



# Identifying impactful sea turtle conservation strategies: a mismatch between most influential and most readily manageable life-stages

Shane A. Richards<sup>1,\*</sup>, Christopher Cvitanovic<sup>2,8</sup>, Michael Dunlop<sup>3</sup>,  
Sabrina Fossette<sup>4</sup>, Linda Thomas<sup>5</sup>, Anton D. Tucker<sup>4</sup>, E. Ingrid van Putten<sup>5,6</sup>,  
Andrea U. Whiting<sup>7</sup>, Scott D. Whiting<sup>4</sup>, Alistair J. Hobday<sup>5,6</sup>

<sup>1</sup>School of Natural Sciences, University of Tasmania, Hobart, Tasmania 7000, Australia

<sup>2</sup>Centre for Marine Science and Innovation, University of New South Wales, Sydney, New South Wales 2052, Australia

<sup>3</sup>CSIRO Environment, Black Mountain, Canberra, Australian Capital Territory 2601, Australia

<sup>4</sup>Biodiversity and Conservation Science, Department of Biodiversity, Conservation and Attractions, Kensington, Western Australia 6151, Australia

<sup>5</sup>CSIRO Environment, Castray Esplanade, Hobart, Tasmania 7000, Australia

<sup>6</sup>Centre for Marine Socioecology, University of Tasmania, Hobart, Tasmania 7000, Australia

<sup>7</sup>School of Environmental and Life Sciences, Charles Darwin University, Darwin, Northern Territory 0871, Australia

<sup>8</sup>Present address: School of Business, University of New South Wales, Canberra, Australian Capital Territory 2600, Australia

**ABSTRACT:** Sea turtles worldwide face a range of threats including sea level rise and warming associated with climate change, predation by invasive species, plastic and light pollution, coastal development, and human interference. Conservation managers have a long history of aiding sea turtle populations, from protecting nests to head-starting hatchlings. Due to these challenges faced by turtles, there is a constant focus on assessing the likely success of proposed conservation interventions to help inform decision-making processes. We develop an age-based, spatially implicit population model for the north-west shelf stock of Australia's endemic flatback turtle *Natator depressus* that estimates the long-term outcomes of a range of onshore and offshore conservation interventions. Analysis of the model shows that young adults contribute most to population growth (i.e. have highest expected future reproductive success); however, this is often the most difficult life stage to manipulate in the field. Observable outcomes of interventions are often delayed for many years, especially for on shore activities (e.g. protecting eggs and hatchlings), due to late age to maturity. The potential impact of warming-induced female bias on population dynamics was also investigated. Although such bias increases population growth rates in the short term, negative effects of the bias (e.g. reduced female mating success) and negative environmental effects (e.g. reduced survival rates, habitat loss) can lead to sustained declines. Population models can rapidly assess climate change and conservation impacts on turtle dynamics and can guide monitoring efforts for real-world application.

**KEY WORDS:** Sea turtles · *Natator depressus* · Anthropogenic threats · Life history · Modelling

## 1. INTRODUCTION

Substantial changes in species' distribution, abundance, and phenology have been documented world-

wide as a result of anthropogenic climate change and other threats associated with human activities (Nash et al. 2017, Pecl et al. 2017). The high rate of long-term change, and the increased frequency of extreme del-

\*Corresponding author: shane.richards@utas.edu.au

eterious environmental events, means that the coping ability of many species is unlikely to provide natural resilience over the remainder of the century (Cockrem 2022). Even if greenhouse gas emissions were dramatically reduced, committed warming of 1.5–2.0°C is now almost certain (IPCC 2023). A range of interventions have been proposed for aiding marine species to cope with climate change (Hobday et al. 2015, Mason et al. 2021). These options can be expensive and/or risky to test in the field and may also involve time delays of many years before an outcome is detected in long-lived species. In the face of rapid environmental change, waiting many years to see if an intervention was successful may no longer be practical.

Expert-based screening tools (e.g. Hobday et al. 2015, Simpson et al. 2015, Moon et al. 2021) and quantitative models (e.g. Crouse et al. 1987, Heppell et al. 1996, Piacenza et al. 2017, Condie et al. 2021, Jensen et al. 2022) have been developed to assess the outcome of different management interventions for marine systems. Clarke et al. (2021) suggests that a robust analytical framework for assessing the need and ramifications of any intervention is required before it is deployed. The most appropriate analytical approach will vary between species, and different options are available depending on the level of life-history knowledge available. For data-limited species, simulation and uncertainty testing is critical when exploring intervention options. Population modelling provides a cheap, transparent, and rapid alternative framework, relative to potentially risky field manipulations, for initially investigating and assessing potential expensive and long-term intervention options.

Sea turtles are considered to be particularly vulnerable to climate change (Poloczanska et al. 2009, Fuentes et al. 2010a, Butt et al. 2016), a threat which is compounded by other human activities, such as coastal development (e.g. Fuentes et al. 2020). Rising temperatures are a driver of sea level rise, which is predicted to threaten turtle breeding areas and nesting sites (Fuentes et al. 2010b, Butt et al. 2016). Rising temperatures also add an additional risk, as sex determination in turtles is temperature dependent; more hatchlings are female at warmer temperatures (Stubbs et al. 2014, Butt et al. 2016, Jensen et al. 2018). Sea turtles also face threats such as predation by invasive species, plastic pollution, coastal development and light pollution, and direct human interference (Heppell et al. 2003). Conservation managers have a long history of aiding sea turtle populations, which are often necessarily aimed at single threats, including: reduced fishery bycatch, and protection of nests from predation (Simpson et al. 2015).

The flatback turtle *Natator depressus* is endemic to Australia and has the smallest migratory range of any sea turtle species (Pendoley et al. 2014). Flatback turtles nest on inshore islands and on the mainland from Mon Repos in southern Queensland to Exmouth in northern Western Australia (Limpus 2007, FitzSimmons et al. 2020). Flatback turtles are threatened by a range of anthropogenic and environmental impacts (Limpus 2007, Whittock et al. 2014), and as a result, they are listed as vulnerable under the Australian Commonwealth Environment Protection and Biodiversity Conservation (EPBC) Act of 1999.

This study focuses on the north-west shelf stock of flatback turtles within the Pilbara region, which have a nesting range between Port Hedland and the Exmouth Gulf (FitzSimmons et al. 2020). Most of the rookeries are subjected to exposure and risk from anthropogenic sources such as townships and resource sector extraction and ports (Fossette et al. 2021). Over the last 2 decades, sea turtle research and monitoring has increased in Western Australia, mostly associated with resource industry funds. One example of this is the North-West Shelf Flatback Turtle Conservation Program (NWSFTCP), which is an environmental offset associated with the Gorgon Gas Project at Barrow Island and contributes 62.5 million AUD over 60 yr for regional flatback turtle conservation, science, and education.

Here we present a spatially implicit, age-dependent meta-population model for the north-west shelf stock of the Australian flatback turtle; however, it could be applied to other species and locations. The model provides a framework for investigating turtle population dynamics in response to management interventions, and helps identify the types of interventions (e.g. life stages targeted) that are more likely to enhance population persistence. A sensitivity analysis identified the life-history parameters that most influence population growth rate, and we calculated the age-dependent future reproductive potential of individuals. The model was then used to predict the impact of conservation interventions that manipulate these important life-history parameters, either at a local scale (e.g. increasing egg survival at a specified rookery) or regionally (e.g. reducing juvenile and adult mortality rates at feeding grounds). Importantly, these model-based experiments reveal expected time lags between interventions and observable responses to interventions. The model is also used to explore potential impacts of climate warming on population persistence via its effect on biasing offspring sex ratios in favour of females, as well as reducing egg and offshore survival, and nesting habitat. By

integrating conservation and environmental impacts, the model provides a framework that can help identify potentially impactful management strategies amid long-term environmental uncertainty.

## 2. MATERIALS AND METHODS

### 2.1. Model description

The model tracks the age distribution and maturation of turtles, and each individual's association with a nesting site, which could change throughout their lifetime. The model is spatially implicit (i.e. we do not explicitly consider site locations or the distances between them). Let  $J_{i,a,t}^s$  and  $A_{i,a,t}^s$  be the number of juvenile and adult turtles of sex  $s = \{f: \text{female}, m: \text{male}\}$  associated with site  $i$  in year  $t$  that are of age  $a$  (years), respectively. Thus, the numbers of juvenile and adult turtles of sex  $s$  associated with site  $i$  in year  $t$  are given by  $J_{i,t}^s = \sum_a J_{i,a,t}^s$  and  $A_{i,t}^s = \sum_a A_{i,a,t}^s$ . These numbers define population abundance just before mating. Each year, adult females mate (1 or more times; Theisinger et al. 2009) with probability  $b$ . Mated females in year  $t$  return to their associated site,  $i$ , to lay eggs with probability  $(1 - f_{i,t})$ , otherwise they choose another site to lay eggs. Those that choose to not nest at their associated site, here referred to as transients, choose their new site weighted by the maximum number of undisturbed nests that the site can support,  $K_{i,t}$  (i.e. rookery size). In this case, the probability that a mated transient female, currently associated with site  $i$ , chooses site  $j$  in year  $t$ , is given by

$$\kappa_{i,j,t} = \frac{K_{j,t}}{\sum_k K_{k,t}} \quad (1)$$

In reality, we expect site switching to be relatively uncommon and site choice to be more complex than described here; however, this simplistic approach prevents unrealistic oscillatory movement patterns between rookeries.

The number of females of age  $a$  that lay eggs at site  $i$  in year  $t$  is

$$B_{i,a,t} = (1 - f_{i,t})bA_{i,a,t}^f + \sum_j \kappa_{j,i,t} f_{j,t} bA_{j,a,t}^f \quad (2)$$

The total number of females that lay eggs at site  $i$  in year  $t$  is  $B_{i,t} = \sum_a B_{i,a,t}$ .

Successful transients switch their site association to the current chosen site with probability  $q$ , which implies that site associations for females after breeding are updated according to

$$\tilde{A}_{i,a,t}^f = (1 - b f_{i,t} q) A_{i,a,t}^f + b q \sum_j \kappa_{j,i,t} f_{j,t} A_{j,a,t}^f \quad (3)$$

The total number of clutches of eggs laid at each site is  $cB_{i,t}$  where  $c$  is the average number of clutches per breeding female per year. Clutches may become damaged by turtles during nesting (e.g. Girondot et al. 2002, Tiwari et al. 2006), and the final number of undamaged clutches at site  $i$  in year  $t$  is  $C_{i,t} = wC_{1,i,t} + (1 - w)C_{2,i,t}$  where

$$C_{1,i,t} = \min\{K_{i,t}, cB_{i,t}\} \quad (4)$$

and

$$C_{2,i,t} = K_{i,t} \left( 1 - \left( 1 - \frac{1}{K_{i,t}} \right)^{cB_{i,t}} \right) \quad (5)$$

$C_{1,i,t}$  and  $C_{2,i,t}$  estimate undamaged clutch numbers when clutches are actively avoided and when clutches are randomly distributed among the potential  $K_{i,t}$  clutch locations. Thus,  $w$  is a tuning parameter that allows control of nest disturbance due to density dependence ( $0 \leq w \leq 1$ ); larger values of  $w$  result in greater numbers of undisturbed clutches. For each site, the proportion of clutches that are damaged is  $1 - C_{i,t}/(cB_{i,t})$ .

On average, each clutch contains  $E$  eggs, and eggs survive to the hatchling stage within site  $i$  with probability  $s_{E,i,t}$ . Hatchlings emerge from the nest and successfully traverse the beach to sea with probability  $s_{H,i,t}$ . Successful dispersal to offshore waters requires hatchlings navigating and surviving nearshore waters, which occurs with probability  $s_{Y,i,t}$ . For the remainder of their first year, their probability of survival is  $s_{J1}$ . The proportion of eggs at site  $i$  in year  $t$  that survive their first year is

$$s_{1,i,t} = s_{E,i,t} s_{H,i,t} s_{Y,i,t} s_{J1} \quad (6)$$

These different survival terms are included as different threats, and management interventions can be specific to these different stages in a site-specific and time-dependent manner.

The number of 1 yr old female and male juveniles associated with each site is

$$J_{i,1,t}^f = \frac{r_t}{1 + r_t} C_{i,t} E s_{1,i,t} \quad (7)$$

and

$$J_{i,1,t}^m = \frac{1}{1 + r_t} C_{i,t} E s_{1,i,t} \quad (8)$$

where  $r_t$  is the sex ratio of offspring (females per male) in year  $t$ . This ratio is expected to increase over time due to environmental warming (Stubbs et al. 2014).

Flatback turtles reach sexual maturity, on average, at age  $\tau_j$  years. Specifically, the probability a turtle of age  $a$  will be mature is

$$M_a = \frac{e^{\alpha(a - \tau_j)}}{1 + e^{\alpha(a - \tau_j)}} \quad (9)$$

where  $\alpha$  is a positive parameter that describes how quickly animals transition from juvenile to adult

when near age  $\tau_j$ . For simplicity, we assume that maturation rates are the same for males and females.

The annual probability a juvenile of age  $a$  matures is

$$m_a = \frac{M_{a+1} - M_a}{1 - M_a} \quad (10)$$

Assuming juveniles (i.e. immature individuals 1 yr or older) and adults survive each year with probabilities  $s_J$  and  $s_A$ , respectively, juvenile cohort abundances progress according to

$$J_{i,a+1,t+1}^s = s_J(1 - m_a)J_{i,a,t}^s \quad (11)$$

and for adults,

$$A_{i,a+1,t+1}^m = s_J m_a J_{i,a,t}^m + s_A A_{i,a,t}^m \quad (12)$$

and

$$A_{i,a+1,t+1}^f = s_J m_a J_{i,a,t}^f + s_A \tilde{A}_{i,a,t}^f \quad (13)$$

Here, the model sets an upper age limit of 60 yr; the oldest flatback turtle observed by Turner Tomaszewicz et al. (2022) was a 45 yr old male from a sample of 74 individuals.

The model described above imposes population limitation via density dependence acting on clutch survival; however, the model could be extended to allow density dependence to also limit population growth by negatively impacting juvenile and adult survival. For stable environmental conditions that promote population persistence, all sites will approach a stable age distribution, which for females we denote by  $J_{i,a}^{f*}$  and  $A_{i,a}^{f*}$ . The expected future number of nesting seasons (i.e. resulting in 1 or more clutches produced during a season) for a female turtle of age  $a$ , when the population is at equilibrium, and adult females mate each year with probability  $b$ , is

$$W_{i,a} = \frac{b}{J_{i,a}^{f*} + A_{i,a}^{f*}} \sum_{j \geq a} A_{i,j}^{f*} \quad (14)$$

This metric quantifies the future contribution of females to population persistence as a function of their current age (Tuljapurkar & Caswell 1996), which identifies individuals currently in the population that are of high conservation value. Future reproductive success,  $W_{i,a}$ , is expected to initially increase with age until the average age at maturity, as younger individuals are less likely to reach maturity. After that, it declines as individuals approach senescence (i.e. their maximum age), as future mating opportunities decline.

## 2.2. Model analysis

Model parameters are presented in Table 1. Many of these parameters can be estimated from previous

studies; however, some are not well known or likely to vary significantly across sites and/or years. Two parameters that are often uncertain are the probability of hatchling survival shortly after entering the water ( $s_Y$ ), and the subsequent probability young individuals survive their first year ( $s_{J1}$ ). Here, we consider a baseline scenario defined by a set of parameter values (Table 1), which results in an approximately stable population size for all sites. From this scenario, we perform a sensitivity analysis (Tuljapurkar & Caswell 1996) of some key and uncertain parameters. In particular, we assess the sensitivity of annual population growth rate to parameters that can be the focus of conservation efforts, which are either beach-based or offshore. The sensitivity analysis is helpful for identifying impactful conservation efforts. Estimating age-dependent future mating success ( $W_{i,a}$ ) for the baseline scenario also provides useful guidance for which individuals are likely to have the most conservation value, and helps with understanding findings from the sensitivity analysis.

Many potential flatback turtle conservation activities are expected to impact the parameters examined by the sensitivity analysis. For example, reducing lighting at times of hatchling emergence may reduce mis-orientation when turtles are seeking the ocean, which can improve hatchling survival (e.g. Hirama et al. 2021). Similarly, reducing lighting on the water (e.g. jetties and moored boats) may facilitate movement of hatchlings to safer open water (Wilson et al. 2023, this Special). Controlling local predator populations (e.g. ghost crabs, cats, dogs, and foxes) (Avenant et al. 2023), or cooling sand temperature on nesting beaches (Jourdan & Fuentes 2015), may also improve egg and hatchling survival. Turtle survival could also be improved by reducing marine debris (Duncan et al. 2017) and reducing bycatch via turtle exclusion devices (e.g. Crowder et al. 1994). The capacity for these and other activities (e.g. van Putten et al. 2023, this Special) to impact model parameters is expected to vary spatially and temporally, depending on the local threats to turtles, which has motivated the examination of population responses to a broad range of parameter values with the sensitivity analysis.

The sensitivity analyses assume that sites are isolated (i.e.  $f_{i,t} = 0$ ). We next consider a turtle population distributed across multiple sites. Specifically, we consider 5 relatively small and weakly connected rookeries that differ in the number of nests they can support in any given year,  $K_{i,t}$ . The smallest rookery can support 500 nests and the largest can support up to 8000 nests (site sizes increase via doubling). These sizes are consistent with Western Australian flatback

Table 1. Model parameters, their baseline value, and description. References consulted when assigning the baseline values are provided where available.  $i$  and  $t$  subscripts imply that the parameter may change between sites and years, respectively. Square bracketed terms show the range of values reported in the literature

Parameter	Value	Description and sources (where available)
$b$	0.454	Annual probability that a female mates (Limpus 2007, Pendoley et al. 2014) (corresponds to 2.2 yr remigration interval, [1.6–2.8])
$f_{i,t}$	0.01	Probability a mated female switches her site, $i$ , when nesting (i.e. becomes a transient); Limpus (2007) suggests very high fidelity
$q$	0.5	Probability a transient adult changes her site association to switched site (Waayers et al. 2011, Thums et al. 2017)
$K_{i,t}$	500–8000	Maximum number of clutches that can be successful at a site in a given year
$w$	0.75	Weighting describing the propensity of clutches to avoid being disturbed by other nesting females; 2% nest disturbance
$c$	3.4 clutches yr <sup>-1</sup>	Average number of clutches laid per year [2.8–3.4] (Parmenter & Limpus 1995, Limpus 2007, Pendoley et al. 2014)
$E$	48 eggs	Average number of eggs per clutch [44–57] (Parmenter & Limpus 1995, Hewavisenthi & Parmenter 2002, Limpus 2007, Whiting et al. 2008, Pendoley et al. 2014)
$r_t$	1.0	Female:male ratio of offspring (Stubbs et al. 2014)
$\tau_j$	16.3 yr	Age when 50% of turtles are mature (Turner Tomaszewicz et al. 2022)
$\alpha$	0.75 yr <sup>-1</sup>	Rate of maturation at age $\tau_j$ (Turner Tomaszewicz et al. 2022)
$s_{E,i,t}$	0.70	Probability of egg survival [0.48–0.93] (Parmenter & Limpus 1995, Hewavisenthi & Parmenter 2002, Whiting et al. 2008, Pendoley et al. 2014)
$s_{H,i,t}$	0.85	Probability of hatchling survival from nest to water
$s_{Y,i,t}$	0.50	Probability of hatchling survival in nearshore waters
$s_{J1}$	0.05	Probability of survival to age 1 yr, after nearshore dispersal; indirectly inferred using Parmenter & Limpus (1995) and assuming a stable population
$s_j$	0.89	Juvenile annual apparent probability of survival; indirectly inferred using Parmenter & Limpus (1995) estimate of 1/400 hatchlings reaching maturity ( $\sim s_1 s_j^{\tau_j}$ )
$s_A$	0.92	Adult annual apparent probability of survival (Pfaller et al. 2018)

rookeries distributed across individual beaches and islands measuring up to a few kilometres in length (Pendoley et al. 2014, Fossette et al. 2021). Qualitatively, our general conclusions are not strongly influenced by rookery size. Having identified key model parameters and the life stages associated with relatively high conservation value, we next predict population outcomes from multiple site-based conservation scenarios performed at the second-largest site ( $K_{4,t}$  nests). Manipulating the second-largest site provides insights for how relatively larger and smaller neighbouring sites may be impacted by local conservation efforts. These scenarios vary in their duration (number of consecutive seasons) and the life-history stages targeted. We investigate 3 types of intervention that improved turtle success: (1) onshore turtle survival of eggs and/or emergent hatchlings, (2) nearshore early survival of dispersing hatchlings, and (3) offshore survival of older juveniles and adults.

Finally, we used the model to explore potential impacts of an increasing female bias of offspring due to

warming. Understanding the impact of female bias when assessing conservation impacts is important because changes in bias can also change population growth rates. In isolation, an increase in female bias will increase population growth rate, as it increases the number of nesting animals; however, it is also expected that increasing female bias will also reduce female mating success due to a decrease in mating opportunities (Heppell et al. 2022). Increased temperatures are also expected to increase egg mortality (Hewavisenthi & Parmenter 2002) and could also coincide with reduced offshore survival and nesting habitat (Varela et al. 2019).

How potential positive and negative future effects combine to impact long-term population dynamics is unclear (Butt et al. 2016, Hays et al. 2023). We explored this issue by simulating population dynamics, assuming from 2025 the female:male sex ratio increased by 0.05 per year from 1 up to 10, which encapsulates the wide range of female-biased sex ratios observed across marine turtle species (e.g. Hewavisenthi

& Parmenter 2002, Katselidis et al. 2012). We then compared this simulation of increased female bias with simulations where we added a negative population effect that increased over time. Specifically, we considered: reducing female mating success as the female sex ratio increased; reduced egg survival under warming temperatures; reduced juvenile and adult annual survival; and reduced nesting availability. How adult female bias quantitatively impacts female mating success is not well understood; however, to illustrate its potential impact, we assumed that mating success declined by 25% for every unit increase in the female:male ratio. For egg survival, we assumed a gradual decline from 70% to 50% survival over 50 yr, starting in 2025, which is similar to changes simulated by Heppell et al. (2022). Similarly, starting in 2025, we modelled annual relative declines of 0.03% for both  $s_J$  and  $s_A$ , and 1% for beach capacity,  $K_{i,t}$ . These changes in parameter values have been chosen as they illustrate the degree of environmental impact that can result in changes in turtle abundance that are comparable with the simulated conservation impacts.

### 3. RESULTS

The stable, relative age distribution and maturity of females is presented in Fig. 1A for a site where population growth is only weakly limited by the availabil-

ity of nesting sites (i.e. the number of clutches laid is small compared to nest availability) and the environment is described by the baseline parameters (Table 1). In this example, 80.0% of the population is predicted to be immature. The corresponding age-dependent expected number of future mating is presented in Fig. 1B, which shows that young adults are expected to contribute most to future population growth because most juvenile females are unlikely to reach maturity. Those females that do mature are predicted to undertake, on average, approximately 5 seasons of nesting during the remainder of their lifetime, although variation among females will be high.

The sensitivity of population growth rate with respect to life-history parameters is presented in Fig. 2. Not surprisingly, given the importance of young adults (Fig. 1B), population growth is very sensitive to changes in first-year survival, as well as annual juvenile and adult survival (Fig. 2A,C). Here, sensitivity to adult survival is weakened by incorporating senescence via enforcing a maximum age of 60 yr. For the life-history parameters that apply once (Fig. 2A,B), their sensitivity weakens as their baseline value increases, due to diminishing returns. The least sensitive parameters are those associated with beach or nearshore survival.

The first set of conservation scenarios we considered involved onshore activities at the second-largest site that improved egg and young hatchling survival. Spe-

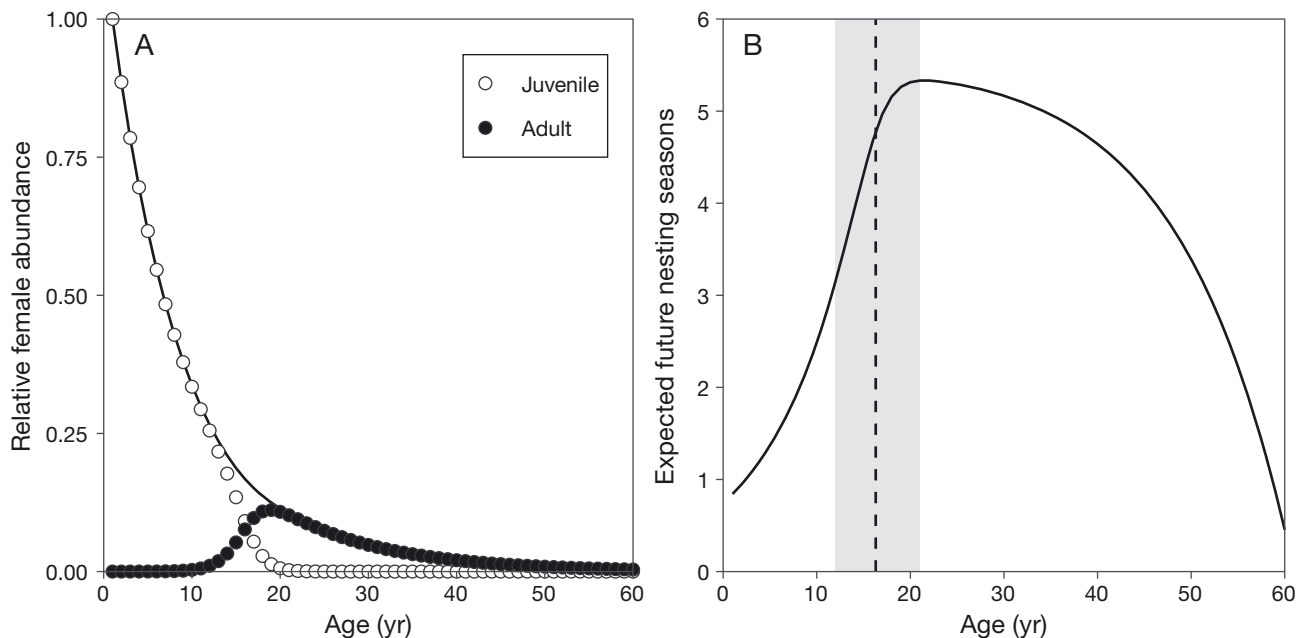


Fig. 1. (A) Stable female age distribution associated with all sites generated by the flatback turtle intervention model when parameterised according to the baseline scenario (Table 1). The line depicts the sum of the adult and juvenile relative abundances. (B) Age-dependent expected future number of nesting seasons. Dashed vertical line: age when 50% of turtles reach maturity; grey shading: ages when between 5 and 95% of animals are mature

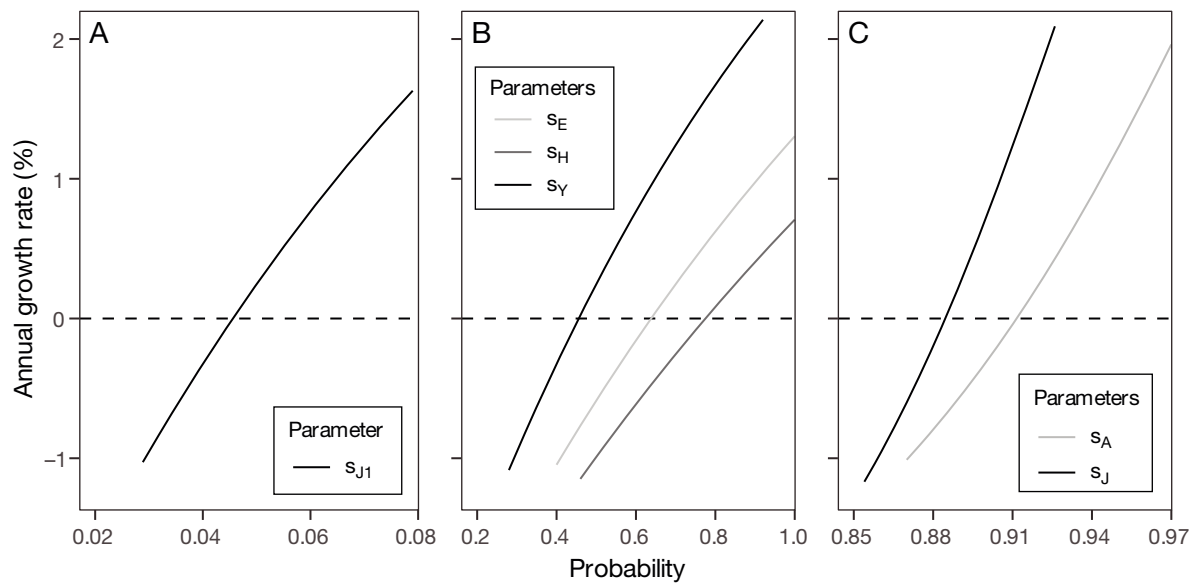


Fig. 2. Sensitivity analyses for the flatback turtle intervention model. Relation between annual population growth and survival parameters that describe life-history probabilities: (A) young turtles during their first year; (B) eggs, and hatchlings traversing the beach and inner-shore waters; and (C) juveniles and adults when offshore. Note the different scales for the probability values. See Table 1 for parameter descriptions and their baseline values

cifically, we assumed optimistic conservation efforts starting in 2025 raising onshore survival, given by the product  $s_E s_{H1}$ , from  $0.7 \times 0.85 = 0.595$  to 0.85 (e.g. via predator removal or exclusion). This level of increase in survival may be achievable if early mortality is largely due to predation or nest disturbance (e.g. King et al. 2023). Scenario 1 assumed that these annual increases in survival were maintained for 15 yr (Fig. 3, top row), whereas Scenario 2 assumed an extreme case of 30 yr of intervention (Fig. 3, second row). Next, we investigated the impact of improving the probability of hatchling survival when within nearshore waters,  $s_Y$ , from 0.5 to 0.75 (Scenario 3). This scenario might reflect reducing attraction of dispersing turtle hatchlings to nearshore structures that concentrate their predators, by reducing lighting near such structures. Scenario 3 also assumed 30 yr of intervention (Fig. 3, third row). Scenario 4 combined both of the 30 yr interventions depicted in Scenarios 2 and 3 (Fig. 3, bottom row). For both target stages, long-term interventions were needed to significantly improve population growth, and combining interventions had a largely additive effect on population abundance at the intervention site (i.e. population change is the sum of the changes due to the individual interventions). Local, site-specific conservation actions had little impact on improving turtle numbers at other sites due to high site fidelity exhibited by adult females.

It is difficult to quickly detect the population-level impact of improving egg and hatchling sur-

vival using subsequent yearly counts of nesting females, as increasing numbers of hatchlings successfully entering or surviving in nearshore waters does not translate to local increases in nesting activity until those individuals first reach sexual maturity, which is  $\tau_j = 16.3$  years later (Fig. 3). In contrast, egg and hatchling conservation interventions rapidly translate to increases in the number of juveniles; however, this age class is difficult to quantify in the field.

Next, we considered annual conservation efforts targeting the older offshore stages, increasing juvenile and adult survival during the years 2025–2055. We increased  $s_j$  from 0.89 to 0.9, and  $s_A$  from 0.92 to 0.93. We assumed that the site associations of juvenile and adult turtles did not impact their likelihood of receiving benefit from the intervention, which would occur if turtles tended to share and mix among feeding grounds (Kale et al. 2022). Unlike onshore interventions, this offshore intervention translated into immediate increases in juvenile and adult numbers, including nesting numbers, and it benefitted all sites (Fig. 4). Benefits were long-lasting, and high site fidelity among mature females tended to result in the smaller sites experiencing density-dependent reductions in nesting success earlier as their numbers increased (Fig. 4).

When female bias in offspring was forced to increase over time (Fig. 5), the predicted sex ratio of the population lagged the sex ratio of offspring by ap-

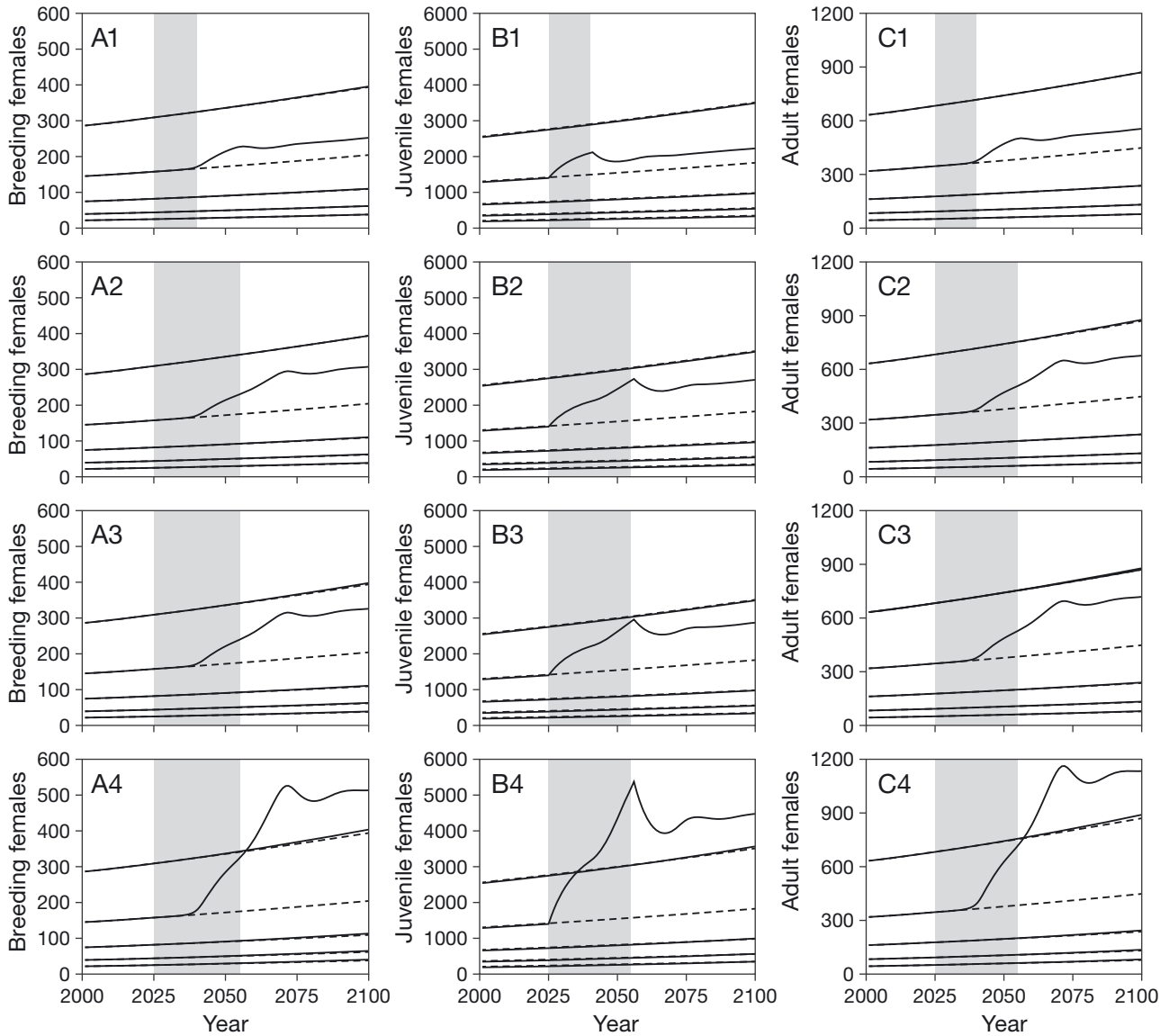


Fig. 3. Predicted outcomes of conservation activities focused on beaches. Lines depict turtle numbers associated with each of 5 relatively small sites that vary in space for nesting:  $K_{1,t} = 500$ ,  $K_{2,t} = 1000$ ,  $K_{3,t} = 2000$ ,  $K_{4,t} = 4000$ , and  $K_{5,t} = 8000$  nests (depicted by lowest to highest lines). Population dynamics for all sites are presented when conservation activities are performed at the second-largest site only (solid lines) and in the absence of any intervention (dashed lines). Columns (A–C) depict life stages ( $B_{i,t}$ ,  $J_{i,t}$ ,  $A_{i,t}$ —breeding, juvenile and adult females—respectively), and rows (1–4) depict distinct conservation scenarios (Scenarios 1–4, respectively). Shaded areas depict the years when conservation activities are performed. Activities are defined by the following modified parameters for Site 4: Scenario 1 (15 yr protecting eggs and hatchlings:  $s_E \times s_H = 0.85$ ); Scenario 2 (same as Scenario 1 except 30 yr spent protecting eggs and hatchlings); Scenario 3 (30 yr protecting young hatchlings when within in-shore waters:  $s_Y = 0.75$ ). Scenario 4 combines Scenarios 2 and 3. In all cases, all other parameters are as presented in Table 1

proximately 29 yr (Fig. 5A), which was longer than age at maturity,  $\tau_j = 16.3$  yr. In isolation, this change in female bias resulted in a substantial increase in population growth (Fig. 5D), and population increase only slowed once the number of undisturbed nests reached beach capacity. However, assuming the negative relation between adult female bias and female mating success depicted in Fig. 5B eventually re-

sulted in severe reductions in the number of mated females (Fig. 5C) such that the population tended towards extinction after an initial population increase (Fig. 5D). Similar trajectories characterised by an initial increase, but subsequent decline, were also observed (Fig. 5D) when we instead incorporated long-term negative effects of reduced egg survival, offshore survival, or beach habitat (Fig. 5C).



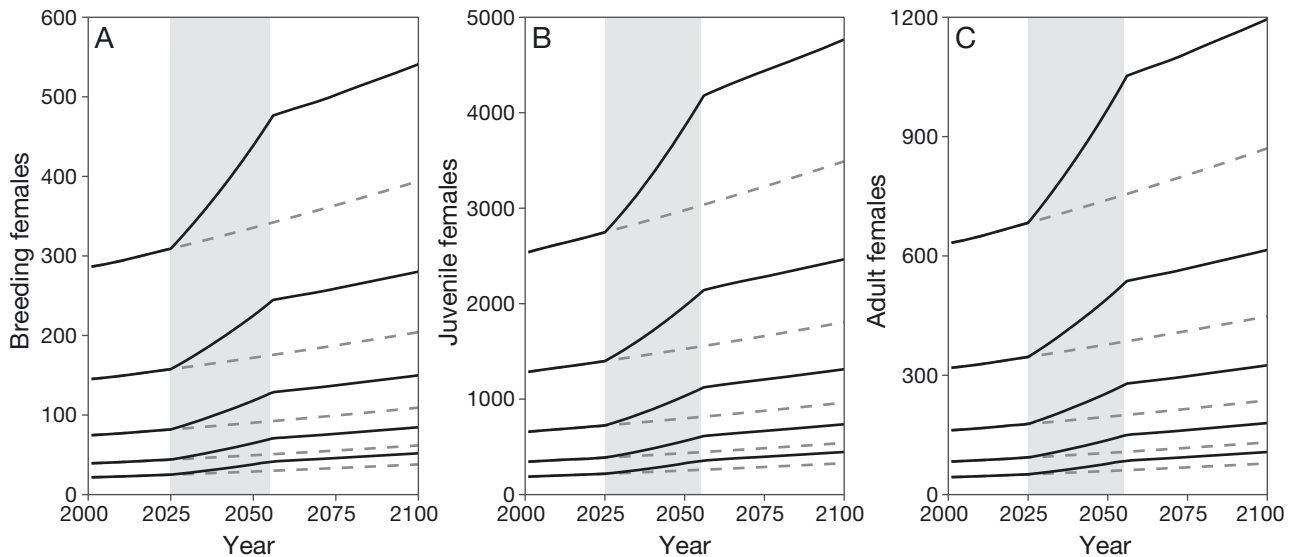


Fig. 4. Predicted outcomes of conservation activities focused offshore, for (A) breeding females, (B) juvenile females, and (C) adult females. Lines depict turtle numbers associated with each of 5 sites that vary in space available for nesting (see Fig. 3). Population dynamics are presented as a result of conservation activities (solid lines) and in the absence of any intervention (dashed lines). Shaded areas depict the years when conservation activities are performed. Conservation activities result in increasing juvenile and adult annual survival: from  $s_j = 0.89$  and  $s_A = 0.92$  to  $s_j = 0.9$  and  $s_A = 0.93$ , from 2025 to 2055

#### 4. DISCUSSION

Here, we have presented a population model that can be used to quickly assess a broad range of proposed conservation interventions, and explored the potential impacts of environmental change on long-term population persistence. Importantly, the modeling analysis suggests that flatback turtle populations can benefit significantly from long-term conservation activities that occur either onshore or offshore. However, high site fidelity meant that local activities targeting eggs and hatchlings typically had little impact on population trajectories predicted at other sites. In general, population dynamics were characterised by long time lags in responses to manipulations, which can lead to difficulty in assessing conservation success (Piacenza et al. 2017). These time lags can also promote non-trivial dynamics when compounded by climate change.

The analysis identified adults, and especially young adults, as the life stage that contributes most to future population growth. Earlier life stages (e.g. eggs and hatchlings) have much lower annual survival rates, resulting in few individuals reaching maturity, which places high conservation value for those that do mature, or are close to maturity (Fig. 1B). Relatively high contributions from young adults to population persistence for long-lived and late-maturing species is a well-known outcome of stage- and age-structured

population models (Crouse et al. 1987, Heppell et al. 1996, Tuljapurkar & Caswell 1996).

Our estimate of approximately 5 nesting seasons per adult female's lifetime is double that provided by Limpus et al. (1984), which was based on a limited data set of 55 tagged females over 9 yr at Mon Repos, Queensland, Australia. How well our estimate reflects mating success exhibited by current flatback populations is unknown, as is the case with most species of sea turtles (Heppell et al. 2003).

Onshore management activities, such as nest protection and improving egg and hatchling survival via predator removal or manipulation of the incubation environment (García et al. 2003, Kurz et al. 2012, Madden Hof et al. 2020), are more readily attainable than activities that target offshore animals. For sites where onshore survival is low, beach activities may be possible that have significant positive impact on very young animals. Unfortunately, many of these individuals are unlikely to survive to maturity once they disperse from their natal beach, which lessens the impact of onshore conservation activities on population persistence (also see Crouse et al. 1987). Nonetheless, improving egg and hatchling survival (ideally concurrently) is predicted to be beneficial if it is sustained over many consecutive years (Fig. 3), and conversely, consecutive years of low egg and hatching survival can lead to a substantial decrease in population growth. Another likely long-term benefit of

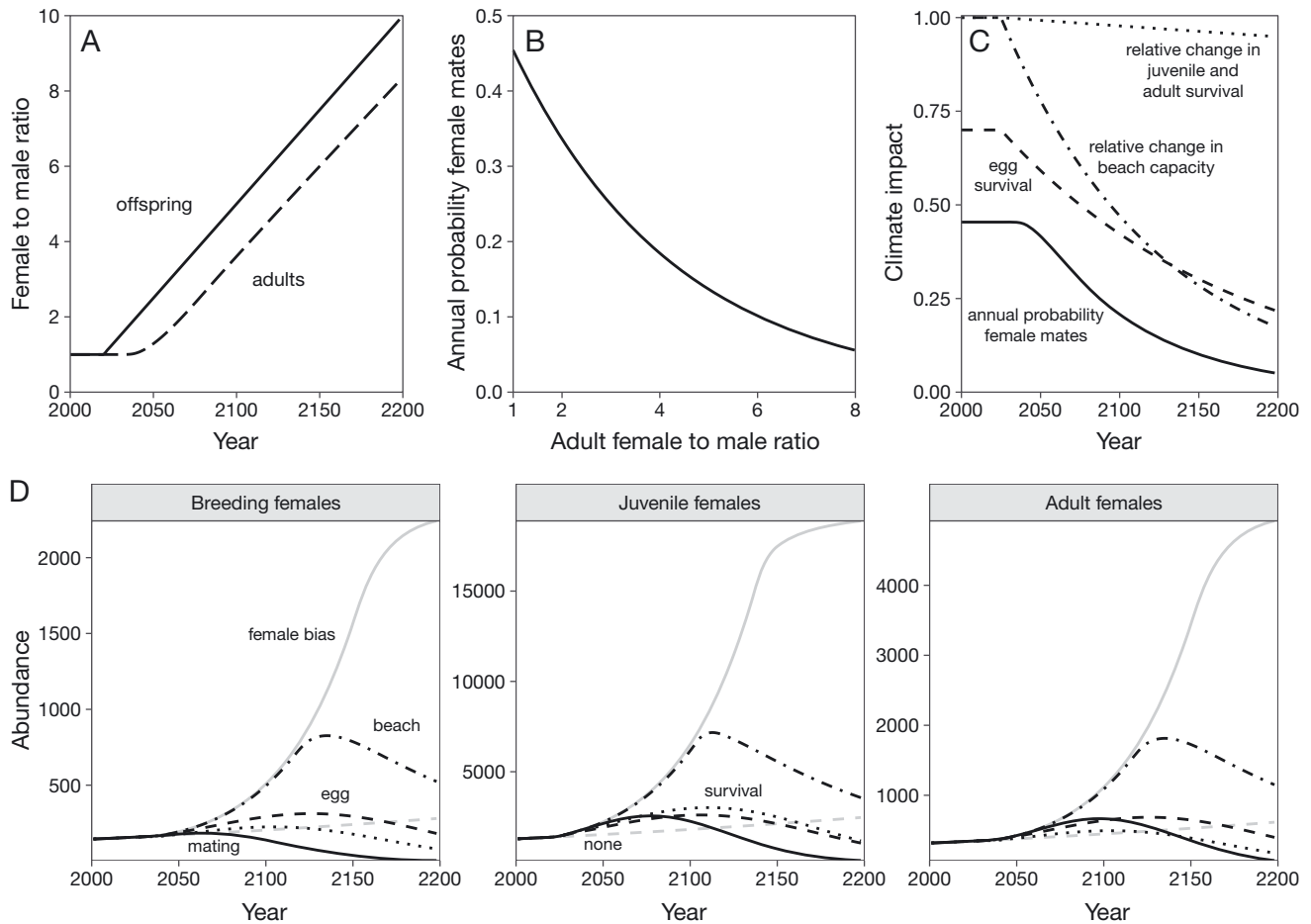


Fig. 5. Simulated long-term population dynamics when environmental warming results in increased female bias in the sex ratio. (A) Assumed impact of warming on the sex ratio of offspring ( $r_t$ ), and the resulting sex ratio of adults. (B) Assumed reduction in annual per-female mating success ( $b(r_t)$ ) as a result of a female-biased adult sex ratio. (C) Four negative impacts associated with increasing female bias that were investigated separately. (D) Predicted population dynamics for turtles associated with the second-largest site ( $K_{4,t} = 4000$  nests), for breeding females, juvenile females, and adult females. Dynamics are presented in the absence of female bias (none: dashed grey line), when female bias depicted in (A) is not associated with any negative effects (female bias: solid grey line), and when female bias is associated with the 4 negative impacts depicted in (C)

beach conservation activities is that they are typically much less costly than offshore conservation measures (Gjertsen et al. 2014).

If turtle monitoring is restricted to counting nesting females or clutch numbers, then assessing the success of onshore conservation activities is not straightforward (Stubbs et al. 2020). In this case, the signal of success is represented by a steady increase in juvenile abundance; however, this signal will not be evident from beach observations until juveniles start maturing around  $\tau_j$  years later and begin returning to beaches as nesting females. In contrast, the model predicts conservation activities will provide faster positive outcomes if they improve offshore survival of juveniles and adults. Positive effects of such interventions (e.g. reductions in turtle mortality caused by

fishery bycatch, decrease in marine debris entanglement/ingestion) should be evident earlier as nesting numbers rise in direct response to increased adult abundance. We refer to this inverse relation between the relative ease of manipulating different life stages (i.e. onshore and offshore) and their relative impact on population growth rate as a conservation mismatch. However, it is important to note that this interpretation of a mismatch focuses exclusively on the anticipated speed of population recovery and neglects consideration of potential benefits to onshore activities, including relative financial costs, practicality, and effort (Gjertsen et al. 2014).

Climate warming acting on increasing the proportion of offspring being female has the potential to result in misleading inference regarding long-term pop-

ulation trends and population status when nesting females are the focus of monitoring. Initial increases in nesting numbers may reflect a relatively fast increase in adult females over males, with adult sex ratios lagging many years with respect to the sex ratio of offspring, due to shifts in the age structure over time. However, high female skew may eventually lead to per capita reductions in mating success (Hays et al. 2023), with the potential to cause a rapid population crash. Alarming, the time lags inherent in the system could result in negative population trends (e.g. nesting female abundances) not being detected until many years after the effects of biased sex ratios have been imbedded in the population. Delayed population collapse in turtle populations, due to increased female bias, has also been predicted using alternative modelling approaches (Heppell et al. 2022). We have shown that increasing female bias may also initially mask other possible negative and long-term detrimental environmental effects, such as reduced egg and offshore survival, and loss of nesting habitat. The climate models presented here serve to illustrate potential difficulties when inferring management success in the presence of environmental change. Additional informed climate simulations are needed to provide a more comprehensive predictive analysis of long-term population dynamics (e.g. Heppell et al. 2022).

Our ability to project population trends under environmental change is also limited by our understanding of how species are likely to adapt to their changing environment. In this example, selection would likely favour genotypes that result in higher offspring survival, and a more even sex ratio, when exposed to the higher temperatures. Whether changes in climate are happening so quickly relative to sea turtle generation time that turtle adaptation can have significant mitigating impacts on population declines is unclear (Charnov & Bull 1989, Heppell et al. 2022). Uncertainty with predicting turtle population responses to climate change is also compounded by uncertainty in temperature effects on food availability (Stubbs et al. 2020).

Estimating population size is difficult in practice due to the offshore lifestyle of juveniles and adults (Theissinger et al. 2009). The model presented here has added utility, as it provides insights about the relationship between nesting females (or clutches), which are more readily observable, and juvenile and adult abundances. For the baseline case, the model predicts that the ratio of adult females and juvenile females, with respect to nesting females, is approximately 2 and 9, respectively (Fig. 3). These estimates, however, assume invariant parameter values and a

relatively stable population (Theissinger et al. 2009), so must be used with caution when populations are increasing or decreasing.

A striking prediction of the model is that conservation activities are only likely to benefit the population if they are sustained over many years (i.e. decades). Stable turtle populations are characterised by females typically being involved in multiple years of nesting (Fig. 1B). As a result, turtle populations can buffer occasional years of low mating or nesting success, which is presumably advantageous in stochastic environments. The converse is that occasional years of high nesting success also have relatively little positive impact on population numbers, necessitating conservation activities to be maintained long-term if they are to ultimately be effective (see also Piacenza et al. 2017).

The model presented here makes several simplifying assumptions that warrant further investigation. For example, the spatially implicit treatment of site locations allowed movement to be modelled using a simple matrix,  $\kappa$ , which was calculated only using site-specific nest carrying capacities,  $K_i$ . However, biased movement between sites due to changing favourable resource and environmental conditions is expected (Waayers et al. 2011, Whittock et al. 2016, Thums et al. 2017, Kale et al. 2022). Our results suggest that site fidelity and site choice by adult females influences the scale that site-specific interventions are likely to have on a population (see also Thums et al. 2017). Our assumption of high site fidelity resulted in the model predicting that onshore conservation activities often had relatively limited impact on turtle numbers associated with other sites, at least in the short term. Nonetheless, identifying which sites are acting as population sources and sinks will help with identifying cost-effective site-specific conservation strategies (Butt et al. 2016).

Here, model parameters have been estimated based on the literature under the assumption that prior studies are broadly indicative of the current and future state of flatback populations; however, stochastic and long-term changes in the environment challenges this assumption. Continued monitoring of offshore survival, nesting activities, and egg/hatchling success across sites, and the development of statistical methodologies for using such data to robustly estimate model parameters will further the utility of the model. Continued refinement of the model in response to new field information will provide an adaptive and transparent approach for helping with the development and assessment of management strategies for the flatback turtle.

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