

ARTICLE

Coastal and Marine Ecology

Quantifying the effects of nest management and environmental change on demography of an endangered sea turtle

Beth E. Ross¹  | Matthew A. Boggie¹  | Angela Anders² | Donna Shaver³

¹U.S. Fish and Wildlife Service, Southwest Region, Science Applications, Albuquerque, New Mexico, USA

²U.S. Fish and Wildlife Service, Southwest Region, Ecological Services, Albuquerque, New Mexico, USA

³National Park Service, Padre Island National Seashore, Corpus Christi, Texas, USA

Correspondence

Beth E. Ross

Email: beth_ross@fws.gov

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Abstract

Understanding the demographic drivers of reintroduced and translocated populations is critical for species establishment and persistence. Given the large number of resources required to conduct ongoing reintroduction and reinforcement programs, additional information on population responses to management practices could help identify key actions that best benefit a species while ensuring economic feasibility. An integrated population model (IPM) can be used to assess and forecast the demographic consequences of different management practices and the interrelationship between management effects, population dynamics, and environmental change. We used an IPM to inform the potential impacts of nest management practices and global climate change on the vital rates of the Texas nesting colony of the endangered Kemp's ridley sea turtle. We used the IPM to estimate population parameters including adult survival, population growth rate, and abundance of nesting females in Texas. Additionally, given potential future scenarios for management and environmental change, we used the IPM to forecast population change and estimate the probability of persistence of the Texas population under future environmental and management scenarios. Future scenarios for nest management that had some level of management (i.e., not all nests were left in situ) resulted in population growth rates that were likely stable or increasing. Scenarios in which all nests were left in situ resulted in stable or decreasing population growth rates as well as a probability of extirpation from Texas >1 ($p(N = 0 \text{ in } 2100) = 0.25\text{--}0.72$). Despite uncertainty in forecasted abundance and population growth rates under all scenarios, our model still predicted stable or increasing population growth rates with a continuation of current nest management practices. In contrast, we found that reduced population growth was expected with reduced nest management effort, and population decline and extirpation was expected with no management. Our IPM framework provides an example of how future management scenarios can be

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evaluated critically to determine population changes through time under future environmental uncertainty.

KEYWORDS

Bayesian statistics, climate change, Gulf of Mexico, Kemp's ridley sea turtle, population viability analysis, sea level rise

INTRODUCTION

To stem the anthropogenically driven global loss of biodiversity, transformative change needs to take place (Díaz et al., 2019). Some species have and will require immediate intervention for reestablishment of self-sustaining populations within their natural range (IUCN/SSC, 2013; Peterson & Bode, 2021; Seddon, 2010; Vitt et al., 2010). These often-costly endeavors require tremendous management and monitoring efforts as well as effective assessment of population viability and demographic response to management practices. Understanding the demographic drivers of reintroduced and translocated populations is therefore critical for species establishment and persistence (Armstrong & Seddon, 2008; Converse, Moore, & Armstrong, 2013). Furthermore, stressors or environmental conditions that led to previous declines of a species need to be mitigated for the establishment of a reintroduced population (IUCN/SSC, 2013). Moreover, future habitat conditions need to be understood in the context of global change to ensure long-term successful reintroduction (Howell et al., 2020). Information about population drivers can better inform potential management actions, reduce key uncertainties related to management actions in the context of global change, and focus resources on efforts that have the largest benefit for conservation (Armstrong & Seddon, 2008; Converse, Moore, Folk, et al., 2013; Runge, 2011).

As most reintroduction programs have focused on avian or mammalian species, less is known about success for reptilian reintroduction programs (Seddon et al., 2014). Reintroduction, reinforcement, and translocation programs, for example, are often conducted to conserve a variety of sea turtle species (e.g., green [*Chelonia mydas*; Blumenthal et al., 2021] and Kemp's ridley [*Lepidochelys kempii*] sea turtles [Caillouet et al., 2015; Shaver & Caillouet, 2015]). In general, sea turtle management efforts involve some level of nest protection (e.g., predator exclusion, moving nests to incubators) and sometimes reintroduction or translocation (Barbanti et al., 2022; Shaver et al., 2020). The life history of organisms such as sea turtles, which are long-lived and slow to reach reproductive age, makes management efforts more challenging as environmental stochasticity likely affects many

age classes and can cause delayed responses to the age structure of the population (Saether et al., 2013). Given the large number of resources required to conduct ongoing reintroduction and reinforcement programs, additional information on population responses to management practices could help identify key actions that best benefit a given species.

The Kemp's ridley sea turtle, for example, has been the focus of a reintroduction program in South Texas since 1978 through translocation of individuals from Tamaulipas, Mexico, to Padre Island National Seashore (PAIS; Shaver & Caillouet, 2015). The species declined to only a few hundred individuals in the 1970s and has since increased to over 100,000 individuals across its range in the Gulf of Mexico through intensive conservation techniques including head-starting, nest management, and translocation efforts (NMFS & USFWS, 2015). Kemp's ridley has a restricted distribution, with nesting almost exclusively limited to the beaches of the western Gulf of Mexico in Mexico (at least 98% of all nests) and Texas (1%–2% of all nests; Gallaway et al., 2016; NMFS & USFWS, 2015; Shaver et al., 2016). Due to threats from sea level rise and coastal development (Fuentes et al., 2020), extreme weather events such as hurricanes (DuBois et al., 2020), and climate change (Bevan et al., 2019), continued reinforcement of the smaller Texas population has been supported to maintain multiple nesting sites along the western Gulf of Mexico as a safeguard against loss of the primary nesting site in Mexico (NMFS & USFWS, 2015). Moreover, it is uncertain how the species will respond to forecasted increasing temperatures, as temperature-dependent sex determination and a limited nesting range make it vulnerable to climate change (Bevan et al., 2019).

While the population overall has experienced increases over the last several decades, the number of females nesting on Texas beaches remains relatively small, and growth of the range-wide population has slowed in recent years (Gallaway et al., 2016). Currently, population estimates are based on the number of nests observed each year (Gallaway et al., 2016), though these estimates lack associated variance estimates, and several demographic and observational processes may obscure underlying population changes. Because females are typically not observed

between release as a hatchling and returning to nest as adults (potentially 10–18 years; Shaver & Wibbels, 2007), and have remigration intervals between breeding of around 2 years (Millan et al., 1989; Rostal, 2007), little is known about the early stages of the Kemp's ridley life cycle (Heppell et al., 2005). Moreover, it is unclear how nest management practices ultimately affect population growth rate of the Texas population.

We developed an integrated population model (IPM) to inform the potential effects of nest management practices and global climate change on the future vital rates of the Texas nesting colony of Kemp's ridley sea turtle. IPMs are a powerful quantitative framework that allow for the integration of multiple datasets and data models that simultaneously estimate population abundance and demographic rates while explicitly accounting for uncertainty across the model structure (Frost et al., 2023; Schaub & Abadi, 2010). We used the IPM to estimate population parameters including adult survival, population growth rate, and abundance of nesting females in Texas. Additionally, we used the IPM to forecast population change and estimate the probability of persistence of the Texas population under future scenarios to provide an adaptive decision context for evaluating management outcomes under uncertain future environmental conditions.

METHODS

Study area and data-sets

Study area

Our study area was coastal Texas, USA (Figure 1). All data were obtained from National Park Service, PAIS. We used data from 1994 to 2021 collected during beach patrols.

Data on Kemp's ridley sea turtles

We used two datasets for our IPM, a capture–recapture dataset of marked adult females and a dataset of nest count and hatchlings released from an indoor incubator facility and outdoor corrals. Monitoring using beach patrols for breeding female turtles and nests began with a few patrols per week in 1986 and has been conducted daily since 1998 (Shaver & Caillouet, 2015). Biologists also conducted patrols on all Texas Gulf of Mexico beaches to some extent after 2005, though not daily in some areas (NMFS et al., 2011). Nests were located from tracks remaining in the sand from females or observation of females laying a nest. Females encountered on the beach were marked using various methods throughout

the study (Shaver & Caillouet, 2015) and genetic information from residual egg material was collected to identify and “mark” unobserved females that had laid nests and left. The majority of females were marked with more than one identifying mark (e.g., a metal tag on a flipper and a Passive Integrated Transponder [PIT] tag), reducing potential bias of parameters due to tag loss (Riecke et al., 2019). Nests were evaluated and categorized as either low risk or high risk based on nest conditions, substrate conditions, and time of nest discovery relative to laying. Nests categorized as high risk included those that were partially depredated, located north of PAIS, laid in higher clay-content soil, laid in areas with seawater inundation, or had ants present in the nest chamber (NMFS et al., 2011; Shaver et al., 2020). Eggs were either placed in corrals (a fenced section of beach above high tide) at South Padre Island (SPI) or PAIS or moved to the incubation facility at PAIS (Shaver et al., 2020). There were, therefore, six categories of potential nest risk and incubation locations used during the study: low-risk nests in incubators, corrals at PAIS, or corrals at SPI; high-risk nests in incubators or corrals at SPI (nests at SPI were not transported to incubators even if at high risk); and nests left in situ with no management (nests that incubate at the original nest location; Table 1). Data from nests from 1994 to 2014 were summarized on an annual basis resulting in a dataset with total number of eggs and total number of hatchlings released. From 2015 to 2021, nest success (number of hatchlings released out of total number of eggs) was individually recorded along with the associated risk level and nest incubation location.

Climate and sea level rise data

We explored several climate variables that may impact the population growth rates of sea turtles. We selected the bioclimatic variable “maximum temperature during the warmest month within a year,” as this variable captures a range of effects that increased temperature would likely have on nesting habitat and turtles during the breeding season (Bevan et al., 2019; Laloë et al., 2017). We limited climate variables spatially to our study area along the Texas Gulf Coast (Figure 1). We used Daymet (Thornton et al., 2022) to estimate monthly minimum and maximum temperature and precipitation from 1994 to 2021, and the R package *dismo* version 1.3-9 (Hijmans et al., 2022) to estimate maximum temperature during the warmest month within a year. We used the R package *FedData* (version 3.0.0; Bocinsky, 2019) to access and download Daymet data. We used the downscaled Coupled Model Intercomparison Project 6 (CMIP6) dataset available through WorldClim (version 2.1) to acquire estimates



FIGURE 1 Study area for Kemp's ridley sea turtle. The black and red areas indicate the current nesting range for Kemp's ridley along the Texas Gulf of Mexico coast of the United States while the red area indicates Padre Island National Seashore.

of maximum temperature during the warmest month for four 20-year time periods, 2020–2040, 2041–2060, 2061–2080, and 2081–2100. We considered two future climate scenarios called Shared Socio-economic Pathways (SSPs) that are based on various levels of socioeconomic development: SSP2-4.5 and SSP5-8.5 (Riahi et al., 2017). SSP2-4.5 (“Middle of the Road” scenario; hereafter “moderate emissions scenario”) is a moderate stable scenario where radiative forcing stabilizes at 4.5 W/m^2 by 2100. SSP5-8.5 (“Fossil-fueled Development – Taking the

Highway” scenario; hereafter “high emissions scenario”) is considered a high radiative forcing scenario where radiative forcing stabilizes at 8.5 W/m^2 in 2100. For each time period, we averaged the estimated maximum temperature during the warmest month over 24 downscaled CMIP6 global climate models and derived a single estimate for that time period within the study area. Spatial resolution of climate data was 1 km^2 .

We used seven NOAA tidal gauge stations (Corpus Christi, Galveston Pier 21, Freeport, Port Isabel, Port

TABLE 1 Current nest management practices for Kemp's ridley sea turtles "current management (continuation)" and future scenarios for nest management at Padre Island National Seashore (PAIS).

Risk level of nest	Nest incubation location	Nest management			
		Current management (continuation)	8% in situ	All corrals	All in situ at PAIS, no mitigation
Low risk	Incubators	40	33	0	0
	Corrals (PAIS)	19	19	59	0
	Corrals (SPI)	24	24	24	24
High risk	Incubators	15	15	0	0
	Corrals (PAIS)	0	0	15	0
	Corrals (SPI)	1	1	1	1
	In situ	1	8	1	75

Note: Nests under the "all in situ at PAIS" scenario would have no additional nest protection or "mitigation" (e.g., cages around nests). Values indicate the percentage of nests comprising each nest management category.

Abbreviation: SPI, South Padre Island.

Mansfield, Rockport, and Sabine Pass) to estimate relative sea level trends across the study area (Figure 1) from 1994 to 2021. After inspecting data for each gauge station and comparing across all gauge stations, we determined there was little variation between relative sea level and averaged across all gauges in the study area. We used projected sea level rise under two different scenarios, global mean sea level rise (GMSL) of 0.5 m by 2100 (moderate scenario) and GMSL of 2.0 m by 2100 (highest scenario), at the same gauge stations (i.e., regional scenarios) for four time periods: 2020–2040, 2041–2060, 2061–2080, and 2081–2100 (Sweet et al., 2022). The regional scenarios can vary from global scenarios. Natural regional variations within shorter timescales, for example, are impacted by estimates of rates and accelerations of tidal change. In contrast, regional variations at longer timescales are driven by factors such as sterodynamic sea level change, changes due to contemporary ice-mass loss and the movement of water between land and ocean, vertical land movement due to glacial isostatic adjustment, tectonics, sediment compaction, and withdrawals of groundwater and fossil fuels (Sweet et al., 2022). After inspecting and comparing the projected sea level rise for each regional scenario at each gauge station, we determined there was little variation between projected sea level and averaged across the seven regional scenarios in the study area.

IPM components

Our IPM consists of three submodels: (1) a model for adult survival based on capture–recapture data, (2) a model for number of offspring per female per year based

on nest and hatchling count data, and (3) a model for number of unique females breeding per year based on identified females in the capture–recapture data. The combined submodels then inform the estimates of abundance of female pre-breeders and adult female breeders and nonbreeders. The IPM framework allows us to fully account for uncertainties related to parameter estimates within each submodel and carry that uncertainty through to the resulting estimates of population growth rate.

1. Capture–recapture submodel for adult survival

We used a multistate model with the hidden Markov process to estimate adult survival and the probability of adults transitioning between three states: breeding, nonbreeding, and dead. The breeding state is defined as a female emerging on land to lay a nest while the nonbreeding state is the remigration interval between breeding attempts. Individuals originally hatched on Texas beaches but breeding as adults at locations outside of Texas (e.g., Tamaulipas, Mexico) would also be classified in the nonbreeding state if a tag was not observed and reported. Individuals transition between breeding, nonbreeding, and dead states with the following transition matrix:

$$\begin{bmatrix} \phi^{\text{ad}}(1 - \psi^{\text{BNB}}) & \phi^{\text{ad}}\psi^{\text{BNB}} & 1 - \phi^{\text{ad}} \\ \phi^{\text{ad}}\psi^{\text{NBB}} & \phi^{\text{ad}}(1 - \psi^{\text{NBB}}) & 1 - \phi^{\text{ad}} \\ 0 & 0 & 1 \end{bmatrix} \quad (1)$$

where columns represent the states of breeding, nonbreeding, and dead at time t , rows represent the

states of breeding, nonbreeding, and dead at time $t + 1$, ϕ_t^{ad} is the apparent survival probability for adult females (both breeders and nonbreeders) from time $t - 1$ to time t , ψ^{BNB} is the transition probability from breeder to nonbreeder, and ψ^{NBB} is the transition probability from nonbreeder to breeder. We set the probability of transitioning from dead to other states to 0 and the probability of remaining in the dead state to 1. Our model for adult survival does not include effects for individual heterogeneity. While this could bias estimates of fecundity (Riecke et al., 2019), we were unable to incorporate individual heterogeneity due to limited sample size and computational limits.

The hidden Markov model also accounts for detection probability during the breeding state, and we constrained the nonbreeding and dead states to have a detection probability set to 0 (i.e., never seen during this state). The observation matrix was defined as

$$\begin{bmatrix} 1 - p_B & p_B \\ 1 & 0 \\ 1 & 0 \end{bmatrix} \quad (2)$$

where the columns represent the observation of 0 or 1, respectively; rows represent the states of breeding, nonbreeding, and dead; and p_B is the detection probability for breeding adult females.

Our hidden Markov model had several assumptions. We assumed the probability of transitioning from breeder to nonbreeder and nonbreeder to breeder was independent of adult female age or previous state and constant throughout the study period. This means the model was not constrained to assume a certain remigration interval for breeding (e.g., 2 or 3 years between breeding). Additionally, individuals seen during false crawls (when female turtles are on the beach and attempt to nest but are unsuccessful and do not lay eggs) were classified as breeders, even if a nest was never detected. We made this assumption because, in our dataset, individuals that false crawled were often observed laying nests in subsequent days, similar to other species of sea turtles (Phillips et al., 2014; Talbert et al., 1980).

2. Nest success and hatchling submodel

Because we had two datasets for nest success and hatchling data (one summarized [1994–2014] and one detailed [2015–2021]), we had two models for nest success. The model based on the nest success data summarized by year (total number of hatchlings, J_t , out of total number of eggs each year, E_t) was specified as

$$J_t \sim \text{Binomial}(E_t, \rho_t) \quad (3)$$

where the probability of an egg hatching, ρ_t , was modeled as

$$\text{logit}(\rho_t) = \alpha_0 + \beta_{\text{CLIM},j} x_{\text{CLIM}}. \quad (4)$$

The probability of an egg hatching depended on the intercept, α_0 , and an effect of maximum temperature during the warmest month, $\beta_{\text{CLIM},j}$. The effects of climate were modeled as random slopes where $\beta_{\text{CLIM},j} \sim \text{Normal}(\mu_{\text{CLIM}}, \sigma_{\text{CLIM}})$ and differed by nest risk and incubation location or for the summarized model here (seven different slopes, six for each nest risk and incubation location and one for this summarized model). The number of hatchlings per year was then modeled as

$$f_t \sim \text{Poisson}\left(\rho_t \times \frac{E_t}{R_t}\right) \quad (5)$$

where R_t was the number of nests per year. The model based on the nest success data for each individual nest, i (number of hatchlings, $J.\text{ind}_i$, out of total number of eggs in that nest, $E.\text{ind}_i$), was specified as

$$J.\text{ind}_i \sim \text{Binomial}(E.\text{ind}_i, \rho.\text{ind}_i) \quad (6)$$

where the probability of an egg hatching, $\rho.\text{ind}_i$, was modeled as

$$\text{logit}(\rho.\text{ind}_i) = \beta_{0,j} + \beta_{\text{CLIM},j} x_{\text{CLIM}} + \beta_{\text{SLR},j} x_{\text{SLR}} \quad (7)$$

where $\beta_{0,j}$ is an intercept that varies by nest risk and incubation location and $\beta_{\text{SLR},j}$ is the effect of sea level rise on egg success which also varies by nest risk and incubation location. The number of hatchlings per female per nest per year was then modeled as

$$f_t \sim \text{Poisson}(\text{mean}(\rho.\text{ind}_i) \times \text{mean}(E_i)). \quad (8)$$

Because nests subject to any currently used nest management practices (incubators and corrals) are not affected by sea level rise, we fixed the slope of $\beta_{\text{SLR},j}$ to zero for all nest risk and incubation locations other than in situ. As we did not have data to model for in situ nests, we assigned a range of priors to determine how sensitive the forecasted population was to a range of effects by climate and SLR (see *Forecasting*). The largest effect was still less than effects of incubation temperature (strongly correlated with air temperature) observed for loggerhead (*Caretta caretta*), olive ridley (*Lepidochelys olivacea*), and green sea turtles (Laloë et al., 2017). We used four priors for $\beta_{\text{CLIM},\text{insitu}}$ and $\beta_{\text{SLR},\text{insitu}}$: $\beta_{\text{CLIM},\text{insitu}}$ and

TABLE 2 Scenarios for forecasting the Kemp's ridley sea turtle integrated population model under different nest management scenarios ("nest management," Table 1), sea level rise ("SLR"), and climate change predictions (Shared Socio-economic Pathway ["SSP"]).

Scenarios	Nest management	SLR	SSP	In situ effect size	$p(\lambda \geq 1)$		Extirpation		
					2042	2100	0.025	0.50	0.975
1	Continuation	0.5 m	2	−1.00	0.55	0.65	NA	NA	NA
2	Continuation	2.0 m	5	−1.00	0.54	0.65	NA	NA	NA
3	Low in situ	0.5 m	2	−1.00	0.53	0.62	NA	NA	NA
4	All corrals	0.5 m	2	−1.00	0.53	0.61	NA	NA	NA
5	All in situ	0.5 m	2	0.00	0.49	0.49	2058	2092	2100
6	All in situ	0.5 m	2	−0.25	0.47	0.41	2056	2091	2100
7	All in situ	2.0 m	5	−0.25	0.47	0.42	2057	2089	2100
8	All in situ	0.5 m	2	−0.50	0.45	0.35	2055	2089	2100
9	All in situ	0.5 m	2	−1.00	0.42	0.20	2053	2084	2100

Note: Additionally, some scenarios involved evaluating the sensitivity to model assumptions about the strength of the effect of temperature and SLR on in situ nests ("In situ effect size"). Results are shown for the probability the population growth of adult breeding Texas females is greater than 1 in 2042 and 2100 (" $p(\lambda \geq 1)$ ") and the year of extirpation for those scenarios in which the population decreases to zero ("Extirpation," median year (0.50) and 95% Bayesian credible intervals shown).

$\beta_{\text{SLR,insitu}} \sim \text{Normal}(0,1)$, $\beta_{\text{CLIM,insitu}}$ and $\beta_{\text{SLR,insitu}} \sim \text{Normal}(-0.25,1)$, $\beta_{\text{CLIM,insitu}}$ and $\beta_{\text{SLR,insitu}} \sim \text{Normal}(-0.5,1)$, or $\beta_{\text{CLIM,insitu}}$ and $\beta_{\text{SLR,insitu}} \sim \text{Normal}(-1,1)$ (Table 2).

3. Population submodel

In addition to estimating survival and state transition probabilities, we used the counts of unique adult breeding females each year to inform the model about changes in abundance. Adult breeding females could have originated from head-started turtles at PAIS or immigrated from other locations (e.g., Tamaulipas, Mexico). We modeled the number of unique adult breeding females per year, y_t , as

$$y_t \sim \text{Poisson}(N_t^{\text{total}}) \quad (9)$$

where $N_t^{\text{total}} = N_t^{\text{B}} + N_t^{\text{Imm}}$, is the sum of the female breeders born in Texas, N_t^{B} , and female breeding immigrants, N_t^{Imm} , each year. We developed the IPM with seven stage classes of pre-breeders (NMFS & USFWS, 2015), and the abundance in a given stage class was a function of the abundance in the previous year and the combined probability of transitioning to the next stage class and surviving ϕ^{pre} . For example, for abundance of females in stage class 7, $N_t^7 \sim \text{Binomial}(N_{t-1}^6, \phi^{\text{pre}})$. The parameter ϕ^{pre} was constant through time and did not vary by stage. Individuals were also not required to transition from stage to stage but could not reach sexual maturity before age 7. The abundance of adult female Texas breeders each year was defined as

$N_t^{\text{B}} \sim \text{Poisson}(N_{t-1}^7 \phi^{\text{pre}} + N_{t-1}^{\text{NB}} \phi_{t-1}^{\text{ad}} \psi^{\text{NBB}} + N_{t-1}^{\text{B}} \phi_{t-1}^{\text{ad}} (1 - \psi^{\text{NBB}}))$. The abundance of adult female nonbreeders originating from Texas each year, N_t^{NB} , was defined as $N_t^{\text{NB}} \sim \text{Poisson}(N_{t-1}^{\text{NB}} \phi_{t-1}^{\text{ad}} (1 - \psi^{\text{NBB}}) + N_{t-1}^{\text{B}} \phi_{t-1}^{\text{ad}} \psi^{\text{NBB}})$. Abundance in stage class 1 was defined as $N_t^1 \sim \text{Poisson}(f_{t-1} \phi^{\text{pre}} N_{t-1}^{\text{total}} \delta \gamma)$ where δ is the mean probability of hatchlings being female, and γ is the average number of nests per female per year. The mean probability of a hatchling being female was calculated from genetically sexed late-stage embryos and hatchlings that had died during development (Shaver & Caillouet, 2015). To calculate the number of nests per female per year, n_{fem} , we averaged the number of nests per female per year, $n_{\text{fem}} = R_t / y_t$.

Forecasting

In coordination with PAIS and U.S. Fish and Wildlife Service-Ecological Services, we evaluated potential future nest management scenarios (Table 2). Potential options for future nest management were as follows: a continuation of current management practices (defined by the percent of nests allocated to each nest risk and incubation location from 2015 to 2021), an increase of in situ nests up to 8% from the current 1% through a reduction in low-risk nests in incubators (hereafter "low in situ"), moving all current nests from incubators to corrals (hereafter "all corrals"), and leaving all nests in situ at PAIS (but still using the corral at SPI, hereafter "all in situ"). As we did not have additional data to estimate hatching probability for high-risk nests in the corral at PAIS, we assumed they would have a similar hatching probability as low-risk

nests in corrals. We forecast the IPM for 79 years to 2100, which encompasses at least four generations for Kemp's ridley sea turtle. Along with these future management scenarios, we included potential future climate and sea level rise conditions (Table 2). To compare among scenarios, we estimated the probability the population growth rate, λ , was ≥ 1 at 2042 and 2100, the geometric mean of λ across the forecast period, and the average (and 95% Bayesian credible intervals [BCI]) year of extirpation. We defined the year of extirpation as the last year with $N^B > 0$.

Model implementation

The IPM was developed in R (v. 4.2.0, R Core Team, 2022) using Nimble (de Valpine et al., 2021). We ran 3 MCMC chains for 200,000 samples, discarding the first 100,000 samples and thinning to every 10th sample. We assessed convergence visually and using a Gelman–Rubin statistic (Gelman & Rubin, 1992). We evaluated goodness-of-fit using a posterior predictive check with a χ^2 test on the total abundance (N^{total}) as this parameter was estimated based on all submodels.

RESULTS

Biologists observed 813 unique adult females during beach patrols, whether from genetic or visual identification. From 1994 to 2014, a total of 1661 nests were managed that yielded 156,345 eggs and 130,523 hatchlings. From 2015 to 2021, 1597 nests were monitored resulting in 150,726 eggs and 127,490 hatchlings. The remains of 2484 embryos and hatchlings were used to calculate the probability of a hatchling being female (mean = 0.73, SD = 0.13). Our goodness-of-fit test indicated adequate fit ($p = 0.71$) with data simulated from the model being slightly underestimated relative to the original data.

Results for adult survival

Average annual adult survival throughout the study period was 0.88 (95% BCI = 0.84–0.92), though there was considerable uncertainty in the first decade of the study (1994–2004, Figure 2). While estimates of adult survival decreased between 2018–2019 and 2020–2021, this is

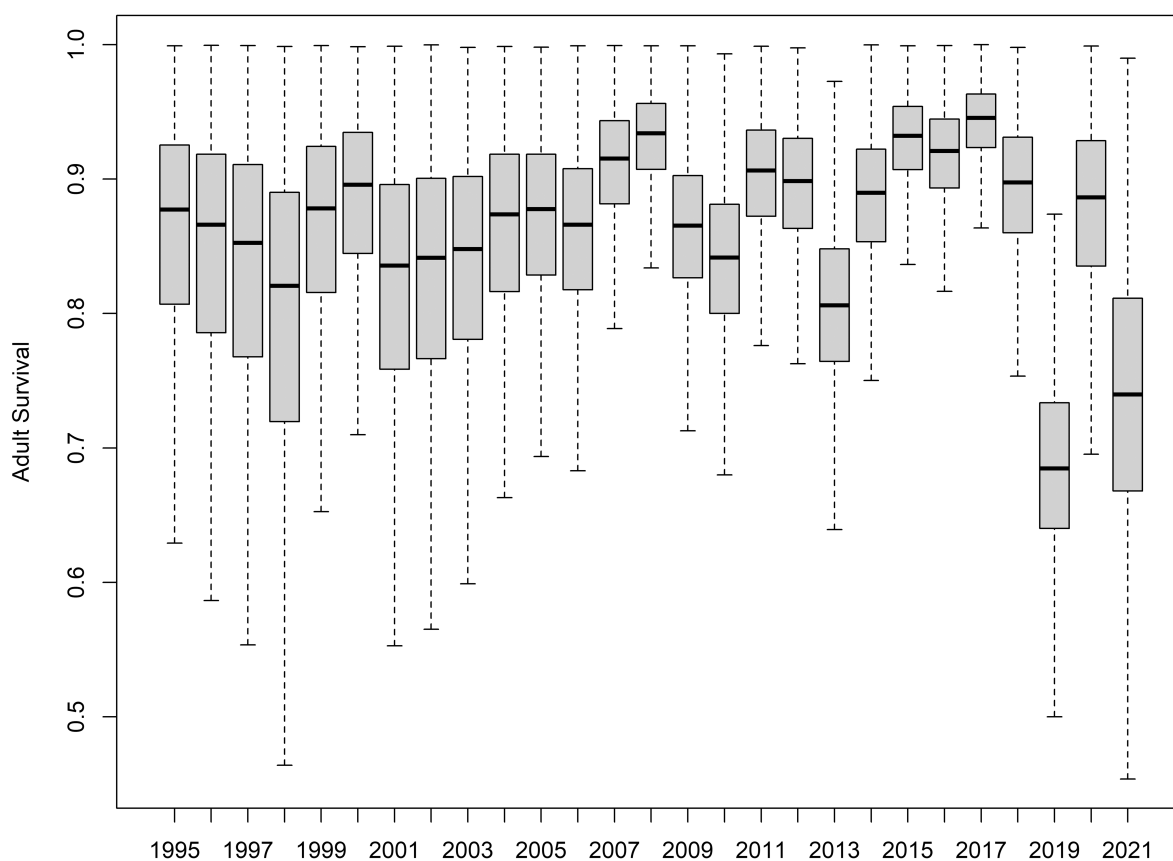


FIGURE 2 Survival of adult female Kemp's ridley sea turtles on the Texas Gulf of Mexico coast from 1995 to 2021. The horizontal line indicates the average survival through the study period. Boxplots indicate the median (dark middle line), 25% and 75% Bayesian credible intervals (BCIs; box limits), and 95% BCI (whiskers).

likely due to changes in sampling effort rather than changes in adult survival, as sampling effort was lower than in other years. Detection probability throughout the study period was 0.98 (95% BCI = 0.87–0.99). The probability of a nonbreeder transitioning to a breeding state was 0.35 (95% BCI = 0.31–0.40), while the probability of a breeder transitioning to a nonbreeding state was 0.94 (95% BCI = 0.93–0.96).

Hatching probability

Of the six nest risk and incubation locations, low-risk nests had higher hatching probability than high-risk nests (Figure 3). There was no statistical difference

between low-risk nests in incubators ($\rho = 0.89$, 95% BCI = 0.88–0.90) and corrals ($\rho = 0.86$, 95% BCI = 0.88–0.89) at PAIS. Hatching success was lower at SPI for both low- ($\rho = 0.70$, 95% BCI = 0.69–0.71) and high-risk ($\rho = 0.67$, 95% BCI = 0.62–0.71) nests in corrals. High-risk nests in incubators had lower hatching success ($\rho = 0.79$, 95% BCI = 0.78–0.80) than low-risk nests in incubators but higher than high-risk nests in corrals. The posterior distribution for in situ hatching success reflected the prior as there were no additional data to include in the likelihood. Climate change did not affect the overall population mean for hatching success, though some nest risk and incubation location categories were positively or negatively correlated with climate change (Figure 4).

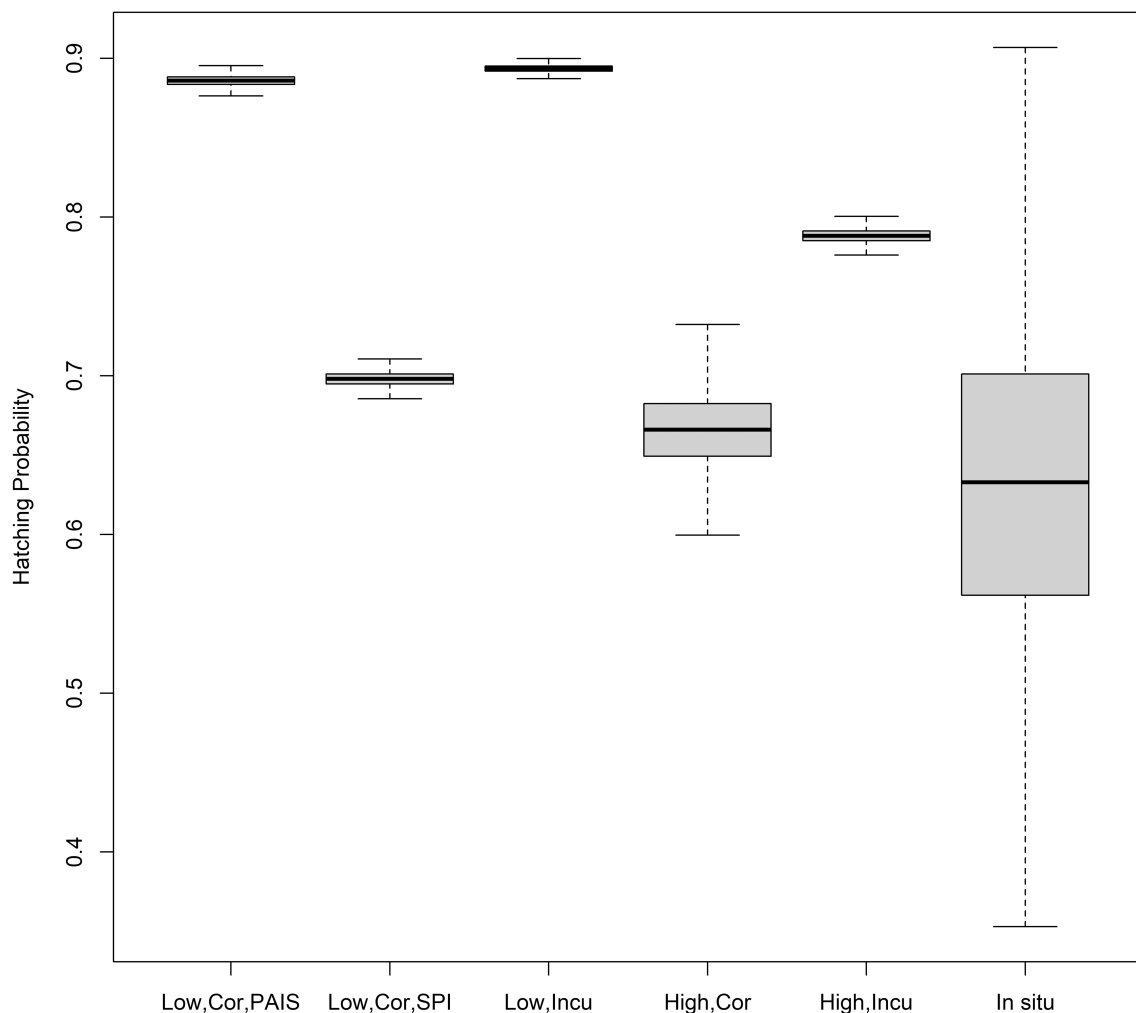


FIGURE 3 Hatching probability from different nest risk and incubation location categories for Kemp's ridley sea turtles nesting on the Texas Gulf of Mexico coast. "Low" corresponds to nests identified by biologists at the time of relocation as low risk, "High" corresponds to high-risk nests, "Cor" refers to nests moved to corrals at either Padre Island National Seashore (PAIS) or South Padre Island (SPI), "Incu" refers to incubators, and "In situ" refers to nests left on the beach without additional management (estimated in Shaver et al., 2020, posterior distribution based only on the prior in this model). Boxplots indicate the median (dark middle line), 25% and 75% Bayesian credible intervals (BCIs; box limits), and 95% BCIs (whiskers).

Population abundance

The abundance of all adult Kemp's ridley sea turtles (breeders and nonbreeders from Texas and immigrants from outside Texas) increased throughout the study (Figure 5). The number of breeding immigrants in the population increased to a peak in 2009, while the number of breeders and nonbreeders from Texas increased until 2018 and did not statistically change from 2018 to 2021. The population growth rate (λ_t) of Texas breeders included

1 within the 95% BCIs for all years except 2021 (95% BCI for λ_{2021} : 0.56–0.98; Figure 6), though there was large variation associated with λ_t until 2015 (CV of $\lambda_t > 0.2$ for all years from 1994 to 2014).

Forecasting

Under a continuation of current nest management practices (Table 1), the predicted abundance of nesting

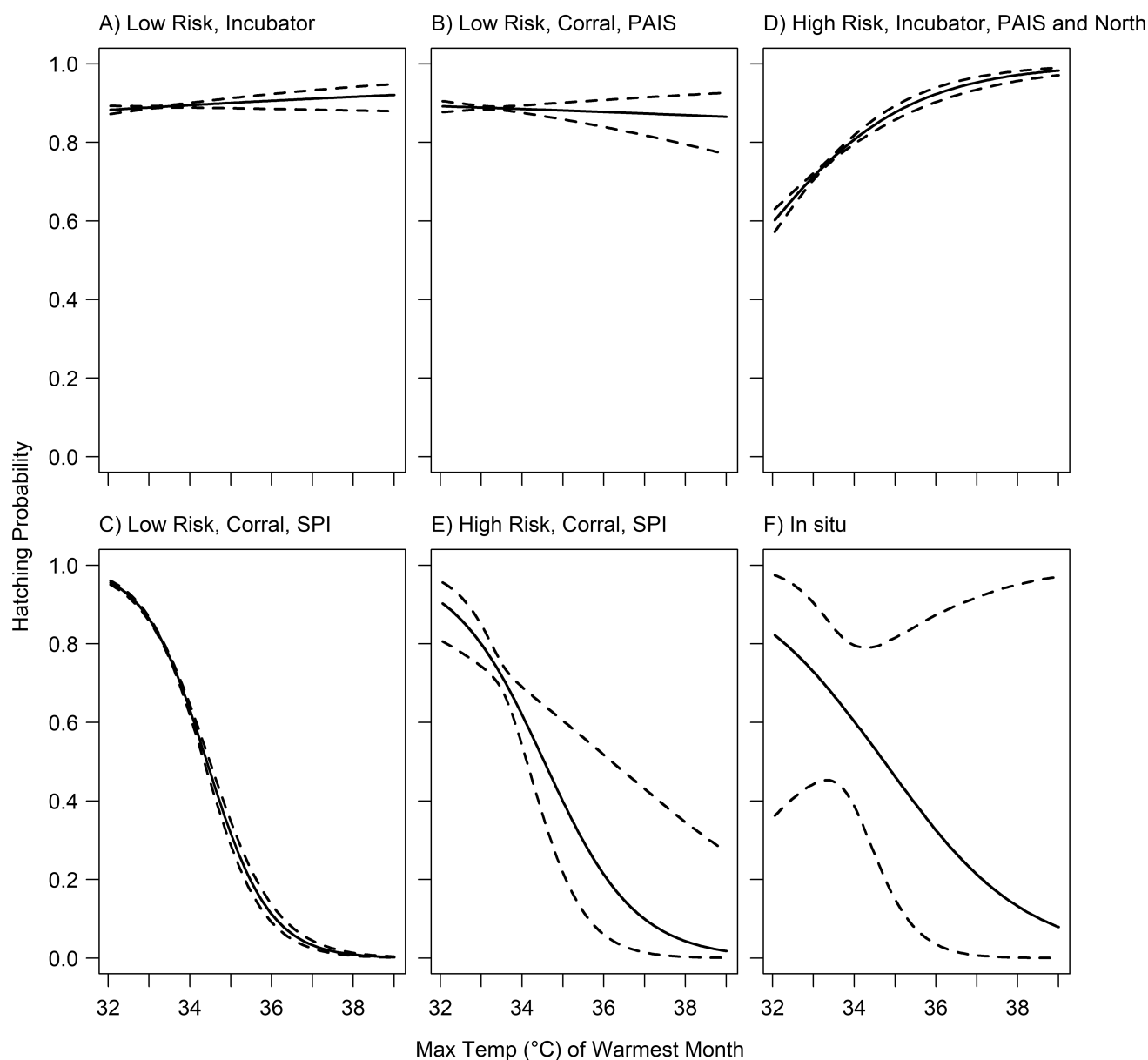


FIGURE 4 Effects of maximum (Max) air temperature (Temp) (in degrees Celsius) during the warmest month of the year on hatching probability of Kemp's ridley sea turtles nesting on the Texas Gulf of Mexico coast under six different nest risk and incubation location categories. "Low" corresponds to nests identified by biologists at the time of relocation as low risk, "High" corresponds to high-risk nests, "Corral" refers to nests moved to corrals at either Padre Island National Seashore (PAIS) or South Padre Island (SPI), and "In situ" refers to nests left on the beach without additional management (estimated in Shaver et al., 2020, posterior distribution based only on the prior in this model). Solid line represents the median of the posterior distribution while the dashed lines represent 95% Bayesian credible intervals.

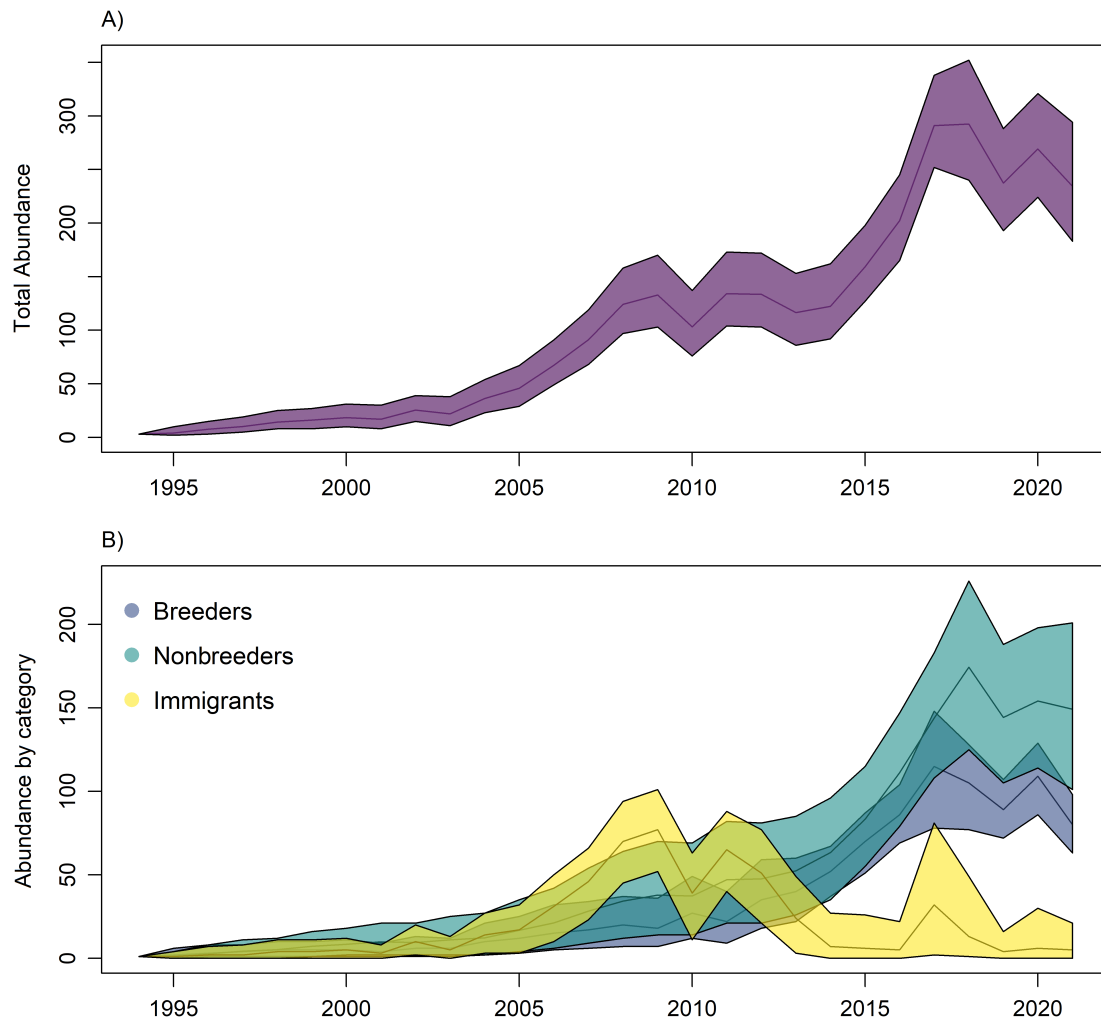


FIGURE 5 Estimates of latent abundance of adult female Kemp's ridley sea turtles found on Texas beaches from 1994 to 2021: (A) all-adult female sea turtles; (B) female breeding (blue, "Breeders," N^B), nonbreeding (green, "Nonbreeders," N^{NB}), and immigrant (yellow, "Immigrants," N^{Imm}) Kemp's ridley sea turtles. Solid lines indicate the medians; polygons indicate the 95% Bayesian credible intervals.

females and population growth rates were similar for the moderate emission (SSP2, Scenario 1) and high emission (SSP5, Scenario 2) scenarios and the mean population growth rate and 95% BCIs during the forecast period was >1 under both scenarios (Figure 7). In Scenario 1, the probability of the population growth rate being ≥ 1 at 20 years into the future (2042) was 0.55 and was 0.65 in 2100, and results were similar for Scenario 2 (Table 2).

The forecasts for the nest management options of limited nests in situ (Tables 1 and 2, Scenario 3) and all eggs in corrals (Tables 1 and 2, Scenario 4) indicated a high probability of a stable population in the future, though the 95% BCIs of the mean population growth rate did include instances of a decreasing population (Figure 7). The probability of the population growth rate being ≥ 1 at 20 years into the future (2042) for Scenarios 3 and 4 was 0.53, and in the year 2100 was 0.62 for Scenario 3 and

0.61 for Scenario 4 (Table 2). None of Scenarios 1–4 resulted in population extirpations (Table 2).

Our range of priors for the effect of climate or SLR on in situ nest success covered scenarios with no effect of climate or SLR (0, Scenario 5) up to a decrease from 82% hatching success down to 8% hatching success for climate and SLR alone (-1 , Scenario 9, Figure 8). Forecasts based on leaving all nests in situ (Scenarios 5–9) had increased uncertainty in their outcome and the mean population growth rate was less than 1 and included zero in 95% BCIs in all cases (Figure 9). As the effect of climate change and sea level rise increased (from 0, Scenario 5 to -1 , Scenario 9), the probability of the population growth rate including 0 increased as well as the probability of $N^B = 0$ (Figure 9). The probability of the population growth rate being ≥ 1 at 2042 and 2100 decreased as the effect of global change increased as did the median year of extirpation for those populations where $N^B = 0$ (Table 2).

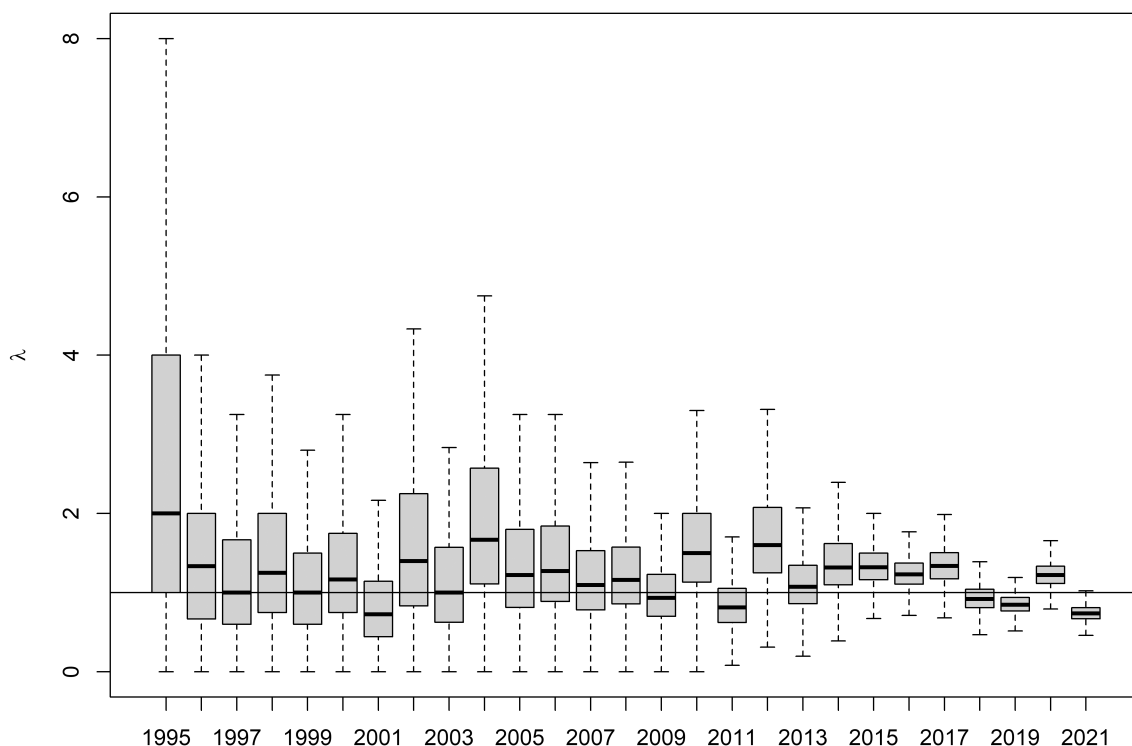


FIGURE 6 Population growth rate (λ) of adult female breeding (N^B) Kemp's ridley sea turtles on the Texas Gulf of Mexico coast from 1995 to 2021. Boxplots indicate the median (dark middle line), 25% and 75% Bayesian credible intervals (BCIs; box limits), and whiskers represent the 95% BCIs. The horizontal line indicates a stable population of $\lambda = 1$.

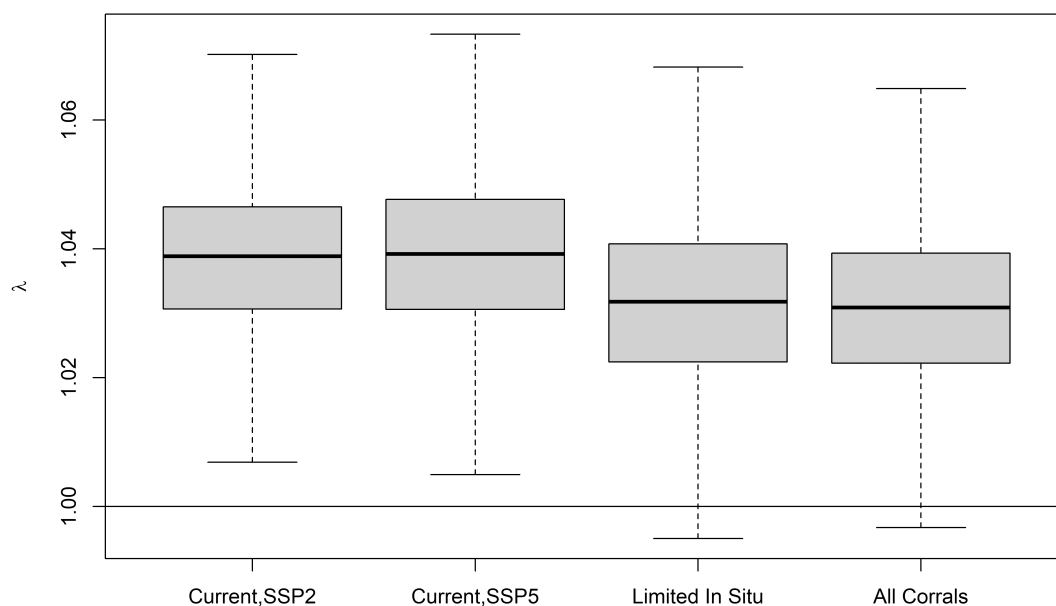


FIGURE 7 Geometric mean of population growth rate (λ) for adult breeding female (N^B) Kemp's ridley sea turtles on Texas beaches across forecast years (2022–2100) for Scenarios 1 ("Current, SSP2"), 2 ("Current, SSP5"), 3 ("Limited In Situ"), and 4 ("All Corals") in Table 2. Boxplots indicate the median (dark middle line), 25% and 75% Bayesian credible intervals (BCIs; box limits), and 95% BCIs (whiskers). The horizontal line indicates a stable population of $\lambda = 1$.

DISCUSSION

Our IPM framework provides an example of how future management scenarios can be evaluated critically to

determine population changes through time while accounting for potential environmental change. Our evaluation of population drivers and expected future changes found that nest management practices play a key role in

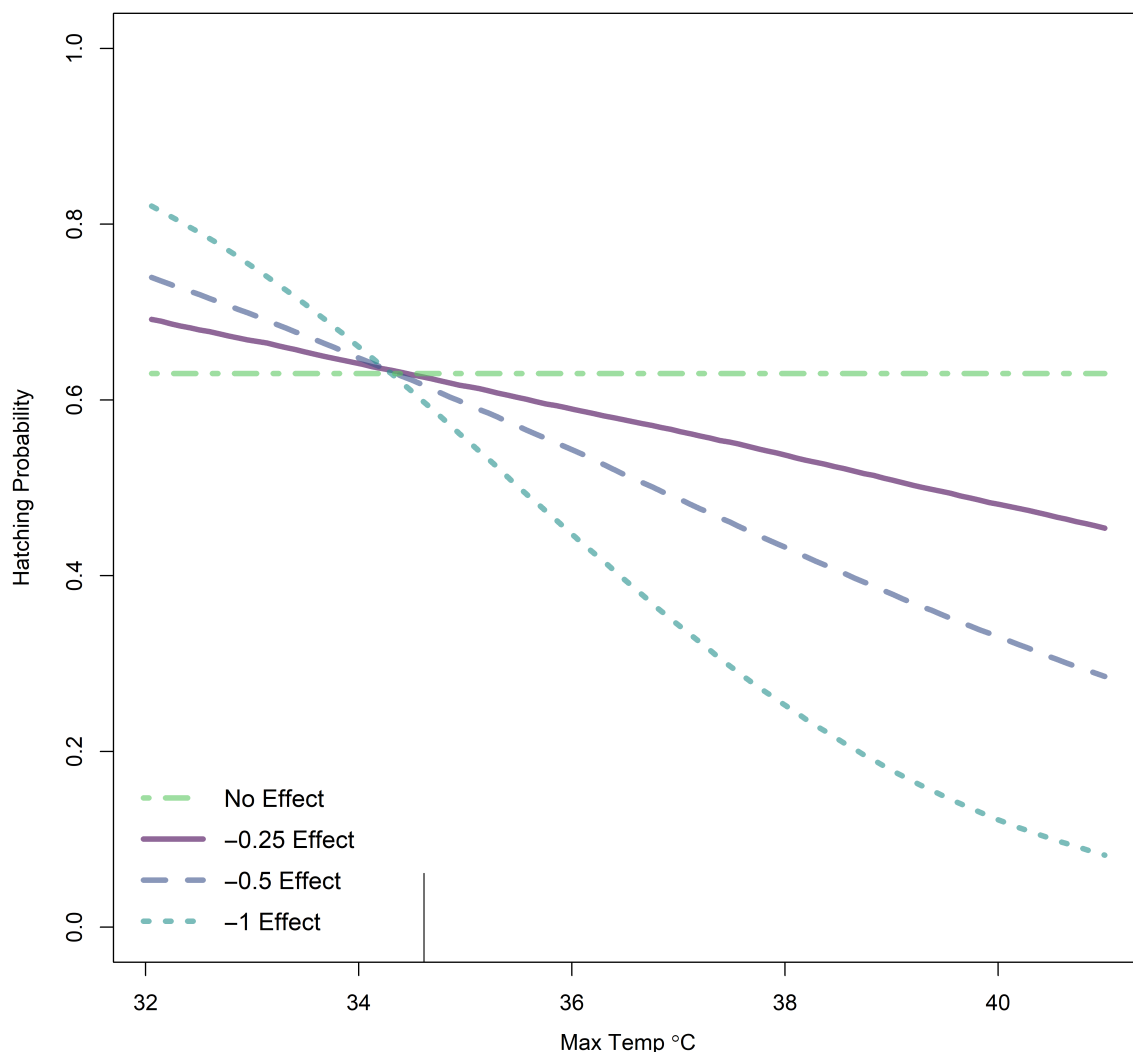


FIGURE 8 Range of effect sizes used to describe the relationship of hatching probability of Kemp's ridley sea turtle and increases in the maximum air temperature (in degrees Celsius) for Scenarios 5–9 (Tables 1 and 2). The vertical line on x-axis indicates the historic (to the left) and forecast (to the right) values for maximum air temperature under SSP2.

sustaining the Texas population of Kemp's ridley sea turtle. Despite uncertainty in forecasted abundance and population growth rates under all scenarios, our model still predicted stable or increasing population growth rates with a continuation of current nest management practices. In contrast, we found that reduced population growth was expected with reduced nest management effort, and population decline and extirpation were expected with no management.

We found that a continuation of nest management practices would have the highest probability of a stable or increasing population in the future. As the protection involved in future nest management scenarios decreased, the probability of a stable population compared to current management also decreased, but the mean population growth rate was still higher than the no-management scenario (i.e., leaving all nests in situ). Due to lower survival,

increased temperatures, and sea level rise, scenarios based on leaving all nests in situ resulted in a higher probability of extirpation of the species from Texas, with greater than 70% probability of extirpation in some scenarios. In our forecasting, as the negative effect of maximum temperature and sea level rise increased on in situ nests, the probability of a stable population decreased, and extirpation was predicted sooner. While our model assumed a constant ratio of female hatchlings, increases in temperature will likely result in increased number of females in in situ nests. There is uncertainty in how this may affect population forecasts, as additional females could result in an increase in the breeding population if not limited by males, but if the population is male-limited, could result in population declines (Laloë et al., 2016). Based on the currently available data, leaving all Kemp's ridley nests in situ would result in a declining nesting colony on beaches in

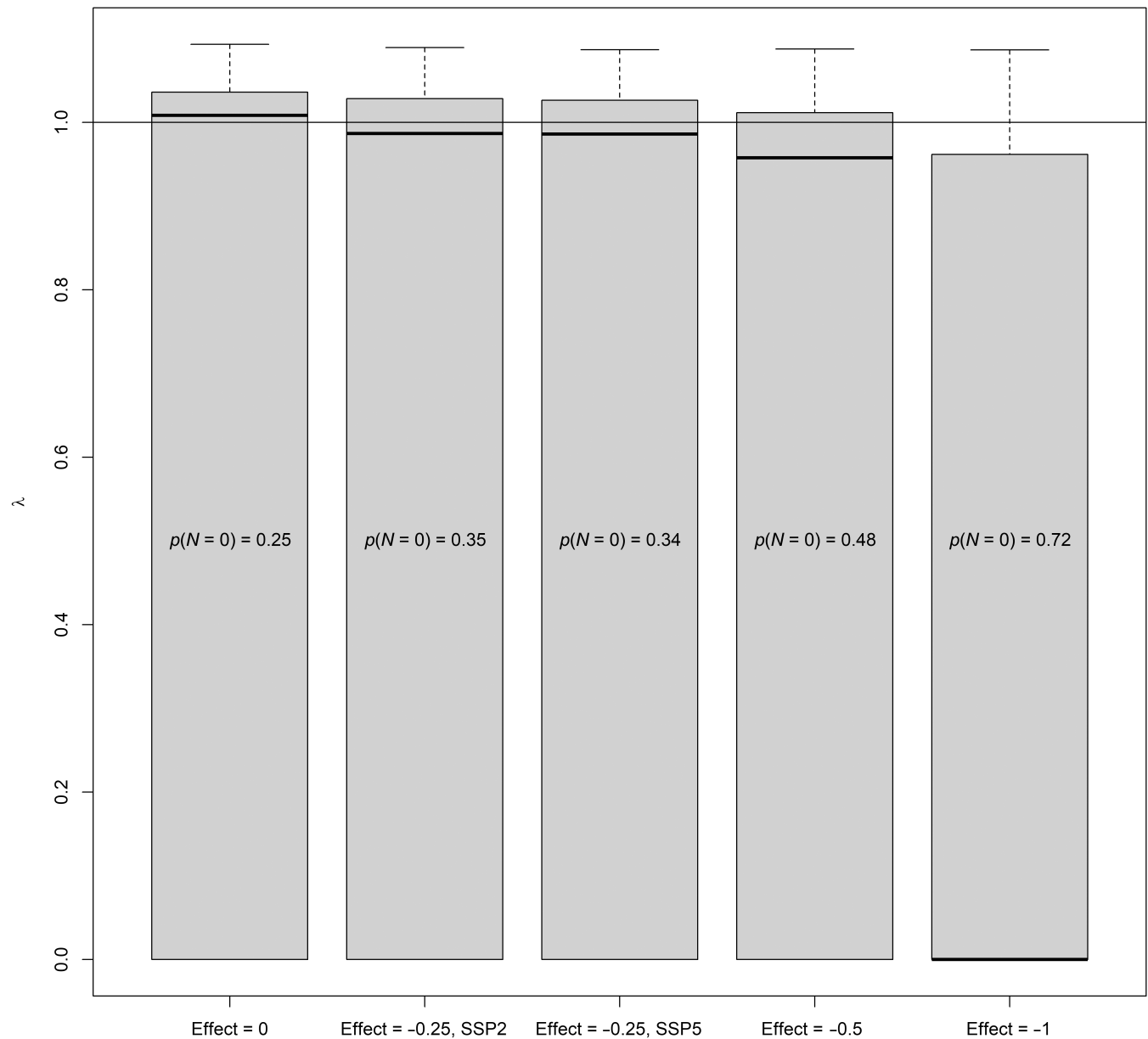


FIGURE 9 Geometric mean of population growth rate (λ) for adult breeding female (N^B) Kemp's ridley sea turtles on Texas beaches across forecast years (2022–2100) for Scenarios 5 (“Effect = 0”), 6 (“Effect = −0.25, SSP2”), 7 (“Effect = −0.25, SSP5”), 8 (“Effect = −0.5”), and 9 (“Effect = −1”) in Table 2. Boxplots indicate the median (dark middle line), 25% and 75% Bayesian credible intervals (BCIs; box limits), and 95% BCIs (whiskers). The horizontal line indicates a stable population of $\lambda = 1$. $p(N = 0)$ is the proportion of instances when the abundance of adult breeding females on Texas beaches (N^B) was 0 in 2100.

Texas and some reinforcement of the population through nest management is required to maintain the Texas nesting colony.

While females nesting on Texas beaches were largely immigrants from the Mexico population until around 2010, the number of breeding females born in Texas has been increasing and is currently similar to the number of immigrants. Better understanding the location of where females hatched provides insights into the success of reintroduction and reinforcement efforts in Texas and aligns with genetic

analyses (Frey et al., 2014). As the model forecasts indicate reinforcement through nest management is likely still needed to maintain the Texas colony, managers could use detection probability of breeding females to estimate the proportion of nests being missed in a season. Ongoing mark–recapture monitoring of breeding females also allows for continued estimation of the proportion of Texas-born and immigrant breeders to ensure outcomes of the reinforcement program align with population recovery goals. With continued monitoring, the model could likely

eventually incorporate monitoring effort into detection probability and some temporal variation in remigration interval (probability of nonbreeder becoming a breeder) to monitor changes in these parameters going forward as they may be changing (Gallaway et al., 2016).

Our estimates of adult survival (84%–92%) align with a relatively slow life-history strategy (Saether & Bakke, 2000), similar to other studies on Kemp's ridley (Heppell et al., 2005) and other sea turtle species (Gerber & Heppell, 2004). Because Kemp's ridley is a relatively long-lived species, environmental stochasticity, including variation due to anthropogenic factors, is likely to affect many age classes and would cause delayed responses in the age structure of the population (Saether et al., 2013). Historic events, such as the Deepwater Horizon oil spill in 2010 (Gallaway et al., 2016), may have negatively affected adult survival, but may have also affected other stage classes of the species that are not monitored by PAIS (e.g., pre-breeding). Delayed maturity and the long-lived nature of the species may make it challenging to fully quantify the effects of environmental perturbations on the population (Saether et al., 2013), and thereby actively manage the population.

Our model provides important insights into the ecology and conservation of Kemp's ridley sea turtle, as well as providing opportunities for future development. For example, density dependence may be affecting resources available to adults, thus limiting the number of nesting attempts in a year or causing a longer remigration interval (Caillouet et al., 2018), and we were unable to include density dependence in our model. Additionally, our model and forecasting relied on an estimate of in situ nest success from one study at PAIS (Shaver et al., 2020), which did not include the probability of hatchlings surviving from hatching to entering the Gulf of Mexico; therefore, the true value for this parameter may be lower than that included in our model, resulting in conservative estimates of survival. Ongoing monitoring of nests under varying environmental conditions and management activities, including in situ conditions, would help to reduce uncertainty in model predictions.

CONCLUSIONS

Reintroduction and reinforcement programs can be a sizeable investment that not only need to be justified but also monitored and adapted for efficacy. A key challenge for these programs is quantifying demographic responses to management efforts while accounting for dynamic environmental conditions. Our IPM provides a powerful and adaptive decision framework for determining future management scenarios while concurrently accounting for

the effects of climate change and sea level rise on a species with a unique life history. Due to climate change and the impacts of anthropogenic stressors, our results suggest that there will likely be a need for some level of nest management moving forward to maintain the Texas breeding colony. With continued monitoring and data collection, the utility of our IPM can be further increased by updating the model and determining the necessary level of nest management and monitoring needed to achieve population goals while balancing the operational costs of running such a program.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Historic data on temperature and precipitation from 1994 to 2021 are available through the FedData R package (v. 3.0.0, Bocinsky, 2019). Forecast temperature data can be obtained through WorldClim at <https://www.worldclim.org/>. Data on tidal gauge stations are available from NOAA at <https://oceanservice.noaa.gov/hazards/sealevelrise/sealevelrise-data.html>. Data related to the Kemp's ridley sea turtle are sensitive and not available publicly. Data for nest counts and mark-recapture data for adult females are available to qualified researchers from Padre Island National Seashore by contacting the Chief of the Division of Sea Turtle Science and Recovery. Novel code (Ross et al., 2024) is available from Zenodo: <https://zenodo.org/doi/10.5281/zenodo.12785872>.

ORCID

Beth E. Ross  <https://orcid.org/0000-0001-5634-4951>

Matthew A. Boggie  <https://orcid.org/0000-0002-8984-0203>

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