

# Investigating differences in population recovery rates of two sympatrically nesting sea turtle species

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## Keywords

conservation management; demographic model; green turtle; loggerhead turtle; management priorities; monitoring; population recovery.

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## Introduction

Long-lived, migratory species may be particularly at risk of extinction (Hutchings et al., 2012; Lewison et al., 2004) because they are likely to encounter diverse threats over a lifetime (Lascelles et al., 2014). Such species require long-term international conservation management, which is usually most successful when informed by an understanding of specific life-history traits and their variation (Dulvy et al., 2014; Ward-Paige et al., 2012).

Although global declines in marine megafauna have occurred in the past and continue apace (McCauley et al., 2015), there are conservation success stories, with some populations showing signs of recovery (Lotze et al., 2011;

## Abstract

Estimating life-history traits and understanding their variation underpins the management of long-lived, migratory animals, while knowledge of recovery dynamics can inform the management of conservation-dependent species. Using a combination of nest counts and individual-based life-history data collected since 1993, we explore the drivers underlying contrasting population recovery rates of sympatrically nesting loggerhead (*Caretta caretta*) and green (*Chelonia mydas*) turtles in North Cyprus. We found that nest counts of loggerhead and green turtles from 28 beaches across the island increased by 46% and 162%, respectively over the past 27 years. A Bayesian state-space model revealed that, at our individual-based monitoring site, nesting of green turtles increased annually at four times the rate of that of loggerhead turtles. Furthermore, we found that loggerhead turtles nesting at the individual-based monitoring site had stable reproductive parameters and average adult survival for the species and are the smallest breeding adults globally. Based on results from multiple matrix model scenarios, we propose that higher mortality rates of individuals in all age classes (likely driven by differences in life history and interaction with fisheries), rather than low reproductive output, are impeding the recovery of this species. While the increase in green turtles is encouraging, the Mediterranean population is estimated to have around 3,400 adults and is restricted to the Eastern Basin. The recovery of loggerhead turtles is likely to be compromised until mortality rates in the region are adequately quantified and mitigated. As survival of immature individuals is a powerful driver for sea turtle population numbers, additional efforts should target management at pelagic and neritic foraging areas. Understanding threats faced by immature life stages is crucial to accurately parameterise population models and to target conservation actions for long-lived marine vertebrates.

Magera et al., 2013; Valdivia, Wolf, and Suckling, 2018). Sea turtle populations have suffered severe declines and have been reduced to a fraction of their historical abundance in many locations (Kittinger et al., 2013; McClenachan, Jackson, and Newman, 2006; Van Houtan and Kittinger, 2014). Basic protective measures at nesting beaches have resulted in significant recovery trends for many populations (e.g., Mazaris et al., 2017; Valdivia, Wolf, and Suckling, 2018). The simultaneous reduction in overexploitation at sea has also contributed to population recoveries (Kittinger et al., 2013; Van Houtan and Kittinger, 2014). Nonetheless, many populations remain at low levels and are under threat of extirpation (Mazaris et al., 2017; Valdivia, Wolf, and Suckling, 2018).

Matrix population models can inform our understanding of population demography and dynamics and have been used to identify life-history parameters at which to target management in sea turtles (Casale and Heppell, 2016; Crouse, Crowder, and Caswell, 1987; Heppell, 1998; Mazaris, Fiksen, and Matsinos, 2005). These models require high-quality, long-term data for all life stages, which is challenging to obtain (Hamann *et al.*, 2010; Rees *et al.*, 2016), particularly as the juvenile life stages remain understudied (Wildermann *et al.*, 2018). From available modelling, it is apparent that immature individuals are the most abundant life stage, with mature adults representing only 1% of sea turtle populations (Casale and Heppell, 2016; Heppell, 1998). While removing nesting females and their eggs can undeniably cause populations to collapse (Tomillo *et al.*, 2008), at-sea protection is also key to population recovery (Casale and Heppell, 2016; Crouse, Crowder, and Caswell, 1987; Crowder *et al.*, 1994; Mazaris, Fiksen, and Matsinos, 2005).

In the Mediterranean, loggerhead (*Caretta caretta*) and green turtle (*Chelonia mydas*) populations have declined historically due to commercial exploitation, incidental fisheries interactions, coastal development and elevated predation of eggs and hatchlings (Casale *et al.*, 2018; Casale *et al.*, 2010b). Loggerhead turtles, the more abundant sea turtle species to reproduce in the Mediterranean, nest predominantly in Greece, Turkey, Cyprus and Libya, while green turtle nesting sites are predominantly in Turkey, Cyprus and Syria (Casale *et al.*, 2018). Globally, green and loggerhead turtles are classified as 'Endangered' (Seminoff, 2004) and 'Vulnerable' (Casale and Tucker, 2017), respectively. The Mediterranean loggerhead turtle population is assessed separately as 'Least Concern' owing to recent increases in nesting abundance but remains conservation-dependent (Casale, 2015; Casale *et al.*, 2018).

Sea turtle mortality rates in the Mediterranean are among the highest in the world and are likely due to unsustainable levels of bycatch (Casale and Heppell, 2016; Lewison *et al.*, 2014). Bycatch predominantly impacts post-pelagic individuals of relatively high reproductive value (Wallace *et al.*, 2008), which is of concern for population maintenance and recovery (Casale and Heppell, 2016; Casale, 2011; Levy *et al.*, 2015; Snape *et al.*, 2013).

Monitoring of nesting beaches across North Cyprus has been undertaken since 1993, with an intensive individual-based monitoring and tagging programme concentrated at one site, Alagadi Beach. Following the recent IUCN RedList assessment of Mediterranean loggerhead turtles as 'Least Concern' (Casale and Tucker, 2017), we investigate the long-term population trend for this species in North Cyprus and compare its recovery with that of green turtles, which are expected to be continuing an initial recovery phase described in Stokes *et al.* (2014). We use a Bayesian state-space model to estimate population growth rates for both species, compare this method to the current IUCN method and use stochastic matrix model projections to explore the drivers of the observed recovery patterns. We predict the loggerhead turtle recovery to be impeded by their greater

propensity for fisheries interactions, despite identical conservation policies for the two species on nesting beaches across North Cyprus.

## Materials and methods

### Data collection

Between 1993 and 2019, surveys were conducted every night at Alagadi Beach, thereafter 'the individual-based monitoring site', during the turtle nesting and hatching season (May–September). Nesting females were tagged post-ovulation using flipper and passive integrated transponder (PIT) tags (Broderick and Godley, 1996; Godley, Broderick, and Moraghan, 1999). Neophyte (i.e., first-time nester) classification was determined from 2000 onwards, one modal breeding cycle (3 years) after the introduction of PIT tags as PIT tag loss is substantially less than that of flipper tags (Omeyer *et al.*, 2019a). Recruitment was calculated as the proportion of nesters that were neophytes. Mean female size was calculated for each nesting season from minimum curved carapace length (CCL notch-to-notch) measurements (Bolten, 1999; Omeyer *et al.*, 2018). Within-season observed clutch frequency (OCF) of uniquely identified females was adjusted to estimated clutch frequency (ECF) if internesting intervals of  $\geq 20$  days were observed (Broderick *et al.*, 2002; Appendix S1.1.1). Remigration intervals of uniquely identified females were calculated as the number of years elapsed between breeding seasons for each individual turtle.

Eleven beaches (hereafter 'the long-term beaches' when also including Alagadi Beach; see Stokes *et al.*, 2014 for beach locations) were monitored annually between 1995 and 2019 with daytime surveys conducted daily, or every 1–3 days during the initial and final days of the season when few turtle activities occur. A further 16 beaches were monitored sporadically across seasons between 1993 and 2019. Remote beaches with low levels of nesting were surveyed every 1–3 days throughout the season. All successful and unsuccessful nesting activities were examined (tracks typically retain excellent visibility due to the hot settled weather and lack of rain during the breeding season), and each nest confirmed using a stick to feel the presence of an air pocket above the eggs, with great care not to touch the eggs themselves. Eggs were protected from predation by dogs and foxes in situ using wide aperture wire mesh, secured under the surface of the sand and directly over the egg chamber. Nests were relocated if they were considered 'doomed' due to close proximity to the sea. Unless clutches were just laid, care was taken not to turn the eggs during the process to avoid causing harm to developing embryos that are particularly vulnerable to movement 12 hours after laying (Limpus, Baker, and Miller, 1979). The depth and dimensions of the original egg chamber were recorded and recreated higher up the beach, in line with the original laying position where possible. Occasionally, nests missed at laying were found and recorded on predation or hatching.

Nests were checked for the presence of hatchling tracks during night-time surveys at Alagadi Beach and during the day at all other beaches. Clutch size was determined based on the number of eggshell fragments (approximate reconstruction of hatched eggs from fragments) and unhatched eggs upon excavation (Broderick *et al.*, 2003). Only nests with hatchling tracks present were excavated prior to 1997, and all nests were systematically excavated thereafter. Presumed unhatched nests were excavated 65 days after their lay date to determine clutch size and to analyse their fate. Hatchling emergence success (HES) was calculated from 1997 onwards as the proportion of emergent hatchlings per clutch (Appendix S1.1.1).

### Reproductive parameters and population trends

Matrix models were constructed for loggerhead turtles, as their lifecycle is the better understood of the two species in the region (Appendix S1.1.3). We regressed a number of reproductive traits (female body size, clutch size, clutch frequency, remigration interval and HES) against time (year), using data collected for this species at Alagadi Beach, to check for temporal bias in parameter estimates. To examine the relationship between nest counts and female recruitment for both species, we used Spearman's rank order correlation tests. Statistical modelling was carried out using R v.3.5.1 (R Core Team, 2019) and the 'nlme' (Pinheiro *et al.*, 2013), 'lme4' (Bates *et al.*, 2015) and 'mgcv' (Wood, 2004) packages. Generalised least squares (GLS) modelling, generalised linear modelling (GLM) and generalised linear/additive mixed modelling were used to analyse trends in the data (Appendix S1.1.2; Figures S1–S8). The long-term trend in nest count analysis was restricted to the 12 long-term beaches monitored consistently since 1995.

Consistent, long-term data are not always available for sea turtles. Therefore, to determine trends in nest or female counts for Red List assessments when data are temporally fragmented, the IUCN Marine Turtle Specialist Group (MTSG) compares change between oldest and most recent 3- to 5-year averages, which are calculated from absolute count data. We compare average counts and percentage change estimates obtained using the IUCN MTRG method applied to (1) the raw data (for both nest and female counts) and (2) the estimated female counts derived from the state-space model (see below for details on the state-space model).

### Matrix models

We used an age-classified, female-only, post-breeding birth-pulse, stochastic projection matrix with an annual time step for loggerhead turtles in R (Appendix S1.1.3). To introduce stochasticity, we ran each matrix model over 5,000 iterations, replacing some life-history parameters with a random draw from an appropriate distribution on each iteration. Several matrix models were derived from the initial matrix model by varying one or multiple parameters to explore their

contribution to the contrasting recovery rates (see Tables 1 and 2). On each iteration, we calculated  $\lambda$  (finite growth rate) under stable-stage distribution as the dominant eigenvalue. We report the mean ( $\bar{\lambda}$ )  $\pm$  95% quantiles from all iterations for each model in Table 1.

### State-space model

To calculate the observed  $\lambda$  based on our female count data and to estimate female population sizes at the individual-based monitoring site, we implemented a Bayesian state-space model in JAGS (v.4.3.0, Plummer, 2003) via the 'jagsUI' library (v.1.5.0, Kellner, 2018) for R. We assumed the underlying trend in our count data followed a conventional exponential growth model (Appendix S1.1.4). The model was fitted by running three Monte Carlo Markov chains for 400 000 iterations, with a burn-in of 300 000, and a thinning rate of 10. Visual checks (Figure S9) and the Brooks–Gelman–Rubin diagnostic tool were used to confirm successful chain convergence (all  $\hat{R}$  values  $<$  1.01). We report the growth rate  $\lambda = \exp(\bar{r})$  with posterior standard deviation (SD) and 95% Bayesian credible intervals (BCI) and compare this with  $\bar{\lambda}$  estimates from the various matrix model scenarios.

## Results

### Population trends

#### Nest counts

Nest counts for both species showed clear positive quadratic trajectories across the 12 long-term beaches monitored consistently since 1995 (Table S1, Fig. 1a,b). When applying the IUCN MTSG Red List assessment method which compares change in nest counts between oldest and most recent 3- to 5-year averages (3 years being used here as equivalent to the median remigration interval for the two species at this site, Omeyer *et al.*, 2019a), nest counts at these long-term beaches increased by 49% and 346% for loggerhead and green turtles, respectively (Table S2).

At the wider-island scale, when including a further 16 beaches for which we had 3 consecutive years of data between 1993 and 1997 and between 2017 and 2019, nest counts increased by 46% and 162% for loggerhead and green turtles, respectively (IUCN MTSG Red List assessment method, Table S2, Fig. 2). While nest counts for loggerhead turtles increased, more than 50% of beaches ( $n = 15$ ) saw their average number of nests in the recent time period decrease compared to the oldest time period. In contrast, only five beaches saw a decrease and three beaches saw no increase in the number of clutches laid in recent years for green turtles (Fig. 2).

At Alagadi Beach, our individual-based monitoring site, loggerhead turtle nest counts remained stable over the study period, whereas nesting numbers for green turtles increased exponentially (GLS, Table S1, Fig. 1c,d). Compared to the earliest period, the number of clutches laid decreased by

**Table 1** Finite population growth rates ( $\lambda$ , mean and 95% quantiles reported) for loggerhead turtles calculated using different matrix model projections

Scenario	HES	PSR	$S_{ej}$	$S_{bj}$	ASM	$S_a$	EPC	ECF	RI	$\lambda$
1	0.43 ± 0.17 <sup>a</sup>	0.89 ± 0.01 <sup>b</sup>	0.65 <sup>c</sup>	0.81 <sup>d</sup>	25 <sup>e</sup>	0.83 ± 0.02 <sup>f</sup>	70 ± 10 <sup>g</sup>	1.5 ± 0.02 <sup>g</sup>	3.2 ± 0.20 <sup>g</sup>	0.944 (0.909–0.968)
2	–	–	–	–	–	–	–	3 <sup>h</sup>	–	0.964 (0.928–0.990)
3	–	–	–	–	–	–	–	5	–	0.980 (0.942–1.006)
4	–	–	–	–	21 <sup>i</sup>	–	–	–	–	0.958 (0.920–0.987)
5	–	–	–	–	21 <sup>i</sup>	–	–	3 <sup>h</sup>	–	0.981 (0.940–1.012)
6	–	–	–	–	21 <sup>i</sup>	–	–	5	–	1.001 (0.957–1.032)
7	–	–	0.70 <sup>j</sup>	–	21 <sup>i</sup>	–	–	3 <sup>h</sup>	–	0.993 (0.950–1.024)
8	–	–	–	0.86 <sup>j</sup>	21 <sup>i</sup>	–	–	3 <sup>h</sup>	–	<b>1.018 (0.972–1.051)</b>
9	–	–	–	–	21 <sup>i</sup>	0.88 <sup>j</sup>	–	3 <sup>h</sup>	–	0.997 (0.958–1.024)
10	–	–	0.70 <sup>j</sup>	0.86 <sup>j</sup>	21 <sup>i</sup>	0.88 <sup>j</sup>	–	3 <sup>h</sup>	–	<b>1.044 (1.001–1.074)</b>
11	0.56 ± 0.17 <sup>k</sup>	–	0.70 <sup>j</sup>	0.86 <sup>j</sup>	21 <sup>i</sup>	0.88 <sup>j</sup>	–	3 <sup>h</sup>	–	<b>1.056 (1.020–1.080)</b>
12	–	–	0.72 <sup>l</sup>	0.88 <sup>l</sup>	21 <sup>i</sup>	0.90 <sup>l</sup>	–	3 <sup>h</sup>	–	<b>1.069 (1.023–1.100)</b>
13	0.56 ± 0.17 <sup>k</sup>	–	0.72 <sup>l</sup>	0.88 <sup>l</sup>	21 <sup>i</sup>	0.90 <sup>l</sup>	–	3 <sup>h</sup>	–	<b>1.081 (1.045–1.106)</b>
14	–	–	0.75 <sup>m</sup>	0.91 <sup>m</sup>	21 <sup>i</sup>	0.93 <sup>m</sup>	–	3 <sup>h</sup>	–	<b>1.106 (1.059–1.138)</b>
15	0.56 ± 0.17 <sup>k</sup>	–	0.75 <sup>m</sup>	0.91 <sup>m</sup>	21 <sup>i</sup>	0.93 <sup>m</sup>	–	3 <sup>h</sup>	–	<b>1.118 (1.079–1.144)</b>
16	–	–	–	–	–	–	115 <sup>n</sup>	–	–	0.959 (0.925–0.983)
17	–	–	–	–	–	–	115 <sup>n</sup>	3 <sup>h</sup>	–	0.980 (0.944–1.005)
18	–	–	–	–	21 <sup>i</sup>	–	115 <sup>n</sup>	–	–	0.975 (0.934–1.003)
19	–	–	–	–	21 <sup>i</sup>	–	115 <sup>n</sup>	3 <sup>h</sup>	–	1.000 (0.957–1.029)
20	–	–	–	–	21 <sup>i</sup>	0.97 <sup>o</sup>	–	3 <sup>h</sup>	–	<b>1.034 (1.005–1.056)</b>

ASM (mean), age at sexual maturity; ECF (mean ± SD), estimated clutch frequency; EPC (mean ± SD), eggs per clutch; HES (mean ± SD), hatchling emergence success; PSR (mean ± SE), primary sex ratios; RI (mean ± SD), remigration interval;  $S_a$  (mean ± SD), adult annual survival;  $S_{bj}$  (mean), benthic juvenile annual survival;  $S_{ej}$  (mean), epipelagic juvenile annual survival.

Initial matrix model is shown in italics. The ‘–’ symbol indicates that values are identical to those from the initial matrix model. Bold lambda values are those comparable with, or which exceed, the lambda estimate obtained from the state-space model (1.02, 0.96–1.09).

<sup>a</sup> Mean (1997–2018).

<sup>b</sup> Estimated using temperature dataloggers (1997–2006) for this subpopulation (see Fuller *et al.*, 2013).

<sup>c</sup> Mean annual survival at age 2 for an ASM of 25 (see Casale and Heppell, 2016).

<sup>d</sup> Mean annual survival calculated from 32 estimates presented in Table 1 in Casale *et al.* (2015).

<sup>e</sup> ASM estimates derived for the average SSM for Mediterranean loggerhead turtles.

<sup>f</sup> Annual survival calculated by Omeyer *et al.* (2019a) for this population.

<sup>g</sup> Calculated here.

<sup>h</sup> Median ECF for remigrant green (Stokes *et al.*, 2014) and loggerhead turtles.

<sup>i</sup> Lower end of ASM estimates for Mediterranean loggerhead turtles (Casale *et al.*, 2018).

<sup>j</sup> 5% increase.

<sup>k</sup> Mean between 1997–2003, when more clutches were relocated.

<sup>l</sup> 7% increase.

<sup>m</sup> 10% increase.

<sup>n</sup> Green turtle mean clutch size (Broderick *et al.*, 2003).

<sup>o</sup> Green turtle adult annual survival at the intensive individual-based monitoring site (Omeyer *et al.*, 2019a).

21% for loggerhead turtles, while they increased by 307% for green turtles (IUCN MTSG Red List assessment method, Table S2).

## Female abundance

At the individual-based monitoring site, loggerhead turtle nester abundance showed a shallow quadratic trajectory (Table S1, Fig. 3a), increasing by 2.1% annually based on observed female counts ( $\lambda = 1.02 \pm 0.03$  [mean ± SD], 95% BCI: 0.96–1.09; state-space model). Using IUCN past and recent periods, nester abundance increased by 11% from 28 (mean, 1993–1995) to 31 (2017–2019) nesting females (Fig. 3a, Table S2). Similarly, the state-space model

estimated that female abundance has changed from 22 (95% BCI: 14–32) to 32 (23–45) nesting females over the same period, a mean increase of 55% (–14 to 169) (Fig. 4, Table S2).

Female abundance for green turtles showed a clear positive quadratic trajectory (Table S1, Fig. 3b) and increased at four times the rate of that of loggerhead turtles annually ( $1.09 \pm 0.07$ , 0.93–1.24; state-space model; Fig. 4). Using IUCN past and recent periods, nester abundance for this species increased by 337% from 19 (1993–1995) to 83 (2017–2019) females (Fig. 3b, Table S2), while the state-space model estimated female abundance increased from 11 (5–26) to 77 (37–151) females

**Table 2** Summary of the aim of each matrix model scenario presented in Table 1

Scenario	Aim of the scenario
1	Initial scenario using known parameter estimates for this population
2	Increase clutch frequency to that of remigrant loggerhead turtles to account for potential bias of population-wide estimate
3	Increase clutch frequency towards upper range of clutch frequency estimates to account for potential bias of population-wide estimate
4	Decrease ASM to the lower of estimates to account for potential bias
5	Combination of aims from Scenarios 2 and 4
6	Combination of aims from Scenarios 3 and 4
7	Combination of aims from Scenarios 2 and 4 and increase annual survival by 5% to investigate effect on $\lambda$
8	Same as Scenario 7 but different life stage
9	Same as Scenario 7 but different life stage
10	Same as Scenario 7 but across juvenile and adult life stages
11	Same as Scenario 10 but also increasing egg survival
12	Combination of aims from Scenarios 2 and 4 and increase annual survival by 7% across juvenile and adult life stages to investigate effect on $\lambda$
13	Same as Scenario 12 but also increasing egg survival
14	Combination of aims from Scenarios 2 and 4 and increase annual survival by 10% across juvenile and adult life-stages to investigate effect on $\lambda$
15	Same as Scenario 14 but also increasing egg survival
16	Increase clutch size to that of green turtles to investigate effect of difference in life-history traits between species on $\lambda$
17	Increase clutch size and frequency to that of green turtles to investigate effect of difference in life-history traits between species on $\lambda$
18	Combination of aims from Scenarios 4 and 16
19	Combination of aims from Scenarios 4 and 17
20	Combination of aims from Scenarios 4 and 16 and increase adult annual survival to that of green turtles to investigate effect of difference in life-history traits between species on $\lambda$

Abbreviations: ASM, age at sexual maturity;  $\lambda$ , finite population growth rate.

over the same periods, a mean increase of 700% (126–1862) (Fig. 4, Table S2).

## Recruitment

At the individual-based monitoring site, nest counts and neophyte recruitment were strongly correlated for green turtles (2000–2019;  $\rho = 0.81$ ,  $P < 0.001$ ) but not for loggerhead turtles ( $\rho = 0.10$ ,  $P = 0.687$ , Spearman's correlation test). While nester abundance remained relatively low for loggerhead turtles (1993–2019), the percentage of neophyte nesters has significantly increased by 20% since 2000 (no autocorrelation:  $\chi^2_1 = 0.23$ ,  $P = 0.629$ , linear slope:  $\beta = 0.005 \pm 0.003$ ,  $F = 8.03$ ,  $P = 0.011$ , GLM, Fig. 3a). The absence of an increase in nest counts despite increased recruitment for loggerhead turtles at this site is likely due to low nest site fidelity rather than a decrease in clutch frequency (Appendix S1.2.1 and 2.2) considering the overall increase in nesting numbers across monitored beaches for this species (Fig. 1a,c).

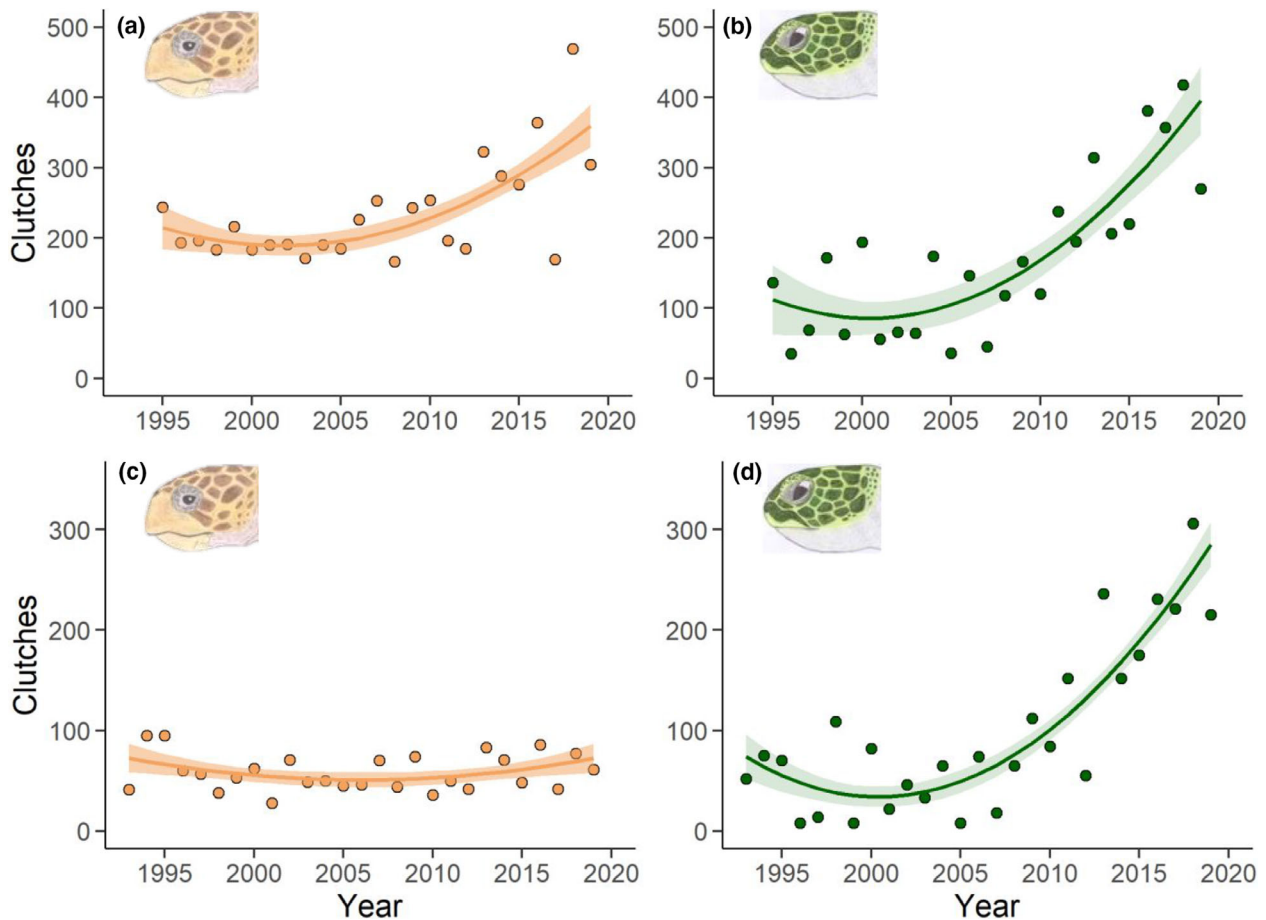
## Matrix models

Parameter estimates are summarised in Table S3. For loggerhead turtles, female body size, clutch size, clutch frequency and remigration interval remained stable over the study period, while HES varied temporally due to changes in translocation practices (Appendix S1.2.2; Figures S2–S8).

Matrix model scenarios and the aim of each scenario are summarised in Tables 1 and 2. The finite loggerhead

population growth rate obtained from the initial matrix model was lower (0.94, 95% CI: 0.91–0.97) than that obtained from the state-space model (1.02, 0.96–1.10) and suggested the population should be decreasing by 5.6% annually. Increasing loggerhead clutch frequency to that of green turtles did not result in comparable  $\lambda$  estimates between loggerhead turtle models (Scenarios 2–3). Similarly,  $\lambda$  estimates only slightly increased when both increasing clutch frequency and decreasing age at sexual maturity (Scenarios 4–6). Obtaining comparable  $\lambda$  estimates between the state-space and the matrix models for loggerhead turtles required a clutch frequency of 3, an age at sexual maturity of 21 years, and a 5% increase in benthic juvenile survival (Scenario 8). For population growth rates to exceed those currently observed at the individual-based monitoring site for loggerhead turtles, survival needed to be increased by 5% across all age classes (Scenarios 10–14). Similarly, obtaining population growth rates that exceed those observed for green turtles at this site ( $1.09 \pm 0.07$ , 0.93–1.24; state-space model) required a 10% increase in survival across all age classes and a 13% increase in HES (Scenario 15).

Compared to loggerhead turtles at this site, green turtles had higher adult survival and produced more eggs and more emergent hatchlings (Table S3; Fig. 5; Appendix S1.2.1). Increasing loggerhead turtle reproductive output to mirror that of green turtles did not result in comparable  $\lambda$  estimates between the matrix model results for loggerhead turtles (Scenarios 16–19) and the state-space model for green turtles ( $1.09 \pm 0.07$ , 0.93–1.24). In contrast, increasing loggerhead turtle adult survival to equal that of green turtles resulted in



**Figure 1** Loggerhead (a and c) and green turtle (b and d) clutches laid across all long-term nesting beaches (a and b) and at the individual-based monitoring site, Alagadi Beach, North Cyprus (c and d) between 1993 and 2019. Data from Panels (c) and (d) are included in Panels (a) and (b). Coloured lines denote generalised least squares model predictions and associated 95% confidence intervals.

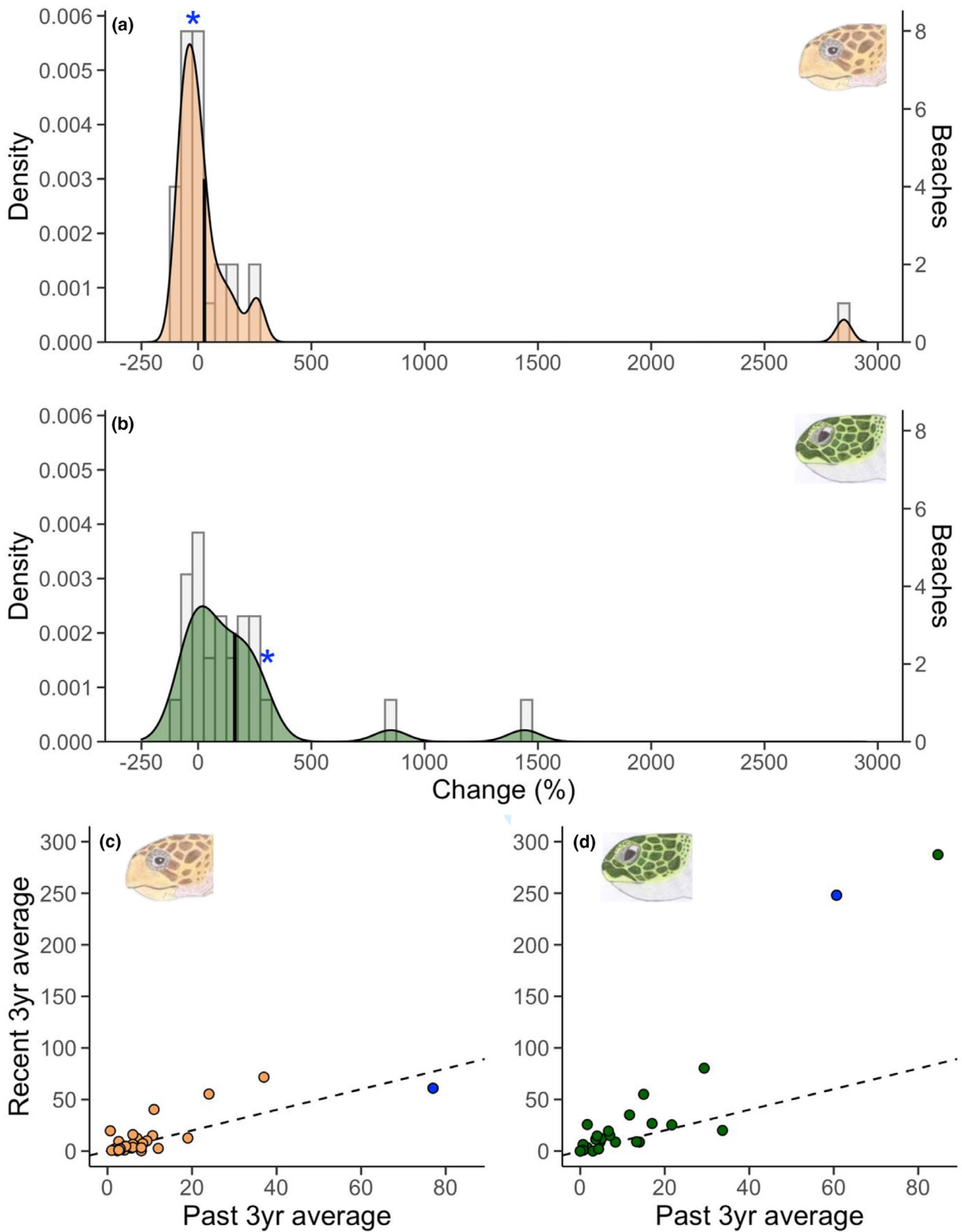
comparable growth rates between the state-space and the matrix models for loggerhead turtles (Scenario 20), although this scenario is unrealistic.

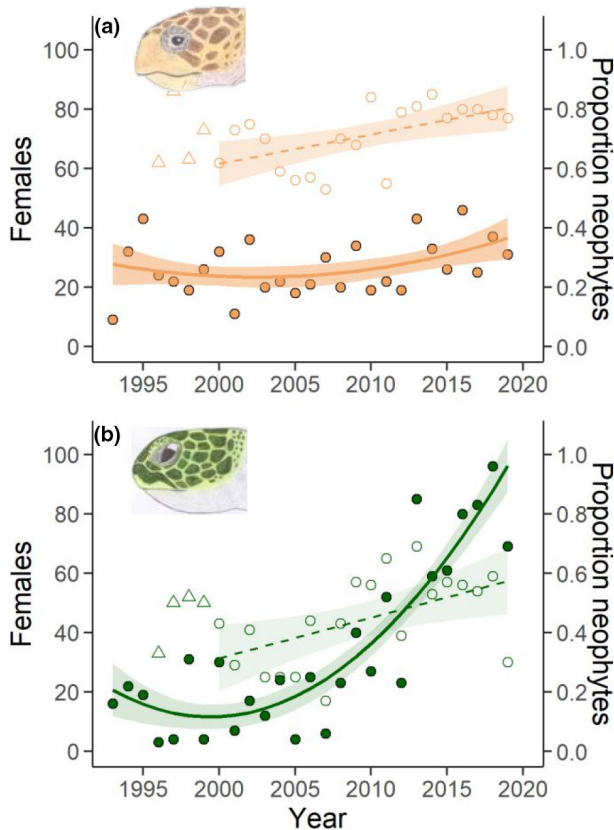
## Discussion

After the interruption of legal trade globally and over a quarter of a century after the commencement of intensive nest protection in North Cyprus (Broderick and Godley, 1996;

Demetropoulos and Hadjichristophorou, 1989), green and loggerhead turtles nesting in North Cyprus have shown differing recovery rates. Six additional years of monitoring have confirmed the suggested initial recovery phase for green turtles described in Stokes *et al.* (2014), and growth in nesting numbers continues exponentially. In contrast, loggerhead turtle nesting numbers have seen a slight increase; this difference cannot be attributed to temporal changes in monitoring practices or reproductive parameters. However, it is possible

**Figure 2** Density plots (primary y axes) of the percentage change in nest count between the oldest and most recent time periods calculated as per International Union for Conservation of Nature (IUCN) Marine Turtle Specialist Group (MTSG) Red List assessment method across all 28 beaches for loggerhead (a) and green (b) turtles, also shown as frequency distributions (secondary y axes). Note that two beaches could not be included in Panels (b) and (d) for green turtles as percentage change could not be calculated due to the absence of clutches being laid in the earliest time period. The IUCN MTSG Red List assessment method compares change between oldest and most recent 3- to 5-year averages, from count data. Black vertical lines in Panels (a) and (b) denote the mean percentage change for all beaches combined. Panels (c) and (d) show the recent average nest count against the oldest average nest count at the same beaches, for loggerhead and green turtles respectively. Dashed lines in Panels (c) and (d) delineate no change in average nest count between time periods. Blue stars (a and b) and blue dots (c and d) denote Alagadi Beach, the individual-based monitoring site (North Cyprus).

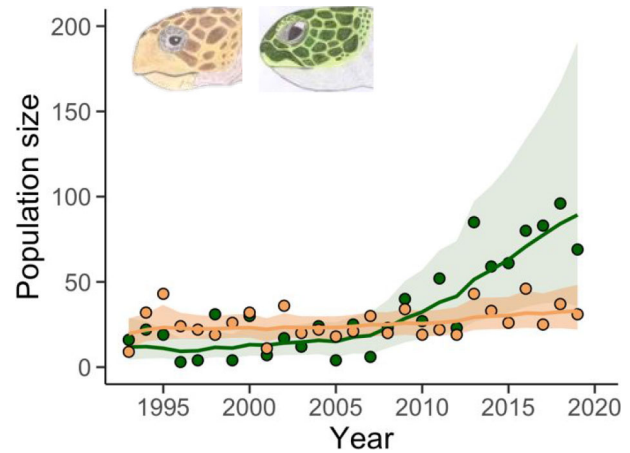




**Figure 3** Nesting (a) loggerhead and (b) green turtles (solid lines, filled circles) and the proportion of those that are neophytes (first-time nesters; dashed lines, open symbols) at the individual-based monitoring site (Alagadi Beach, North Cyprus) between 1993 and 2019. Triangles represent a period of lower certainty before the introduction of passive integrated transponder tags in 1997. Coloured lines denote model predictions (generalised least squares for female counts and generalised linear modelling for proportion of neophytes) and associated 95% confidence intervals.

these populations are recovering from different levels of depletion.

Recruitment of neophytes has driven the increase in nesting numbers for green turtles (Stokes *et al.*, 2014) and is an indicator for population growth (Heppell *et al.*, 2003; Richardson *et al.*, 2006). Although previous genetic examination has shown high philopatry among female loggerhead turtles nesting within Cyprus (Carreras *et al.*, 2006), recent satellite tracking from North Cyprus has revealed within-season multicountry nesting for loggerhead turtles (Snape *et al.*, 2016). Thus, the high proportion of neophyte loggerhead turtles that were recorded laying only one clutch and that were never resighted raises questions: Are these females truly first-time nesters and/or to which rookery do they belong? The relatively low coverage of capture–mark–recapture programmes in the Mediterranean currently prevents these questions from being answered, yet they are key to refining estimates of reproductive parameters and determining rookery-

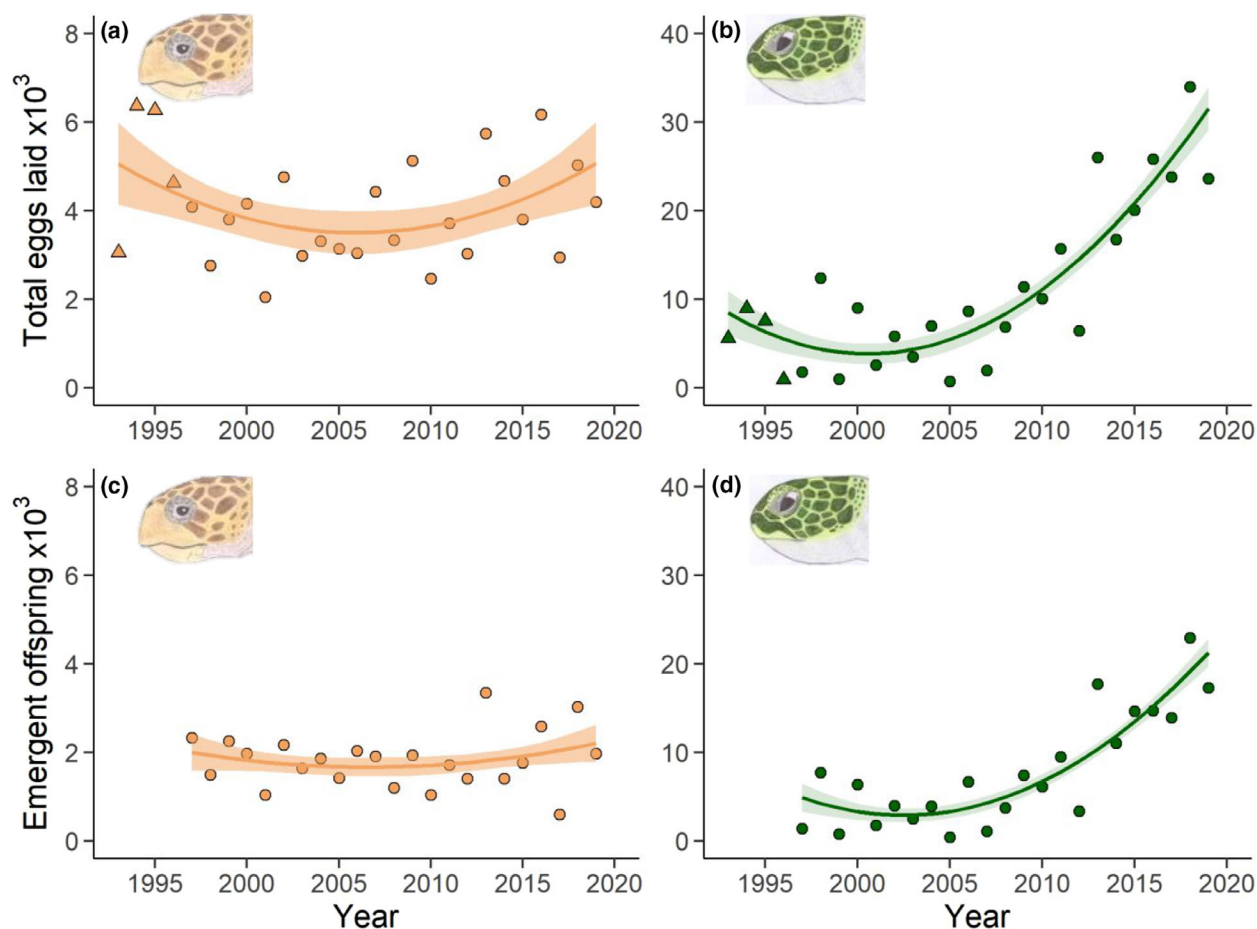


**Figure 4** Annual estimated female population size for loggerhead (orange) and green (green) turtles, based on a Bayesian state-space model fit (coloured lines) to observed female counts (circles) at the individual-based monitoring site (Alagadi Beach, North Cyprus). 95% Bayesian Credible Intervals shown as coloured polygons.

specific population sizes. Genetic analysis could reveal the origin of individuals and whether these are new founders as has been observed in Spain (Carreras *et al.*, 2014), although previous data suggest no evidence of genetic bottleneck and founder effect for Mediterranean loggerhead turtles nesting within the species' known range (Carreras *et al.*, 2006). Additionally, it suggests tag returns likely overestimate remigration interval and underestimate clutch frequency (Pfaller *et al.*, 2013; Rees, Theodorouand, and Margaritoulis, 2020; Tucker, 2010), therefore influencing rookery-specific and regional population size estimates (Weber *et al.*, 2013; Esteban, Mortimer, & Hays, 2017; Casale and Ceriani, 2020). As such, while nest counts are most often used as a proxy of sea turtle population size, it is ideal, although logistically challenging, to count nesting females to estimate population abundance within each regional management unit (Casale and Ceriani, 2020; Shamblin *et al.*, 2017, 2021).

Given the interannual variation in sea turtle nesting numbers (e.g. Broderick, Godley, and Hays, 2001), long-term data series are required for meaningful population assessments (Mazaris *et al.*, 2017; Valdivia, Wolf, and Suckling, 2018). The IUCN MTSG Red List assessment method aims to provide a coarse measure of population trends when long-term data are not available; however, it largely underestimated the increase in nester abundance for both species compared to the state-space model. Additionally, its sensitivity to small deviations resulted in opposing trends in nest counts for loggerhead turtles when comparing results for the individual-based monitoring site and the wider island. Thus, when available, entire time series should be used to account for long-term fluctuations and to accurately reflect observed trends (D'Eon-Eggertson, Dulvy, and Peterman, 2015). Similarly, single monitoring sites cannot be used in isolation to assess population trends for species with low site fidelity, such as loggerhead turtles in the current study.





**Figure 5** Estimated number of eggs laid by (a) loggerhead and (b) green turtles at the individual-based monitoring site (Alagadi Beach, North Cyprus) and resulting emergent offspring (c and d) between 1993 and 2019. Triangles in Panels (a) and (b) denote period of high uncertainty, as only nests that had visibly hatched were excavated prior to 1997; thus, analyses of emergent offspring were performed from 1997. Coloured lines denote generalised least squares model predictions and associated 95% confidence intervals.

Our matrix model scenarios suggest that the difference in recovery rates between sea turtle species in North Cyprus is driven by variation in mortality rates of all age classes rather than reproductive output (Scenarios 5 and 7–15 vs. 16–19). Survival estimates for loggerhead turtles are consistently lower than for green turtles globally (e.g. adult survival, see Omeyer *et al.*, 2019b; Pfäller *et al.*, 2019), likely due to differences in movement patterns and interactions with fisheries. These matrix scenarios reiterate that population trends in sea turtles are heavily driven by juvenile survival (Crouse, Crowder, and Caswell, 1987; Crowder *et al.*, 1994; Mazaris, Fiksen, and Matsinos, 2005; see also Casale and Heppell, 2016). The absence of clear signs of recovery for loggerhead turtles at the individual-based monitoring site, despite stable reproductive parameters, suggests mortality could be hindering the recovery of this population. This is substantiated by the far greater increase in nest counts for green turtles compared to loggerhead turtles when considering the broader scale beach datasets.

Previous modelling of loggerhead turtles in the South-eastern United States found the ‘proportional sensitivity’, or potential to alleviate population decline through increased survival of each particular life stage, to be ‘unresponsive’ for eggs (Crouse, Crowder, and Caswell, 1987; Crowder *et al.*, 1994). High predation levels in the Mediterranean necessitate active clutch protection (Casale *et al.*, 2018) and contrary to results from the United States (Crouse, Crowder, and Caswell, 1987; Crowder *et al.*, 1994), our matrix models indicate a clear effect on population growth rates when further increasing nest success through relocation away from the shoreline for this species (loggerhead turtles only; see also Mazaris, Fiksen, and Matsinos, 2005). While a less powerful driver of growth than increasing benthic juvenile survival by 5%, for example (with around one third of the effect on population growth, Scenarios 5, 8, 10 and 11), this could be seen as an emergency, immediately attainable measure to ameliorate the unavoidable delay in effecting the more complicated task of protecting juveniles and adults in benthic

and pelagic habitats. However, we re-emphasise the conclusion that increased egg survival should not be seen as a substitute for protection of juveniles and adults at sea (Crouse, Crowder, and Caswell, 1987; Crowder *et al.*, 1994). Additionally, green turtle nest success was reduced in relocated nests compared to natural nests. In contrast, loggerhead nest success benefitted from relocation (Table S3). This likely reflects a lower tendency to lay very close to the shoreline due to the larger size and deeper digging habits of green turtles compared to loggerheads at this location (Mediterranean loggerhead turtles are smaller than their global conspecifics). Relocated nests from green turtles are more likely to be from the 'marginal' zone where they may survive inundation and actually benefit from the cooling effects of non-catastrophic washover. These opposing responses to the same conservation management practice from two sympatrically nesting sea turtle species highlight the need for prudent monitoring of hatch success rates and regular review of intervention practices. Nest relocation practices are controversial as they are likely to alter nest temperature and moisture levels, may additionally interfere with natural selection (see Mrosovsky, 2008), and should therefore be viewed as an emergency and temporary measure to safeguard populations at risk of collapse.

The contradicting population growth rates obtained from the two modelling approaches highlight the limitations of population modelling when key parameters and their variations are unknown. Accounting for potential biases in estimates for age at sexual maturity, clutch frequency and survival did not explain the discrepancy between modelled growth rates. The constant survival estimates used for the juvenile age classes in the matrix models are unrealistic, with survival probabilities gradually increasing throughout development with body size, through effects on foraging efficiency (e.g., Marshall *et al.*, 2012), thermal physiology (Spotila *et al.*, 2017) and predation susceptibility (e.g. Salmon and Scholl, 2014), for example. However, age at sexual maturity and survival estimates are scarce for Mediterranean loggerhead and green turtles (Casale *et al.*, 2018), limiting the modelling exercise in the current study. Obtaining population- and size-specific estimates are hindered by the complicated geopolitical context of the region, preventing in-water research in some areas, and artisanal fishing fleets present challenges to establishing onboard observer programmes.

The successful recovery of green turtle populations (e.g., Chaloupka *et al.*, 2008) is thought to be facilitated by their highly localised inshore foraging and nesting grounds, which are more readily and effectively protected than those of species with less predictable habitat use (Broderick *et al.*, 2006). While this distribution makes green turtles relatively easy to protect, it also makes them vulnerable because inadequate protection at major sites can result in population crashes. Loggerhead turtles, in contrast, generally have a complex movement pattern during (Snape *et al.*, 2016, 2018; Tucker, 2010) and outside of the breeding season (Dujon *et al.*, 2018; Haywood *et al.*, 2020a; Snape *et al.*, 2016), which may make them particularly susceptible to anthropogenic activities (Lewison *et al.*, 2014; Wallace *et al.*, 2008).

Additionally, loggerhead turtles recruit to neritic foraging habitats at a larger size than green turtles and continue to transition between pelagic and neritic feeding and among neritic feeding areas as juveniles (Snape *et al.*, 2020).

Incidental capture is highly variable within the Mediterranean (Casale, 2011) and likely impacts nesting aggregations differently based on the genetic origin of individuals within each of the various fishing areas. For example, bycatch (Casale *et al.*, 2010a; Casale, 2011; Nada and Casale, 2011; Turkozan *et al.*, 2018) and intentional killing for meat (Nada and Casale, 2011) result in high sea turtle mortality in the Adriatic Sea, Egypt, the Tunisian Plateau and Turkey: all areas hosting foraging grounds for loggerhead (Bertuccio *et al.*, 2019; Haywood *et al.*, 2020b; Snape *et al.*, 2016) and green turtles nesting in Cyprus (Bradshaw *et al.*, 2017; Stokes *et al.*, 2015) and for other populations and life stages (Casale *et al.*, 2018). North Cyprus itself has high bycatch rates (Casale, 2011; Snape *et al.*, 2016), and it appears that small juvenile green turtles, likely from mixed stocks, are heavily impacted in the local area. Only a few subadults and non-breeding adults of this species are observed in the local small-scale fisheries (Snape *et al.*, 2013) or use foraging sites in Cyprus despite their proximity (Bradshaw *et al.*, 2017; Stokes *et al.*, 2015). Differential bycatch among foraging areas may also explain differential rates of recruitment among foraging areas (Bradshaw *et al.*, 2017).

For many marine vertebrate species, conservation actions have been focussed on terrestrial breeding aggregations where individuals are readily accessible. While this has sufficed for some populations to recover, for others more importance needs to be placed on distant management beyond breeding colonies. Mortality in juvenile life stages has also been shown to have important population-level effects in seabirds (Genovart, Oro, and Tenan, 2018; Sherley *et al.*, 2017). For Mediterranean loggerhead and green turtles, we reiterate the acute need to address anthropogenic mortality rates as a priority to increase survival of post-pelagic individuals (Casale and Heppell, 2016; Casale, 2011; Levy *et al.*, 2015; Snape *et al.*, 2013; Wallace *et al.*, 2008). While increasing reproductive success is undeniably essential for some conservation-dependent species, increasing survival across all age classes, and particularly for juvenile life stages, would have the most profound impact on population growth rates for sea turtles and other long-lived marine vertebrates (Cortés, 2002; Halley, Van Houtan, and Mantua, 2018; Ward-Paige *et al.*, 2012).

Although the increase in green turtle nesting across North Cyprus is encouraging, complacency would be counterproductive. Sustained and more holistic monitoring and conservation efforts, on land and at sea, are required to restore populations to abundances where they can fulfil their ecological roles (Heithaus *et al.*, 2014; Lazar *et al.*, 2011). Many marine vertebrate populations have shown the potential to rebound faster than previously thought (Mazaris *et al.*, 2017; Speed, Cappel, and Meekan, 2018; Valdivia, Wolf, and Suckling, 2018); however, with the exception of Greece (Casale *et al.*, 2018), the recovery of Mediterranean loggerhead turtles is likely to remain compromised until bycatch in the

region is adequately addressed in the long term. Extensive individual-based population monitoring datasets are invaluable in assessing changes in population vital rates and population trends. Nevertheless, additional efforts need to be directed towards a better understanding of the threats faced by juveniles in order to target conservation actions and to accurately parameterise population models necessary for the effective management of many threatened species.

## Author contributions

ACB and BJG conceived the study. LCMO, KLS and RBS led the analysis, with input from ACB and BJG. LCMO led the writing with contributions from all. LCMO, KLS, DB, BAC, SD, WJF, BJG, RTES and ACB contributed to data collection.

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## Data Availability Statement

Data are available from corresponding author upon reasonable request.

## References

- Bates, D., Maechler, M., Bolker, B. & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* **67**, 1–48.
- Bertuccio, V., Costantini, F., Angelini, V., Furi, G., Gobic, K. & Abbiati, M. (2019). Haplotype and biometric patterns in loggerhead turtles from the Adriatic foraging ground. *J. Sea Res.* **147**, 1–9.
- Bolten, A. (1999). Techniques for measuring sea turtles. In *Research and Management Techniques for the Conservation of Sea Turtles*: 110–114. Eckert, S., Bjørndal, K., Abreu-Grobois, F.A. & Donnelly, M. (Eds). Washington, DC: IUCN/SSC Marine Turtle Specific Group Publication 4.
- Bradshaw, P.J., Broderick, A.C., Carreras, C., Inger, R., Fuller, W., Snape, R., Stokes, K.L. & Godley, B.J. (2017). Satellite tracking and stable isotope analysis highlight differential recruitment among foraging areas in green turtles. *Mar. Ecol. Prog. Ser.* **582**, 201–214.
- Broderick, A.C., Frauenstein, R., Glen, F., Hays, G.C., Jackson, A.L., Pelembe, T., Ruxton, G.D. & Godley, B.J. (2006). Are green turtles globally endangered? *Glob. Ecol. Biogeogr.* **15**, 21–26.
- Broderick, A.C., Glen, F., Godley, B.J. & Hays, G.C. (2002). Estimating the number of green and loggerhead turtles nesting annually in the Mediterranean. *Oryx* **36**, 1–9.
- Broderick, A.C., Glen, F., Godley, B.J. & Hays, G.C. (2003). Variation in reproductive output of marine turtles. *J. Exp. Mar. Biol. Ecol.* **288**, 95–109.
- Broderick, A.C. & Godley, B.J. (1996). Population and nesting ecology of the green turtle, *Chelonia mydas*, and the loggerhead turtle, *Caretta caretta*, in northern Cyprus. *Zool. Middle East* **13**, 27–46.
- Broderick, A.C., Godley, B.J. & Hays, G.C. (2001). Trophic status drives interannual variability in nesting numbers of marine turtles. *Proc. R. Soc. B.* **268**, 1481–1487.
- Carreras, C., Monzon-Arguello, C., Lopez-Jurado, L.F., Calabuig, P., Bellido, J.J., Castillo, J.J., Sanchez, P., Medina, P., Tomas, J., Gozalbes, P., Fernandez, G., Marco, A. & Cardona, L. (2014). Origin and dispersal routes of foreign green and Kemp's ridley turtles in Spanish Atlantic and Mediterranean waters. *Amphib. Reptil.* **35**, 73–86.
- Carreras, C., Pascual, M., Cardona, L., Aguilar, A., Margaritoulis, D., Rees, A., Turkozhan, O., Levy, Y., Gasith, A., Auggi, M. & Khalil, M. (2006). The genetic structure of the loggerhead sea turtle (*Caretta caretta*) in the Mediterranean as revealed by nuclear and mitochondrial DNA and its conservation implications. *Conserv. Genet.* **8**, 761–775.
- Casale, P. (2011). Sea turtle by-catch in the Mediterranean. *Fish Fish.* **12**, 299–316.
- Casale, P. (2015). *Caretta caretta* (Mediterranean subpopulation). IUCN Red List Threat. Species 2015 e.T83644804A83646294.
- Casale, P., Affronte, M., Insacco, G., Freggi, D., Vallini, C., Pino D'Astore, P., Basso, R., Paolillo, G., Abbate, G. & Argano, R. (2010a). Sea turtle strandings reveal high anthropogenic mortality in Italian waters. *Aquat. Conserv. Mar. Freshw. Ecosyst.* **20**, 611–620.
- Casale, P., Broderick, A.C., Caminas, J.A., Cardona, L., Carreras, C., Demetropoulos, A., Fuller, W.J., Godley, B.J., Hochscheid, S., Kaska, Y., Lazar, B., Margaritoulis, D., Panagopoulou, A., Rees, A., Tomas, J. & Turkozhan, O. (2018). Mediterranean sea turtles: current knowledge and priorities for conservation and research. *Endanger. Species Res.* **36**, 229–267.
- Casale, P. & Ceriani, S.A. (2020). Sea turtle populations are overestimated worldwide from remigration intervals: correction for bias. *Endanger. Species Res.* **41**, 141–151.
- Casale, P., Freggi, D., Furi, G., Vallini, C., Salvemini, P., Deflorio, M., Totaro, G., Raimondi, S., Fortuna, C. & Godley, B.J. (2015). Annual survival probabilities of juvenile

- loggerhead sea turtles indicate high anthropogenic impact on Mediterranean populations. *Aquat. Conserv.* **25**, 690–700.
- Casale, P. & Heppell, S. (2016). How much sea turtle bycatch is too much? A stationary age distribution model for simulating population abundance and potential biological removal in the Mediterranean. *Endanger. Species Res.* **29**, 239–254.
- Casale, P., Margaritoulis, D., Bradai, N.M., Broderick, A.C., Carreras, C., Demetropoulos, A., Fuller, W.J., Glen, F., Godfrey, M.H., Godley, B.J., Hadjichristophorou, M., Hamza, A., Haxhiu, I., Jony, M., Jribi, I., Kaska, Y., Khalil, M., Kusetogullari, H., Lazar, B., Levy, Y., Misfud, C., Nada, M., Oliver, G., Panagopoulou, A., Rees, A., Saad, A., Tiwari, M., Tomas, J., Türlozan, O. & Ziza, V. (2010b). In *Sea turtles in the Mediterranean: distribution, threats and conservation priorities*: 1–294. Casale, P. & Margaritoulis, D. (Eds). Gland: IUCN/SSC Marine Turtle Specialist Group.
- Casale, P. & Tucker, A.D. (2017). *Caretta caretta* (amended version of 2015 assessment). IUCN Red List Threat Species 2017 e.T3897A119333622.
- Chaloupka, M., Bjørndal, K.A., Balazs, G.H., Bolten, A.B., Ehrhart, L.M., Limpus, C.J., Suganuma, H., Troëng, S. & Yamaguchi, M. (2008). Encouraging outlook for recovery of a once severely exploited marine megaherbivore. *Glob. Ecol. Biogeogr.* **17**, 297–304.
- Cortés, E. (2002). Incorporating uncertainty into demographic modeling: Application to shark populations and their conservation. *Conserv. Biol.* **16**, 1048–1062.
- Crouse, D.T., Crowder, L.B. & Caswell, H.A.L. (1987). A stage-based population model for loggerhead sea turtles and implications for conservation. *Ecology* **68**, 1412–1423.
- Crowder, L.B., Crouse, D.T., Heppell, S.S. & Martin, T. (1994). Predicting the impact of turtle excluder devices on loggerhead sea turtle populations. *Ecol. Appl.* **4**, 437–445.
- D'Eon-Eggertson, F., Dulvy, N.K. & Peterman, R.M. (2015). Reliable identification of declining populations in an uncertain world. *Conserv. Lett.* **8**, 86–96.
- Demetropoulos, A. & Hadjichristophorou, M. (1989). Sea turtle conservation in Cyprus. *Mar. Turt. Newsl.* **44**, 4–6.
- Dujon, A.M., Schofield, G., Lester, R.E., Papafitsoros, K. & Hays, G.C. (2018). Complex movement patterns by foraging loggerhead sea turtles outside the breeding season identified using Argos-linked Fastloc-Global Positioning System. *Mar. Ecol.* **39**, e12489.
- Dulvy, N.K., Fowler, S.L., Musick, J.A., Cavanagh, R.D., Kyne, P.M., Harrison, L.R., Carlson, J.K., Davidson, L.N., Fordham, S.V., Francis, M.P., Pollock, C.M., Simpfendorfer, C.A., Burgess, G.H., Carpenter, K.E., Compagno, L.J., Ebert, D.A., Gibson, C., Heupel, M.R., Livingstone, S.R., Sanciangco, J.C., Stevens, J.D., Valenti, S. & White, W.T. (2014). Extinction risk and conservation of the world's sharks and rays. *Elife* **3**, 1–34.
- Esteban, N., Mortimer, J.A. & Hays, G.C. (2017). How numbers of nesting sea turtles can be overestimated by nearly a factor of two. *Proc. R. Soc. B Biol. Sci.* **284**, 20162581.
- Fuller, W.J., Godley, B.J., Hodgson, D.J., Reece, S.E., Witt, M.J. & Broderick, A.C. (2013). Importance of spatio-temporal data for predicting the effects of climate change on marine turtle sex ratios. *Mar. Ecol. Prog. Ser.* **488**, 267–274.
- Genovart, M., Oro, D. & Tenan, S. (2018). Immature survival, fertility, and density dependence drive global population dynamics in a long-lived species. *Ecology* **99**, 2823–2832.
- Godley, B.J., Broderick, A.C. & Moraghan, S. (1999). Short-term effectiveness of passive integrated transponder tags used in the study of Mediterranean marine turtles. *Chelonian Conserv. Biol.* **3**, 477–479.
- Halley, J.M., Van Houtan, K.S. & Mantua, N. (2018). How survival curves affect populations' vulnerability to climate change. *PLoS One* **13**, e0203124.
- Hamann, M., Godfrey, M.H., Seminoff, J.A., Arthur, K., Barata, P.C.R., Bjørndal, K.A., Bolten, A.B., Broderick, A.C., Campbell, L.M., Carreras, C., Casale, P., Chaloupka, M.Y., Chan, S.K.F., Coyne, M.S., Crowder, L.B., Diez, C.E., Dutton, P.H., Epperly, S.P., FitzSimmons, N.N., Formia, A., Girondot, M., Hays, G.C., Cheng, J.J., Kaska, Y., Lewison, R.L., Mortimer, J.A., Nichols, W.J., Reina, R.D., Shanker, K., Spotila, J.R., Tomas, J., Wallace, B.P., Work, T.M., Zbinden, J.A. & Godley, B.J. (2010). Global research priorities for sea turtles: informing management and conservation in the 21st century. *Endanger. Species Res.* **11**, 245–269.
- Haywood, J.C., Fuller, W.J., Godley, B.J., Margaritoulis, D., Shutler, J.D., Snape, R.T.E., Widdicombe, S., Zbinden, J.A. & Broderick, A.C. (2020a). Spatial ecology of loggerhead turtles: Insights from stable isotope markers and satellite telemetry. *Divers. Distrib.* **26**, 368–381.
- Haywood, J.C., Casale, P., Freggi, D., Fuller, W.J., Godley, B.J., Lazar, B., Margaritoulis, D., Rees, A.F., Shutler, J.D., Snape, R.T.E., Swain-Diaz, N.R., Widdicombe, S. & Broderick, A.C. (2020b). Foraging ecology of Mediterranean juvenile loggerhead turtles: insights from C and N stable isotope ratios. *Mar. Biol.* **167**, 1–15.
- Heithaus, M.R., Alcoverro, T., Arthur, R., Burkholder, D.A., Coates, K.A., Christianen, M.J.A., Kelkar, N., Manuel, S.A., Wirsing, A.J., Kenworthy, W.J. & Fourqurean, J.W. (2014). Seagrasses in the age of sea turtle conservation and shark overfishing. *Front. Mar. Sci.* **1**, 1–6.
- Heppell, S.S. (1998). Application of life-history theory and population model analysis to turtle conservation. *Copeia* **1998**, 367–375.
- Heppell, S.S., Snover, M.L. & Crowder, L.B. (2003). Sea turtle population ecology. In *Biology of Sea Turtles*, Vol. II: 275–306. Lutz, P.L., Musick, J.A. & Wyneken, J. (Eds). Boca Raton, FL: CRC Press, Inc.
- Hutchings, J.A., Myers, R.A., García, V.B., Lucifora, L.O. & Kuparinen, A. (2012). Life-history correlates of extinction risk and recovery potential. *Ecol. Appl.* **22**, 1061–1067.

- Kellner, K. (2018). jagsUI: a wrapper around 'rjags' to streamline "JAGS" analyses. *R Packag. 1.5*.
- Kittinger, J.N., Houtan, K.S.V., Mcclenachan, L.E. & Lawrence, A.L. (2013). Using historical data to assess the biogeography of population recovery. *Ecography (Cop.)* **36**, 868–872.
- Lascelles, B., Notarbartolo Di Sciara, G., Agardy, T., Cuttelod, A., Eckert, S., Glowka, L., Hoyt, E., Llewellyn, F., Louzao, M., Ridoux, V. & Tetley, M.J. (2014). Migratory marine species: Their status, threats and conservation management needs. *Aquat. Conserv. Mar. Freshw. Ecosyst.* **24**, 111–127.
- Lazar, B., Gracan, R., Katic, J., Zavodnik, D., Jaklin, A. & Tvrtkovic, N. (2011). Loggerhead sea turtles (*Caretta caretta*) as bioturbators in neritic habitats: an insight through the analysis of benthic molluscs in the diet. *Mar. Ecol.* **32**, 65–74.
- Levy, Y., Frid, O., Weinberger, A., Sade, R., Adam, Y., Kandanyan, U., Berkun, V., Perry, N., Edelist, D., Goren, M., Bat-Sheva Rothman, S., Stern, N., Tchernov, D. & Gil, R. (2015). A small fishery with a high impact on sea turtle populations in the eastern Mediterranean. *Zool. Middle East* **61**, 300–317.
- Lewison, R.L., Crowder, L.B., Read, A.J. & Freeman, S.A. (2004). Understanding impacts of fisheries bycatch on marine megafauna. *Trends Ecol. Evol.* **19**, 598–604.
- Lewison, R.L., Crowder, L.B., Wallace, B.P., Moore, J.E., Cox, T., Zydelski, R., McDonald, S., DiMatteo, A., Dunn, D.C., Kot, C.Y., Bjorkland, R., Kelez, S., Soykan, C., Stewart, K.R., Sims, M., Boustany, A., Read, A.J., Halpin, P., Nichols, W.J. & Safina, C. (2014). Global patterns of marine mammal, seabird, and sea turtle bycatch reveal tax-specific and cumulative megafauna hotspots. *Proc. Natl. Acad. Sci.* **111**, 5271–5276.
- Limpus, C.J., Baker, V. & Miller, J.D. (1979). Movement induced mortality of loggerhead eggs. *Herpetologica* **35**, 335–338.
- Lotze, H.K., Coll, M., Magera, A.M., Ward-Paige, C. & Airoldi, L. (2011). Recovery of marine animal populations and ecosystems. *Trends Ecol. Evol.* **26**, 595–605.
- Magera, A.M., Mills Flemming, J.E., Kaschner, K., Christensen, L.B. & Lotze, H.K. (2013). Recovery trends in marine mammal populations. *PLoS One* **8**, e77908.
- Marshall, C.D., Guzman, A., Narazaki, T., Sato, K., Kane, E.A. & Sterba-Boatwright, B.D. (2012). The ontogenetic scaling of bite force and head size in loggerhead sea turtles (*Caretta caretta*): Implications for durophagy in neritic, benthic habitats. *J. Exp. Biol.* **215**, 4166–4174.
- Mazaris, A.D., Fiksen, Ø. & Matsinos, Y.G. (2005). Using an individual-based model for assessment of sea turtle population viability. *Popul. Ecol.* **47**, 179–191.
- Mazaris, A.D., Schofield, G., Gkazinou, C., Almpnidou, V. & Hays, G.C. (2017). Global sea turtle conservation successes. *Sci. Adv.* **3**, e1600730.
- McCauley, D.J., Pinsky, M.L., Palumbi, S.R., Estes, J.A., Joyce, F.H. & Warner, R.R. (2015). Marine defaunation: Animal loss in the global ocean. *Science (80-)* **347**, 1255641.
- McClenachan, L., Jackson, J.B.C. & Newman, M.J.H. (2006). Conservation implications of historic sea turtle nesting beach loss. *Front. Ecol. Environ.* **4**, 290–296.
- Mrosovsky, N. (2008). Against oversimplifying the issues on relocating turtle eggs. *Environ. Manage.* **41**, 465–467.
- Nada, M. & Casale, P. (2011). Sea turtle bycatch and consumption in Egypt threatens Mediterranean turtle populations. *Oryx* **45**, 143–149.
- Omyer, L.C.M., Casale, P., Fuller, W.J., Godley, B.J., Holmes, K.E.K.E., Snape, R.T.E. & Broderick, A.C. (2019a). The importance of passive integrated transponder (PIT) tags for measuring life-history traits of sea turtles. *Biol. Conserv.* **240**, 108248.
- Omyer, L.C.M., Fuller, W.J., Godley, B.J., Snape, R.T.E. & Broderick, A.C. (2018). Determinate or indeterminate growth? Revisiting the growth strategy of sea turtles. *Mar. Ecol. Prog. Ser.* **596**, 199–211.
- Omyer, L.C.M., Fuller, W.J., Godley, B.J., Snape, R.T.E. & Broderick, A.C. (2019b). The effect of biologging systems on reproduction, growth and survival of adult sea turtles. *Movement Ecology* **7**, 1–12. <https://doi.org/10.1186/s40462-018-0145-1>
- Pfäller, J.B., Bjørndal, K.A., Chaloupka, M., Williams, K.L., Frick, M.G. & Bolten, A.B. (2013). Accounting for imperfect detection is critical for inferring marine turtle nesting population trends. *PLoS One* **8**, e62326.
- Pfäller, J.B., Williams, K.L., Shamblyn, B.M. & Giron dot, M. (2019). Genetic determination of tag loss dynamics in nesting loggerhead turtles. *Mar. Biol.* 166–197.
- Pinheiro, J., Bates, D., DebRoy, S. & Sarkar, D.; Team, T. R. C (2013). nlme: Linear and Nonlinear Mixed Effects Models. *R Packag.* 186.
- Plummer, M. (2003). JAGS: A Program for Analysis of Bayesian Graphical Models using Gibbs Sampling. *3rd International Workshop on Distributed Statistical Computing (DSC 2003)*; Vienna, Austria 124.
- R Core Team. (2019). *R: A language and environment for statistical computing. R foundation for statistical computing.* Vienna, Austria.
- Rees, A.F., Alfaro-Shigueto, J., Barata, P., Bjørndal, K., Bolten, A., Bourjea, J., Broderick, A., Campbell, L., Cardona, L., Carreras, C., Casale, P., Ceriani, S., Dutton, P., Eguchi, T., Formia, A., Fuentes, M., Fuller, W., Giron dot, M., Godfrey, M., Hamann, M., Hart, K., Hays, G., Hochscheid, S., Kaska, Y., Jensen, M., Mangel, J., Mortimer, J., Naro-Maciel, E., Ng, C., Nichols, W., Phillott, A., Reina, R., Revuelta, O., Schofield, G., Seminoff, J., Shanker, K., Tomás, J., van de Merwe, J., Van Houtan, K., Vander Zanden, H., Wallace, B., Wedemeyer-Strombel, K., Work, T., Godley, B., Van De Merwe, J.P., Van Houtan, K.S., Zanden, H.B., Vander, W.B., Wedemeyer-Strombel, K., Work, T. & Godley, B. (2016). Are we working towards global research priorities for

- management and conservation of sea turtles? *Endanger. Species Res.* **31**, 337–382.
- Rees, A.F., Theodorouand, P. & Margaritoulis, D. (2020). Clutch frequency for loggerhead turtles (*Caretta caretta*) nesting in Kyparissia Bay, Greece. *Herpetol. Conserv. Biol.* **15**, 131–138.
- Richardson, J.I., Hall, D.B., Mason, P.A., Andrews, K.M., Bjorkland, R., Cai, Y. & Bell, R. (2006). Eighteen years of saturation tagging data reveal a significant increase in nesting hawksbill sea turtles (*Eretmochelys imbricata*) on Long Island. *Antigua. Anim. Conserv.* **9**, 302–307.
- Salmon, M. & Scholl, J. (2014). Allometric growth in juvenile marine turtles: Possible role as an antipredator adaptation. *Zoology* **117**, 131–138.
- Seminoff, J.A. (2004). *Chelonia mydas*. *IUCN Red List Threat. Species 2004 e.T4615A11037468*.
- Shamblin, B.M., Dodd, M.G., Griffin, D.B.B., Pate, S.M., Godfrey, M.H., Coyne, M.S., Williams, K.L., Pfaller, J.B., Ondich, B.L., Andrews, K.M., Boettcher, R. & Nairn, C.J. (2017). Improved female abundance and reproductive parameter estimates through subpopulation-scale genetic capture-recapture of loggerhead turtles. *Mar. Biol.* **164**, 1–14.
- Shamblin, B.M., Dodd, M.G., Pate, S.M., Godfrey, M.H., Pfaller, J.B., Williams, K.L., Ondich, B.L., Steen, D.A., Darrow, E.S., Hillbrand, P., Boettcher, R., Coyne, M.S. & Nairn, C.J. (2021). In search of the “missing majority” of nesting loggerhead turtles: improved inter-seasonal recapture rates through subpopulation-scale genetic tagging. *Mar. Biol.* **168**, 1–14.
- Sherley, R.B., Ludynia, K., Dyer, B.M., Lamont, T., Makhado, A.B., Roux, J.P., Scales, K.L., Underhill, L.G. & Votier, S.C. (2017). Metapopulation tracking Juvenile penguins reveals an ecosystem-wide ecological trap. *Curr. Biol.* **27**, 563–568.
- Snape, R.T.E., Beton, D., Broderick, A.C., Çiçek, B.A., Fuller, W.J., Özden, Ö. & Godley, B.J. (2013). Strand monitoring and anthropological surveys provide insight into marine turtle bycatch in small-scale fisheries of the Eastern Mediterranean. *Chelonian Conserv. Biol.* **12**, 44–55.
- Snape, R.T.E., Bradshaw, P.J., Broderick, A.C., Fuller, W.J., Stokes, K.L. & Godley, B.J. (2018). Off-the-shelf GPS technology to inform marine protected areas for marine turtles. *Biol. Conserv.* **227**, 301–309.
- Snape, R.T.E., Broderick, A.C., Cicek, B.A., Fuller, W.J., Glen, F., Stokes, K.L. & Godley, B.J. (2016). Shelf life: neritic habitat use of a turtle population highly threatened by fisheries. *Diver. Distrib.* **22**, 797–807.
- Snape, R.T.E., Schofield, G. & White, M. (2020). Delineating foraging grounds of a loggerhead turtle population through satellite tracking of juveniles. *Aquat. Conserv. Mar. Freshw. Ecosyst.* **30**, 1476–1482.
- Speed, C.W., Cappo, M. & Meekan, M.G. (2018). Evidence for rapid recovery of shark populations within a coral reef marine protected area. *Biol. Conserv.* **220**, 308–319.
- Spotila, J.R., Oconnor, M.P. & Paladino, F.V. (2017). Thermal biology. In *Biology of Sea Turtles*, Vol. I.: 297–314. Boca Raton: CRC Press.
- Stokes, K.L., Broderick, A.C., Canbolat, A.F., Candan, O., Fuller, W.J., Glen, F., Levy, Y., Rees, A.F., Rilov, G., Snape, R.T., Stott, I., Tchernov, D. & Godley, B.J. (2015). Migratory corridors and foraging hotspots: critical habitats identified for Mediterranean green turtles. *Divers. Distrib.* **21**, 665–674.
- Stokes, K.L., Fuller, W.J., Glen, F., Godley, B.J., Hodgson, D.J., Rhodes, K.A., Snape, R.T.E. & Broderick, A.C. (2014). Detecting green shoots of recovery: the importance of long-term individual-based monitoring of marine turtles. *Anim. Conserv.* **17**, 593–602.
- Tomillo, P.S., Saba, V.S., Piedra, R., Paladino, F.V. & Spotila, J.R. (2008). Effects of illegal harvest of eggs on the population decline of leatherback turtles in Las Baulas Marine National Park, Costa Rica. *Conserv. Biol.* **22**, 1216–1224.
- Tucker, A.D. (2010). Nest site fidelity and clutch frequency of loggerhead turtles are better elucidated by satellite telemetry than by nocturnal tagging efforts: Implications for stock estimation. *J. Exp. Mar. Biol. Ecol.* **383**, 48–55.
- Turkozan, O., Yılmaz, C., Uçar, A.H., Carreras, C., Ergene, S., Aymak, C. & Karaman, S. (2018). Local differentiation in the origin of stranded loggerhead turtles, *Caretta caretta*, within an eastern Turkey foraging area. *Ocean Coast. Manage.* **153**, 70–75.
- Valdivia, A., Wolf, S. & Suckling, K. (2018). Marine mammals and sea turtles listed under the U.S. Endangered Species Act are recovering. *PLoS One* **14**, e0210164.
- Van Houtan, K.S. & Kittinger, J.N. (2014). Historical commercial exploitation and the current status of Hawaiian green turtles. *Biol. Conserv.* **170**, 20–27.
- Wallace, B.P., Heppell, S.S., Lewison, R.L., Kelez, S. & Crowder, L.B. (2008). Impacts of fisheries bycatch on loggerhead turtles worldwide inferred from reproductive value analyses. *J. Appl. Ecol.* **45**, 1076–1085.
- Ward-Paige, C.A., Keith, D.M., Worm, B. & Lotze, H.K. (2012). Recovery potential and conservation options for elasmobranchs. *J. Fish Biol.* **80**, 1844–1869.
- Weber, N., Weber, S.B., Godley, B.J., Ellick, J., Witt, M. & Broderick, A.C. (2013). Telemetry as a tool for improving estimates of marine turtle abundance. *Biol. Cons.* **167**, 90–96.
- Wildermann, N.E., Gredzens, C., Avens, L., BarriosGarrido, H.A., Bell, I., Blumenthal, J., Bolten, A.B., McNeill, J.B., Casale, P., Di Domenico, M., Domit, C., Epperly, S.P., Godfrey, M.H., Godley, B.J., González-Carman, V., Hamann, M., Hart, K.M., Ishihara, T., Mansfield, K.L., Metz, T.L., Miller, J.D., Pilcher, N.J., Read, M.A., Sasso, C., Seminoff, J.A., Seney, E.E., Williard, A.S., Tomás, J.,

Vélez-Rubio, G.M., Ware, M., Williams, J.L., Wyneken, J. & Fuentes, M.M.P.B. (2018). Informing research priorities for immature sea turtles through expert elicitation. *Endanger. Species Res.* **37**, 55–76.

Wood, S. (2004). Stable and efficient multiple smoothing parameter estimation for generalized additive models. *J. Am. Stat. Assoc.* **99**, 673–686.

## Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

**Appendix S1.** Materials and Methods.

**Figure S1.** Trend in detection probability and detectability for loggerhead turtles.

**Figure S2.** Female body size for loggerhead turtles.

**Figure S3.** Clutch size for loggerhead turtles.

**Figure S4.** Remigration intervals (RIs) for loggerhead turtles.

**Figure S5.** Loggerhead turtles recorded laying one clutch.

**Figure S6.** Observed and estimated clutch frequencies (OCF and ECF respectively) for loggerhead turtles.

**Figure S7.** Relationship between observed (a) and estimated (b) clutch frequency and RI for loggerhead turtles.

**Figure S8.** Hatchling emergence success for loggerhead turtles.

**Figure S9.** Colour-coded lognormal residuals of observed versus predicted abundance indices (coloured points), and a loess smoother (black line) through all residuals to highlight any systematically auto-correlated residual patterns.

**Table S1.** Summary statistics for GLS model outputs.

**Table S2.** Applying the IUCN Marine Turtle Specialist Group Red List assessment method to obtain trends in female and nest abundance comparing two 3-year time periods.

**Table S3.** Comparison of life-history parameters of loggerhead and green turtles nesting at the intensive individual-based monitoring site, Alagadi Beach.