we used CoSMoS version 3.1 (Barnard et al. 2018) both accessed via the Our Coast Our Future web platform (www.ourcoastourfuture.org, Point Blue Conservation Science and USGS 2021). We selected sea level rise increments of 50 cm, 100 cm and 200 cm which correspond to State of California guidance of projections of sea level rise based on medium-high risk assumptions of sea level rise (Ocean Protection Council, 2018) for 2040, 2070 and 2100 the same time periods used for future climate projections. The projections for future sea level rise are also given for mean high water (MHW) conditions but we found some differences in the MHW line from the DEM and from CoSMoS projections for current conditions. We calculated the Euclidean distance between the MHW line provided by the CoSMoS models for current sea levels and the MHW line we created from the DEM. We then calculated the mean difference between these 2 distances across all cells within each beach group location. We used these mean differences to transform future distances from the CoSMoS models slightly to adjust for the differences in the present-day layers. We used the Spatial Analyst toolbox in ArcGIS 10.8.1 to create the distance to MHW layers.

We summarized the results of the future spatial predictions by calculating the spatial difference between future hatching success and historic hatching success for each scenario; all combinations of sea level rise/climate change, predator exclosure, nest initiation date). We then calculated the spatial mean of these differences within each beach segment. These calculations were all done in R (R Core Team 2020) using the raster package (Hijmans 2020).

RESULTS

Dataset Characteristics: Temporal and Spatial Trends

The dataset analyzed comprised 6,050 initiated clutches (i.e., nesting attempts), 5556 in Monterey Bay and 494 in Point Reyes. Of these, fledging success was assessed for 3139 clutches that hatched: 2851 in Monterey Bay and 288 in Point Reyes.

Clutch initiation was almost entirely in the months of March through July (only 2 clutches were initiated outside this period), with 87.5% of clutches initiated in April, May, or June (Figure 2). Thus, the primary active months of breeding (from egg laying until fledging) comprised March, April, May, June, July, and August. The number of clutches analyzed per year varied from 229 to 554 (mean = 356; Table 2).

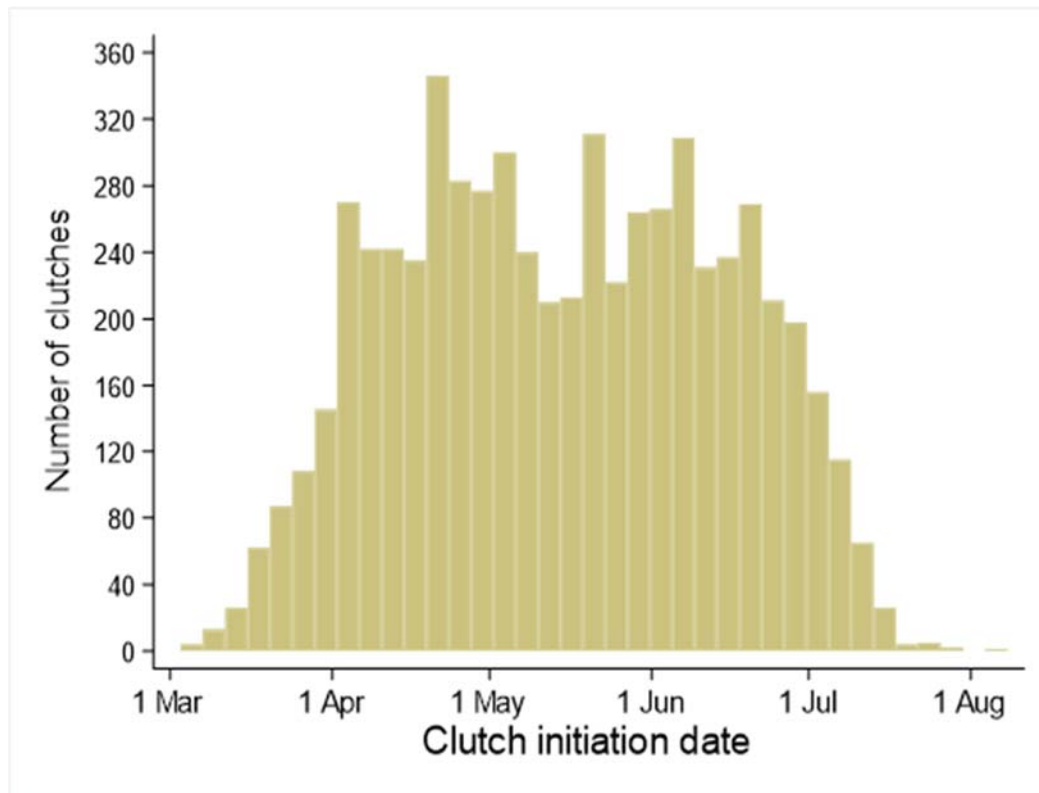


Figure 2. Distribution of clutch initiation dates (n = 6050). Initiation date is the day the first egg is laid.

Table 2. Sample size (number of clutches analyzed) for each year for Point Reyes National Seashore (PRNS) and Monterey Bay (MOBA).

YEAR	PRNS	MOBA	Total
2003	22	207	229
2004	37	299	336
2005	19	335	354
2006	24	266	290
2007	28	297	325
2008	21	269	290
2009	21	269	290
2010	15	309	324
2011	15	352	367
2012	7	338	345
2013	21	438	459
2014	44	438	482
2015	49	495	544
2016	42	302	344
2017	45	313	358
2018	50	380	430
2019	34	249	283
Total	494	5,556	6,050

The distribution of the distance to mean high water from all nest locations ($n = 6050$) is shown in Figure 3. By far most nests are located within 100 m of mean high water, three quarters of the nests were located within 102 m of MHW, though nests were located as far as 570 m from MHW.

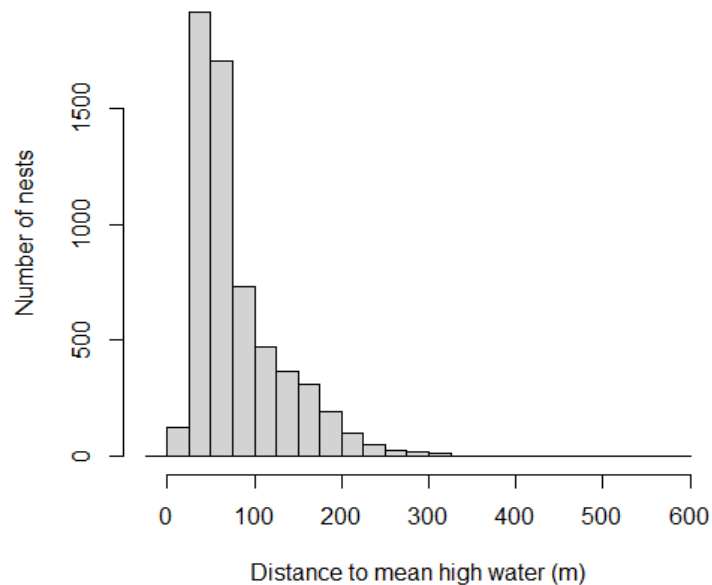


Figure 3. Histogram of the distance from mean high water (m) from each nest location.

Annual variation for temperature variables is displayed in Figure 4, for Tmin May, Tmin June, Tmin Oct, and Tmax Feb, respectively. These are the only four climate variables that were significantly associated with hatching success or fledging success, as documented below. Figure 4 displays the mean temperature for each area in each year, though we note that statistical analysis was of the nest-location-specific temperature (see Methods, above).



western snowy plover chicks on hatch day, Jenny Erbes photo

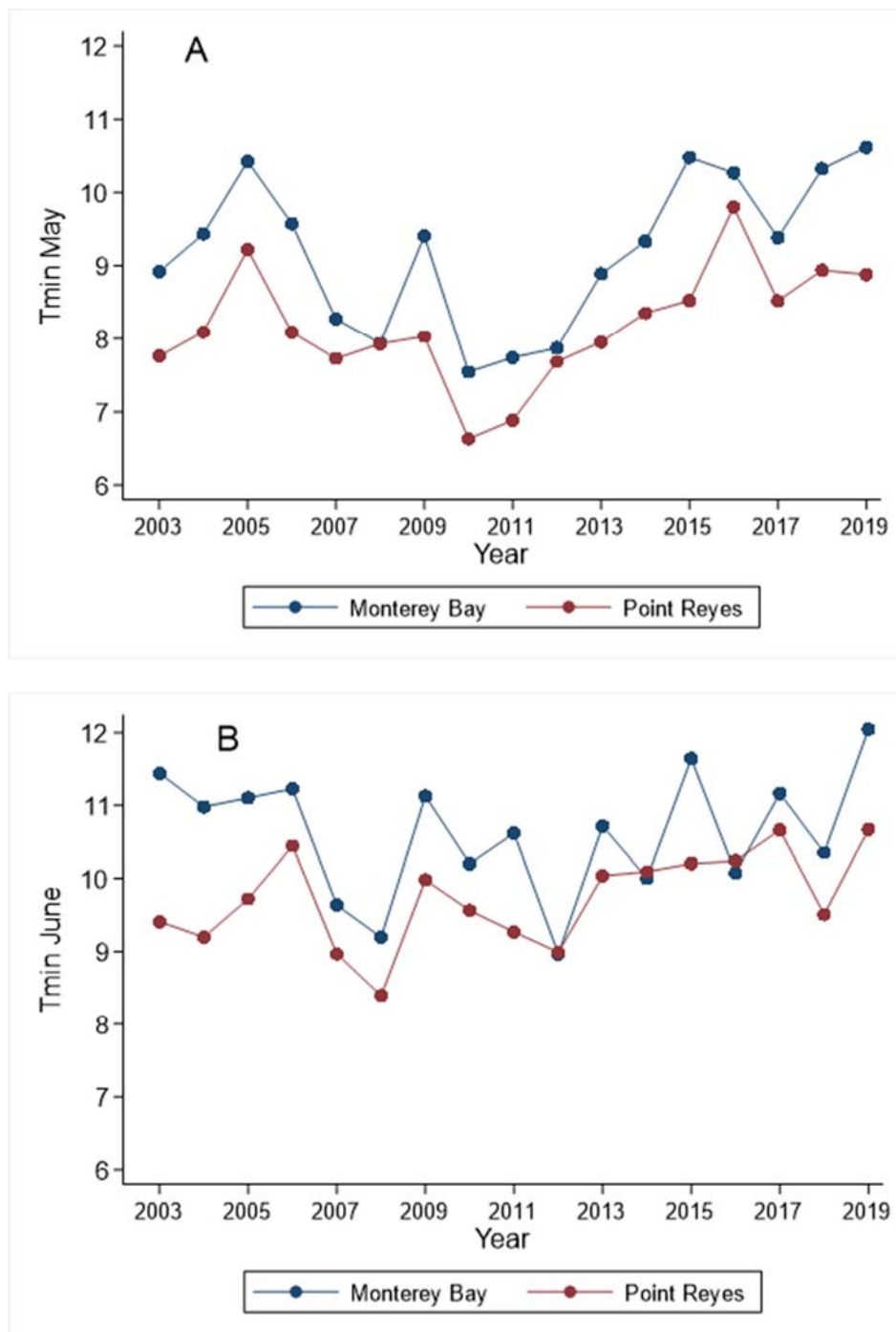


Figure 4. Annual variation in mean monthly temperature for Monterey Bay and Point Reyes, for nests analyzed. A) Minimum temperature May. B) Minimum temperature June. C) Minimum temperature for the October preceding breeding (e.g., October 2002 value is shown for breeding year 2003). D) Maximum temperature February.

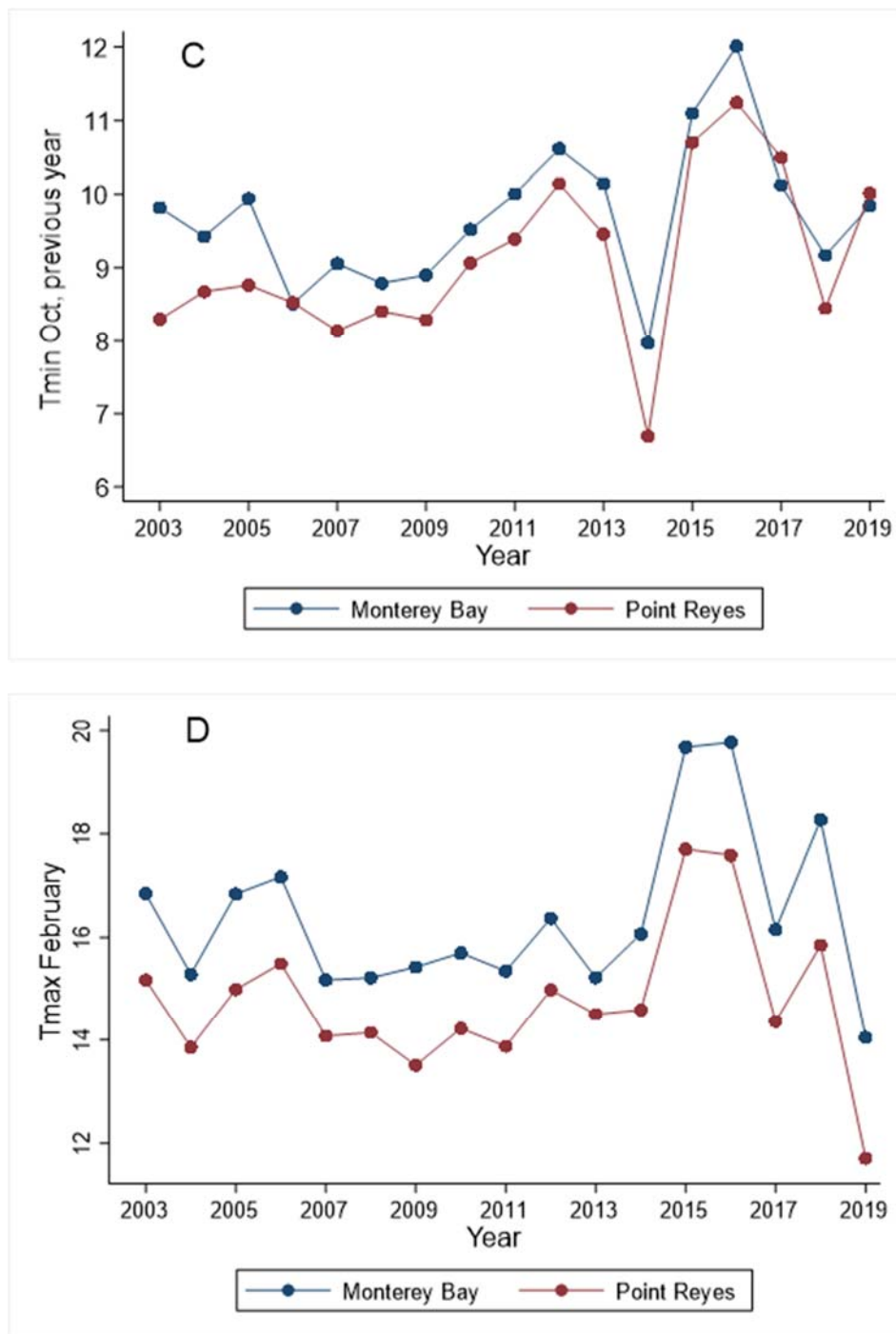


Figure 4 (cont.). Annual variation in mean monthly temperature for Monterey Bay and Point Reyes, for nests analyzed. A) Minimum temperature May. B) Minimum temperature June. C) Minimum temperature for the October preceding breeding (e.g., October 2002 value is shown for breeding year 2003). D) Maximum temperature February.

Hatching success and fledging success both exhibited strong year-to-year variation. Figure 5 displays annual variation for each area for hatching success and fledging success.

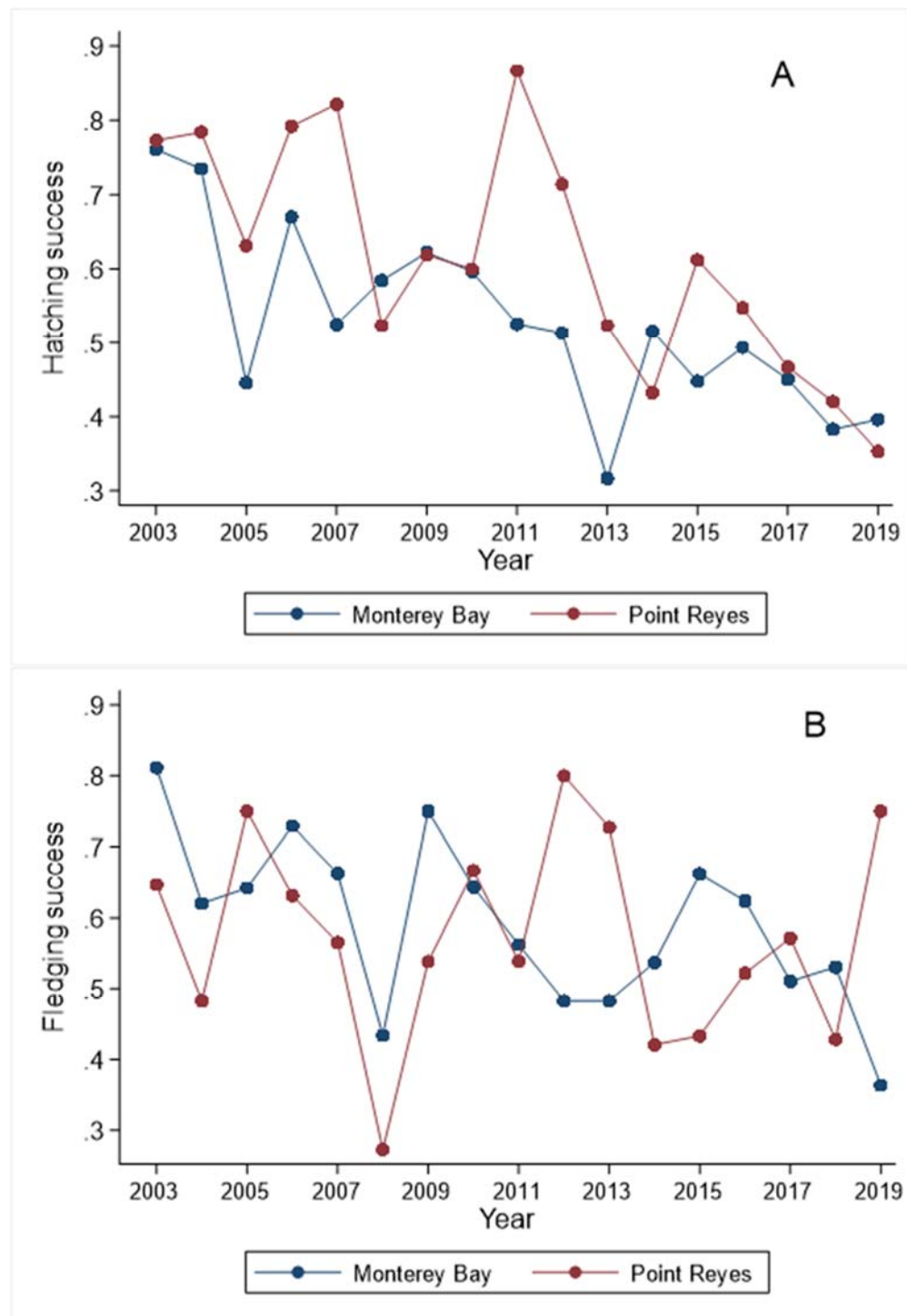


Figure 5. Annual variation in A) hatching success and B) fledging success for each area.

Statistical Analysis of Historic Data

Effects of Habitat and Climate on Hatching Success

The final statistical model for hatching success is summarized in Table 3. Date of clutch initiation was an important predictor and was modeled as a cubic function (Figure 6), with a minimum hatching success evident for clutches initiated in April. The final model included “group location,”

which demonstrated strong variation (Table 3). While there was marked variation in hatching success within the two areas, overall, Monterey Bay and Point Reyes did not differ significantly with respect to hatching success.

Table 3. Final statistical model for probability of hatching success, results of logistic regression. Clutch initiation date (“clutchinitdate”) is scored as 1 = 1 Mar, 32 = 1 Apr, etc. Quadratic and cubic terms shown also. Predator Exclosure (“PredExcl”) is scored as no exclosure (= 0) or predator exclosure (= 1). The coefficients for Group Location are shown relative to the baseline value for “CentralNorth”. Group Locations within Monterey Bay area denoted (MOBA) and within Point Reyes (PRNS). Separate slopes are fit for non-excused and excused nests for Tmin May (slopes differ, $P = 0.014$) and for Tmin Oct (slopes differ, $P = 0.009$).

HATCH SUCCESS	Coef.	Std. Err.	z	P> z	[95% Conf.Interval]	
clutchinitdate	-0.091	0.014	-6.370	0.000	-0.118	-0.063
clutchinitdate^2	0.001	0.000	6.910	0.000	0.001	0.002
clutchinitdate^3	0.000	0.000	-6.470	0.000	0.000	0.000
PredExcl	-4.415	1.575	-2.800	0.005	-7.503	-1.327
Group Location						
NorthBeach(PRNS)	-0.431	0.172	-2.500	0.012	-0.769	-0.093
Kehoe(PRNS)	-0.241	0.226	-1.070	0.285	-0.684	0.201
RestorationArea(PRNS)	-0.312	0.370	-0.840	0.400	-1.037	0.414
Limantour(PRNS)	-1.025	0.409	-2.510	0.012	-1.826	-0.223
North(MOBA)	-0.741	0.143	-5.180	0.000	-1.022	-0.461
PajaroRiver(MOBA)	-0.324	0.113	-2.880	0.004	-0.545	-0.103
CentralSouth(MOBA)	0.686	0.111	6.170	0.000	0.468	0.904
SalinasRiver(MOBA)	0.640	0.111	5.750	0.000	0.422	0.858
NorthMarina(MOBA)	0.591	0.115	5.140	0.000	0.365	0.816
FortOrd(MOBA)	1.519	0.130	11.730	0.000	1.266	1.773
Monterey(MOBA)	0.386	0.276	1.400	0.162	-0.155	0.928
Effect of Tmin May: Without and with PredExcl						
0	-0.156	0.029	-5.320	0.000	-0.214	-0.099
1	0.252	0.163	1.540	0.122	-0.068	0.571
Effect of Tmin Oct: Without and with PredExcl						
0	-0.168	0.029	-5.710	0.000	-0.226	-0.110
1	0.116	0.104	1.110	0.265	-0.088	0.321
Distance MHW	0.002	0.001	2.660	0.008	0.000	0.003
Intercept	3.886	0.482	8.060	0.000	2.941	4.831

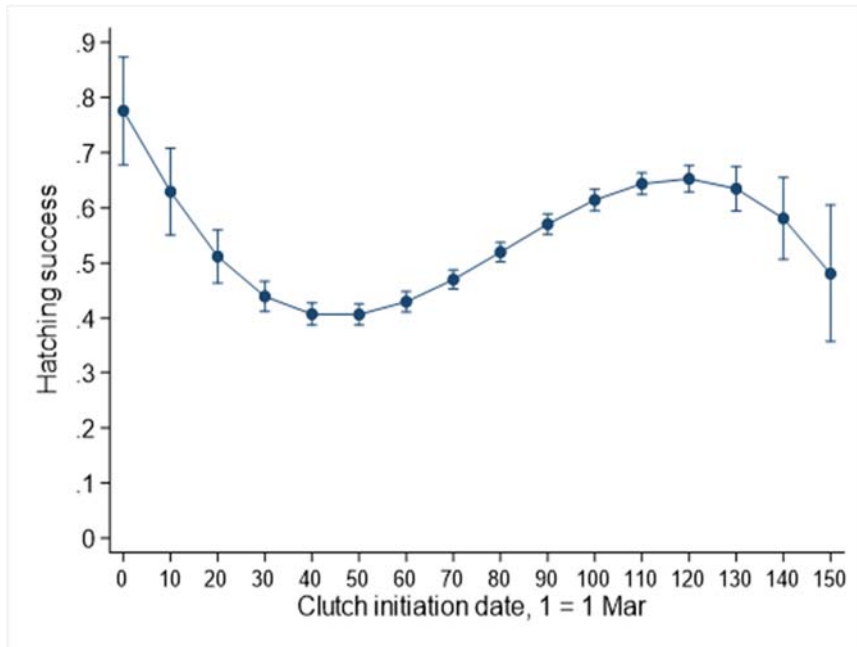


Figure 6. Predicted relationship of hatching success to clutch initiation date, as obtained from the final statistical model (Table 3); the cubic term is significant, $P < 0.001$. Shown are the 95% CIs around predicted estimates.

The only habitat variable included in the final model, other than group location, was Distance to MHW. The estimated effect of Distance to MHW was included in our model projections (Table 3) and is illustrated in Figure 7. While there was also evidence of an effect of distance to backshore, the effect of Distance to MHW was a stronger predictor. Hatching success increased with increasing distance to MHW ($P = 0.008$; Figure 7); the effect appeared linear (no significant quadratic term) and did not differ between areas, nor did it differ between exclosed and non-excused nests.

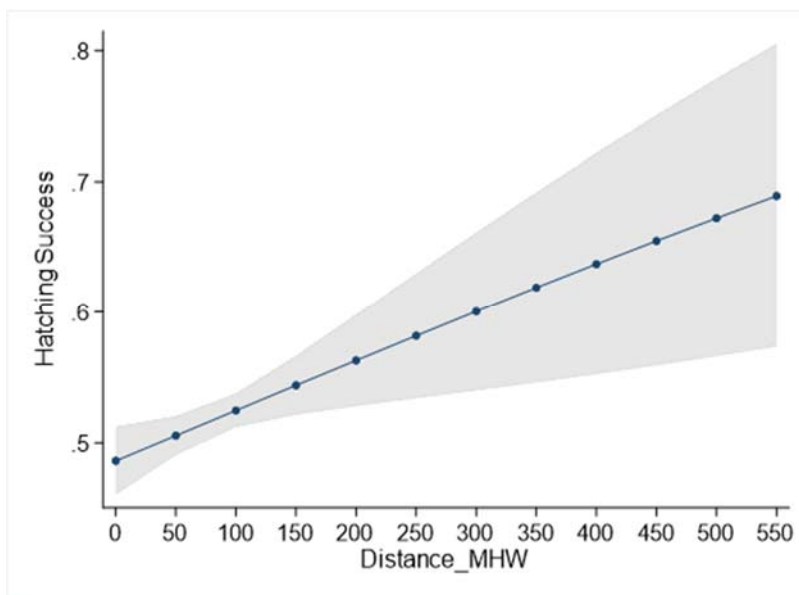


Figure 7. Predicted relationship of hatching success to distance to mean high water (Distance_MHW) as obtained from the final statistical model ($P = 0.008$; Table 3). Shading depicts the 95% CI around predicted estimates.

The final statistical analysis indicated two climate variables affected hatching success: T_{min} May and T_{min} Oct. The effect of each variable was strong and independent of the other, as evidenced in the final statistical model (Table 3). No precipitation variable was significant. The effect of T_{min} May is illustrated in Figure 8. For exclosed nests there was no significant effect of T_{min} May ($P > 0.1$), but for non-excused nests, the effect was strong, hatching success decreasing from nearly 60% to about 45%, as May temperatures increased. Minimum temperature for May was a better predictor than the three month-average (April-May-June).

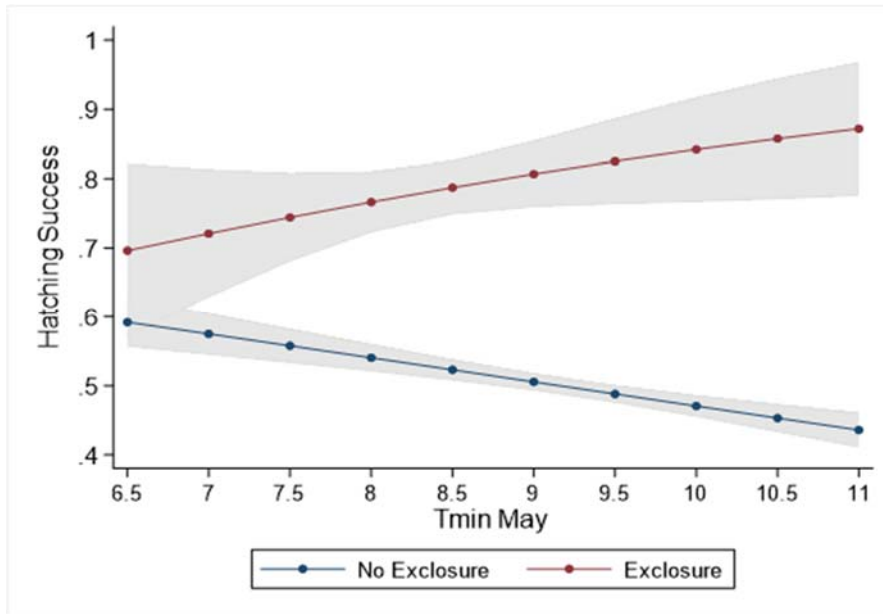


Figure 8. Predicted relationship of hatching success to T_{min} May, as obtained from the final statistical model (Table 3). For exclosed nests, the effect is not significant ($P > 0.1$), but for non-excused nests the effect is significant, $P < 0.001$. Shading depicts the 95% CI around predicted estimates.

The effect of T_{min} Oct, which is the October before the onset of the breeding season, was also very significant; the effect is illustrated in Figure 9. As with T_{min} May, the effect of T_{min} Oct was significantly positive for non-excused nests ($P < 0.001$) but was not significant for exclosed nests ($P > 0.2$). The magnitude of the effect of T_{min} Oct for non-excused nests was substantial: hatching success varied from over 60% for the lowest values of T_{min} Oct to under 40% for the highest values (Figure 9). The effects of T_{min} May and T_{min} Oct on hatching success did not differ between the two areas.

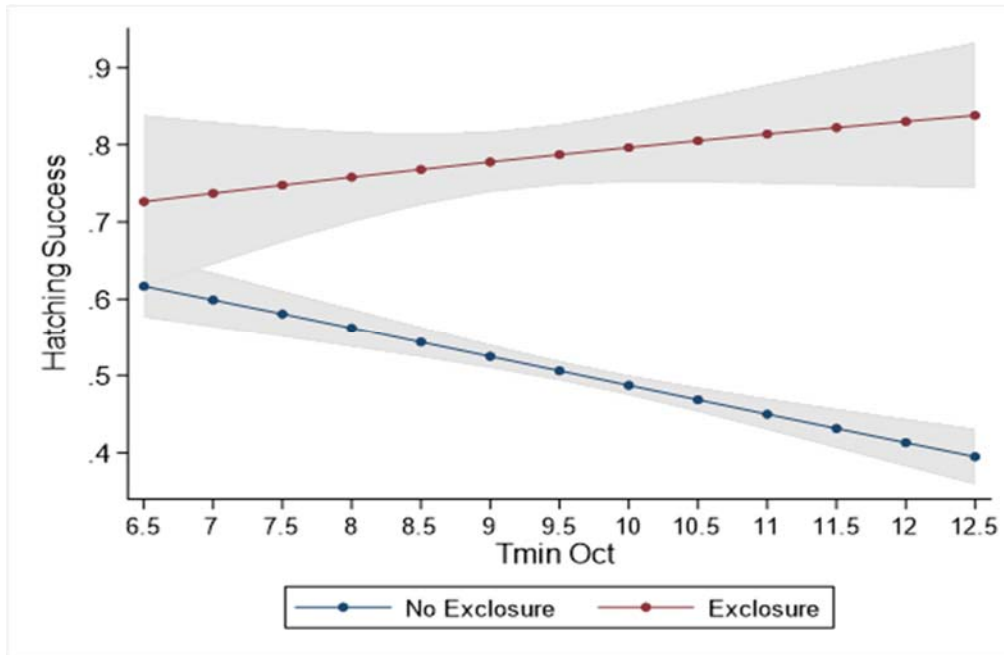


Figure 9. Predicted relationship of hatching success to Tmin Oct, as obtained from the final statistical model (Table 3). For exclosed nests, the effect is not significant ($P > 0.2$), but for non-exclosed nests the effect is significant, $P < 0.001$. Shading depicts the 95% CI around predicted estimates.

Effects of Climate and Habitat on Predation as a Cause of Nest Failure

That the effects of Tmin May and Tmin Oct were confined to non-excused nests suggests that predation played an important role in modulating hatching success or failure. We examined this possible linkage by analyzing the probability that, if a nest failed, failure was due to predation.

Among nests whose cause of nest failure was known, the probability that nest failure was due to predation increased as Tmin May increased (Logistic regression coefficient, $\beta = 0.243 \pm 0.054$, $P < 0.001$, Figure 9). Similarly, as Tmin Oct increased, the probability that nest failure was due to predation increased (Logistic regression coefficient, $\beta = 0.201 \pm 0.054$, $P < 0.001$, Figure 10). This effect was only found for non-excused nests. Thus, as Tmin May and Tmin Oct increased, nest failure rates increased, and among failed nests, the probability that failure was due to predation also increased.

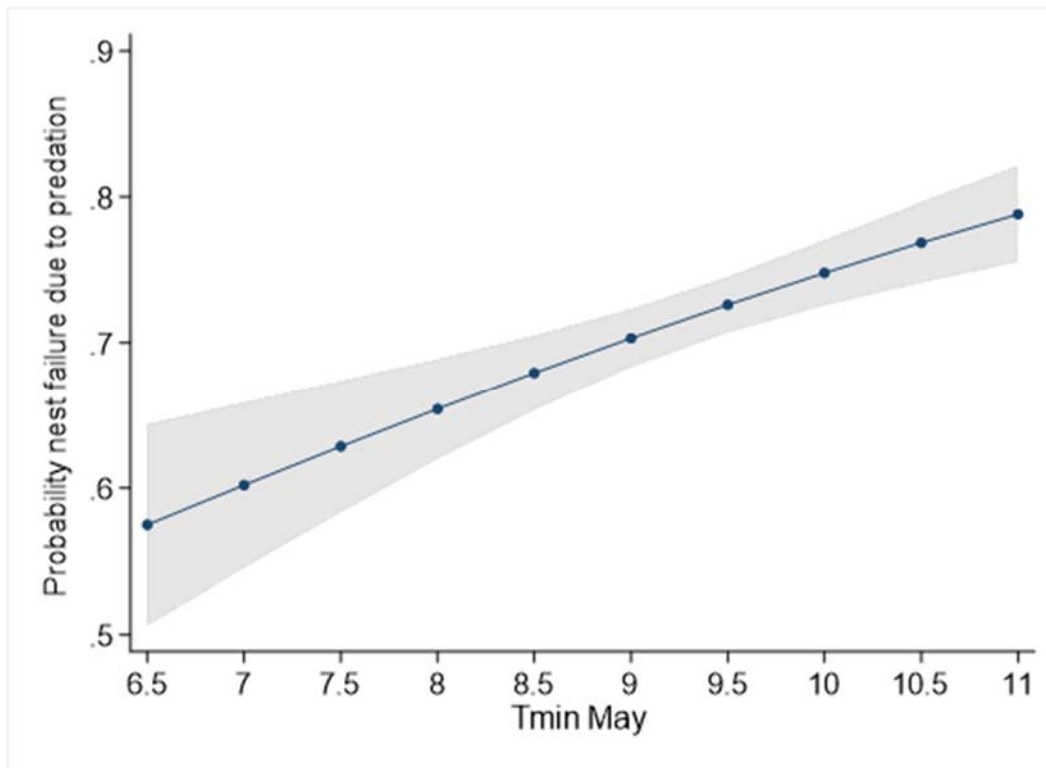


Figure 10. Probability that nest failure was due to predation in relation to Tmin May ($P < 0.001$). Shaded area depicts the 95% CI around the estimates.

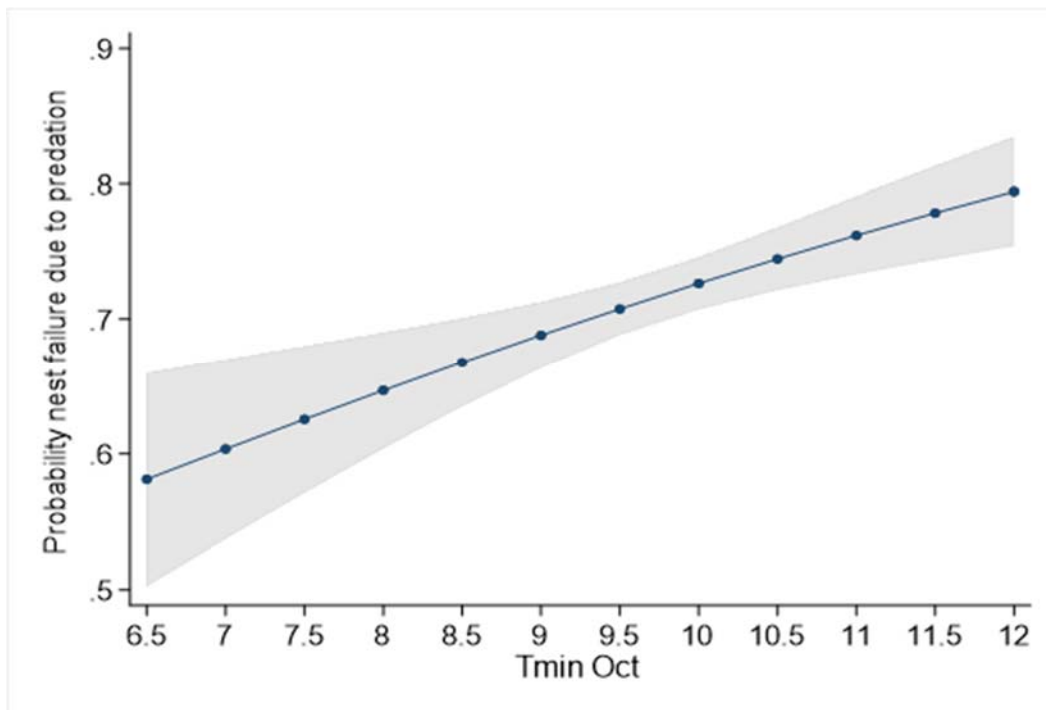


Figure 11. Probability that nest failure was due to predation in relation to Tmin Oct ($P < 0.001$). Shaded area depicts the 95% CI around the estimates.

With increasing distance to MHW, the estimated probability that nest failure was due to predation increased, from less than 70% for nests <50 m from MHW to over 90% for nests > 400 m from MHW (Figure 12; Logistic regression coefficient, $\beta = 0.00477 \pm 0.00142$, $P = 0.001$).

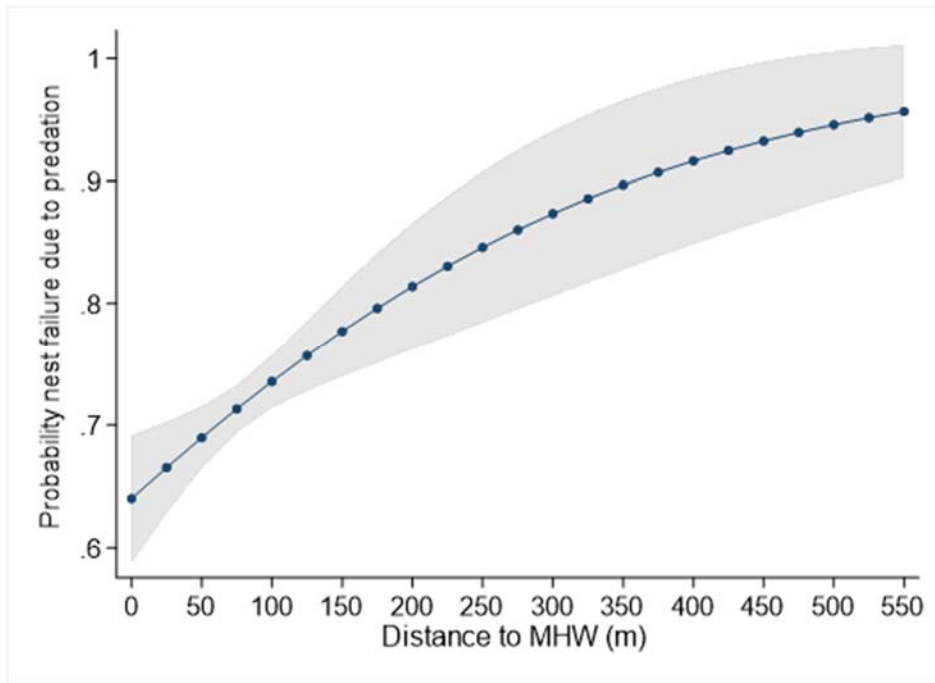


Figure 12. Probability that nest failure was due to predation in relation to Distance to MHW ($P = 0.001$). Shaded area depicts the 95% CI around the estimates.

The effect of Distance to MHW illustrates a trade-off with respect to predation. If we reanalyze hatching success but exclude depredated nests, we find that with increasing Distance to MHW, the probability of nest failure decreases ($P < 0.001$). That is, there are two opposing forces at play: with increasing Distance to MHW, failure due to causes other than predation decreases, but at the same time the probability of predation increases as indicated in Figure 12. With respect to hatching success, predation-related nest failure reduces but does not eliminate the advantage observed for nests with increasing distance to MHW. The net result, as illustrated in Figure 7 is a modest increase in hatching success with increasing Distance to MHW.

Effects of Climate and Habitat on Fledging Success

We analyzed the same set of climate and habitat variables, including group location, with respect to fledging success, for clutches that successfully hatched. The final statistical model included a cubic effect of date (analyzed as clutch initiation date); results are illustrated in Figure 13 and Table 4. For fledging success, clutches initiated in April and May had the highest probability of success ($P < 0.001$ for the cubic term). No habitat variable was significant. Group location also was significant ($P < 0.001$), but there was no overall difference in fledging success between the two major areas. Two climate variables were significant. First, fledging success increased with increasing Tmax Feb, but only for Monterey Bay ($P < 0.001$); the effect of Tmax Feb for Point Reyes was not significant ($P > 0.3$) (Table 4). The difference in slopes was significant ($P = 0.042$) and is illustrated in Figure 14. Second, fledging success increased with increasing Tmin June ($P < 0.001$), illustrated in Figure 15. However, there was no significant difference in the effect of Tmin June on fledging success comparing the two areas ($P > 0.2$), both areas demonstrated positive slopes.

Table 4. Final statistical model for probability of fledging success, results of logistic regression. Clutch initiation date (“clutchinitdate”) is scored as 1 = 1 Mar, 32 = 1 Apr, etc. Quadratic and cubic terms shown also. The coefficients for Group Location are shown relative to the baseline value for “CentralNorth”. Separate slopes are fit for Monterey Bay (MOBA) and Point Reyes (PRNS) for the effect of Tmax Feb (slopes differ, P = 0.042). No significant difference in slopes for Tmin Jun.

FLEDGE SUCCESS	Coef.	Std. Err.	z	P> z	[95% Conf.	
clutchinitdate	0.083	0.019	4.470	0.000	0.047	0.120
clutchinitdate^2	-0.001	0.000	-3.950	0.000	-0.002	-0.001
clutchinitdate^3	0.000	0.000	3.090	0.002	0.000	0.000
Tmin Jun	0.183	0.048	3.790	0.000	0.088	0.278
Group Location						
NorthBeach(PRNS)	3.287	1.403	2.340	0.019	0.538	6.036
Kehoe(PRNS)	2.802	1.393	2.010	0.044	0.072	5.531
RestorationArea(PRNS)	2.049	1.550	1.320	0.186	-0.988	5.086
Limantour(PRNS)	4.357	1.596	2.730	0.006	1.229	7.485
North(MOBA)	0.529	0.243	2.170	0.030	0.052	1.005
PajaroRiver(MOBA)	0.111	0.151	0.730	0.465	-0.186	0.407
CentralSouth(MOBA)	0.328	0.158	2.070	0.038	0.018	0.639
SalinasRiver(MOBA)	0.233	0.149	1.560	0.120	-0.060	0.525
NorthMarina(MOBA)	-0.180	0.161	-1.120	0.264	-0.495	0.136
FortOrd(MOBA)	-0.075	0.159	-0.470	0.636	-0.388	0.237
Monterey(MOBA)	-0.219	0.417	-0.530	0.599	-1.038	0.599
Effect of Tmax Feb: By Area						
PRNS	-0.089	0.089	-1.000	0.317	-0.263	0.085
MOBA	0.099	0.027	3.690	0.000	0.046	0.152
Intercept	3.886	0.482	8.060	0.000	2.941	4.831

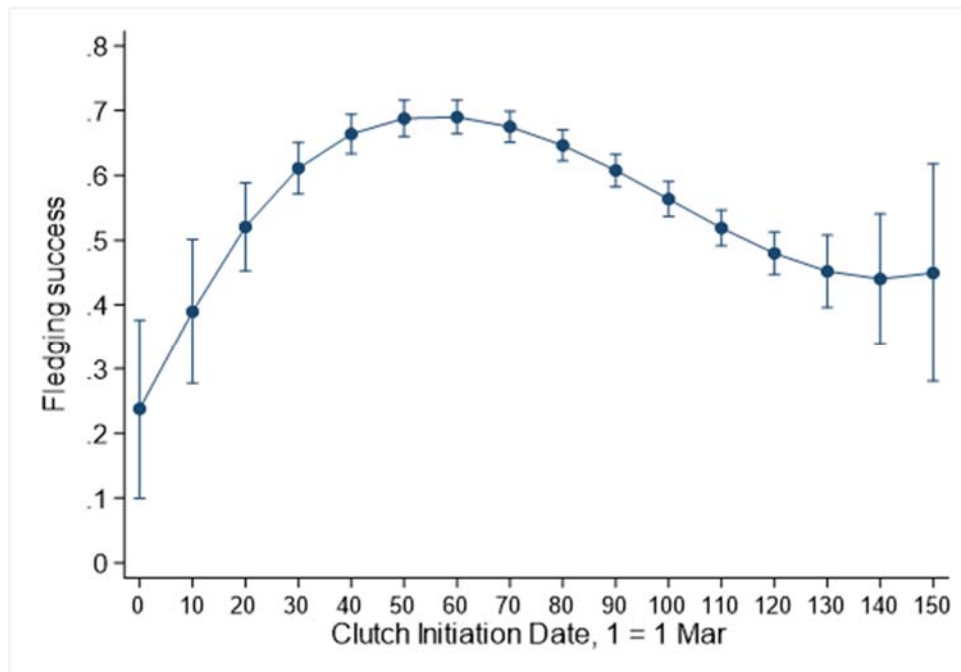


Figure 13. Predicted relationship of fledging success to clutch initiation date, as obtained from the final statistical model (Table 4); the cubic term is significant, $P = 0.002$. Shown are the 95% CIs around predicted estimates.

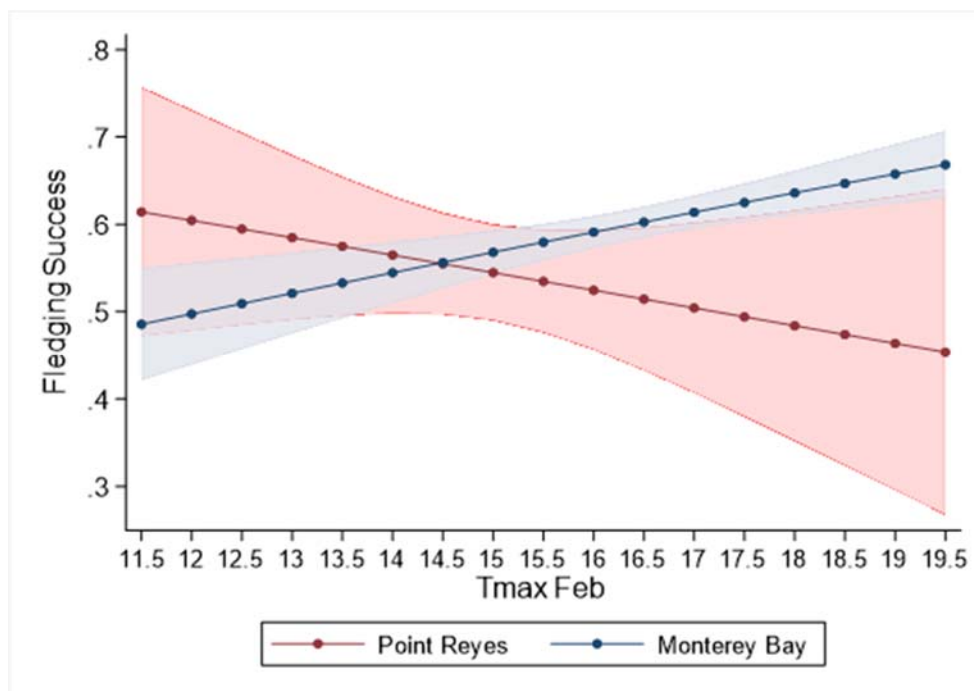


Figure 14. Fledging success in relation to Tmax February, as estimated by the final statistical model (Table 4). The effect of Tmax Feb differed between Monterey Bay ($P < 0.001$) and Point Reyes ($P > 0.3$). Shaded areas indicate 95% CIs of the estimates.

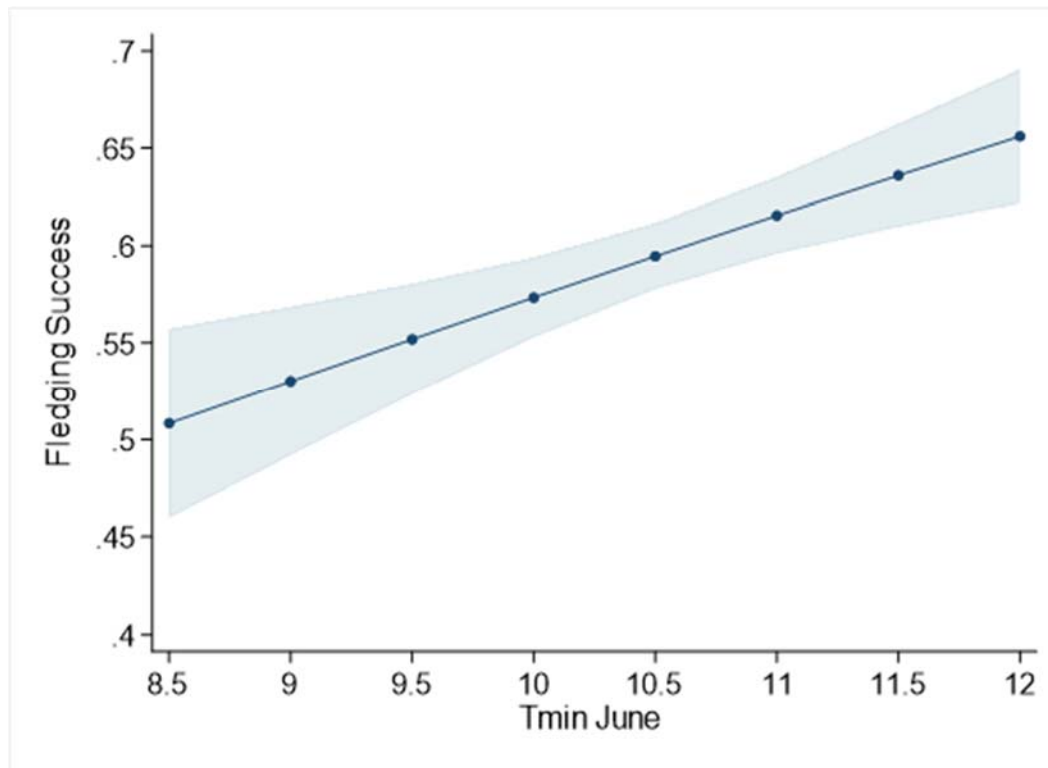
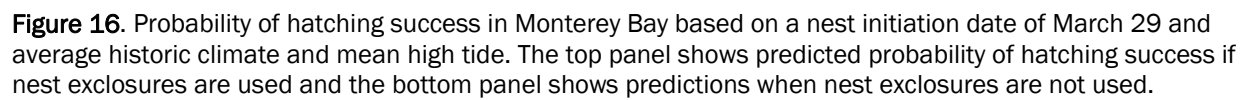


Figure 15. Fledging success in relation to Tmin June, as estimated by the final statistical model (Table X-3). The effect of Tmin June did not differ between Monterey Bay and Point Reyes ($P > 0.2$). Shaded areas indicate 95% CIs of the estimates.

Spatial Variation

Projecting our models spatially across the study area shows the potential improvement in snowy plover hatching success that could be achieved using predator exclosures as we find substantially higher predicted hatching success when we assume that exclosures are used everywhere (Figures 16 and 17.) For example, we predict hatching success > 0.6 in Monterey (Figure 16) and > 0.46 in Point Reyes across all beach habitat if exclosures are used.



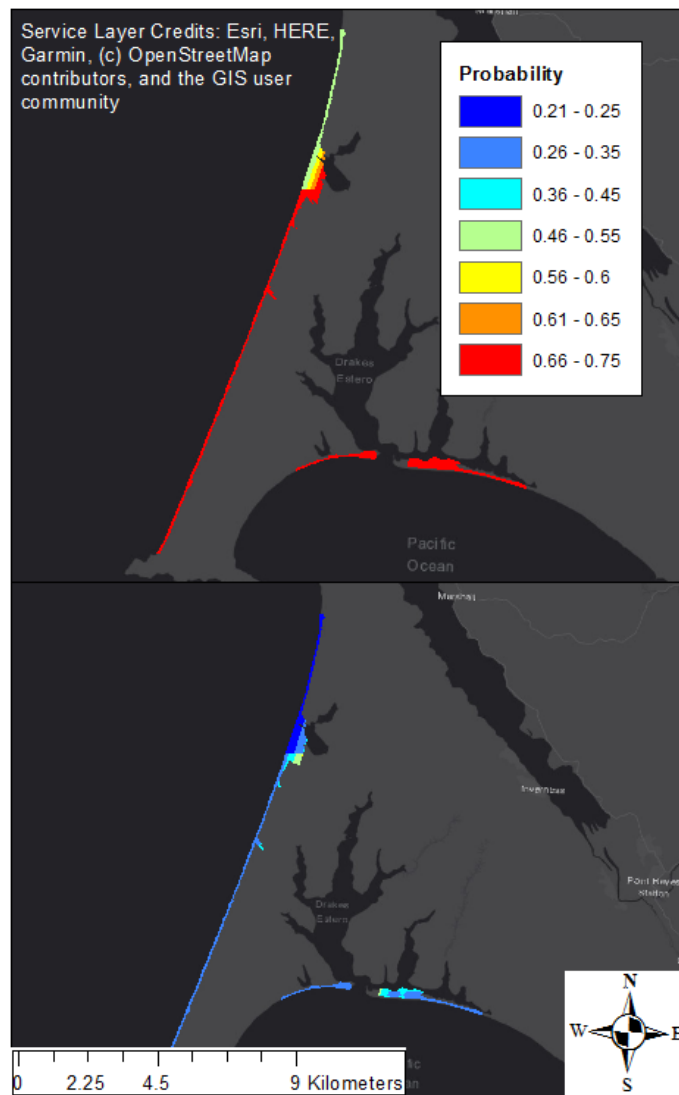


Figure 17. Predicted probability of hatching success in Point Reyes based on a nest initiation date of March 29 and average historic climate and mean high tide. The top panel shows predicted probability of hatching success if nest exclosures are used and the bottom panel shows predictions when nest exclosures are not used.

We also find some spatial variability in hatching success depending on when nests are initiated. For example, while the northern half of Monterey Bay has low hatching success in general, we project the highest hatching success in the north when nests are initiated on July 2 as compared to the other dates of March 29 or May 4 (Figure 18). The effect of nest initiation in Point Reyes is more spatially consistent with the entire area increasing in predicted hatching success when nests are initiated on July 2 as opposed to the two earlier dates (Figure 19).

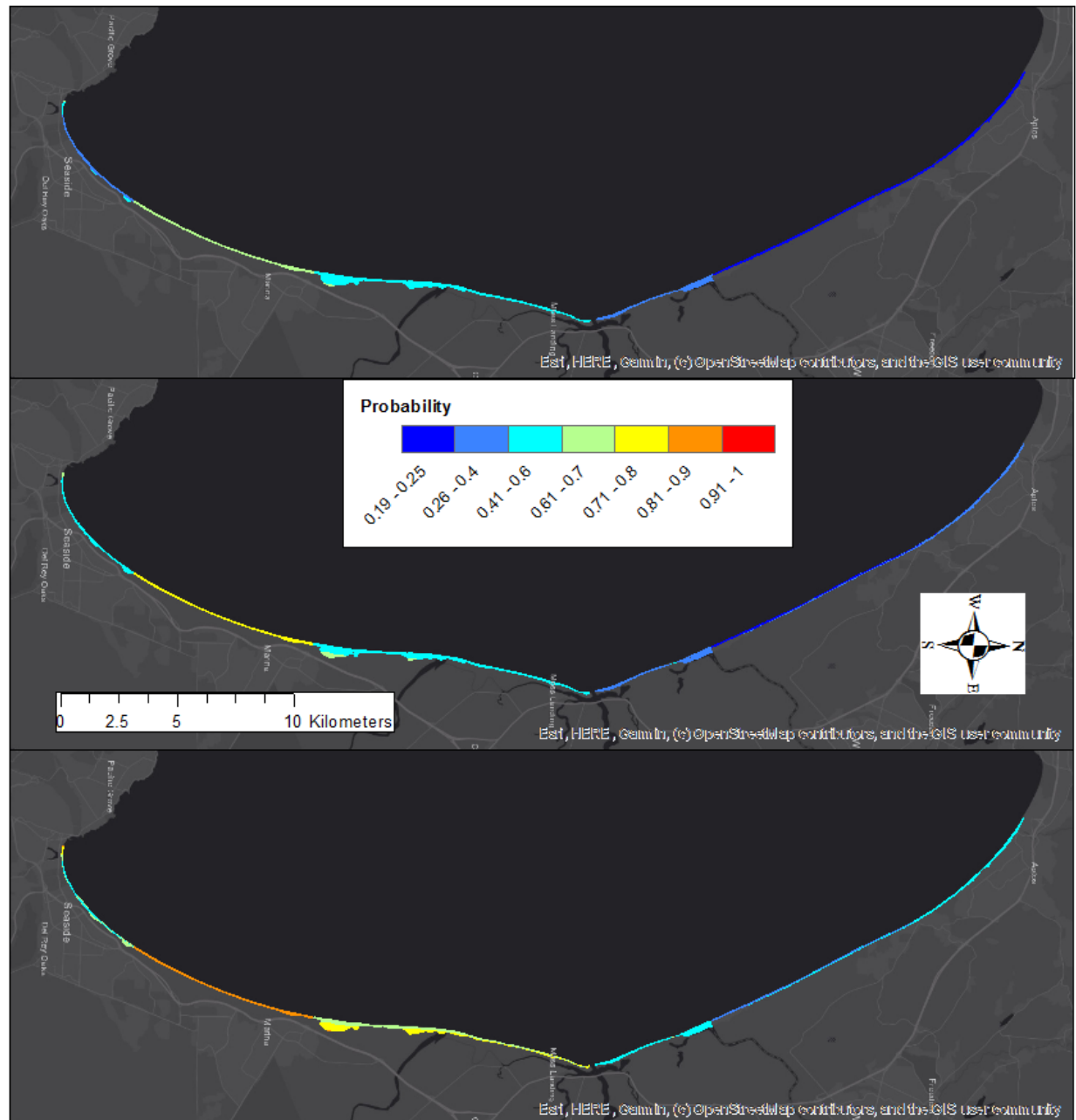


Figure 18. Predicted probability of hatching success in Monterey Bay based on average historic climate and mean high tide and no nest exclosures used. The panels, from top to bottom, show predictions based on nest initiation dates respectively of March 29, May 14, and July 2.

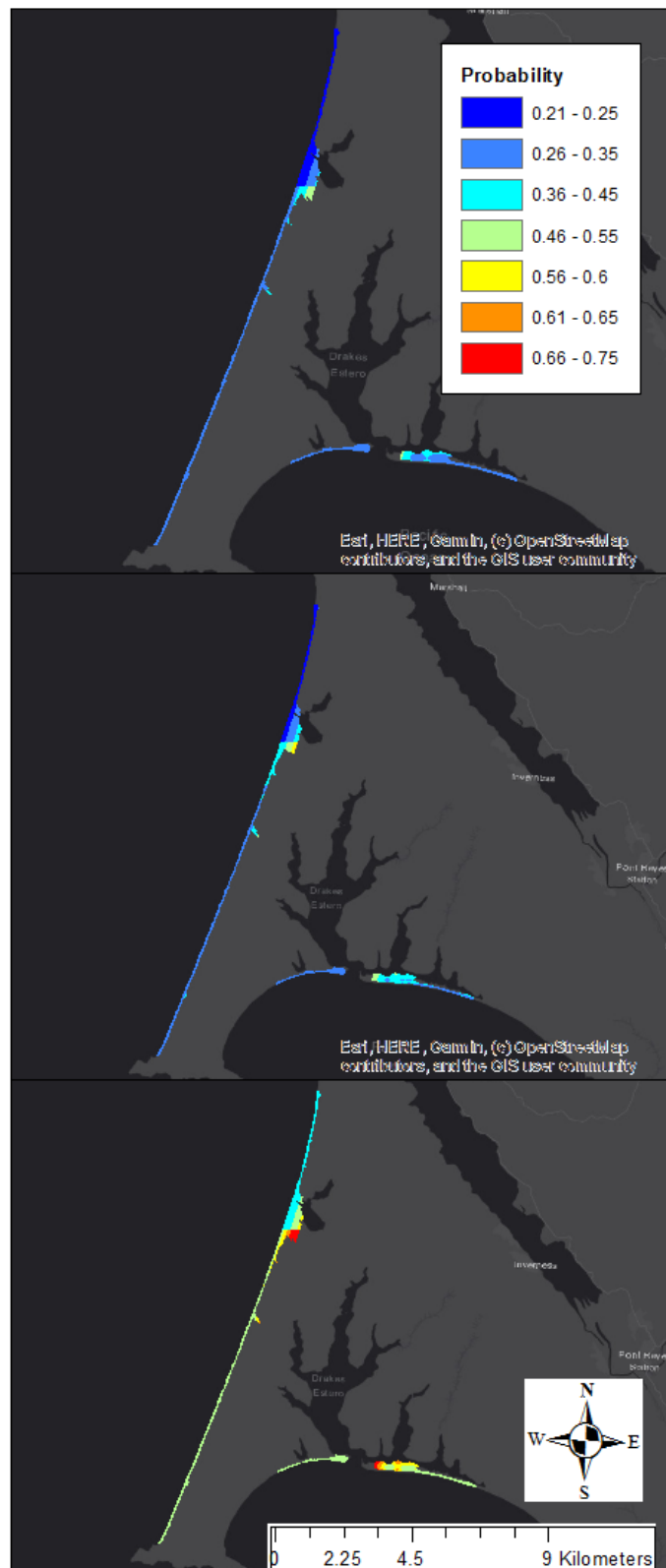


Figure 19. Predicted probability of hatching success in Point Reyes National Seashore based on average historic climate and mean high tide and no nest exclusions used. The panels, from top to bottom, show predictions based on nest initiation dates respectively of March 29, May 14, and July 2.

In Monterey Bay, we found a contrasting spatial pattern between predicted probabilities of fledging success as opposed to hatching success. Hatching success was consistently highest in the southern half of Monterey Bay (Figure 18) whereas fledging success was consistently highest in the northern half of Monterey Bay (Figure 20) irrespective of nest initiation date. We found that spatial patterns of fledging success are strongly tied to the group locations in Point Reyes. Across each of the nest initiation dates we selected for the spatial predictions, Kehoe and a large portion of the Restoration Area consistently have the highest predicted probability of fledging success (Figure 21). In contrast, the predicted probabilities of fledging success in North Beach varies depending on when nests are initiated (Figure 21).

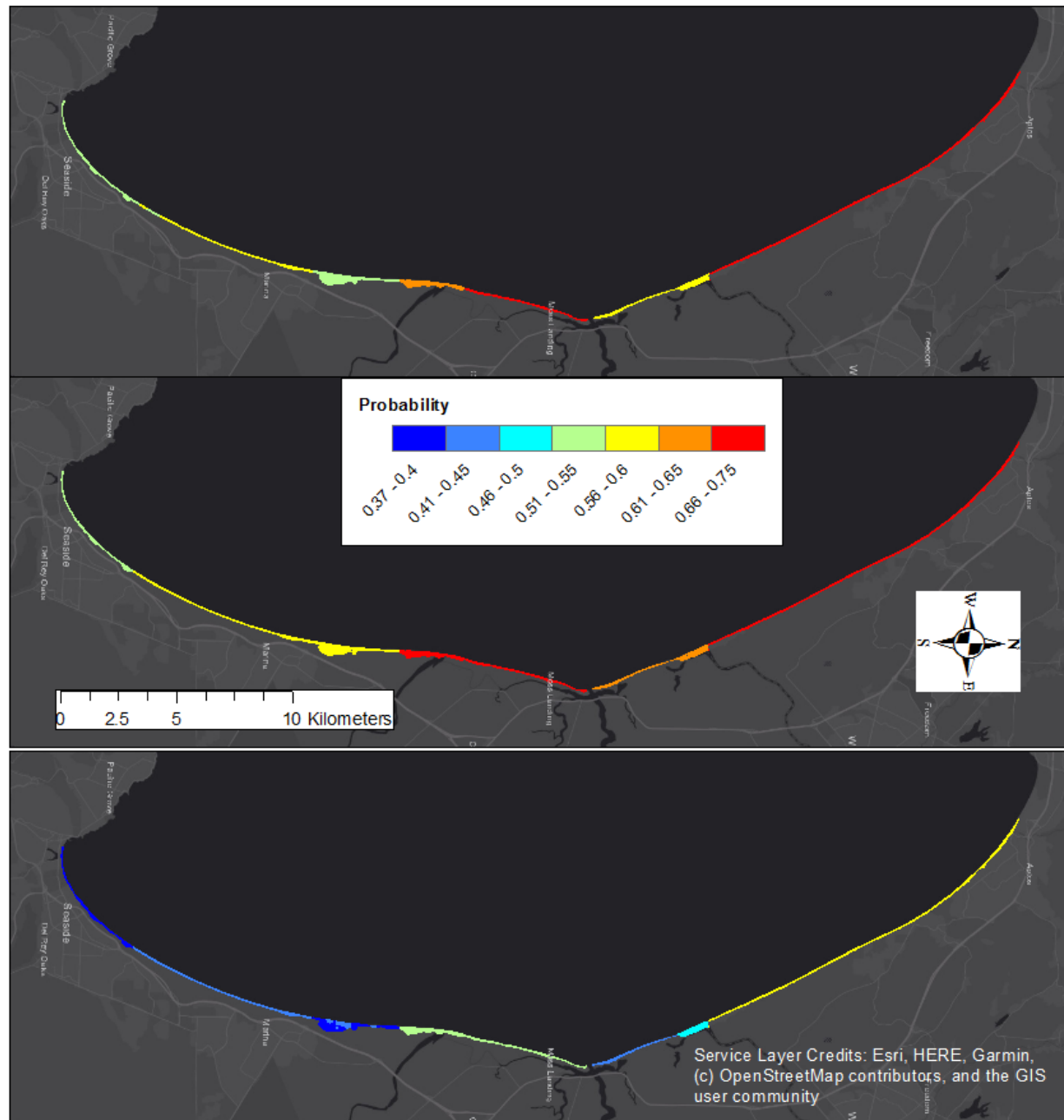


Figure 20. Predicted probability of fledging success in Monterey Bay. The panels, from top to bottom, show predictions based on nest initiation dates respectively of March 28, May 23, and July 3.

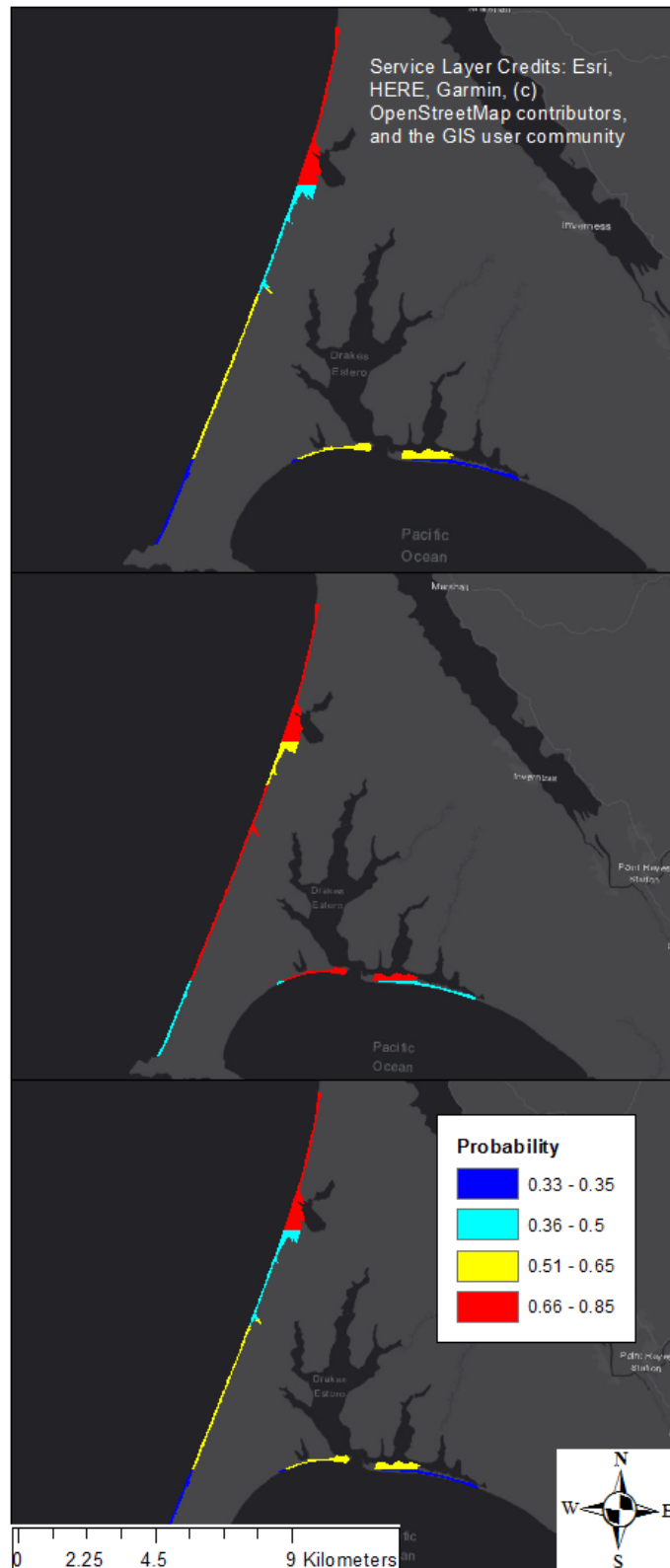


Figure 21. Predicted probability of fledging success in Point Reyes National Seashore. The panels, from top to bottom, show predictions based on nest initiation dates respectively of March 28, May 23, and July 3.

Future Projections: Sea Level Rise and Climate

Sea level rise

In both Monterey Bay and Point Reyes, sea level rise will decrease the nesting habitat available for snowy plovers with each increment of increasing sea levels (Tables 5 and 6). The only exception to this pattern is in the Restoration Area in Point Reyes that is beyond the extent of future sea levels, and we don't project any loss of habitat in this location (Table 6).

The North Marina beach segment MX has by far the most remaining habitat in Monterey Bay with 200 cm of sea level rise (48.8 ha), followed next by the SX in the Salinas River (18.9 ha, Table 5). All other segments have < 10 ha remaining with 200 cm of sea level rise (Table 5). In total we project that the Monterey Bay study region will lose 294.4 ha of habitat (52.1% decrease) to high tide inundation with 200 cm of sea level rise.

Table 5. Hectares of beach habitat available in Monterey Bay with 200, 100, 50, and 0 cm of sea level rise, in descending order of total hectares at 200 cm. Each row presents the data for a unique beach segment.

Name	GroupLoc	200 cm	100 cm	50 cm	0 cm
MX	NorthMar	48.8	53.3	54.8	55.2
SX	SalinasR	18.9	30.1	37.6	38.4
PS	PajaroR	9.9	12.5	16.7	17.4
RD	North	6.9	16.4	22.3	24.6
FO	FortOrd	6.9	14.7	16.3	17.5
MA	NorthMar	6.7	11.1	11.9	12.2
SN	SalinasR	6.0	8.2	9.1	9.2
NC	Monterey	5.7	8.8	9.9	10.4
ZB	PajaroR	5.4	5.9	6.7	6.8
RR	FortOrd	5.3	9.5	11.5	12.4
JR	CentralNo	5.1	12.2	16.8	18.6
HI	Monterey	4.7	7.0	7.4	7.9
SG	NorthMar	4.0	5.4	5.8	5.9
MD	CentralSo	3.4	7.8	10.8	11.6
CE	North	3.3	12.7	17.1	14.7
MP	CentralSo	2.3	8.4	13.7	16.1
MB	Monterey	1.8	5.3	6.1	7.2
MN	NorthMar	1.4	2.3	2.8	3.1
NM	North	1.0	6.0	10.5	14.7
RO	FortOrd	1.0	7.4	9.7	10.6
ME	North	0.9	10.7	17.0	17.0
PH	North	0.6	6.7	12.2	15.4
NO	North	0.5	2.7	4.4	5.0
MO	North	0.5	3.5	4.3	4.5
NT	North	0.3	2.6	4.1	5.4
ZS	CentralNo	0.3	1.3	2.4	2.7
PJ	CentralSo	0.1	0.7	1.4	1.7

As compared to Monterey Bay, the beach segments in Point Reyes retain substantially more sandy beach habitat with 200 cm of SLR; every segment except Drake's spit retains 14 ha or greater (Table 6). While we project that all the segments will lose habitat to high tide inundation at 200 cm of sea level rise except the Restoration Area, the remaining habitat should be large enough to support plover populations. In total, we project that Point Reyes will lose 79.8 ha (30.5% decrease) of sandy beach habitat to permanent high tide inundation with 200 cm of sea level rise.

Table 6. Hectares of beach habitat available in Point Reyes with 200, 100, 50, and 0 cm of sea level rise, in descending order of total acreage at 200 cm. Each row presents the data for a unique beach segment.

Segment	GroupLoc	200 cm	100 cm	50 cm	0 cm
Restoration Area (RA)	RestArea	77.0	77.0	77.0	77.0
North Beach (NP/NB)	NorthB	49.9	56.4	59.2	62.0
South Beach (SB)	NorthB	22.0	26.3	27.9	30.1
Kehoe (K)	Kehoe	15.9	21.4	23.8	25.9
Limantour (L)	Limantour	14.6	23.6	44.5	56.3
Drake's Spit (D)	Limantour	2.2	2.7	4.7	10.1

Hatching Success

Within the remaining habitat within the study extent, we found that the effects of climate change and sea level rise on hatching success were very sensitive to whether predator exclosures were used. When we project that exclosures are not used, predicted hatching success declines consistently across the century irrespective of when nests are initiated (Figures 22 and 23). The main difference between Point Reyes and Monterey Bay is that predicted hatching success does not decline substantially in 2040 in Point Reyes whereas predicted probability of hatching success declines between 0.05 and 0.1 in 2040 in Monterey Bay. In contrast, when exclosures are used, we predict that the probability of hatching success will increase consistently throughout the 21st century, although the increase is somewhat muted between 2070 and 2100 with a nest initiation date of July 2 in Monterey Bay (Figure 22).

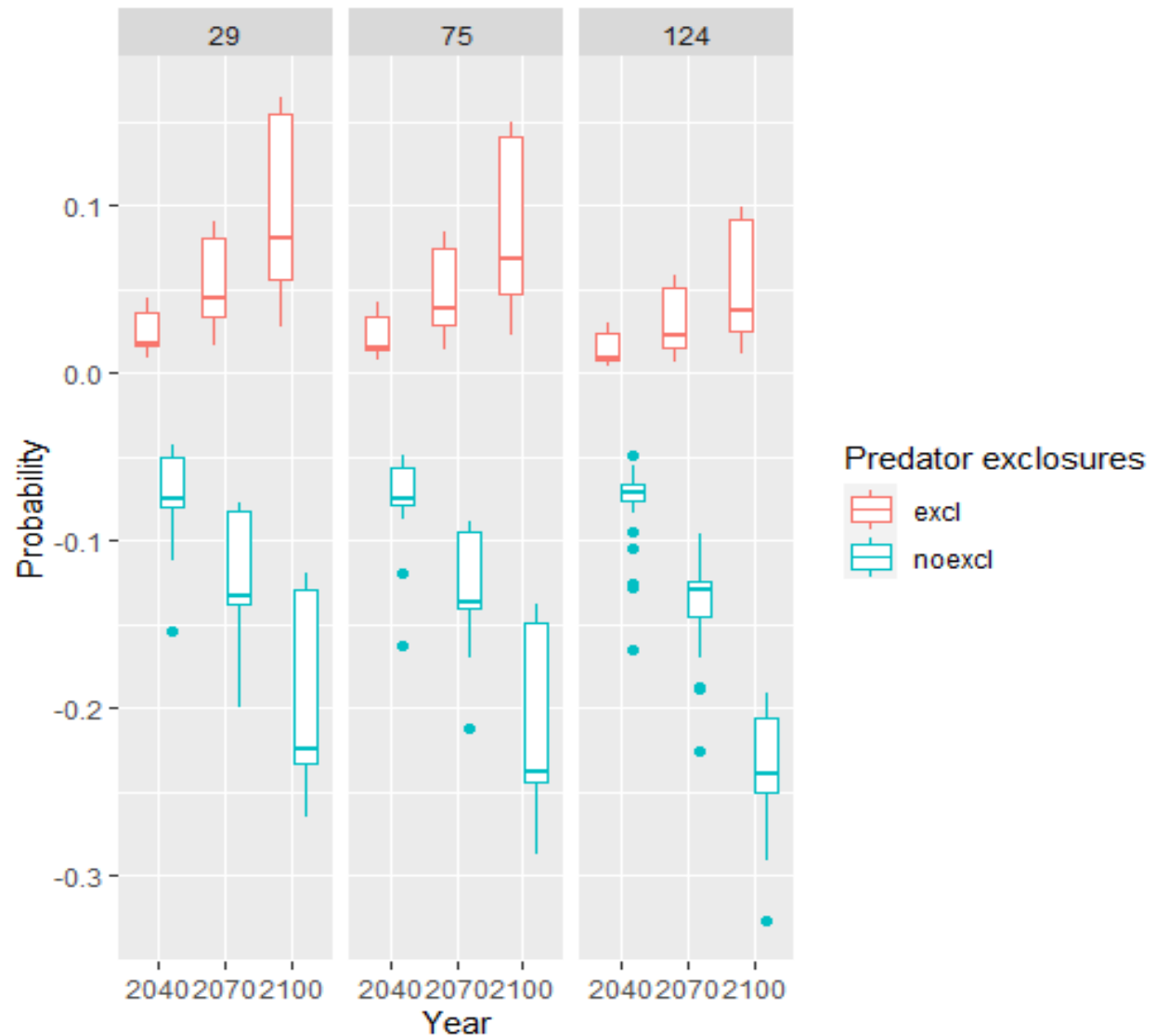


Figure 22. Boxplots of the change in the predicted probability of hatching success summarized across all beach segments in Monterey Bay (n = 27) in response to projected future climate change and increasing sea levels at 2040, 2070 and 2100. Colors indicate whether predator exclusions were used (excl) or not (noexcl) to protect nests. Each panel presents predictions for the number of days after March 1 in which nests were initiated.

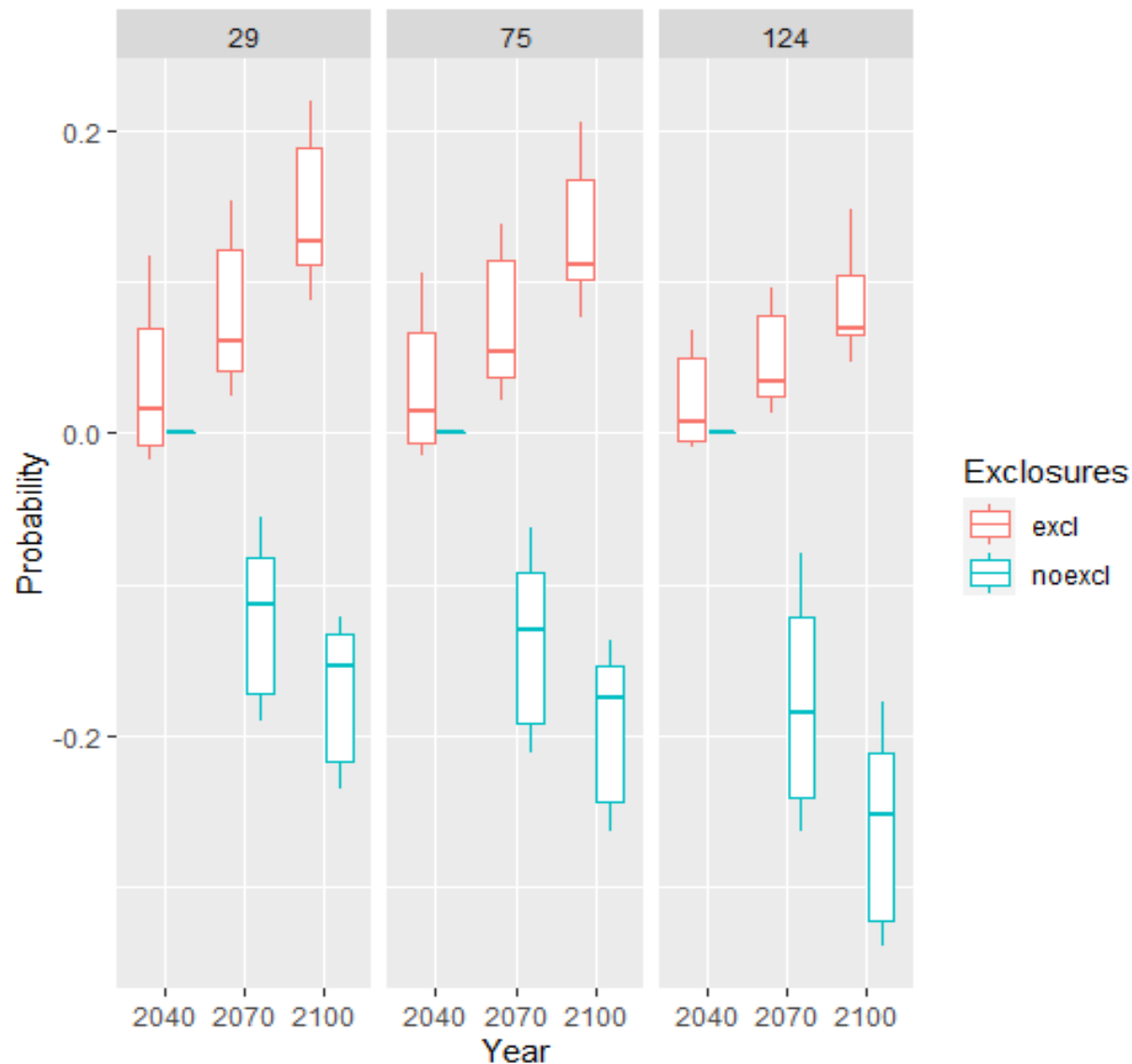


Figure 23. Boxplots of the change in the predicted probability of hatching success summarized across all beach segments in Point Reyes (n = 4) in response to projected future climate change and increasing sea levels at 2040, 2070 and 2100. Colors indicate whether predator exclusions were used (excl) or not (noexcl) to protect nests. Each panel presents predictions for the number of days after March 1 in which nests were initiated.

We found substantial variation in the change in habitat across the beach segments with the future projections (Figure 24). Segments such as CE, ME, MO, RD, NT, PH, and ZB could see on average improvements in the probability of hatching success greater than 0.1 with climate change if predators are excluded. When predator exclusions are not used, we find that these same segments see less of a decline in the probability of hatching success as compared to other segments.

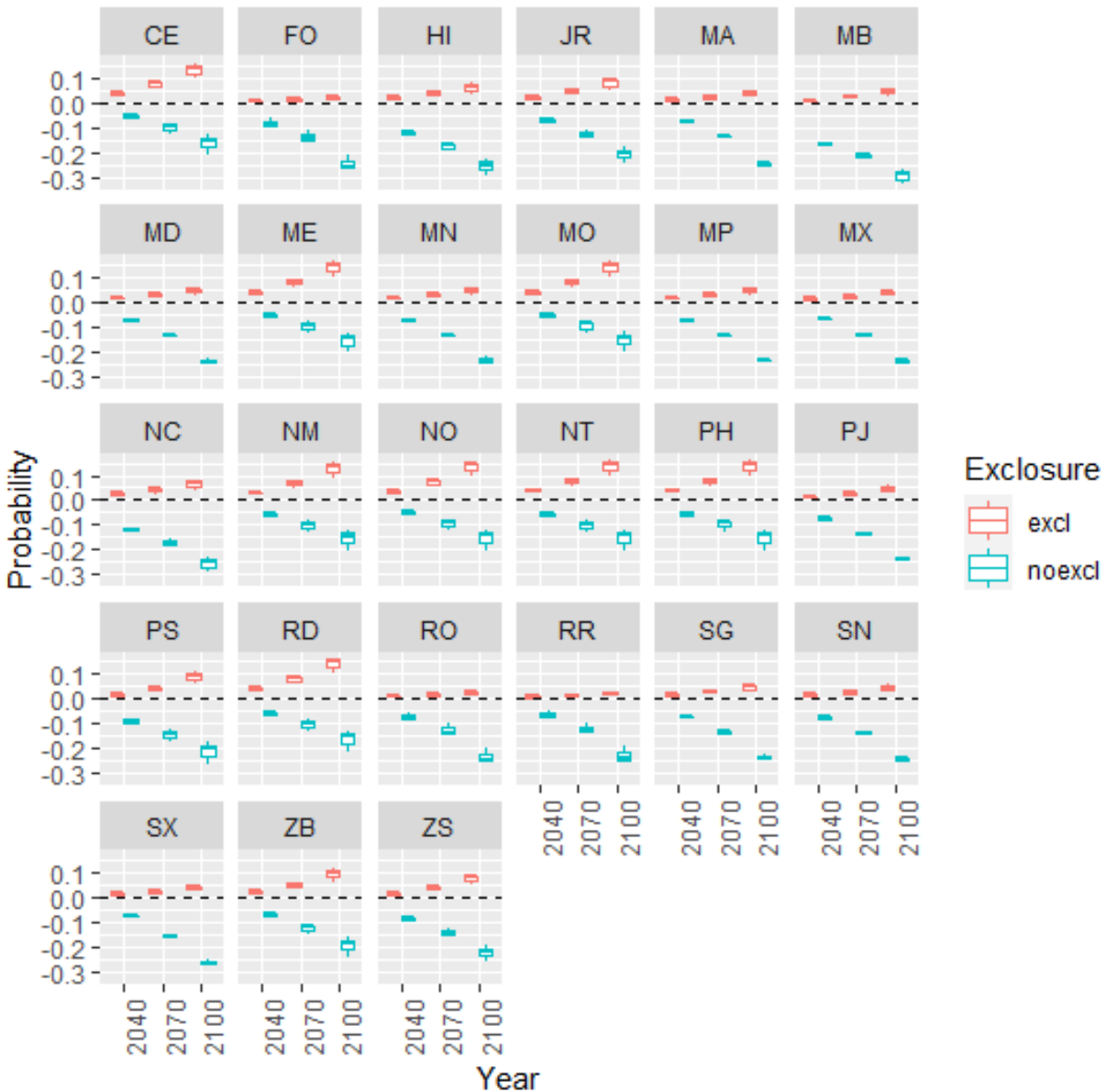


Figure 24. Boxplots of spatial summaries of the change in the predicted probability of hatching success in Monterey Bay for all beach segments in response to projected future climate change and increasing sea levels. Colors indicate whether predator exclusions are used (excl) or not (noexcl). The black dashed line indicates zero change in the probability of hatching success.

In Point Reyes, we project that Kehoe and North Beach (North B) will experience the greatest increase in the probability of hatching success by 2100 in Point Reyes, between 0.1 and 0.2, if predator exclusions are used (Figure 25). We project that the Restoration Area, despite not losing any habitat to increasing sea levels, and Limantour could experience the greatest decline in the probability of hatching success if predator exclusions are not used (Figure 25); in both cases the probability of hatching success declines by approximately 0.2 by 2070 (Figure 25).

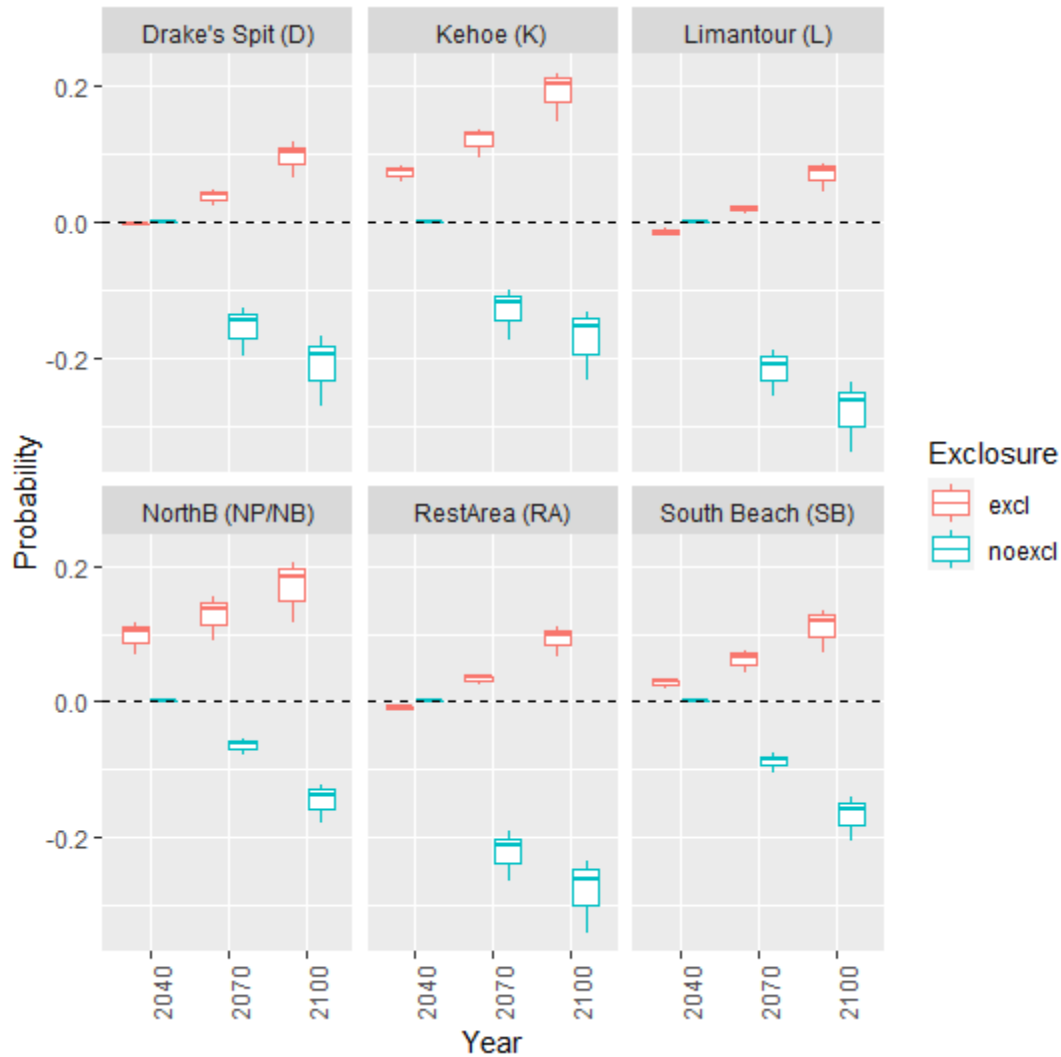


Figure 25. Boxplots of spatial summaries of the change in the predicted probability of hatching success in Point Reyes for all beach segments in response to projected future climate change and increasing sea levels. Colors indicate whether predator exclusions are used (excl) or not (noexcl). The black dashed line indicates zero change in the probability of hatching success.

Fledging Success

For all Monterey segments and all segments at Point Reyes except the Restoration Area and Kehoe, we find that warming temperatures will lead to improved fledging success (Figures 26 & 27). Generally, we project that the probability of fledging success will increase by between 0.05 - 0.1 by 2040 and increase by between 0.15 to over 0.2 by 2100 within Monterey Bay segments (Figure 26). In Point Reyes, we project a much more substantial improvement in fledging success at Drake's Beach, Limantour, and South Beach (Figure 27). For example, we project between a 0.3 - 0.4 increase in the probability of fledging success by 2040 at Limantour (Figure 27).

In contrast to the rest of the study area, we project relatively unchanged (North Beach) or declining fledgling success (Kehoe and Restoration Area) with future climate change (Figure 27). While our models predict a positive response to warming minimum temperatures in June (Figure 14), the models also project a negative (although not significant) effect of increasing February maximum temperatures at Point Reyes (Figure 15). The future climate models we used predict greater

February warming at North Beach, Kehoe, and Restoration Area as compared to the other beach segments at Point Reyes. However, the relatively low sample size of fledged nests at Point Reyes contributes to relatively large standard errors for these spatial predictions.

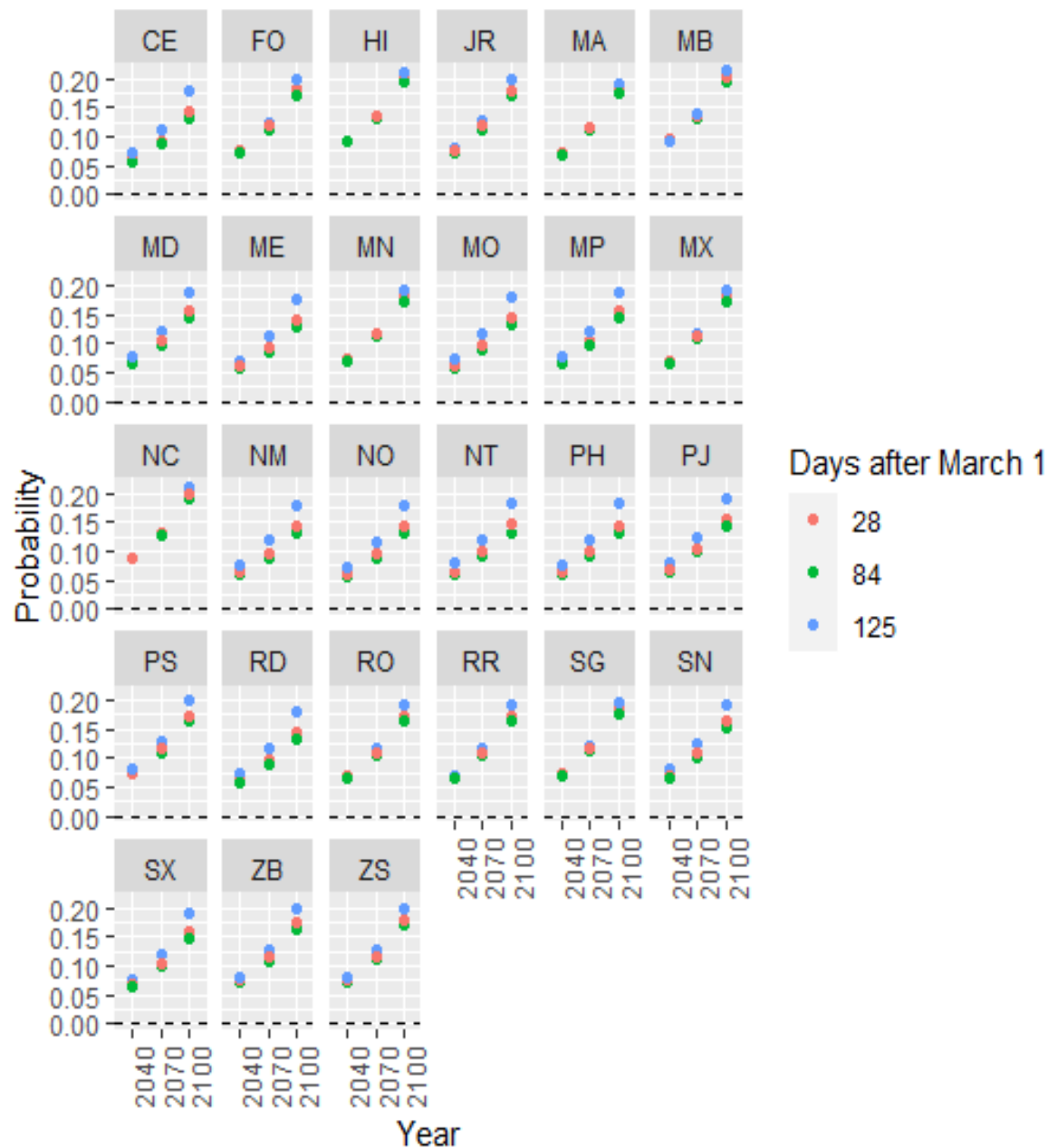


Figure 26. Summary of spatial summaries of the change in the predicted probability of fledging success in Monterey Bay for all beach segments in response to projected future climate change and increasing sea levels. Colors indicate the number of days after March 1 that nests were initiated. The black dashed line indicates zero change in the probability of fledging success.

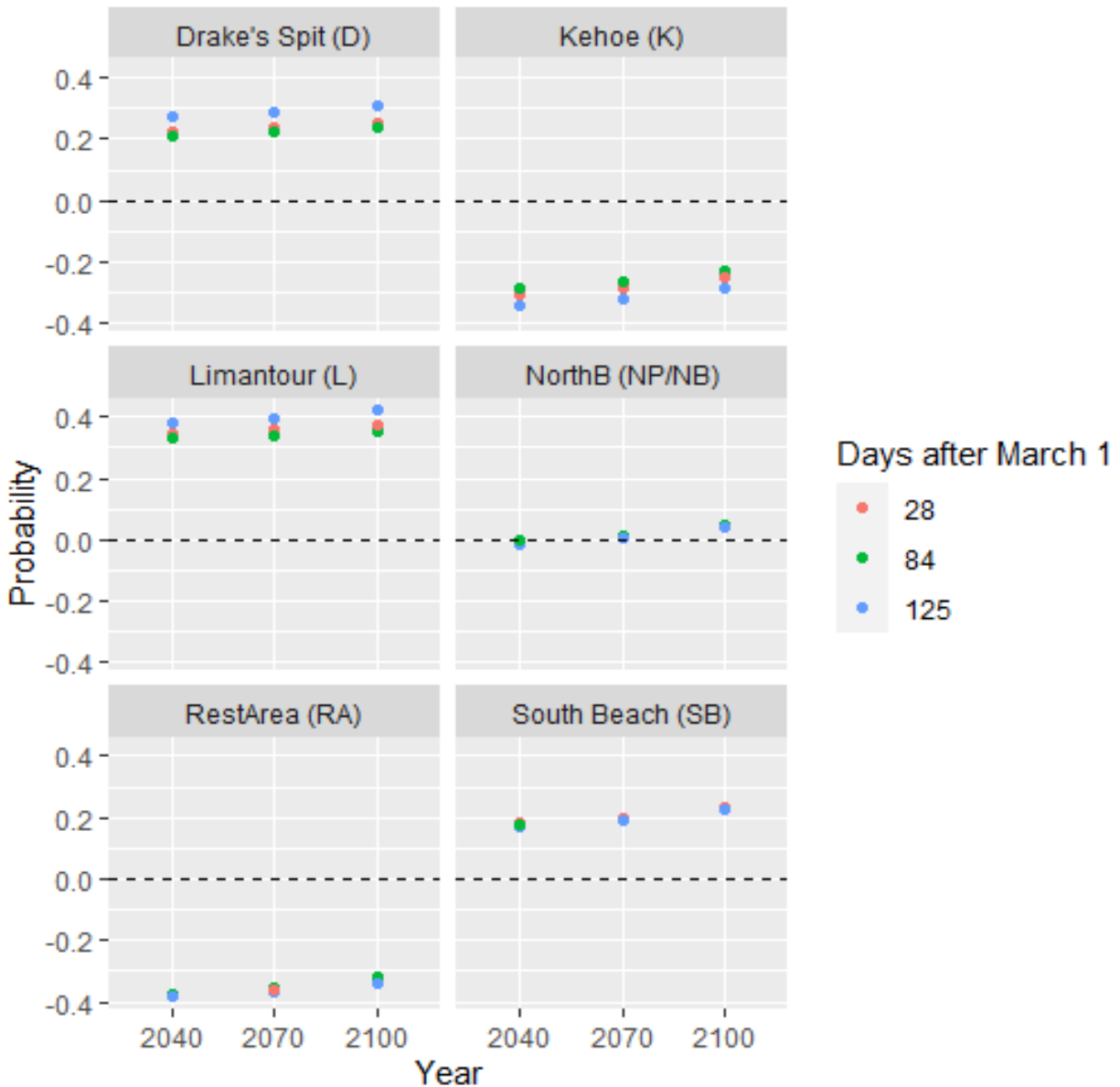


Figure 27. Summary of spatial summaries of the change in the predicted probability of fledging success in Point Reyes for all beach segments in response to projected future climate change and increasing sea levels. Colors indicate the number of days after March 1 that nests were initiated. The black dashed line indicates zero change in the probability of fledging success.

DISCUSSION

In this study we found a significant link between plover hatching success and habitat conditions; the greater the distance a nest was located from mean high water the higher the probability of hatching, regardless of whether a nest was protected by an enclosure. Our findings also indicate that nesting habitat above mean high water at Monterey Bay and Point Reyes will decrease significantly as sea level rises and yet the influence of beach width on snowy plover reproductive success is not well understood. Patrick and Colwell (2013) found that plovers selected wider beaches for nesting but did not document the relationship between hatching success and beach width. Nesting farther above

mean high water probably confers many benefits including protection from flooding by ocean tides and waves, lower levels of disturbance from human recreation, and possibly a more open viewshed which may aid in detection of approaching predators.

However, for nests that failed, the probability that predation was the cause of nest failure actually increased at greater distances above mean high water. The predator risk hypothesis posits that selection of more open nest sites aids in rapid predator detection, reducing the risk of individual mortality during incubating but increasing the risk of nest exposure to egg predators and environmental factors (e.g., wind, temperature fluctuations; Fraser and Catlin 2019). The pattern that we observed in this study suggests that nests located farther above mean high water were more vulnerable to predators. Possible explanations for this pattern are that nests that were farther above mean high water had more occluded viewsheds (either from vegetation or topography) resulting in delayed detection of predators, because predator abundance was greater farther above mean high water, or because egg predators targeted this habitat. Other studies have shown that snowy plovers nesting in more vegetated areas are at greater risk of individual mortality, presumably because their view of approaching predators is more occluded (Amat and Masero 2004), and this mortality risk drives selection of more open nest sites (Gomez-Serrano and Lopez Lopez 2014, Stenzel and Page 2019). In this study, our findings suggest that at Point Reyes and Monterey Bay, there is a trade-off between nesting high enough above mean high water to escape loss from environmental factors and an increasing risk of nest predation as distance from mean high water increases. This highlights both the vulnerability of nests to future increases in sea level and the importance of predator management, including use of individual nest exclosures, to reduce predator pressure so that plovers can safely move above the high tide line to increase their chances of hatching a nest. Our results also may indicate the need for protection of ecosystem processes and anthropogenic interventions (e.g., habitat restoration) that reduce vegetative cover and/or modify topography to positively influence nest success (Dinsmore et al. 2014, Leja 2015, Neuman et al. 2019), but further studies are necessary to substantiate a causal link between vegetation cover and the patterns we detected.

In this study, predicted hatching success was highly sensitive to the use of nest exclosures at both Point Reyes and Monterey Bay (Figures 22 and 23). Similar positive effects of exclosures on snowy plover hatching rates have been documented at other areas (Hardy and Colwell 2008, Dinsmore et al. 2014), however, exclosures can increase the risk of nest abandonment and plover mortality if predators learn that exclosures are associated with incubating plovers (Neuman et al. 2004, Hardy and Colwell 2008, Eberhardt-Phillips et al. 2016). Further, exclosures have been linked to lower annual survival rates of adult snowy plovers (Gaines et al. 2020) and this negatively impacts population viability because this vital rate is the most critical for population stability (Nur et al. 2007). These same negative effects of exclosures have been documented for many other imperiled shorebird species (Isaksson et al. 2007, Barber et al. 2010).

Climate change is expected to affect bird populations in several ways. Extreme climate fluctuations may induce spatial synchrony across geographically distinct populations, warming temperatures may result in temporal mismatches between nest phenology and resource availability, cause changes in the timing of migration, and cause geographic distributions to shift northward (Crick 2004, Dunn and Winkler 2010, Haig 2019). In this study we documented significant links between temperature and plover reproductive rates, with warmer temperatures associated with lower hatching rates and higher fledging rates. There is mounting evidence that warmer temperatures are causing bird species to begin laying earlier (Dunn and Winkler 2010), and though we did not examine that relationship in this study, there is evidence that the populations we studied do show a shift to earlier nest initiation when spring temperatures are warmer and that this earlier nest initiation leads to greater overall fecundity (Hudgens et al. 2020). In addition, our models found a somewhat complicated pattern

between nest initiation date and hatching success in that the earliest nests, prior to March 10, had the highest probability of hatching success but we also found that hatching success declined for nests initiated between March 10 and late May and then increased between late May and early July. Since we did not attempt to model explicitly how the effects of temperature cause plovers to change the timing of nest initiation, our results of changes in hatching and fledging success in response to warming temperatures may only tell part of the story.

Warmer temperatures also were linked with increased fledging success, which may to some degree compensate for the negative effects of warmer temperatures on hatch rates, though we did not determine the relative impacts of these two demographic rates on future population viability. One possible explanation for the effect of warmer temperatures on chick survival is that warmer temperatures confer direct thermoregulatory benefits for young chicks which increases their survival beyond the most vulnerable early stage of chick-rearing. Plover chick survival increases with increasing age and younger chicks (0-10 days old) are brooded by adults more than 50% of the time, compared with 17% of the time for older chicks (Colwell et al. 2007). Hudgens et al. (2020) examined the effect of warmer temperatures on the number of fledglings produced per male each year and found that annual fecundity per male increased with warmer temperatures, primarily because this allowed breeding males the opportunity of re-nesting and fledging second broods. Another possible explanation for the positive impact of warm temperatures on fledging probabilities is that warmer temperatures reduce physiological stress on breeding adults in the year prior to nesting, allowing them to be in better body condition which will benefit them during the following breeding season. Hudgens et al. found that colder temperatures over winter negatively affected the survival of adult snowy plovers (Hudgens et al. 2020). Though the mechanism for this negative effect is not well understood, it may be related to less abundant food resources, the greater energy expenditures needed to thermoregulate in colder temperatures, or both. Alternatively, beach invertebrates may simply become more active at the surface of the sand and in sheltered wrack microhabitats when it is warmer, providing shorebirds with greater access to foraging opportunities (Pienkowski 1983, Davis and Keppel 2021), that could lead to improved body condition.

Warmer temperatures in the future, especially extreme heat events, may result in increased levels of human use of beaches at the two study areas, which is of concern for plovers because increased human use may result in lower fledging success. Ruhlen et al. (2003) found that at Point Reyes, snowy plover chicks were more likely to disappear on weekend days, when human use of beaches was greater, as compared to weekdays. In this study, we did not account for increasing levels of human-caused disturbance on plover hatch or fledge rates in the future, so our results with respect to positive trends in fledge rates should be viewed with caution.

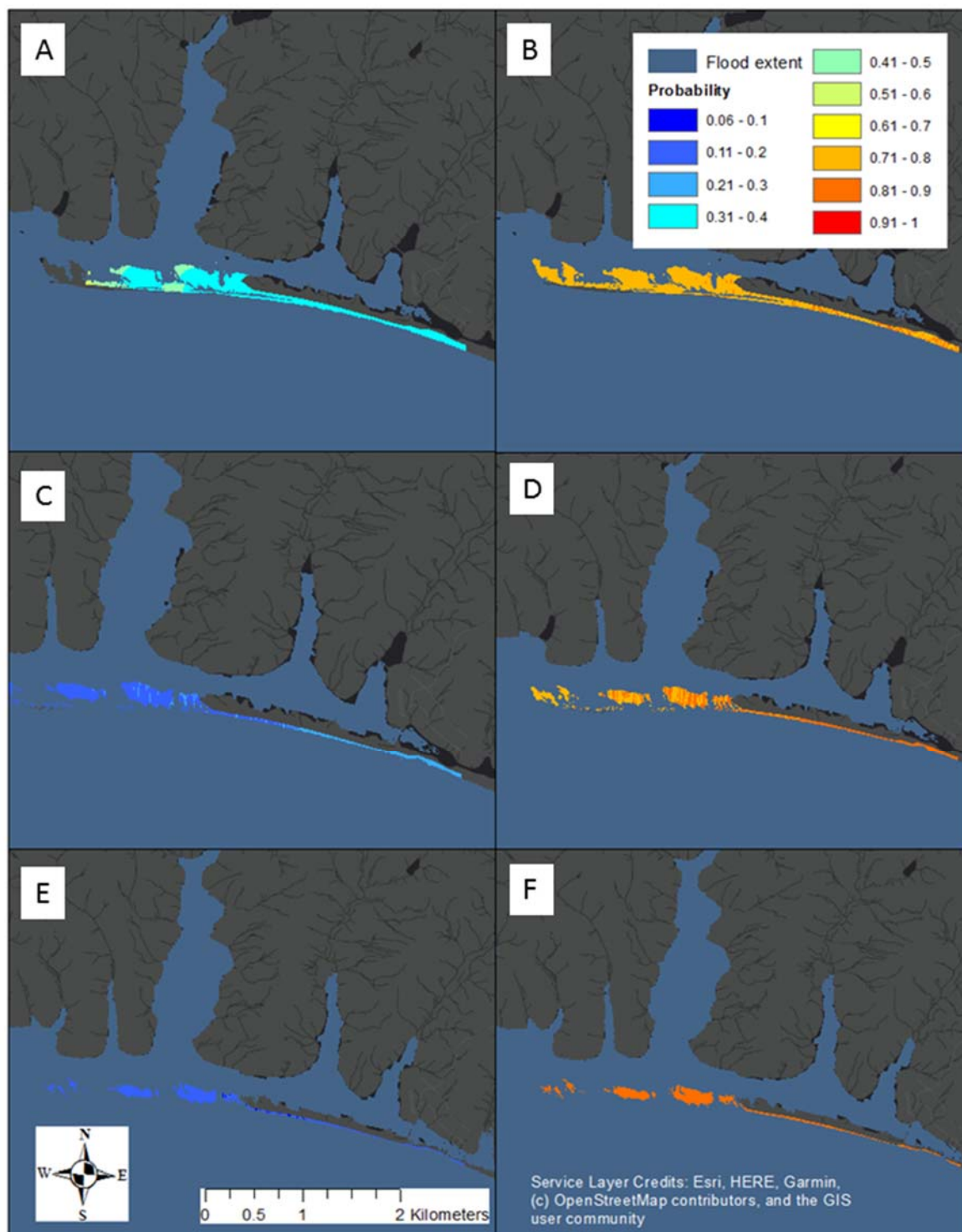


Figure 28. Maps of predicted hatching success (colored areas) based on climate change scenarios of 2040 (A & B), 2070 (C & D) and 2100 (E & F) at Limantour Beach in Point Reyes. Panels A, C and E assume no predator exclosures are used while panels B, D and F assume predator exclosures are used for all nests. All maps assume a nest initiation date of May 24. The areas in dark blue in each panel shows locations that CoSMoS models project to be inundated at mean high water with sea level rise of 50 cm (A & B), 100 cm (C & D) and 200 cm (E & F).

Because of these major findings, we suspect that a warmer climate primarily will affect snowy plover reproductive success in a net negative way, even given the higher predicted fledging rates. Hudgens et al. (2020) found that warming would increase plover survival and fecundity, but they did not consider the potential decreases in habitat availability that will be driven by sea level rise and acknowledged that the net positive effects of warming on the demographic rates they examined could be obviated by habitat loss (Figure 28). In this study we found that habitat availability at the two regions will decrease due to sea level rise and that each study area showed patterns of vulnerability. Our models of sea level rise project that much of the existing beach habitat will be lost and a narrowing of much of what remains (Figure 28). However, our study did not allow for the migration of beach habitat inland. In some parts of our study area, there is ample opportunity for existing dunes to erode, creating new beach habitat that our models do not consider. Management should target these areas to ensure that natural habitat evolution is allowed to proceed so that new habitat is created as sea levels rise. In addition, our results indicate that protecting nests from predators may improve plover reproductive success in a warming climate, but future approaches will likely need to be adapted to changing predator and environmental conditions.

FURTHER RESEARCH

Our findings identify important interactions between reproductive success, predators, and environmental conditions. Future work should focus on elucidating the mechanisms that are causing these patterns. For example, our results indicate that warmer temperatures can reduce hatching success through an interaction with predation. Devising the most appropriate adaptation solutions will require a more complete understanding of the link between temperature and predation of plover nests. This may require directly studying how plover predators respond to increasing air temperature. A promising avenue would be to expand the approach we took in this study to include plover populations in more southern areas in California that have warmer air temperatures than occur in Monterey or Point Reyes. Similarly, we need to uncover why nests are more vulnerable to predation the further they are located from mean high water. It is possible that management could modify beach habitats in ways that would improve hatching success at greater distances from mean high water. This will be increasingly important as sea levels rise and the amount of habitat at greater distances from mean high water is reduced substantially.

Future projections of sea level rise effects on plover habitat should allow for an evolving shoreline. Although the CoSMoS models of future sea levels indicate that a substantial proportion of today's sandy beaches in the study area will be lost to increasing sea level, it is possible that sandy beach habitats will move inland as sea levels increase. Because much of the beaches and adjacent habitat within Monterey Bay and Point Reyes are publicly owned and managed as parks, there is less development that could constrain habitat migration than there is on much of the rest of the California coast. However, we do not yet know if beaches backed by high dunes or bluffs will evolve in ways that support high quality beach habitat as sea levels rise. Future efforts could include more explicit projections for how these beach habitat types might change in response to rising seas.

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REFERENCES

- Adams, D, M Koenen, K Peterlein, D Press, and SG Allen. 2014. Snowy plover monitoring protocol for Point Reyes National Seashore: Version 7.1. Natural Resource Report NPS/SFAN/NRR—2014/850. National Park Service, Fort Collins, Colorado. NPS 612/126255, August 2014
- Barnard, PL, LH Erikson, AC Foxgrover, PL Limber, AC O'Neill, and S Vitousek, 2018, Coastal Storm Modeling System (CoSMoS) for Central California, v3.1 (ver. 1h, March 2021): U.S. Geological Survey data release, <https://doi.org/10.5066/P9NU062B>.
- Barnard, PL, Erikson, LH, Foxgrover, AC, Finzi Hart, JA, Limber, P, O'Neill, AC, van Ormondt, M, Vitousek, S, Wood, N, Hayden, MK, and Jones, JM, 2019. Dynamic flood modeling essential to assess the coastal impacts of climate change. Scientific Reports, Volume 9, Article #4309, 13 pp., <http://dx.doi.org/10.1038/s41598-019-40742-z>.
- Crick, HQP. 2004. The impact of climate change on birds. *Ibis* 146 (Suppl.1): 48–56
- Davis, JG and G Keppel. 2021. Fine-scale environmental heterogeneity and conservation management: Beach-cast wrack creates microhabitats for thermoregulation in shorebirds. *Journal of Applied Ecology* 58: 1291-1301, <https://doi.org/10.1111/1365-2664.13865>
- Defeo O, McLachlan A, Schoeman DS et al. 2009. Threats to sandy beach ecosystems: a review. *Estuarine, Coastal and Shelf Science*, 81:1–12.
- Dinsmore, SJ, DJ Lauten, KA Castelein, EP Gaines and MA Stern. 2014. Predator exclosures, predator removal, and habitat improvement increase nest success of snowy plovers in Oregon, USA. *Condor* 116:619–628.
- Dunn, PO and DW Winkler. 2010. Effects of climate change on timing of breeding and reproductive success in birds. In AP Moller, W Fiedler, P Berthold (eds.). *Effects of Climate Change on Birds*. Oxford University Press, Oxford, UK.
- Eberhart-Phillips, LJ, BR Hudgens, and MA Colwell. 2016. Spatial synchrony of a threatened shorebird: regional roles of climate, dispersal and management. *Bird Conservation International* 1:119-135.
- Faillace, CA, and BW Smith. 2016. Incubating snowy plovers (*Charadrius nivosus*) exhibit site-specific patterns of disturbance from human activities. *Wildlife Research* 43: 288-297.
- Flint, LE and AL Flint, 2014, California Basin Characterization Model: A Dataset of Historical and Future Hydrologic Response to Climate Change, (ver. 1.1, May 2017): U.S. Geological Survey Data Release, <https://doi.org/10.5066/F76T0JPB>.
- Gaines EP, SJ Dinsmore, and MT Murphy. 2020. Effects of management for productivity on adult survival of snowy plovers. *Journal of Field Ornithology* 91:130–141.

Gardali T, Seavy NE, DiGaudio RT, Comrack LA. 2012. A climate change vulnerability assessment of California's at-risk birds. PLoS ONE 7(3): e29507. doi: 10.1371/journal.pone.0029507.

Haig, SM. 2019. Changing Climates and Challenges to Charadrius Plover Success throughout the Annual Cycle. Pp. 45–62. In M. A. Colwell and S. M. Haig (editors). The Population Ecology and Conservation of Charadrius Plovers Studies in Avian Biology (no. 52), CRC Press, Boca Raton, FL.

Hardy, MA, and MA Colwell. 2008. The impact of predator exclosures on snowy plover nesting success: A seven-year study. Wader Study Group Bulletin, 115:161–166.

Hijmans, RJ. 2020. raster: Geographic Data Analysis and Modeling. R package version 3.3-7. <https://CRAN.R-project.org/package=raster>

Himmelstoss, EA, AS Farris, RE Henderson, MG Kratzmann, Ergul, Ayhan, Zhang, Ouya, JL Zichichi, ER Thieler, 2018, Digital Shoreline Analysis System (version 5.0): U.S. Geological Survey software release, <https://code.usgs.gov/cch/dsas>.

Hosmer, DW, S Lemeshow, and RX Sturdivant. 2013. Applied Logistic Regression Analysis, Third Edition, John Wiley and Sons Inc., New York.

Hubbard, DM, and JE Dugan. 2003. Shorebird use of an exposed sandy beach in southern California. Estuarine, Coastal and Shelf Science. 58S: 169-182.

Hutto, SV, Higgason KD, Kershner JM, Reynier WA, Gregg DS. 2015. Climate change vulnerability assessment for the north-central California coast and ocean. Marine Sanctuaries Conservation Series ONMS-15-02. U.S. Department of Commerce, National Oceanic and Atmospheric Administration, Office of National Marine Sanctuaries, Silver Spring, MD. 473 pp.

Lau, M. 2020. Breeding Western Snowy Plover Monitoring at Point Reyes National Seashore, Marin County, California, 2020 Annual Report. Natural Resource Report NPS/SFAN/NRR.

Neuman, K, L Stenzel, C Eyster, B Barbaree, E Haile, D Dixon, C Hickey, and A Palkovic. 2021. Reproductive Success and Breeding Population Size of Snowy Plovers in the Monterey Bay Region, 2020. Point Blue Conservation Science, Petaluma, CA.

Neuman, KK, RW Stein, CR Eyster, and T Gardali. 2019. Climate-smart conservation of beaches and dunes for western snowy plover recovery, in Monterey Bay, California. Point Blue Conservation Science. Contribution #2301. Petaluma, CA.

Neuman, KK, Stenzel LE, Warriner JC, Eyster C, Barbaree B, D Dixon D, Haile E, Palkovic A, Hickey C. 2019. Reproductive success and breeding population size of snowy plovers in the Monterey Bay region, California, in 2019. Point Blue Conservation Science, unpublished report. 40pp.

Neuman, KK, LA Henkel, GW Page. 2008. Shorebird use of sandy beaches in central California. Waterbirds 31: 115-121.

Nielsen, K, Morgan, SG and J Dugan 2013. Baseline characterization of sandy beaches in California's North-Central coast region. Final Report. California Marine Life Protection Act Initiative. 118 pp.

- National Research Council. 2012. Sea-Level Rise for the Coasts of California, Oregon, and Washington: Past, Present, and Future. Washington, DC: The National Academies Press. <https://doi.org/10.17226/13389>.
- Nur, N, GW Page and LE Stenzel. 2007. Population viability analysis for Pacific coast Snowy Plovers. Appendix D in: Recovery plan for the Pacific coast population of the Western Snowy Plover (*Charadrius alexandrinus*). U.S. Fish & Wildlife Service, Sacramento, CA.
- Ocean Protection Council (2018) State of California Sea-Level Rise Guidance, 2018 Update. https://opc.ca.gov/webmaster/ftp/pdf/agenda_items/20180314/Item3_Exhibit-A OPC SLR Guidance-rd3.pdf
- Point Blue Conservation Science and U.S. Geological Survey. Our Coast Our Future (OCOF). Web application, Petaluma, California. www.ourcoastourfuture.org (accessed August 10, 2021).
- Pienkowski, MW. 1983. Surface activity of some intertidal invertebrates in relation to temperature and the foraging behaviour of their shorebird predators. *Marine Ecology Progress Series*, 11: 141-150.
- R Core Team (2020). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
- Ruhlen, TD, S Abbott, L Stenzel, and GW Page. 2003. Evidence that human disturbance reduces Snowy Plover chick survival. *Journal of Field Ornithology* 74:300-304.
- Schlacher, TA, DS Schoeman, J Dugan, M. Lastra, A Jones, F Scapini, A McLachlan. 2008. Sandy beach ecosystems: key features, management challenges, climate change impacts, and sampling issues. *Marine Ecology* 29: 70-90.
- StataCorp. 2019. STATA 16.1. StataCorp LLC. College Station, Texas.
- Stenzel, LE and GW Page. 2019. Breeding Biology of *Charadrius* Plovers. Pp. 91–125 in Colwell and Haig (editors). *The Population Ecology and Conservation of Charadrius Plovers* (no. 52), CRC Press, Boca Raton, FL.
- van de Pol, M, BJ Ens, D Heg, L Brouwer, J Krol, M Maier, KM Exo, K Oosterbeek, T Lok, CM Eising, and K Koffijberg. 2010. Do changes in the frequency, magnitude and timing of extreme climatic events threaten the population viability of coastal birds? *Journal of Applied Ecology*, 47, 720–730.
- Veloz, S, N Nur, L Salas, D Jongsomjit, J Wood, D Stralberg, and G Ballard. 2013. Modeling climate change impacts on tidal marsh birds: Restoration and conservation planning in the face of uncertainty. *Ecosphere* 4:1–25.
- Vitousek, S, PL Barnard, P Limber, L Erikson, and B Cole. 2017. A model integrating longshore and cross-shore processes for predicting long-term shoreline response to climate change. *Journal of Geophysical Research: Earth Surface* 122:782–806.