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Twenty-eight years of decline: nesting population demographics and trajectory of the north-east Queensland endangered hawksbill turtle (*Eretmochelys imbricata*)

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Highlights

- First long-term *Eretmochelys imbricata* nesting data set from northern Great Barrier Reef
- Multiple monitoring indices all point to alarming decline in *Eretmochelys imbricata* nesting density.

ABSTRACT

Globally, hawksbill turtles (*Eretmochelys imbricata*) are listed as Critically Endangered, the cause of which is largely attributed to excessive historical take by the tortoiseshell industry. Yet few long-term data analyses describing population trend or survivorship exist. Here we analyse a long-term dataset for a globally significant western Pacific *E. imbricata* nesting population on Milman Island, northern Great Barrier Reef. Three demographic indicators were used: (1) number of egg clutches laid, (2) nester abundance and survival, and (3) the body-size distribution of nesters (curved carapace length, CCL). Models were developed for a time series from the 1990 - 91 to 2016 -17 nesting season that included 21 years of sampling, with predicted trends evaluated against samples from the 2017-18 nesting season. The number of clutches laid and nester abundance rate of decline varied over the study period, but the decline was markedly similar with a 58 and 57% overall reduction, respectively. Annual survival rate was high (0.972, 95% CI = 0.965 to 0.977), but was not estimated separately for all years. Models predicted that the current rate of decline would lead to nesting extirpation by 2036 (95% CI: 2026-2058) and 2032-2037 (95% CI: from 2020 to increasing), for the models of nester abundance and number of eggs laid, respectively; and aligned with the observed values for the test data set (2017-18 season).

The rate of decline of *E. imbricata* nesting at Milman Island highlights the urgency to understand and mitigate risks faced by this endangered population and more broadly across the western Pacific.

Keywords: Hawksbill turtle, *Eretmochelys imbricata,* population abundance, tortoiseshell, Great Barrier Reef, capture-mark-recapture.

Introduction

Centuries of *Eretmochelys imbricata* take by the tortoiseshell (bekko) industry have resulted in the prohibition of international trade (Appendix I Conventional on International Trade in Endangered Species, CITES), and a global listing as 'Critically Endangered'(Mortimer and Donnelly 2008) . Despite the development of regional and international conservation agreements and legislative protection designed to reduce trade, threats to the viability of *E. imbricata* populations in the western Pacific Ocean remain, including: unrestricted legal and illegal take; incidental catch in active fisheries or discarded ghost nets; and, loss or degradation of nesting and foraging habitat (Humber et al., 2014; Kinch & Burgess, 2009; Lam et al., 2011; Mortimer & Donnelly, 2008; Wallace et al., 2011). Although considered major threats to *E. imbricata* populations throughout the region, the level of take and incidental catch remain uncertain in many western Pacific countries (CITES, 2018; Wallace et al., 2011). In spite of Japan withdrawing its reservation to take *E. imbricata* under Appendix I of the Convention on International Trade in Endangered Species (CITES) (Marine Turtle Newsletter 1994), the continued take of *E. imbricata* for food and tortoiseshell is considered the greatest contemporary threat to *E. imbricata* survival (GBR Marine Park Authority, 2014; Wallace et al., 2011). Several aspects of climate change impacts on foraging ground and nesting habitat viability has been elucidated (Montero et al 2018), nesting success and offspring sex ratios for this nesting cohort remains unknown. Confounded by the current lack of comprehensive genetic stock assignment, stock boundaries and 'management unit' delineation (Fitzsimmons & Limpus, 2014; Vargus et al., 2016), it also remains unclear how these threats affect *E. imbricata* populations at a stock level.

Genotypic mixed-stock-analysis, flipper tagging and satellite telemetry have revealed breeding migrations of *E. imbricata* between north-eastern Australian rookeries and south-western Pacific regions including Vanuatu, New Caledonia, Solomon Islands and Papua New Guinea (PNG) (Bell & Jensen, 2018; Fitzsimmons & Limpus, 2014; Hamilton et al., 2015; Vargus et al., 2016). There are currently two genetically distinct nesting stocks described in this region: 1) Solomon Islands; and, 2) one stock managed as two subpopulations – Arnhem Land, and north-east Queensland, in Australia (Broderick et al., 1994; Vargus et al., 2016).

The south-western Pacific region was highly exploited throughout the nineteenth and twentieth centuries to meet the demand of the tortoiseshell trade (Hamilton et al., 2015; Kinch & Burgess, 2009; Limpus, 2009;;), which was concentrated in the northern Great Barrier Reef (GBR), where *E. imbricata* were once abundant. However, conservation initiatives undertaken at both nesting (Arnavon Islands in the Solomon Islands) and foraging grounds (Howick Group) has resulted in some recovery of this nesting cohort (Bell & Jensen, 2018; Hamilton et al., 2015). Few other robust estimates of population trends for this region exist. Where data exists, nesting density at many other major rookeries lack sufficient data, are approaching extirpation, or continue to decline (Meylan & Donnelly 1999; Mortimer & Donnelly, 2008).

Australian *E. imbricata* are listed as "Vulnerable" (*Environment Protection and Biodiversity*

Conservation Act, 1999) and "Endangered" under Queensland legislation (*Nature Conservation Act, 1992*). *Eretmochelys imbricata* nest in low density on islands in the northern GBR and Torres Strait areas of eastern Australia (Limpus, 1980; Miller et al., 1995). Based on nesting density surveys during the 1980-90s, Milman Island, located in remote far northern GBR, (Figure 1) was identified as supporting a high-density *E. imbricata* nesting population. It was selected as Queensland's primary index nesting beach for monitoring long-term variability of the north-east Queensland stock representative of multiple nesting sites over a large spatial area, and what was once considered to be one of the world's largest *E. imbricata* stocks (Limpus 2009; Limpus & Miller 2008; Loop et al., 1995; Meylan & Donnelly, 1999; Miller et al. 1995). The island and surrounding waters have, since 2004, received the highest level of State and Federal zoning protection, classified as a National Park "Scientific" and "Preservation" zone[s], within the GBR Marine Park.

Here we provide the first comprehensive analysis of a 28-year dataset (1990 - 91 to 2016 - 17 season) to ascertain the north-east Queensland stock population trend. The potential for substantial fluctuations in nester abundance and life-history traits such as age-at-maturity and nesting phenology lhighlights the need for multiple lines of evidence to diagnose trends (Piacenza et al. 2016). We therefore examined changes in demographic parameters of *E. imbricata* at Milman Island using three independent datasets: (1) egg production using nonlinear models (autoregressive generalised additive models, GAM), (2) survival, nester abundance, remigration interval and number of clutches laid per female using multistate open robust design models (MSORD) (Kendall, 2004; Kendall & Nichols, 2002) and (3) the distribution of nester body size. Body-size distribution has been used extensively for exploited populations (Genner et al., 2010; Graham et al., 2005; Hutchings, 2005), as a fitness-related phenotypic trait that can relate directly to population stability (Anderson et al., 2008) and as an early warning signal of population collapse (Carvalho et al., 2018; Clements et al., 2017). Finally, we evaluate the predictive models of nester abundance and egg production against the observed rates for the 2017 - 18 nesting season. Together these approaches provide more robust evidence of nesting turtle population demographics and trajectories, and essential quantitative evidence critical to support future conservation management of the north-east Queensland *E. imbricata* stock before an unviable population may lead to extirpation.

METHODS

Study area and data set

Milman Island (143^0 00’ 57”E, 11^0 10’ 08” S) is an uninhabited, densely-wooded sand cay located approximately 23 km off mainland Australia, in the far northern section of the GBR Marine Park, Queensland (Figure 1). The island is approximately 2.4 km in circumference. An intertidal reef flat (area ~ 560 ha) extends around much of the island, preventing access by nesting turtles at low tide. *Eretmochelys imbricata* nest or attempt to nest on beaches around the entire island, typically on a rising tide after sunset (1930-2300 h) (Loop et al., 1995).

Monitoring teams patrolled the beach after sunset whenever turtles had tidal access to nesting sites. Monitors were trained in data collection, utilized minimal disturbance methods and were routinely scrutinized for competency to ensure data collection consistency.

Turtles were double-tagged on the trailing edge of each front flipper using uniquely numbered titanium tags (Limpus, 1992). Nesting, measurement, laparoscopy and tagging data were collected using standard protocols (as described in Dobbs et al. 1999; Limpus & Miller, 2008) and stored in the Queensland Turtle Research Database.

Eretmochelys imbricata nesting on Milman Island peaks between January and February (Loop et al 1995; Dobbs et al. 1999; Limpus & Miller, 2008). The monitoring period varied among years because of logistical constraints and cyclones (Table S1, online supplement). Over the 28-year period from the 1990 to 2017 nesting season, no data were collected during 2000, 2002 and from 2011 to 2014 (Table S1). For the 22 years where data were collected, the sampling period effort ranged from 12 to 117 nights (average = 43 nights per season), with most surveys being undertaken from January 15 to February 15, in order to cover the peak nesting activity (Figure S1). Data were analysed as "nesting season[s]" (Table S1) because most nesting occurred as a peak over the tropical wet season (December to March) and thereby spanned two calendar years (Figure S1).

Statistical approach

Trends in the number of clutches laid: We modelled the trend in the number of clutches laid using a generalised additive model (GAM) in the 'mgcv' package of R (v 1.8-26, Wood & Wood, 2018). This model predicted the number of clutches laid on a given day as a nonlinear function of nesting year (i.e. the long-term trend) and days within a nesting season (i.e. the seasonal effect). The long-term trend was modelled with a penalised thin plate regression spline and the seasonal effect was modelled with a cyclic cubic spline. The model was fit to all monitoring data from 1990-1991 to 2016-2017 (Table 1), and the predictive performance of the model was evaluated against the 2017 - 18 data.

Initial modelling indicated adequate fit of lognormal and Tweedie error distributions, and we therefore chose the simpler lognormal form, where the response variable was transformed [log(x+1)]. Finally, because of serial autocorrelation in the residuals with a lag of 1 year (Phi = 0.31), the final model included an autoregressive process of order 1 ('corAR1' parameter) and was fitted using the Restricted Maximum Likelihood (REML) approach.

For comparison with earlier studies (Limpus, 2009; Limpus & Miller, 2008), we also used a standardised measure of clutches laid. This represents the nightly average number of clutches laid from January 15 to February 15 (standard period; Dobbs et al., 1999, Limpus & Miller, 2008) (excluding years with $\leq$ 20 nights of sampling, Table 1). The long-term trend in clutches laid was modelled with a weighted GAM where the average clutches laid per standard season was the response variable and year was the explanatory variable. The regression was weighted by the inverse of the number of nights sampled because the sampling effort varied between nesting seasons (Table 1).

Capture mark-recapture (CMR) models: We used the multistate open robust design model (MSORD), which was developed to deal with several hawksbill-specific nesting behaviour (Kendall & Bjorkland, 2001). These included: (1) not all females migrate to the nesting area every year (breeding omission or skipped breeding), (2) females arrive and leave the nesting area in a staggered manner, and (3) females lay multiple clutches and do not nest every night (i.e. they nest at ~ 14-day intervals) (Loop et al., 1995). The two states in this multistate framework are 'nesters' and 'unobservable', where the latter state represents turtles that have skipped nesting and are therefore unobservable at the rookery. Live encounter histories were compiled and analysed for all nesting females captured between November 15 to April 30 of each nesting season. Encounter histories were pooled into 14-day sampling periods within each nesting season, which reflected the ca. 14-day nesting cycle (or internesting interval) known for the Milman rookery (Loop et al., 1995). The primary sampling occasions consisted of 27 annual austral summer nesting seasons from 1990-1991 to 2016-2017, and secondary sampling occasions consisted of 12 successive sampling periods (each 14 days long). Capture histories were therefore comprised of 324 occasions (i.e. 27 primary x 12 secondary samples), coded as ‘1’ if an individual turtle was caught, ‘0’ if it was not caught, or ‘.’ if no sampling occurred for a given secondary sample. Tag loss was assumed to be minimal because turtles were double tagged. Analyses were conducted using the software MARK (v. 9.0, White & Burnham, 1999) through RMark (Laake, 2013) in R (v 3.4, R Development Core Team, 2018).

Goodness of fit and tests of assumptions: There are no established procedures for assessing the goodness-of-fit of MSORD models (Kendall, 2004; Pradel et al., 2005). Instead, we tested the underlying CMR assumptions separately for each of the primary periods under the fully-time varying Cormack-Joly-Seber model implemented in the software U-CARE (v 2.3.2, Choquet et al., 2006; Choquet et al., 2009). We then added the X^2 values of each test and the degrees of freedom for each test to calculate the global goodness-of-fit, and to estimate the variance inflation factor ($\hat{c}$), which is a measure of overdispersion, as the quotient between the sum of the X^2 statistics divided by the sum of the degrees of freedom (following García-Cruz et al., 2015).

Model construction: Model parameters included survival probability (S), temporary emigration probability (Ψ), entry/arrival probability ($pent$), departure probability (Φ) and capture probability (p). The complexity of MSORD models meant that it was not feasible to fit all 12,936 combinations of the parameter specifications that we considered. Instead, we tested different parameter structures one-by-one and retained those that reduced Akaike Information Criterion (AIC) by more than 2 points, or in the case of overdispersion, quasi AIC (QAIC) (Burnham & Anderson, 2002; García-Cruz et al., 2015). This was undertaken for each of the five parameters (Ψ, $pent$, Φ, p and S); the other four parameters were set to be time-invariant. We then constructed the final model using the parameter specifications with the lowest AIC values. Where an examination of parameter estimates and/or parameter counting indicated that parameters were not adequately identified (e.g. boundary effects or singularities), we proceeded to the second-ranked parameter specification, or if necessary, by choosing a simpler parameter formulation. In all models, capture probability was fixed to zero for years where sampling did not take place (2000-2001, 2002-2003, 2011-2012, 2012-2013, 2013-2014 and 2014-2015).

Each parameter was allowed to vary (a) between nesting years (primary samples), (b) between 14-day sampling periods (secondary samples) and (c) between strata ('nester' or 'unobservable'). More complex formulations were also considered (Figure 2). Other terms included in the candidate model set were based on specific biological predictions. Firstly, because hawksbill nesting seasons have a quasi-Gaussian shape (Dobbs et al., 1999; Girondot, 2017; Fig. S1), we used a cubic spline to allow *pent* to peak in the middle of the season. Secondly, because the probability of an individual leaving the nesting ground is expected to increase as a function of the number of egg clutches laid, we included a linear function between Φ and time since arrival to the island (following García-Cruz et al., 2015). Finally, because of the high energetic demands of reproduction and migration, nesting in consecutive years is very rare (Kendall et al., 2019). We therefore also set the probability of transitioning from the nester to the unobservable (non-breeding) state ($\Psi^{\text{n to u}}$) to one.

Because analysing long-term trends in *S* was a focus of the study, we tested a number of alternative hypotheses (Table 1), including (1) constant *S*, (2) *S* varied over time, (3) *S* varied between turtles tagged in different nesting seasons and (4) *S* varied with marked cohort and time.

We modelled the long-term trend in nester abundance using a GAM, where the response variable was the number of nesters and the explanatory variable was nesting season. The GAM was weighted by the inverse standard error of the nester abundance estimates. Model predictions were then compared to the observed number of nesters in the 2017-2018 nesting season, and the observed number of nesters adjusted by recapture probability (i.e. tagged females/recapture probability). This latter estimation was based on the formula for the derived estimate (Cooch & White, 2017), and used the average recapture probability for years with same sampling effort as 2017-2018 (2001-2002, 2004-2005, 2009-2010 and 2010-2011).

Nester size and recruitment rates

To characterise changes in CCL frequency distribution over time we used the ‘sm’ library (Bowman & Azzalini, 2018) in R to compare annual kernel density plots with the first nesting season (following García-Cruz et al., 2015). A permutation test was used to compare differences between size distributions (Bowman & Azzalini, 1997). Sample sizes in this analysis ranged from 102 turtles in 1991-1992 to 566 in 1998-1999.

As an indicator of the rate of recruitment into the nesting population, we also analysed available laparoscopy data (1991-1992 to 1997-1998; 1999-2000; 2003-2004 to 2006-2007) to differentiate between turtles breeding for the first time (recruit) and turtles that had nested before (repeat). Data prior to 1999-2000 were taken from Limpus & Miller (2008). The temporal trend in new recruits was analysed by a binomial GAM where the response variable was ‘recruit’ or ‘repeat’ nesters and the explanatory variable was nesting season. The significance of the nesting season effect was estimated by a bootstrapped log-likelihood ratio test (LRT).

RESULTS

Annual trend in the number of egg clutches laid

The number of clutches laid declined significantly over the study period (autoregressive GAM, nesting seasons: estimated degrees of freedom, edf 3.428, $F = 2.47$, $p < 0.01$; seasonal effect: edf = 4.14, $F = 3.43$, $p < 0.01$; Figure 3). The overall adjusted r^2 (0.161) showed considerable variation within and between years, suggesting that factors not included in the analysis affected egg production. Fitted model values were then back transformed and averaged for each year, which indicated that the average number of clutches laid per night declined by 58% from 1990-1991 to the 2016-2017 nesting season. This decline was the steepest from 1990-1991 to 1999-2000 (7.08 clutches·night^{-1} to 4.42 clutches·night^{-1}, or 38%), and from 2010-2011 to when monitoring started again in 2015-2016 (26% decline).

The average number of clutches laid per night in the standard period also declined over the study period (Figure 4, edf = 2.90, $F = 3.54$ $p = 0.04$; adjusted $r^2 = 0.43$) and followed the same trend as the autoregressive GAM described above. This model suggested an overall decline of 50% from the 1990-1991 nesting season to the 2016-2017 nesting season.

MSORD model selection

A total of 2,831 individually-tagged female *E. imbricata* were included in this analysis. Overall the variance inflation factor ($\hat{c} = 1.80$) indicated slight but statistically significant overdispersion (Global $X^2 = 315.2$, df = 175, $p < 0.001$). We therefore used QAIC in model selection and adjusted confidence intervals accordingly (Cooch & White, 2017). The Goodness of Fit tests for each of the 19 nesting seasons (i.e. seasons with > 2 secondary samples) indicated the presence of transient turtles (i.e. turtles not observed again within a nesting season after their first capture) within the 1992-1993, 1995-1996, 1996-1997 and 2005-2006 nesting seasons (TEST.3R, p values from 0.01 to 0.03). Capture heterogeneity ('trap dependence') was evident in 1995-1996, 1997-1998, 1998-1999 and 1999-2000 (TEST2.CT, p values < 0.01). TEST.3M was also significant for 1992-1993 and 1995-1996, whereas TEST.CL was significant only for the 1997-1998 season.

These results point towards the need to consider appropriate models with the arrival and departure probabilities of turtles within a season. The QAIC values of the fitted MSORD models also suggested that the entry (*pent*) and departure (Φ) varied between secondary samples, as expected for species with staggered arrivals to, and departures from rookeries. However, because secondary samples were not taken from the first and last secondary samples in every year, all parameters were not estimable in the fully time-dependent models (see also Figure S1 in supplementary online material). We therefore used the 'time since marking' formulation for Φ and a nonlinear smoother for *pent* (B-spline function of 'days since the start of the nesting season'). These formulations were based on a trade-off of high QAIC rank and parameter estimation 'Time-since-marking' models are often used to account for 'transience' or 'trap dependence' detected by the TEST.3R or TEST2.CT tests (Cooch & White, 2017; Gimenez et al., 2018).

The model with a simple Ψ parameter, where the probability of transitioning from breeder to a non-breeder or non-breeder to breeder was constant had greater weight of evidence (w_i) support than the model that allowed Ψ to vary over time. The model that allowed p to vary between nesting seasons had the highest weight of evidence. However, the QAIC rank 2 model that also included a term allowing p to vary between secondary samples and between nesting seasons (Figure 2) resulted in more reliable estimation of the other parameters. We therefore used this formulation to compare different alternative hypotheses for changes in survival of nesters over the study period.

The model ranked the best by the weight of evidence criteria (Rank 1, Table 1) indicated that *E. imbricata* nester survival varied between nesting seasons and between marked cohorts. Turtles marked with tags earlier in the study tended to have lower survival than cohorts tagged later in the study. However, because of nesting seasons with few or no samples, we were not able to estimate survival over time for every marked cohort. Similarly, the model that allowed survival to vary between nesting seasons (Rank 2, Table 1) was not able to estimate survival in every season because of seasons with few or no samples. Estimates of survival ranged from 0.96 (0.80-0.99) in 1993-1994 to 0.84 (0.72 to 0.92) in 1998-1999.

The third-ranked model assumed constant survival, which was estimated to be 0.972 (SE= 0.003; 95% CI = 0.965 to 0.977). This model also had the highest estimability for the other parameters (Table 1) and was therefore used in the final model, which featured a constant survival parameter, a constant $\Psi^{u\text{ to }n}$ ($\Psi^{n\text{ to }u} = 1$), an additive term for *p* (secondary sample + nesting year) (Figure 3), a polynomial spline for *pent* and a time-since-arrival term for Φ.

Predictions from the final CMR model

Recapture probabilities (‘*p*’) were the highest in 1992-1993 (0.69, Figure 5), with reliable estimates for 19 nesting seasons (i.e. the 1991-1992 and 2015-2016 seasons were excluded because of low sample size). Recapture probability was not estimable for the first secondary sample (1, Nov 15 - 28) because sampling in the first secondary sample only took place in the 1994-1995 and 1997-1998 nesting seasons (Table S1 and Figure S1 in online supplement). Recapture probability for the remaining secondary samples ranged from 0.09 in the last secondary sample (12) to 0.55 in secondary sample 6.

The final model structure for *pent* suggested a staggered, nonlinear trend of arrivals at the nesting area, which was consistent with the time-after-arrival function for Φ that suggested individual turtles left the nesting area after all of their clutches were laid (rather than all at once; Figure 5). Consequently, the modelled residence probability declined over the secondary samples, consistent with the pattern of staggered arrivals, a peak nesting period (Figure 5) and departures once all clutches had been laid.

Overall, the estimated number of nesters declined over the study period with trend for cyclic variation suggesting extrinsic variables influenced nesting migrations (Figure 5d). The number of nesters fluctuated from year to year, but an overall decline from a maximum of 437 (423-452) in 1996-1997 to a minimum of 141 (137 to 147) nesting females in the 2016-2017 nesting season was apparent. A GAM fitted to the nester abundances (weighted by 1/SE) indicated a linear decline across the study period, corresponding to an overall decline of 57% from the 1990-1991 to the 2016-2017 nesting season.

The MSORD model estimated that an average of 5.92 (95% CI= 5.69-6.16) clutches were laid by each female per year, based on the recapture histories of 2,831 turtles over the period from November 15 to April 30 for the 21 years with data. However, we caution that annual estimates are likely to be biased because turtles possibly arrived before sampling commenced and departed after sampling finished (*sensu* Cooch & White, 2017).

Forecasted nesting and nester abundance trends

Each model was then extrapolated to predict the year when less than one turtle nested per year (MSORD model) or less than one nest was laid per year (standard period and GAM models), assuming that the current rate of decline continues unabated. The forecast also assumed that most nesting occurs over the nesting season from November to April.

The standard-period model for the average nightly clutches laid over the standard period (January 15 to February 15) predicted less than one clutch per year by 2032-2033, with the 95% CIs ranging from as early as 2020-2021 to an increase over the forecast period (2017-2018 to 2080-2081) (Figure 6a). However, the predicted average number of clutches laid was close to the observed nightly clutches for the 2017-2018 season (Figure 6a).

The more comprehensive GAM model of nightly clutches laid (autoregressive GAM) predicted less than one clutch per year by 2037-2038, but with wide 95% confidence intervals spanning extirpation in 2024-2025 to an increasing number of clutches laid (Figure 6b). The predicted average number of clutches laid was within the range of the observed nightly clutches for the 2017-2018 season (Figure 6b).

Finally, the GAM fitted to the MSORD nester abundance estimates suggested less than one nester per year by 2036-2037 (95% CI from 2026-2027 to 2058-2059) (Figure 6c). The predicted nester abundance for the 2017-2018 nesting season aligned with the observed number of nesters (Figure 6c). However, when the observed number of nesters in 2017-2018 was adjusted for recapture probability using an ad-hoc Horvitz Thomson estimator (i.e. estimated number of nesters = number of observed females/average capture probability), more turtles were observed than expected in 2017-2018 (Figure 6c).

Nester size (CCL) and recruitment

Significant differences ($p < 0.05$) were found in nester CCL between the first nesting season

(1990-1991) and 1992-1993, 1996-1997, 1998-1999, 2008-2009, 2010-2012, 2016-2017 and 2017-2018 (Figure 7). In all cases, a leftwards shift occurred suggesting that the size of nesters became smaller than 1990-1991. This was particularly pronounced in the latter nesting seasons of the study (>2007-2018), with the exception of 2015-2016 when left skewness was evident but not significant, likely resulting from the relatively small sample size (*n*=110)

Although the proportion of recruit breeders tended to increase from 1990-1991 to 2006-2007 (Supplementary online material, Figure S2), there was considerable variation among years and the overall effect of nesting season was not significant (LRT: 3.412, $p = 0.257$, 1,000 bootstrap replicates). Excluding years with less than 20 samples, the highest proportions of recruit breeders occurred in 2003-2004 and 2005-2006 (21-27% recruit breeders) and the lowest in 1991-1992 (10%) and 1994-1995 (12%).

Discussion

The number of nesting *E. imbricata* on Milman Island has declined by 57% between the 1990-1991 and 2016-2017 nesting seasons, with a corresponding 58% decline in the number of clutches laid. Should this severe decline continue, our models predict nesting extirpation could occur between the 2032-2033 and 2036-2037 seasons, (with 95% CIs from 2020-2021 to increasing). Assuming this nesting cohort and site is representative of the north-east Queensland stock and the larger south-western Pacific population in general, these results are alarming. Particularly so, as Milman Island receives a comparatively high level of protection within the GBR Marine Park in comparison to other critical nesting sites (Commonwealth of Australia, 2017).

Although this is the longest-term dataset available for *E. imbricata* of any genetic stock within the region, limitations on interpreting population trends must be acknowledged. Because of logistical and resource constraints, not all years were monitored, and the sample period timing was inconsistent in some years. We addressed these issues by using statistical models that accounted for varying sampling effort and by making assumptions that certain parameters such as the remigration interval and the timing of arrival and departure did no not vary between nesting seasons over the monitoring period. Importantly, we used three different demographic indicators and tested the predictions of our model against the last year of data. All three indicators uncovered a similar pattern of population decline and the predictions agreed with the 2017 - 2018 data.

Overall, estimated annual survival was high (0.972, 95% CI= 0.965 to 0.977) and comparable to those reported for *E. imbricata* populations at Varanus Island off the Pilbara coast (0.947; Prince & Chalpouka, 2012), and Long Island, Antigua rookery, in the Atlantic Caribbean (0.95; Richardson et al., 1989; Kendall et al., 2019). However, we were not able to model survival for all nesting seasons separately, because some years were not sampled or had low sampling effort. A northern GBR foraging *E. imbricata* population with similarly high survivorship rate (0.92) also showed an overall decline of adult females between 1996 and 2008 (Bell, 2012). Whilst only 15% of this foraging population originated from the north-east Queensland nesting stock (Bell & Jensen, 2018), high survival coupled with adult female decline suggests failed hatching success at nesting beaches, and/or low survival through to maturation.

Comparisons of survival models in this study suggested a cohort by time effect (Table 1) but we did not have the data to fully parameterise the model. One explanation for this may be differential mortality between stock components, i.e. the abundance of nesters from foraging grounds where turtles are subject to high harvest mortality may have declined faster than for nesters from areas with greater protection. Beyond the GBR, other known (and critical) nesting and foraging habitat lies outside of this protection (Commonwealth of Australia, 2017).

Milman Island is afforded the highest level of marine reserve protection within the GBR (with little to no take of nesting turtles or their eggs), and adult females have been shown to have high survivorship probabilities. During the Austral summer, the island produces both male and female *E. imbricata* offspring with hatchling emergence success >85% (Limpus & Miller, 2008). A rapid and ongoing decline in the number of nesting females is therefore likely to be a result of historical and contemporary tortoiseshell take in unprotected foraging areas within the stock's geographical range, possibly leaving an older cohort of 'protected' adult turtles to survive.

This contemporary exploitation of female turtles is reflected by the observed decline in the average size of nesters, which was more pronounced in the latter decade of sampling. A reduction in average body size is characteristic of an exploited population, and can affect the resilience and capacity of populations to recover (Anderson et al., 2008). The smaller sizes and trend of increased proportion of new breeders prior to 2006 (Figure S2) could imply the early stages of population recovery from commercial exploitation. Nevertheless, a substantial increase in recruitment to the nesting population is unlikely given that both nester abundance and the number of clutches laid continued to decline. Other explanations for the reduction in nester body size cannot be ruled out, including maturation at smaller sizes or cohort effects.

Understanding the cause[s] of the population decline and the potential for the stock to recover is difficult without supplementary data from foraging grounds, which is required to achieve a more representative description of the demographic composition. Current understanding of the foraging grounds used by Milman Island nesters is imperfect. A limited number of titanium flipper tags (~30) have been recovered from *E. imbricata* throughout the western Pacific region. A turtle tagged while nesting on Milman Island in 1993-1994 was subsequently found dead near Meruake, Indonesia (Miller et al., 1998). Other tags have been recovered in PNG, Western Gulf of Carpentaria, and in northern GBR/Torres Strait (Limpus & Miller, 2008, Limpus et al., 2013). In 2008, a nester tracked with a satellite-linked tag was found to forage in the Torres Strait region (Cturtle.org/tracking). Although limited, these data suggest the stock's geographical range likely extend[ed] to neighbouring countries of Indonesia and PNG. A better understanding of the location and threats within foraging areas and breeding migration routes is essential for identifying and mitigating the cause[s] of decline at the nesting beach). Further defining the nesting distribution of this genetic stock/management unit to confirm Milman Island's suitability or representativeness as an index site for a larger spatial scale nesting cohort is important. Additional studies are required to understand whether historic and continued exploitation have resulted in genetic change (see Allendorf et al., 2008) within the stock's likely geographical range and the consequences for conservation management.

Our estimate of the number of *E. imbricata* clutches laid per year (5.9 yr^{-1}) was much greater than earlier studies on Milman Island (1990-1995, 2.5 yr^{-1}; Loop et al., 1995) and elsewhere (3.8 clutches laid over a similar period in the Solomon Islands; Hamilton et al., 2015). This is likely to be because we derived this parameter from the MSORD model, which accounted for varying probabilities of recapture, arrival and departure over the nesting season (and hence the fact that not all laying events were observed for every turtle). The number of clutches laid per female is likely to be underestimated from census data unless all turtles are observed for all laying events during the nesting season.

The remigration interval of 6.7 years (95% CIs: 6.3-7.1) estimated from our MSORD model was also considerably longer than the 3.4 years earlier reported (Loop et al. 1995). However, our estimate is likely to have been upward biased by the assumption that the remigration interval was constant. This assumption was necessary because of missed nesting seasons. Another possible explanation for greater remigration intervals could be escalating coral bleaching events in the northern GBR (AIMS, 2017) that are impacting the quality of the foraging ground, which could in turn affect the breeding condition and the onset of vitellogenesis. As *E. imbricata* play an important role in shaping reef structure and dynamics (Leon & Bjorndal, 2002) and aid in reef recovery, both management and conservation efforts should focus on arresting further decline of the Milman Island subpopulation, and more broadly the north-east Queensland stock across south-west Pacific, at all critical nesting and foraging grounds.

Conclusion

Our results provide the longest running CMR demographic study to record a decline in a nesting *E. imbricata* population within the south-west Pacific or greater Asia-Pacific region. Should the long-term decline in *E. imbricata* nesting on Milman Island continue, it could transition from one of the world's largest nesting *E. imbricata* cohorts to an unviable nesting level within 100 years of it first being described. Even though *E. imbricata* breeding populations are likely to consist of multiple rookeries within a region rather than a sole rookery (Broderick et al., 1994), effective conservation is difficult to achieve when individual countries afford different levels of protection to the nesting beaches, migratory routes and feeding grounds. Urgent conservation effort and tangible management action over multi-geopolitical areas is required to mitigate threats causing the continued decline of the north-east Queensland stock. Until threats to the stock are better spatially quantified and defined, interim moratoriums on turtle take should be considered, while ongoing monitoring of the nesting population on Milman Island will be important to determine the effectiveness of conservation actions.

Acknowledgements

We would like to thank Dr Colin Limpus for his foundation work essential to our understanding of the population at Milman Island. We would like to acknowledge the financial and volunteer support from Earthwatch Institute, Japanese Bekko Association, Reef Joint Field Management Program and World Wide Fund for Nature-Australia. This work would also not have been possible without the support of so many people that gave their energy and time unselfishly in undertaking field work at Milman Island. This work was conducted under the Queensland Department of Agriculture Animal Ethics approval number: SA 2015/11/526.

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TABLES AND FIGURES

Table 1: comparison of different models for the survival of hawksbill nesters, based on information theoretic weight of evidence (w_1) and the number of estimated parameters. Other parameters (Ψ, pent, ϕ and p) were specified according to Figure 2. QAIC: quasi-Akaike information criterion.

Model rank	Hypothesis	Formula (refer to Fig 2)	No. of param.	No. param. estimated	QAIC	ΔQAIC	w_i
1	Varies between marked cohorts and nesting seasons	S_{tc}	90	53	23408.74	0.00	0.999
2	Varies between nesting seasons	S_t	67	45	23459.96	51.22	<0.001
3	Constant over time	$S\cdot$	40	38*	23460.24	51.50	<0.001
4	Varies between marked cohorts	S_c	65	47	23484.14	75.39	<0.001
5	Linear relationship between survival and nesting season plus varies between marked cohort	$\text{logit}(S) = \beta_0 + \beta_1 t + c$	90	50	28422.04	5013.29	<0.001
6	Quadratic relationship between survival and nesting season plus varies between marked cohorts	$\text{logit}(S) = \beta_0 + \beta_1 t + \beta_1 t^2 + c$	66	49	28422.55	5013.29	<0.001
7	Quadratic relationship between survival and nesting season	$\text{logit}(S) = \beta_0 + \beta_1 t + \beta_1 t^2$	41	39	28483.75	5075.01	<0.001
8	Linear relationship between survival and nesting season	$\text{logit}(S) = \beta_0 + \beta_1 t$	41	39	28483.76	5075.01	<0.001

* model did not estimate p in 2015-2016 or in the last secondary sample (12). We therefore did not estimate nester abundance for these samples.

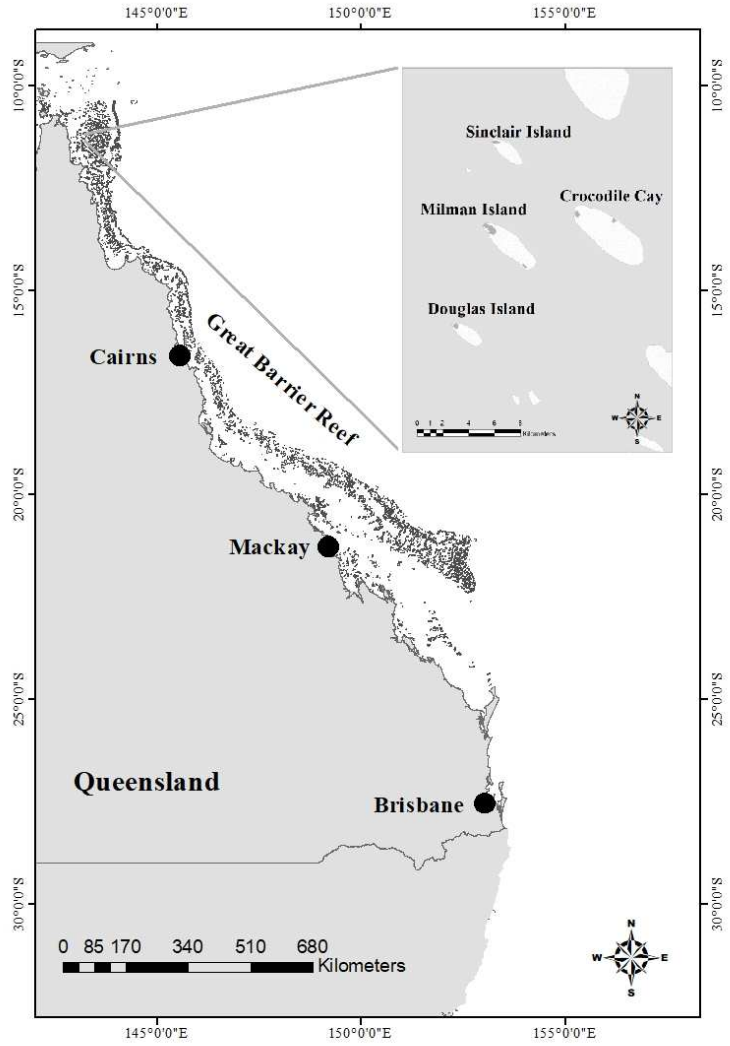

Figure 1. Location of Milman Island, in north east Australia.

Survival	**Temporary migration**	**Entry/arrival Departure**	**Departure**	**Capture probability**
$\begin{Bmatrix} \boldsymbol{S}\cdot \\ S_t \\ S_{tc} \\ S_c \\ S_s \\ S_{t,s} \\ \mathrm{logit}(S) = \beta_0 + \beta_1\, t \\ \mathrm{logit}(S) = \beta_0 + \beta_1\, t + \beta_1\, t^2 \\ \mathrm{logit}(S) = \beta_0 + \beta_1\, t + c \\ \mathrm{logit}(S) = \beta_0 + \beta_1\, t + \beta_1\, t^2 + c \end{Bmatrix} +$	$\begin{Bmatrix} \boldsymbol{\Psi}^{\boldsymbol{n\ to\ u}} = \boldsymbol{\Psi}^{\boldsymbol{u\ to\ n}} \\ \Psi^{n\ to\ u} \neq \Psi^{u\ to\ n} \\ \Psi_{f=1}^{n\ to\ u} = \Psi^{u\ to\ n\ (a)} \\ \Psi_{f=1}^{n\ to\ u} \neq \Psi^{u\ to\ n} \end{Bmatrix} +$	$\begin{Bmatrix} \mathrm{pent}\cdot \\ \mathrm{pent}_t \\ \mathrm{pent}_s \\ \mathrm{pent}_{t,s} \\ \mathrm{mlogit}(\mathrm{pent}) = \beta_0 + \beta_1 ns^{(b)} \\ \mathbf{mlogit}(\mathbf{pent}) = \mathbf{B_0} + \boldsymbol{f}(\boldsymbol{ns})^{(c)} \end{Bmatrix} +$	$\begin{Bmatrix} \Phi\cdot \\ \boldsymbol{\Phi}_{\boldsymbol{arrival}} \\ \Phi_c \\ \Phi_t \\ \Phi_s \\ \Phi_{t,s} \end{Bmatrix} +$	$\begin{Bmatrix} p\cdot \\ p_t \\ p_{t,s} \\ p_{t:s*} \\ p_{s*} \\ p_{effort\ (days)} \\ p_{t,s} \\ p_{s(f=0)} \\ \boldsymbol{P}_{\boldsymbol{t,s(f=0)}} \end{Bmatrix}$

[(a)] where ‘*n to u*’ denotes the transition from nester to unobservable state, ‘*u to n*’ the reverse transition and ‘*f*’ a parameter that was fixed.

[(b)] where ‘*ns*’ is the number of elapsed days in a nesting season (arbitrary coded as since October 1 for each year) and β denotes a coefficient.

[(c)] a polynomial spline function (B-spline basis)

Figure 2: full set of parameters considered in the multistate open robust design (MSORD) mark-recapture analyses. Inclusion of parameters in the final model was based on information theoretic criteria and parameter identifiability. The notation ‘·’ denotes that a given parameter was held constant, the subscript ‘*t*’ denotes a parameter that was allowed to vary between primary sessions (nesting seasons), the subscript ‘*s*’ denotes parameters that varied between secondary sampling periods (i.e. fortnightly periods within a year) and ‘*c*’ represents turtles tagged in a given year (tagging cohort). Grey text indicates over-parameterised models (e.g. singularities or boundary-value estimates).

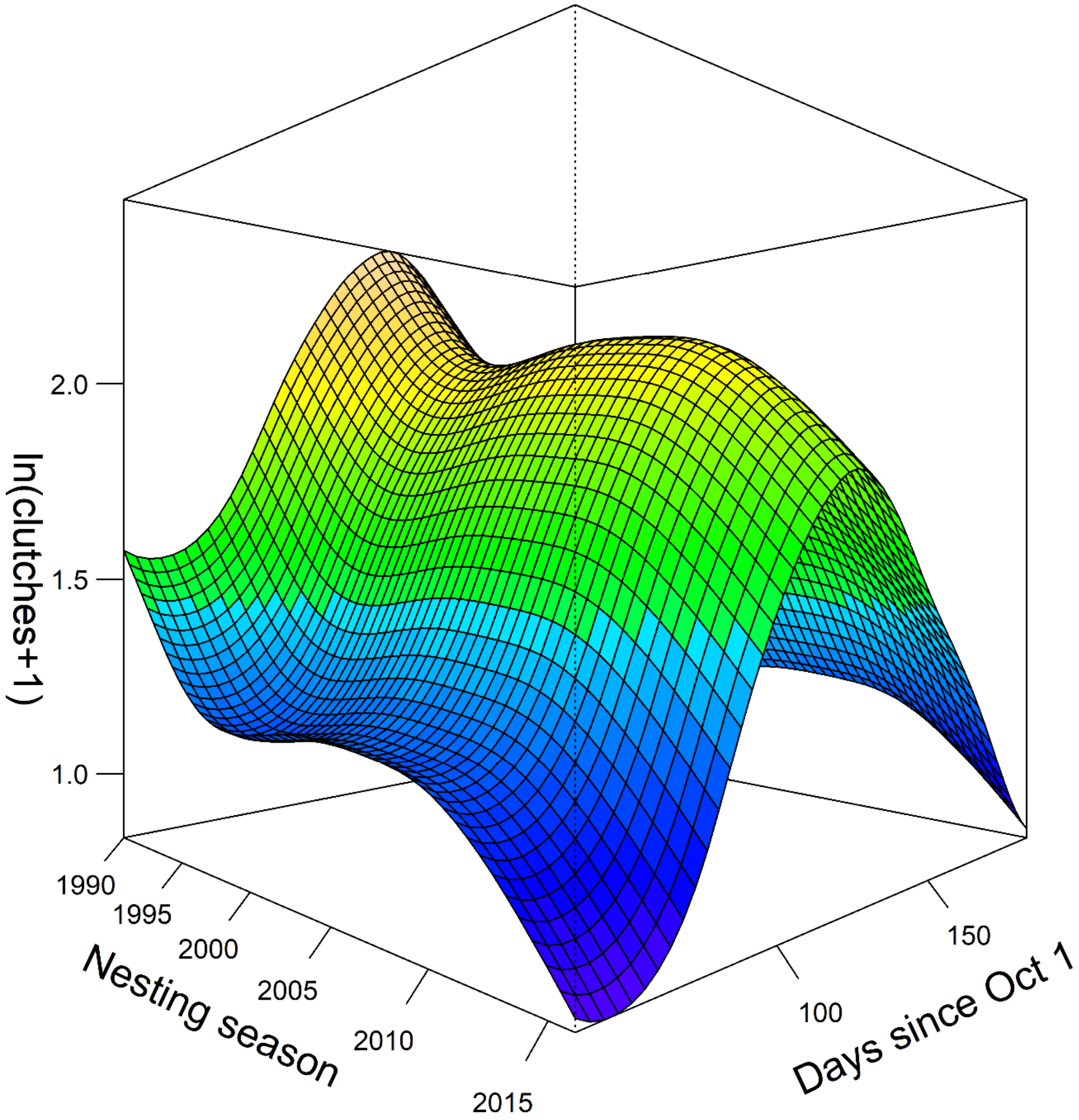

Figure 3: modelled number of clutches laid per night by *E. imbricata* (log transformed) as a function of nesting year (the long-term trend) and the number of days that had elapsed since the start of each nesting season (the seasonal effect, coded as days since October 1).

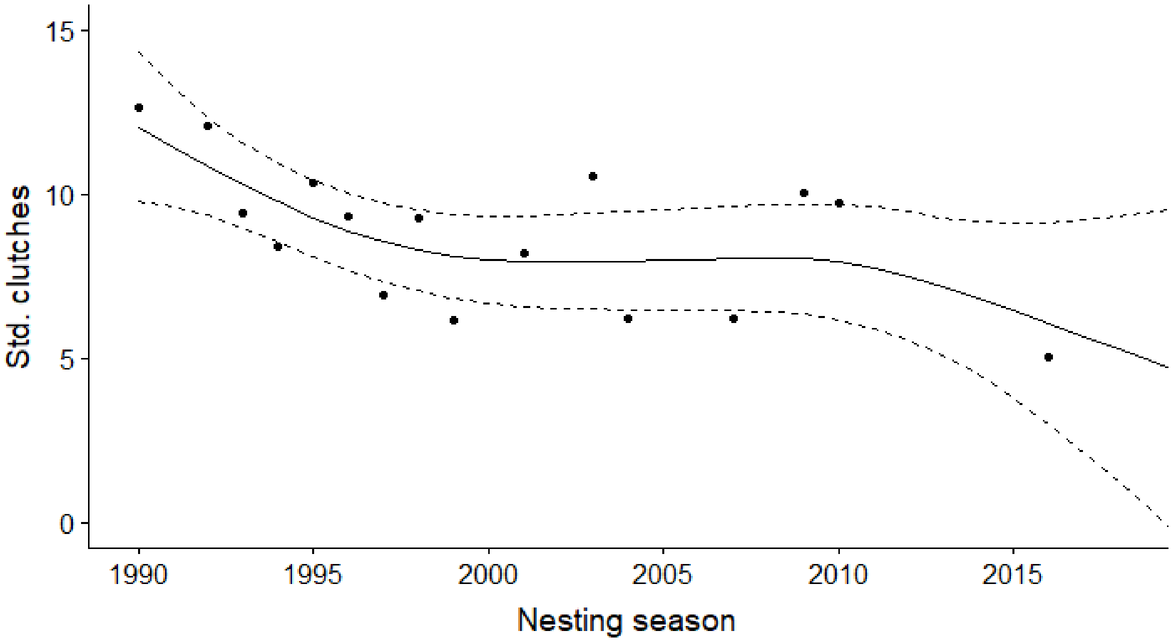

Figure 4: Average number of clutches laid per night (Std.clutches) for a standard period in each year. The solid black line is the fit of a GAM (± 95% confidence intervals), weighted by sampling effort.

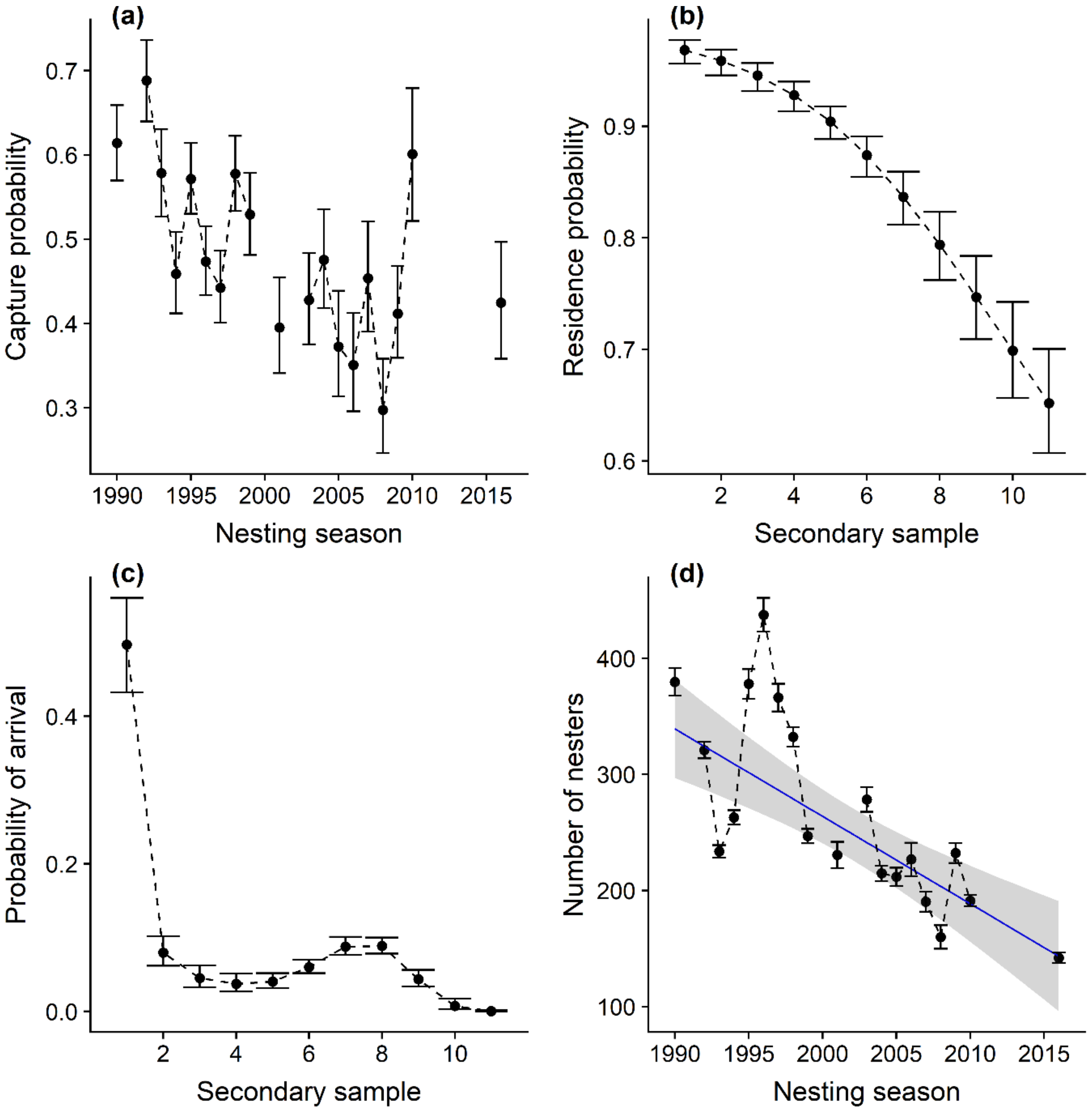

Figure 5: parameters in the final CMR model (±95% confidence intervals): (a) capture probability averaged for each nesting season, (b) probability of residence as a function of secondary sample (fortnightly from November 15), (c) probability of arrival as a function of secondary sample and (d) number of nesters in each nesting season, where the blue trend line represents a GAM (grey region: 95% CIs, weighted by 1/SE). Nesting seasons with no data (2000-2001, 2002-2003, 2011-2012 to 2014-2015) or limited sampling effort (1991-1992 and 2015-2016) were excluded from (a) and (d).

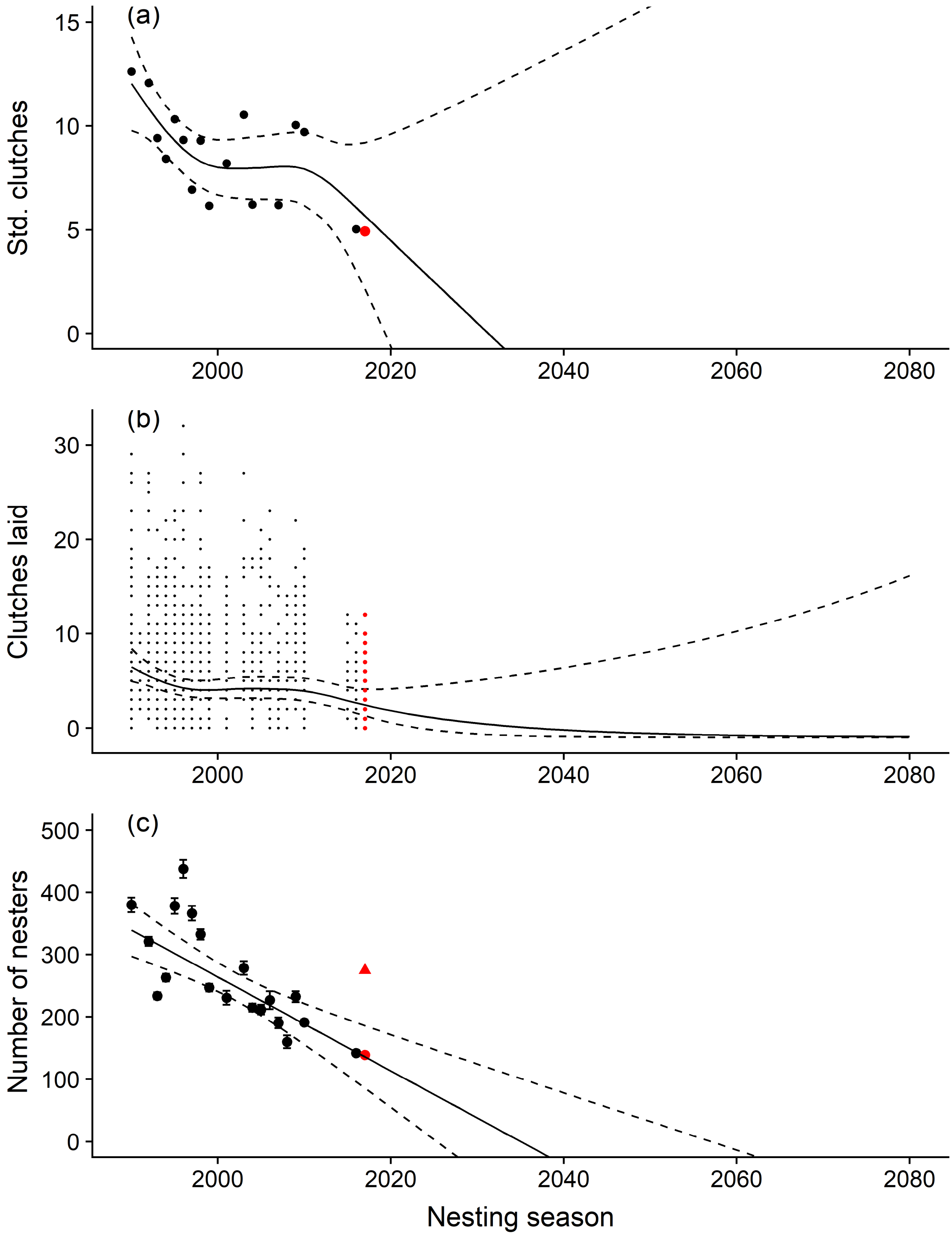

Figure 6: projected trends based on the results of the current analyses (± 95% CI) for (a) average clutches per night for the standard census period between January 15 and February 15 (GAM weighted by sampling effort), (b) clutches per night over the whole period (back

transformed from a lognormal autoregressive GAM (see Figure 3) and (c) MSORD estimates of number of nesters (trend modelled by a GAM). In fig (b) the small circles represent observed clutches per night and the dark larger circles the average clutches per night for each season. In fig (a), an average of 1 clutch per year is predicted by 2032-2032 (95% CI from 2020-2021 to >2080). In fig (b) an average of < 1 clutch per year is predicted by 2037-2038 (95% CI from 2024-2025 to >2080). In fig (c) less than one nester per year is predicted by 2036-2037 (95% CI from 2026-2027 to 2058-2059). Data from the 2017-2018 nesting season are in red, in fig (c) the red circle represents the number of tagged females and the red triangle represents the number of tagged females divided by an estimate of p.

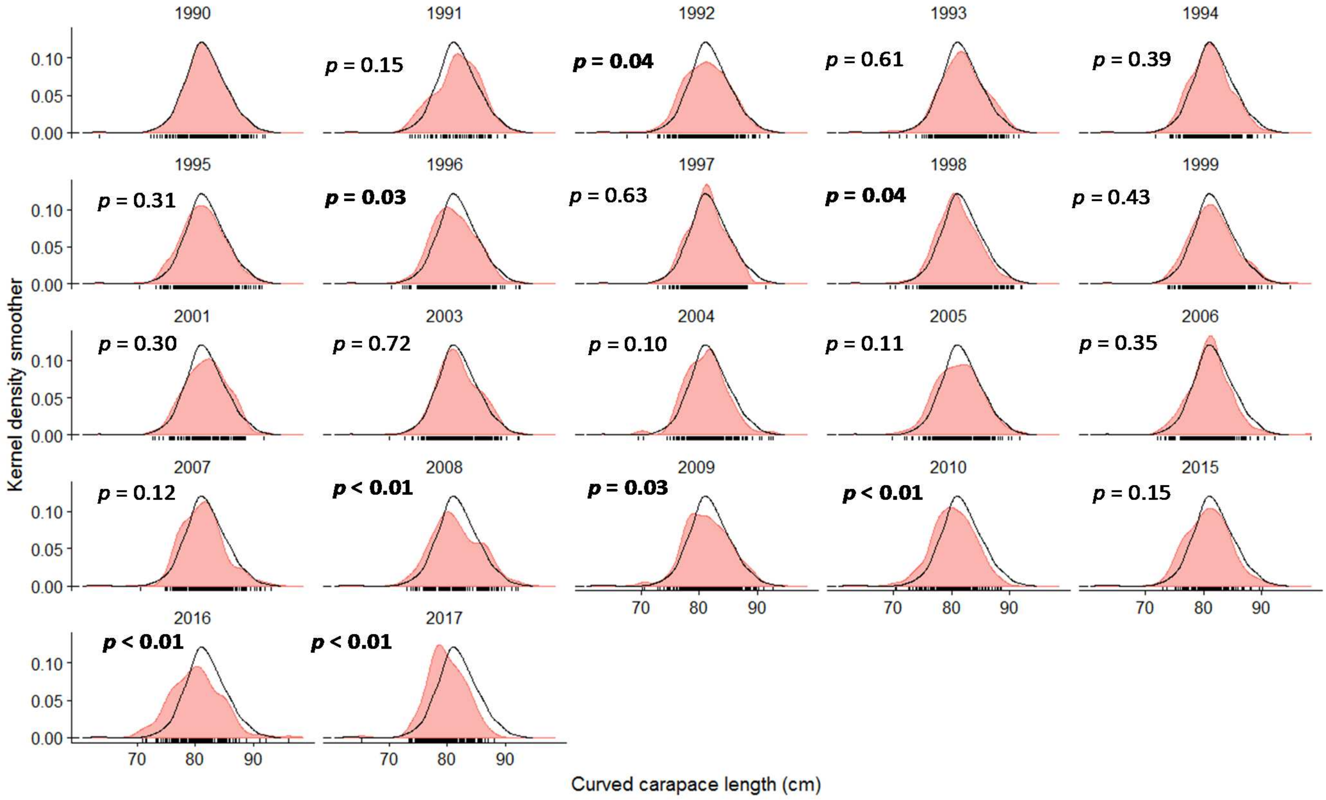

Figure 7: the distribution of nester sizes (CCL, cm) from the 1990-1991 to the 2017-2018 nesting seasons. The first nesting season is used as a reference to compare subsequent nesting seasons. Kernel density estimators were used to smooth the length-frequency histograms, and *p* values represent the significance of permutation tests.

Supplementary Material

Table S1. Surveys dates and sample sizes for Milman Island nesting turtle census, and the models that the data were used in: Std.: standard period model; GAM; MSORD and CCL (nester size distribution). Refer to the methods for more details. [1] included in the MSORD model but annual estimates were excluded because of low sample size.

Season	Sampling period	Finished	No. of nights sampled	Models
1990	11/01/1991	27/03/1991	76	Std, GAM, MSORD, CCL
1991	04/02/1992	18/02/1992	15	GAM, MSORD[1], CCL
1992	15/01/1993	03/04/1993	79	Std, GAM, MSORD, CCL
1993	14/01/1994	22/03/1994	68	Std, GAM, MSORD, CCL
1994	26/11/1994	14/02/1995	81	Std, GAM, MSORD, CCL
1995	19/12/1995	13/04/1996	117	Std, GAM, MSORD, CCL
1996	02/12/1996	28/02/1997	89	Std, GAM, MSORD, CCL
1997	23/11/1997	08/03/1998	106	Std, GAM, MSORD, CCL
1998	20/12/1998	02/03/1999	72	Std, GAM, MSORD, CCL
1999	19/12/1999	03/03/2000	74	Std, GAM, MSORD, CCL
2000	-	-	0	-
2001	13/01/2002	14/02/2002	32	Std, GAM, MSORD, CCL
2002	-	-	0	-
2003	14/01/2004	09/02/2004	26	Std, GAM, MSORD, CCL
2004	23/01/2005	20/02/2005	28	Std, GAM, MSORD, CCL
2005	08/01/2006	29/01/2006	22	GAM, MSORD, CCL
2006	14/01/2007	01/02/2007	18	GAM, MSORD, CCL
2007	08/01/2008	17/02/2008	42	Std, GAM, MSORD, CCL
2008	11/2/2009	01/02/2009	22	GAM, MSORD, CCL

2009	10/01/2010	8/2/2010	30	Std, GAM, MSORD, CCL
2010	19/01/2011	15/02/2011	28	Std, GAM, MSORD, CCL
2011	-	-	0	-
2012	-	-	0	-
2013	-	-	0	-
2014	-	-	0	-
2015	26/01/16	6/2/2016	12	GAM, MSORD[1], CCL
2016	19/01/2017	15/02/2017	28	Std, GAM, MSORD, CCL
2017	15/1/18	15/2/18	31	Used to validate model predictions (Std, GAM, MSORD)

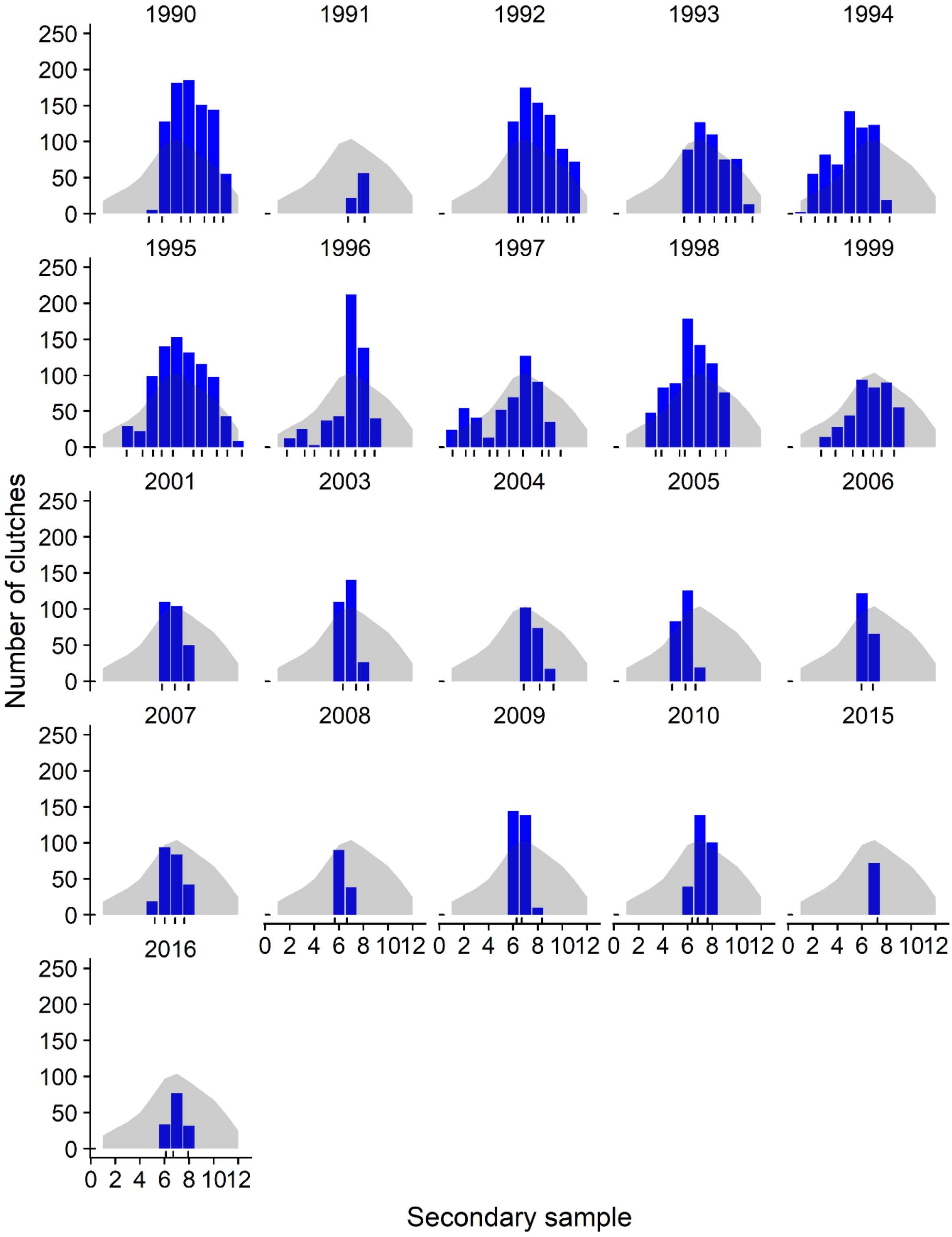

Figure S1: number of clutches laid per nesting year and secondary sample (fortnights from November 15 to April 20 of each year). The grey shaded area represents the overall average (GAM).

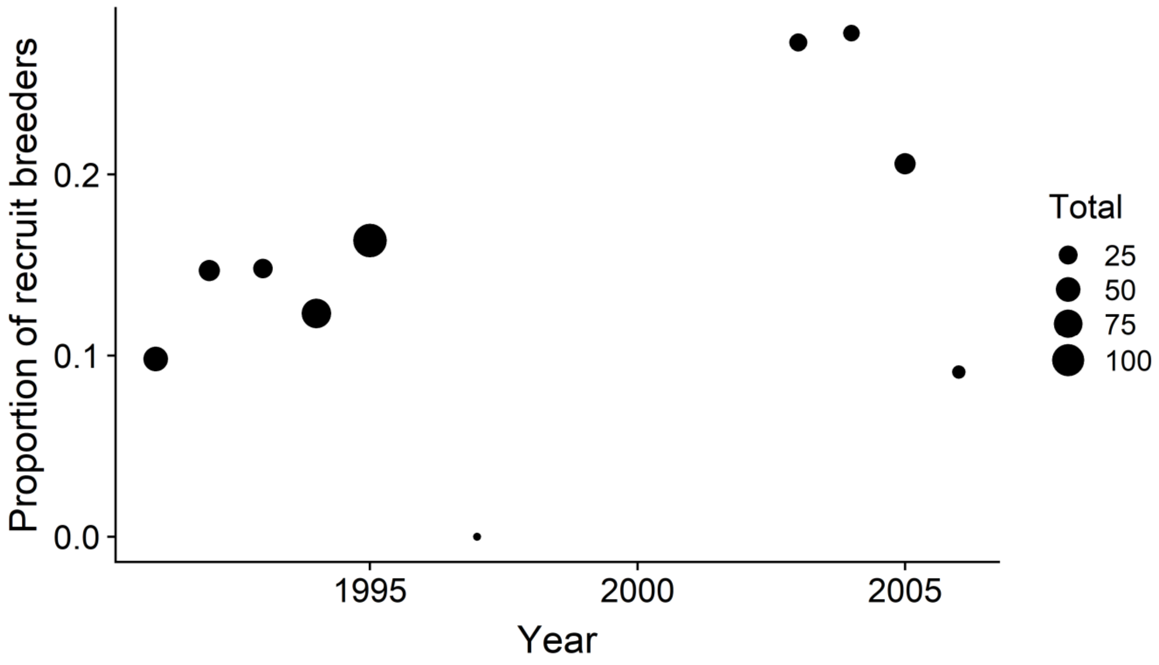

Figure S2: proportion of new recruit hawksbill turtles nesting at Milman Island 1990-2006, where the size of the points is proportional to the total number of turtles that were examined (from 6 turtles in 1997-1998 to 110 turtles in 1995-1996).