Detecting green shoots of recovery - the importance of long-term individual based monitoring of marine turtles

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Abstract

Population monitoring is an essential part of evaluating the effectiveness of management interventions for conservation. Coastal breeding aggregations of marine vertebrate species that come ashore to pup or nest provide an opportunistic window of observation into otherwise widely dispersed populations. Green turtle (*Chelonia mydas*) nesting on the north and west coasts of northern Cyprus has been monitored consistently and exhaustively since 1993, with an intensive saturation tagging programme running at one key site for the same duration. This historically depleted nesting population is showing signs of recovery, possibly in response to nest protection approaching two decades, with increasing nest numbers and rising levels of recruitment. Strong correlation between year to year magnitude of nesting and the proportion of new breeders in the nesting cohort implies that recruitment of new individuals to the breeding population is an important driver of this recovery trend. Recent changes in fishing activities may be impacting the local juvenile neritic stage, however, which may hinder this potential recovery. Individuals returning to breed after two years laid fewer clutches than those returning after three or four years, demonstrating a trade-off between remigration interval and breeding output. Average clutch frequencies have remained stable around a median of three clutches a year per female despite the demographic shift towards new nesters, which typically lay fewer clutches in their first season. We show that where local fecundity has been adequately assessed, the use of average clutch frequencies can be a reliable method for deriving nester abundance from nest counts. Index sites where individual based monitoring is possible will be important in monitoring long-term climate driven changes in reproductive rates.

Keywords: population monitoring, clutch frequency, neophyte, remigration interval, green turtle, trade-off

Introduction

Population monitoring is integral to conservation biology (Goldsmith 1991), and forms an essential part of evaluating the effectiveness of active conservation management (Nichols & Williams 2006). Present-day conservation monitoring must not only endeavour to detect changes in population status, but also climate change driven alterations to reproductive rates, developmental biology (Milligan et al. 2009) and spatio-temporal displacements (Parmesan & Yohe 2003). For many marine, nocturnal or otherwise cryptic species, detection poses additional challenges, and direct monitoring may be difficult, impractical or impossible. Various indirect survey methods are used as indices of abundance, such as redd (nest) counts for salmonids (eg. Rieman & Myers 1997), egg-mass counts for pond breeding amphibians (eg. Raithel et al. 2011), acoustic monitoring for loquacious species (eg. anurans, Crouch & Paton 2002; whales, Simard et al. 2010), and camera trapping, live trapping, hair detection and road casualty data for terrestrial mammals (eg. George et al. 2011, Swan et al. 2013). For marine vertebrates, breeding aggregations are often monitored as an index of overall population status (eg. whales, Andriolo et al. 2010, Fretwell et al. 2014), and species that come ashore to pup or nest present a logistical opportunity to count individuals with greater accuracy and much reduced cost (e.g. sea lions, Pitcher et al. 2007).

The vast majority of marine turtle monitoring research is based at nesting beaches. The accessibility of females during this narrow window has made nester abundance a common response variable for sea turtle population trend monitoring (Heppell et al. 2003). Population assessments based solely on abundance of nesting females have drawn criticism (Bjorndal et al. 2010) and should ideally be combined with in-water foraging ground surveys, which are expensive and labour-intensive (Seminoff et al. 2003). Large discrepancies exist in levels of available funding, however, and nesting beach studies are often the only feasible approach to implement monitoring over long time frames at low expense (Meylan 1995; Gerrodette & Taylor 1999).

Studies of sea turtle reproductive ecology rely heavily on the practice of tagging individuals to elucidate breeding frequency and fidelity to nesting areas (Balazs 1999). In the past, tag loss has been a major confounding variable, with reports of 78% documented tag loss and upper retention estimates of just six years in early studies (Mortimer & Carr 1987). Tag retention rates have since been enhanced with improved tag design and the introduction of PIT (Passive Integrated Transponder) tags. These developments have increased the accuracy of neophyte/ remigrant classification, reducing uncertainty in the quantification of neophyte turtles and overall nester abundance (McDonald & Dutton 1996).

Most marine turtle populations display obligate skipped breeding behaviour due to the high energy demands of migration and reproduction (Prince & Chaloupka 2012), females laying a variable number of clutches within a breeding season (termed clutch frequency) every few years (the remigration interval). Individuals must attain a threshold body condition before embarking on a breeding migration, and so their remigration interval varies in response to fluctuations in environmental conditions (Solow et al. 2002). The low trophic status of the green turtle (*Chelonia mydas*) makes it particularly susceptible to environmental stochasticity, driving large inter-annual oscillations in numbers of nesting females (Limpus & Nicholls 1988; Broderick et al. 2001). The intrinsic variability characteristic of green turtle nesting makes longevity in monitoring programmes essential for identifying underlying population trends (Broderick et al. 2003; Heppell et al. 2003; Jackson et al. 2008). Individual plasticity and inter-population variation in clutch frequency add further uncertainty when deriving nesting population estimates from nest abundance counts (Van Buskirk & Crowder 1994; Rivalan et al. 2006). Many studies divide nest counts by an average value of clutch frequency to give estimated annual nester abundance or vice versa (e.g. Seminoff 2004; Troeng & Rankin 2005; Beggs et al. 2007). A simplistic model of stochastic nesting behaviour, applied to a loggerhead turtle nest count series with known nester abundance, indicated that this method has the potential to produce biased estimates of population trends (Mazaris et al. 2008). Thus more studies of individually marked populations are needed.

Green turtles in the Mediterranean have a history of severe exploitation (Sella 1995). Contemporary rookeries of modest size remain at a handful of sites in Turkey, Cyprus, Syria and Israel (Kasparek et al. 2001; Broderick et al. 2002; Canbolat 2004; Yalcin-Ozdilek 2007; Rees et al. 2008), with ca. 30% of Mediterranean nesting in Cyprus. Modern threats in the Mediterranean include fisheries bycatch and mass tourism (Casale & Margaritoulis 2010); this population has been highlighted as a conservation priority owing to its 'High Risk-High Threat' status (Wallace et al. 2011).

Since 1993, an extensive monitoring programme has conducted comprehensive surveys of the nesting beaches of the north and west coasts of northern Cyprus, located in the Eastern Mediterranean (for beach locations see Fig. 1). Intensive survey effort has been concentrated at Alagadi, where continual night patrols of this 2 km stretch of beach for the duration of the breeding season have allowed exhaustive tagging. Here, we examine the apparent recovery of the population, and reveal the range of insights that long-term individual based monitoring can provide.

Materials and methods

Daytime monitoring of marine turtle nesting activity was conducted every 1-3 days on beaches with significant nesting on the north and west coasts of northern Cyprus for the duration of the breeding season (end of May to end of September) each year between 1993 and 2013 (less complete monitoring was undertaken in 1992; see Fig. 1 for beach locations). Daytime monitoring involves thorough examination of all nesting activity during the early morning, location of eggs if present, and protection from depredation by stray dogs and foxes using a wide mesh wire screen secured into the sand above the nest (carried out exhaustively since 1994). An intensive night monitoring and tagging programme has been conducted at Alagadi (comprising two coves 1.2 and 0.8 km in length) over the same time period (see Broderick et al. 2002, 2003 for detailed methods). Patrols are undertaken at sufficient frequency to encounter all females nesting at this beach. Internal PIT tags have been administered in addition to external flipper tags to all turtles nesting at this breeding site since 1997.

Neophyte/ remigrant analyses were conducted on a subset of the data from 2000 onwards due to increased accuracy of neophyte classification three years (one full nesting cycle for most females) following the introduction of PIT tagging.

Long intervals between observed nesting events within a nesting season are indicative that a female has laid elsewhere on a nearby beach. Thus, the number of clutches laid per season at Alagadi by each marked individual (observed clutch frequency, OCF) is adjusted where turtles have internesting intervals of 20 days and over to give the expected clutch frequency (ECF; Frazer & Richardson 1985, see also Broderick et al. 2002 for bimodal distribution of internesting interval data). The remigration interval (RI) for remigrant turtles is calculated as the number of years since that individual was last recorded nesting at Alagadi.

Statistical tests and modelling were carried out using R version 2.14.2 (R Development Core Team 2012), and packages “nlme” (Pinheiro et al. 2012) and “lme4” (Bates et al. 2011). Tests of correlation were performed using Spearman’s rank order correlation coefficient. LOESS (locally weighted) regressions were fitted to RI and ECF time series data with degree one (linear) and a span of 0.75. Time series analyses of yearly nest counts were conducted using generalized least squares (GLS) modelling to account for temporal autocorrelation in the data.

Clutch frequencies were regressed against explanatory variables using generalized linear mixed modelling (GLMM), fitted using the Laplace approximation, restricted maximum likelihood estimates (REML) and stepwise model simplification. GLMMs allow statistical analysis of non-normal data with random effects, which quantify the variation across units/ grouping factors of the fixed effect parameters (Bolker et al. 2009). In this case, models had Poisson error structure and logarithmic link function, with zero-truncation. Explanatory variables included categorical fixed effects for neophytes (first time nesters; true or false) and remigration interval (two vs. three or four years), a fixed covariate of body size, and random effects for individual (to avoid pseudoreplication where females have returned to nest in subsequent years) and year (to account for interannual variation in magnitude of nesting arising from environmental stochasticity). GLMM was also used to regress body size against neophyte/ remigrant nesters whilst accounting for pseudoreplication of individuals. The significance of removing model terms was assessed by likelihood ratio tests using maximum likelihood estimates (Crawley 2007), in order of least significance and with a threshold of p=0.05. Model residuals were checked for overdispersion, normality and homoscedasticity.

Results

The annual green turtle nesting abundance for Alagadi and the total across the north and west coasts is shown in Figure 2. The high interannual variation typical of green turtle nesting is evident (combined nesting range: 35-335 nests per season, mean ± standard deviation (SD): 13 ± 77.1), following a two to three year pseudo-cyclical pattern. The coefficient of variation (CV=SD/mean: 0.59) lies within the range previously reported for this species by Broderick et al. (2001; 0.41-1.08). Nesting abundance on the two coasts is significantly correlated ($r_{(19)}$=0.72, p<0.001) showing a synchrony in reproductive cycles across this area. Comparison of nest count models at Alagadi and across the two coasts demonstrated significant autocorrelation at a time lag of one year (GLS, Alagadi: φ=-0.729, $\chi^2_{(1)}$=11.274, p<0.001; overall: φ=-0.449, $\chi^2_{(1)}$=4.224, p=0.04). Having accounted for this autocorrelation, nest counts showed a significant quadratic trajectory through time (Fig. 2; Alagadi linear slope: β=-10.663 ± 2.790; Alagadi quadratic slope: β=0.709 ± 0.135, $\chi^2_{(1)}$=17.471, p<0.0001; overall linear slope: β=-20.878 ± 5.405; overall quadratic slope: β=1.259 ± 4.817, $\chi^2_{(1)}$=14.379, p=0.0001). This indicates that nesting in the region has stabilised and may now be increasing. This trend was also significant for nester abundance at Alagadi (Fig. 3a; autocorrelation at one year: φ=-0.743, $\chi^2_{(1)}$=10.711, p=0.001; linear slope: β=-3.151 ± 0.929; quadratic slope: β=0.231 ± 0.045, $\chi^2_{(1)}$=17.079, p<0.0001). Recruitment (as measured by the proportion of nesters that are neophytes) has followed a similar quadratic trend (linear slope: β=-0.103 ± 0.016; quadratic slope: β=0.005 ± 0.001, $\chi^2_{(1)}$ =22.005, p<0.0001), but with no significant autocorrelation. Record numbers of nests, nesters and neophytes were observed at Alagadi in 2013 (236 nests, 85 nesting females, 57 neophytes). There has been no trend in survey effort, detection probability (imperfect detection of nests or individuals), or detectability (beach fidelity) over the study period (see Supplementary Figure S1 and Pfaller et al. 2013).

We confirmed that the recent trajectory describes a significant increase in nests, nesters and recruitment, by considering the number of nests and nesters post-2000, which corresponds with the local minimum of all our quadratic fitted lines. Since 2001, there has been a significant increase through time in the number of nests across all beaches ($\beta=15.993 \pm 3.063$, $\chi^2_{(1)}=11.938$, $p=0.0006$), the number of nests on Alagadi ($\beta=9.799 \pm 1.605$, $\chi^2_{(1)}=15.516$, $p=0.0001$), the number of nesting females on Alagadi ($\beta=3.493 \pm 0.606$, $\chi^2_{(1)}=14.398$, $p=0.0001$) and rates of recruitment ($\beta=0.029 \pm 0.009$, $\chi^2_{(1)}=8.399$, $p=0.004$).

A comparison of observed and estimated nester abundance is shown in Figure 3a. Here, the known number of females nesting each year at Alagadi is used to test the accuracy of estimates derived using nest counts and average values of clutch frequency. Estimated nester abundance is taken as the quotient of annual nest abundance divided by an average clutch frequency of three (Seminoff 2004; also the overall mean and median clutch frequency from the current study). Estimated nester abundance and actual/ observed nester abundance were highly correlated ($r_{(19)}=0.97$, $p<0.0001$). Conclusions drawn from these abundance series about the population trend at this breeding aggregation would be analogous.

The tagging programme based at Alagadi has revealed a strong correlation between the number of nests and the proportion of neophytes since 2000 ($r_{(12)}=0.94$, $p<0.0001$; Fig. 3b). This strong correlation between the proportion of neophytes in the nesting cohort and the magnitude of nesting implies that recruitment of new individuals into the breeding population is an important driver of year to year nester abundance, an encouraging sign of a population in recovery. The reduced correlation between the number of nesters and the proportion of neophytes seen prior to 2000 provides evidence that the introduction of PIT tagging has had a significant effect on the accuracy of neophyte/ remigrant identification. First time nesters at Alagadi are significantly smaller than remigrant nesters (GLMM, $\chi^2_{(1)}$=84.95, p<0.0001; mean CCL 87.7 ± 6.5 cm for neophytes cf. 92.0 ± 5.9 cm for remigrants), re-affirming their classification as true neophytes. The intensity of survey effort at this site has afforded near perfect attribution of nests to known females (98% since 2000, 93% since comprehensive monitoring began in 1993).

Figure 4a shows RIs observed for the marked green turtle population at Alagadi between 1994 and 2013. The majority of remigrants return after 2, 3 or 4 years [87%; median RI: 3, interquartile (IQ) range: 3-4, n=212]. The low incidence of unusually long RIs most likely reflects individuals with lower site fidelity, who may have nested elsewhere in Cyprus, or further afield, undetected. The majority (78%) of remigrant turtles observed over three or more seasons varied their RI from one breeding season to the next (n=51, see Fig. 4b), exemplifying the high levels of modulated periodicity green turtles show in response to environmental stochasticity. Despite this, the annual average RI has remained relatively stable over the study period (see Fig. 5a), fluctuating mostly between three and four years. Lower RIs at the beginning of the time series are an artefact of time since tagging began; only those remigrants with lower than average remigration interval can be re-encountered within the first three years of monitoring.

Median ECF across all years and nesters was three (IQ range: 1-4, n=485). No long-term trend in median clutch frequency is apparent from the data (see LOESS smoother Fig. 5b). Instead, median ECF is correlated with the number of nesters present in a given season ($r_{(19)}$=0.52, p=0.02), with three of the four lowest nesting seasons having a low average ECF, indicating that females breeding in poor nesting years may be in suboptimal body condition. Median clutch frequency is more variable in the early part of the time series, stabilising as the number of females increases, effectively increasing the sample size and reducing susceptibility to skewed averages. ECF varies between neophytes and remigrants (see Fig. 6a-b), with neophytes most likely to lay a single clutch (40%, n=194), and the majority of remigrants laying three to five clutches (77%, n=212). GLMM showed the effect to be significant, with remigrants laying an average of 0.6 clutches more than neophytes, whilst accounting for individual and year to year variation ($\chi^2_{(1)}$=37.198, p<0.0001). Female body size had a statistically significant but biologically insignificant effect on clutch frequency ($\chi^2_{(1)}$=7.689, p<0.01), with a 10 cm increase in curved carapace length (CCL) increasing ECF by an average of 0.04.

RI was found to have a significant effect on clutch frequency, with short RIs of less than three years reducing ECF by almost a quarter (0.23), once variation across individuals and years was accounted for (GLMM, $\chi^2_{(1)}$=4.009, p<0.01). Body size did not have significant effect to be included in the model. Female nesters returning after a short interval of two years are most likely to lay three clutches (40%, n=48, Fig. 6c), whilst those returning after three or four years are more likely to lay four or five clutches (57%, n=136, Fig. 6d-e).

A total of 273 nesting females have been tagged at Alagadi since 1992. Forty percent of neophytes nesting between 2000 and 2008 (n=55) did not remigrate to this site in subsequent breeding seasons (we do not include 2009-2013 as these neophytes may yet return).

Discussion

Evaluation of indirect survey method reliability is essential for accurate population monitoring. Validated indices are the primary tool for tracking changes in abundance of many cryptic species of conservation concern (eg. carnivore track counts and camera trap surveys, Balme et al. 2009). Long-term individual based monitoring of green turtles at Alagadi, northern Cyprus has provided fundamental and applied insights into sea turtle nesting ecology. Our data suggest that estimation of nesting population size from nest abundance data is reliable, provided that fecundity is adequately monitored at relevant localised index sites to provide the ‘proportionality’ information required to interpret these data (Gerrodette & Taylor 1999). Green turtles nesting at Ascension Island in the South Atlantic are larger in size, migrate further (~2300 km, Luschi et al. 1998) and have a longer period of suitable nesting conditions than those nesting in the Mediterranean, and thus perhaps unsurprisingly have a higher average clutch frequency of around 6 nests per season (Weber et al. 2013) compared to the average of 3 detected in the current study. Clutch frequencies derived through tagging efforts alone where complete survey is not possible or site fidelity is low will be underestimated, leading to inflated population assessments. Studies augmenting capture-mark-recapture methods with the use of tracking (Tucker 2010, Weber et al. 2013) and ultrasonography (Blanco et al. 2012) technologies can improve clutch frequency estimates in such cases. Breeding rates will likely be affected by long-term changes in foraging conditions, highlighting the importance of ongoing monitoring at index sites to ascertain multifaceted responses to climate change.

Saturation tagging at Alagadi has revealed clutch frequencies that are significantly different among groups (eg. neophytes vs. remigrants), but that are temporally stable across groups. Reduced clutch frequency in neophyte turtles as seen here has previously been reported in green turtles (Carr et al. 1978), as well as in leatherback (Tucker & Frazer 1991), loggerhead (Hawkes et al. 2005) and hawksbill turtles (Beggs et al. 2007). It is likely that this phenomenon is caused by both increasing physiological capacity with age, and changes in nesting behaviour such as site fidelity (Carr et al. 1978). Individual green turtles lay increasingly large clutches across (Bjorndal & Carr 1989) and within (Broderick et al. 2003) breeding seasons, indicating an increase in reproductive efficiency or capacity. Low subsequent remigration rates of neophytes tagged at Alagadi (this study) suggests lowered site fidelity in new breeders. Broderick et al. (2002) found that single-clutch neophyte females have a lower probability of remigrating to Alagadi in subsequent years than those with higher clutch frequencies (0.3 cf 0.8). Satellite telemetry of internesting loggerhead turtles in Florida has revealed a higher site fidelity in remigrants compared to new breeders (Tucker 2010). Such 'leaky' female nest site fidelity facilitates genetic mixing of the maternal lineage across nesting sites (Lee et al. 2007), and may promote resilience to loss of breeding sites through behavioural adaptation.

Our finding that females remigrating after three or four years lay extra clutches in comparison to those remigrating after two years supports the notion that suboptimal foraging conditions can be compensated for by building up energy reserves over a longer interval. A similar relationship between remigration interval and likely clutch frequency has been observed in leatherback turtles (Rivalan et al. 2005), and Van Buskirk and Crowder (1994) describe a comparable trade-off in interspecific reproductive effort resource allotment. Many iteroparous species may skip a breeding year if conditions are not favourable (eg. fat dormouse, Pilastro et al. 2003); this may partly be compensated for if a higher reproductive output can be attained in the following breeding season (eg. four-toed salamander, Harris & Ludwig 2004). The implications for population assessment are that short term fluctuations in breeding activity may be misinterpreted unless populations are monitored in the long term (Hays 2000), and that breeding frequency should be monitored at the individual level where possible in order to detect long term change in the scaling factors used for conversion of monitoring indices to population estimates.

The recent upward trend in nest numbers in northern Cyprus may signal the beginning of a recovery phase for this sub-population following the cessation of a heavy harvest and intensive screening of nests against unnaturally elevated predation levels. Recruitment can be viewed as a measure of cohort strength (Heppell et al. 2003), and rising numbers of neophytes as seen in this population are an early indication of population growth (Richardson et al. 2006). Similar nest protection schemes have had measurable success some 20 years later (Garduño-Andrade et al. 1999; Dutton et al. 2005). There is, however, considerable uncertainty surrounding the time it takes for green turtles to reach breeding age; published age at sexual maturity estimates for wild green turtles range from 27 (Frazer & Ladner 1986) to 40 (Limpus & Chaloupka 1997) years. Evidence from living tags, however, has shown that male and female green turtles released from the Cayman Island Turtle Farm (a conservation facility/ tourist attraction/ turtle meat supplier in the Caribbean) as hatchlings can breed at 19 and 17 years respectively (Bell et al. 2005). If this species can indeed reach sexual maturity at less than 20 years, then it is possible that sustained reduction in nest depredation across two decades has aided in the early stages of recovery of this historically depleted breeding aggregation.

Behavioural reproductive mechanisms such as natal philopatry and polyandry contribute to the resilience of sea turtles (Bell et al. 2009), which have shown encouraging recovery potential and rebound capacity in response to long-term protection (Garduño-Andrade et al. 1999; Broderick et al. 2006; Richardson et al. 2006; Marcovaldi & Chaloupka 2007). The complex life cycle of this group, and others involving multiple distinct habitats and delayed sexual maturity, makes adequate protection particularly challenging (Heppell et al. 2003); protective measures on the nesting beach will not be effective if threats at sea are not addressed (Dutton et al. 2005), and the potential for trophic uncoupling of resources and ability to shift ranges under changing climatic conditions are important considerations for such species (Møller et al. 2008; Robinson et al. 2009).

Nest count series should be used in conjunction with data regarding other life stages wherever possible (Bjorndal et al. 2010). Encouragingly, genetic studies at Alagadi have revealed a greater number of males than females in the breeding population (Wright et al. 2012a; Wright et al. 2012b), suggesting that the population increase observed here has occurred across demographic groups. However, a recent assessment of sea turtle bycatch in northern Cyprus (Snape et al. 2013) has found a high incidence of juvenile green turtle mortality. Potential increased fishing effort in the region following changes in trade regulation between northern Cyprus and southern Cyprus (Snape *pers. obs.*) may impede the recovery of this population.

Monitoring projects must be cost-effective in the long-term in order to ensure the longevity of data required to make meaningful estimations of population trends (Schroeder & Murphy 1999). Re-sampling assessments of extant data from comprehensively monitored nesting sites have found that temporal sub-sampling within the breeding season could save up to 50% of monitoring costs with little loss of statistical power (Jackson et al. 2008; Sims et al. 2008, Whiting et al. 2013). The efficacy of these more parsimonious sampling regimens is reliant on consistency in the temporal distribution of the nesting season, however, which has been shown to be variable in accordance with both long- (Weishampel et al. 2004) and short- (Hawkes et al. 2007) term fluctuations in sea surface temperature.

Furthermore, complete sampling of the breeding season yields additional advantages in localities where remedial conservation measures such as nest protection and surveillance of illegal take are beneficial (eg. Bell et al. 2007).

A range of strategies is required to cover the breadth and depth necessary to detect changes in biological parameters and spatio-temporal distributions that are likely to occur in response to climate change. Index sites such as Alagadi, where long-term and consistent individual based monitoring is possible, can offer valuable insights into survival and reproductive rates that other localities can use in converting more basic density indices into population estimates. Long-term datasets are vital in documenting change, but are often difficult to maintain with variable funding stability through time (Hays et al. 2005). Monitoring programmes with a core set of simple, robust and inexpensive measurements may have a greater likelihood of remaining consistent and sustainable in the long-term (Bennun 2001; Lovett et al. 2007).

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Figures

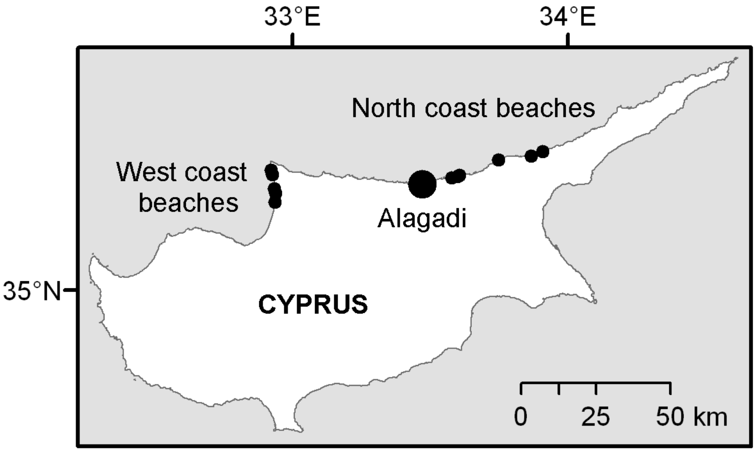


Figure 1. Turtle nesting beaches monitored in the current study.

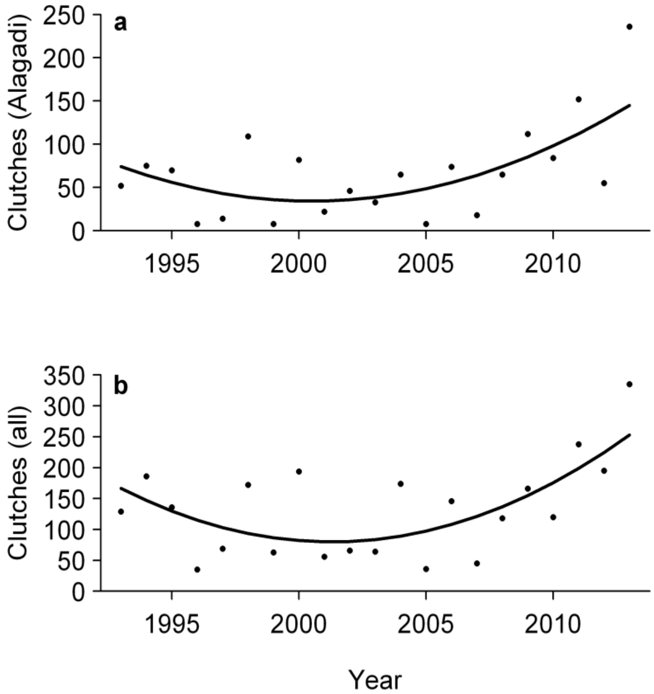


Figure 2. Green turtle clutches on a) Alagadi beach and b) across all monitored sites against time, with quadratic trend lines (solid lines). These data build on the data 1993-2000 presented in Broderick et al. (2002).

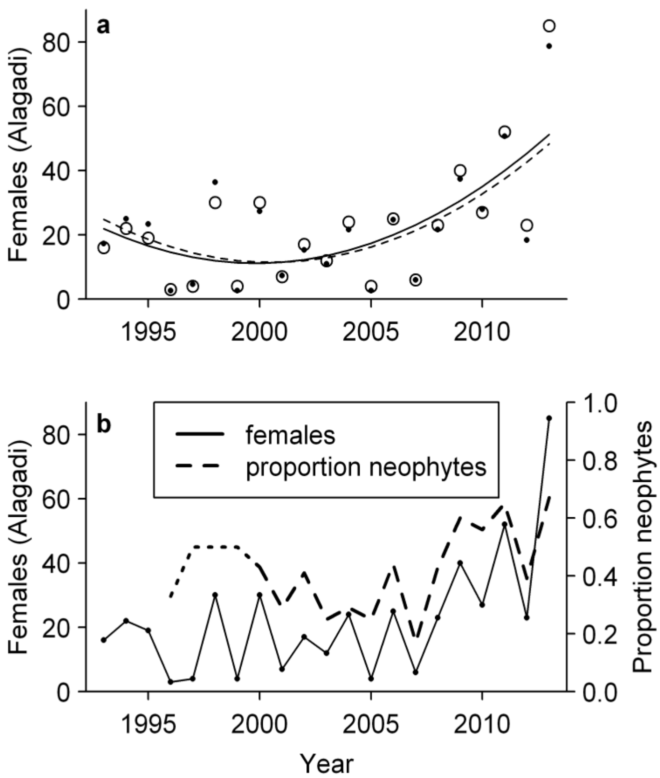


Figure 3. Green turtle nesting at Alagadi from 1993 to 2013. a) Number of females nesting at Alagadi as observed through intensive tagging effort (black dots; data for 1993-2000 previously presented in Broderick et al. (2002)), and as predicted by dividing annual nest counts by the grand mean expected clutch frequency for this population (3; open circles). Nesting population trends estimated using these two measures are almost identical (solid line: actual data, dashed line: predicted data). b) Correlation between the number of nesting females (solid line), and the proportion of those that are first time nesters (dotted/ dashed line) at Alagadi over the same time period. The dotted portion indicates lower confidence in neophyte/ remigrant identification prior to 2000.

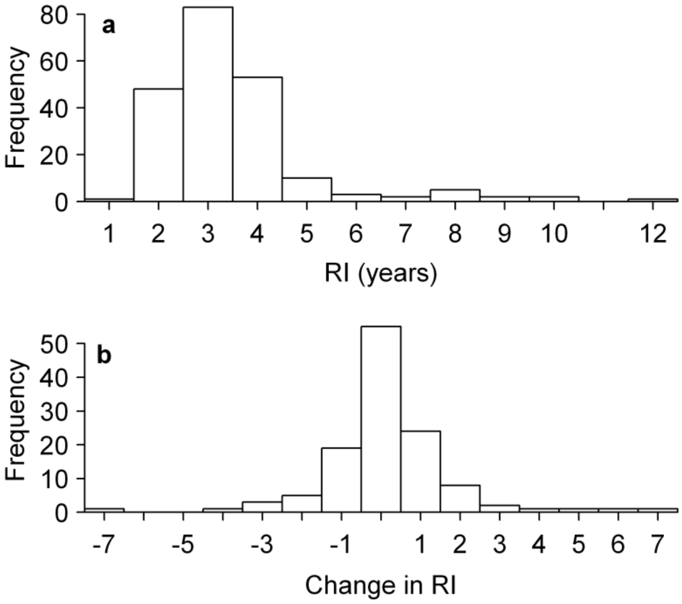


Figure 4. Remigration interval (RI) of green turtles returning to nest at Alagadi. a) Observed RIs (1994-2013). b) Change in RI for green turtles nesting at Alagadi during three or more seasons, taken as the increase/ decrease in RI compared to the previous RI recorded for each individual.

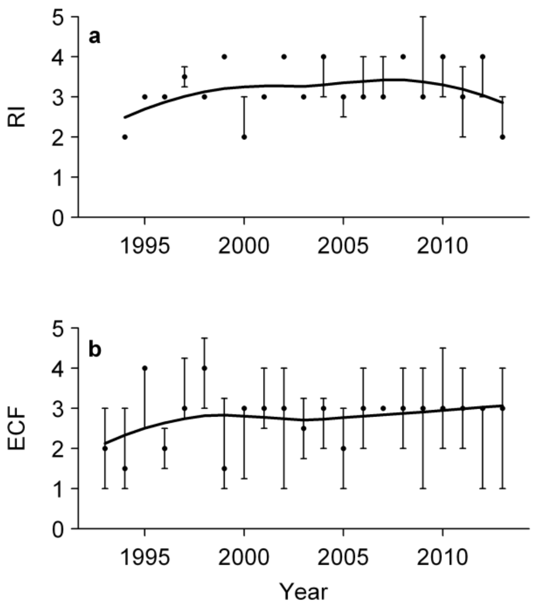


Figure 5. Breeding frequency of green turtles at Alagadi from 1993 to 2013. a) Yearly median and interquartile range for remigration interval (RI) and b) expected clutch frequency (ECF) for nesting at Alagadi, each with locally weighted regression line (LOESS smoother).

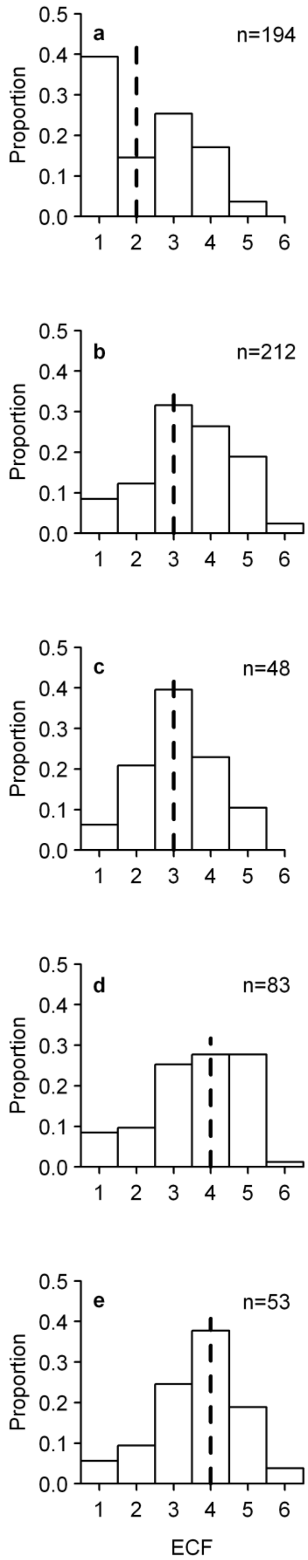
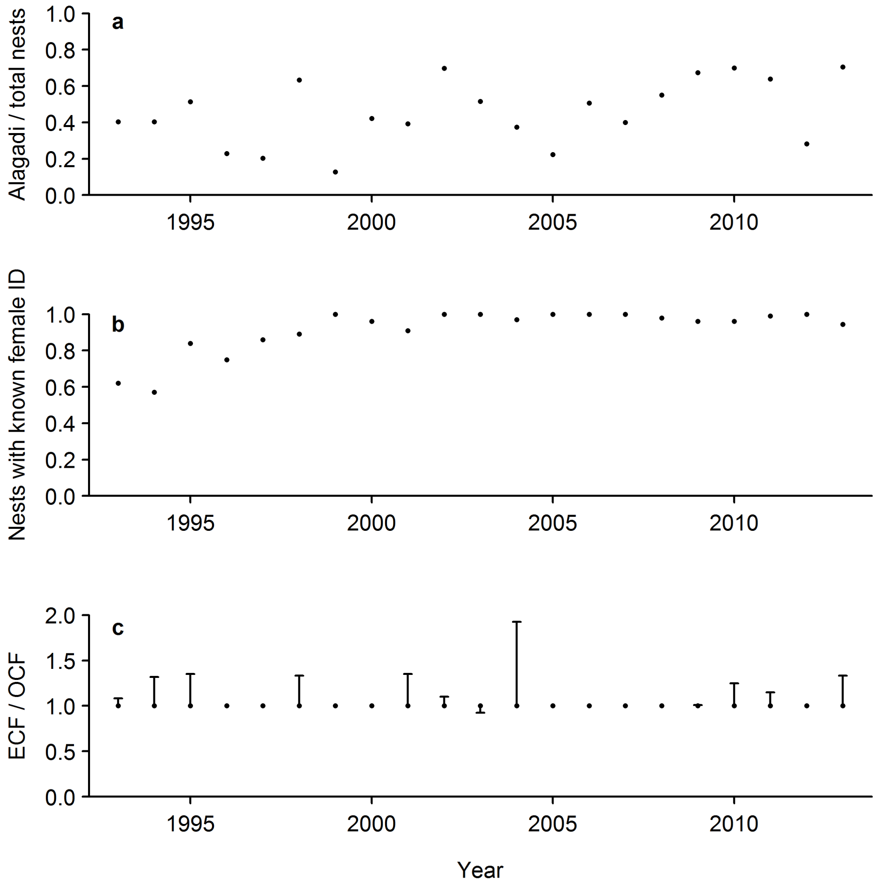


Figure 6. Expected clutch frequency (ECF) for a) neophyte (2000 - 2013), b) all remigrant, c) two year remigrant, d) three year remigrant and e) four year remigrant green turtles nesting at Alagadi (1994 to 2013). Dashed lines are median values.



Supplemental Figure S1. Lack of trend in fidelity and detectability. a) Proportion of all nests recorded across the north and west coasts that are laid at Alagadi. b) Proportion of nests laid at Alagadi that are assigned to a particular female (through witnessing of oviposition). c) Yearly median ratio of OCF:ECF (ratios were calculated for each individual female), with 5^{th} - 95^{th} percentiles displayed as error bars.