

INVESTIGATING LIFE-HISTORY TRAITS OF ADULT MEDITERRANEAN SEA TURTLES

Submitted by

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I certify that all material in this thesis that is not my own work has been identified and that no material has been previously submitted and approved for the award of degree by this or any other University.

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Green turtle nesting for the first time at Alagadi Beach, North Cyprus in 2016.

Photo credit: Lucy C.M. Omeyer.

ABSTRACT

The management of species of conservation concern requires high-quality life-history data to model and assess population stocks. This is particularly important for long-lived, migratory species with slow life-histories. In the case of sea turtles, the estimation of demographic parameters is a priority for the species globally and, in particular, in the Mediterranean Sea. In this thesis, I focus on green (*Chelonia mydas*) and loggerhead (*Caretta caretta*) turtles which nest sympatrically at Alagadi Beach, North Cyprus, where intensive monitoring and saturation tagging have been undertaken since 1993. This thesis aims to make use of this 26-year individual-based dataset both to further and to challenge current knowledge and theories surrounding life-history traits. More specifically, in **Chapter 2**, I review the state of knowledge of the growth strategy of adult sea turtles and life-history trade-offs. I highlight that, although studies of turtles in captivity have provided insights into changes in energy allocation at sexual maturity, there is a lack of data regarding the temporal variation in post-maturity growth rates in wild individuals. Thus, in **Chapter 3**, I provide evidence suggesting that, contrary to previous thinking, green and loggerhead turtles do not grow throughout their life. This clearly has implications for our understanding of ageing and longevity of the species. Additionally, in **Chapter 4**, I offer the first study of the effects of biologging device attachment on growth, reproduction and survival of nesting females. While the absence of an effect at this study site is promising considering how widely this technique is used in sea turtles, I stress the need for similar studies elsewhere to confirm this finding. Furthermore, I examine in **Chapter 5** the importance of passive integrated transponder (PIT) tags and show that they greatly improve estimates of flipper tag loss and life-history and demographic parameters, essential for population assessments. Lastly, I use results from previous chapters in **Chapter 6** to investigate the difference in recovery rates of the two species. I propose that high bycatch rates in the Mediterranean Sea are hampering the recovery of loggerhead turtles at this study site, whereas green turtles are showing signs of exponential recovery. In conclusion, this thesis emphasises the importance of long-term studies to refine life-history models and provides new and improved data for Mediterranean sea turtles, which can be used in regional and global IUCN Red List assessments.

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Chapter 2: Growth rates of adult sea turtles

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LCMO collated the data and led the writing, with contributions from ACB and BJG.

Chapter 3: Determinate or indeterminate growth? Revisiting the growth strategy of sea turtles

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ACB and BJG conceived the study and LCMO led the analyses and the writing. All authors contributed to data collection and writing of the manuscript.

Chapter 4: The effect of biologging systems on reproduction, growth and survival of adult sea turtles

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Chapter 5: The importance of passive integrated transponder (PIT) tags for measuring life-history traits of sea turtles

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ACB and BJG conceived the study, KEH and LCMO assembled the data, PC developed the tag loss models and LCMO led the analysis with input from PC, ACB and BJG. LCMO led the writing of the manuscript with contributions from all authors. LCMO, WJF, BJG, KEH, RTES and ACB all contributed to data collection.

Chapter 6: Investigating differences in population recovery rates of two sympatric sea turtle species

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ACB and BJG conceived the study, LCMO and KLS assembled the data, RBS developed the Bayesian state-space model and greatly assisted LCMO with the development of the matrix models. KLS analysed the population trend data, while LCMO analysed the vital rates data. ACB and BJG provided input on all analyses. LCMO led the writing of the manuscript with contributions from all authors. LCMO, KLS, SD, WJF, BJG, RTES and ACB all contributed to data collection.

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LIST OF NOTATIONS AND ABBREVIATIONS

Notations

A – projection matrix model

B – breeding state

β – slope

\hat{c} – quasi-likelihood over-dispersion coefficient

cm – centimetre

cm yr⁻¹ – centimetre per year

ϵ_t – observation residual for year t

f – fecundity

F – fertility

F – F statistic

g – grams

i – iteration

I_t – trend in count data in year t

km – kilometres

L_α – size at sexual maturity

L_∞ – asymptotic size

mm – millimetres

mo – month

n – sample size

NB – non-breeding state

N_t – vector holding the numbers in each time step

P/p – probability

p – encounter probability

p_B – probability of recapture in the breeding state

List of notations and abbreviations

p_{NB} – probability of recapture in the non-breeding state

ϕ – autocorrelation value

\hat{R} – potential scale reduction factor

\bar{r} – estimable mean population rate of change

r_t – annual rate of change at time t

ρ – correlation coefficient

S – survival rate

S_a – annual survival of adults

S_{bj} – annual survival of benthic juveniles

S_{ej} – annual survival of epipelagic juveniles

S_h – annual survival of hatchlings

S_1 – survival rate the first year after first capture

S_2 – survival rate in subsequent years

t – time

t – t statistic

y_t – count for year t

yr(s) – year(s)

$\Delta AICc$ – difference between the Akaike's information criteria corrected for small sample size value of a model and the lowest of all AICc values

$^{\circ}C$ – degrees Celsius

% – percentage

% of body size year⁻¹ – percent of body size per year

♀ – female

♂ – male

$\psi_{B \rightarrow NB}$ – breeding transition probability from the breeding to the non-breeding state

$\psi_{NB \rightarrow B}$ – breeding transition probability from the non-breeding to the breeding state

χ^2 – chi-squared value

√ – presence

List of notations and abbreviations

× – absence

λ – finite population growth rate

$\bar{\lambda}$ – mean population growth rate

λ_t – growth rate in year t

σ – standard deviation

σ_ε^2 – observation variance

σ_η^2 – estimable process error variance

Abbreviations

AIC – Akaike's information criterion

AICc – Akaike's information criterion corrected for small sample size

ARO – annual reproductive output

AS – age-at-size method

ASM – age at sexual maturity

BCI – Bayesian credible interval

CAGR – compound annual growth rates

C – clutch size

CCL – curved carapace length

CH – capture history

CI – confidence intervals

CMR – capture-mark-recapture

CV – coefficient of variation

D – number of dead full-term hatchlings

df – degrees of freedom

d.o.y – day of the year

DPS – distinct population segment

ECF – estimated clutch frequency

Edf – estimated degrees of freedom

List of notations and abbreviations

EFS – external fundamental system

EPC – eggs per clutch

Fig. – figure

FmvBGF – Faben's modified von Bertalanffy growth function

GAMM – generalised additive mixed model

GLM – generalised linear model

GLMM – generalised linear mixed model

GLS – generalised least square

GLS tags – global location sensing tags

GoF – goodness of fit

GR – growth rate method

H – number of hatched eggs

HES – hatchling emergence success

ID – identification

ind. – independence of tag loss between tags

IQR – interquartile range

IUCN – international union for conservation of nature

LAG – line of arrested growth

LGM – logistic growth model

MCMC – Monte Carlo Markov chains

MeanCCL – mean curved carapace length

MTCP – marine turtle conservation project

na or N/A – not applicable

n-ind. – non-independence of tag loss between tags

OCF – observed clutch frequency

PIT tag – passive integrated transponder tag

PSR – primary sex ratios

PTT – platform terminal transmitter

qAICc – quasi-likelihood Akaike's information criterion corrected for small sample size

List of notations and abbreviations

RI – remigration interval

RMU – regional management unit

SCL – straight carapace length

SD – standard deviation

SE – standard error

Sk – skeletochronology

SPOT – society for the protection of turtles

SRO – seasonal reproductive output

SSM – size at sexual maturity

SvBGF – seasonalised von Bertalanffy growth function

TDR – time depth recorder

TH – tag history

tsm – time-since-marking

Unk – unknown

vBGF – von Bertalanffy growth function

YearsSFC – years since first capture

CHAPTER 1: GENERAL INTRODUCTION

Life-history theory traditionally recognises seven key traits affecting an individual's life-history strategy. These include growth, age- and size-specific reproductive investments and lifespan (Stearns 1992). Life-history traits are thought to have evolved under strong natural selection in order to optimise individual fitness (Smith 1991). Variation in these traits results from the partitioning of finite energy resources among competing needs (Gadgil & Bossert 1970), such that the fitness of any one trait cannot be maximised without leading to cost in others (Stearns 1989). Further variation in life-history traits can arise within and among populations and species as a result of both intrinsic and extrinsic factors (Stearns 1992). With the sixth mass extinction event currently underway (Ceballos et al. 2017), the management of species of conservation concern requires knowledge of life-history traits and their variation, in particular for long-lived species. In the absence of these parameters, population models and stock assessments cannot be derived accurately.

Sea turtles represent an excellent study system in which to investigate life-history trade-offs and life-history trait variation. Indeed, sea turtles are circumglobally distributed (Wallace, DiMatteo, et al. 2010), are slow growing with a 'bet-hedging' life-history strategy (Avens et al. 2015) and delay sexual maturity for decades (van Houtan et al. 2014, 2016). As fecundity and body size tend to be correlated in sea turtles (e.g. Broderick et al. 2003), studying the temporal variation in post-maturity growth rates can give us an insight into changes in energy allocation to growth after sexual maturity, which has implications for our understanding of ageing in this taxon. However, the cryptic life-cycle of sea turtles has made estimating other life-history traits, such as age at sexual maturity, generation times and survivorship, particularly problematic in wild populations. This has led to the need to estimate population- and species-specific demographic parameters being highlighted as a research priority for sea turtles (Hamann et al. 2010, Rees et al. 2016, Casale et al. 2018).

Conservation status

All seven sea turtle species are of conservation concern and are listed on the IUCN Red List of Threatened Species. Kemp's ridley (*Lepidochelys kempii*, Marine Turtle Specialist Group 1996) and hawksbill (*Eretmochelys imbricata*, Mortimer & Donnelly 2008) turtles are critically endangered, while green turtles (*Chelonia mydas*, Seminoff 2004) are classified as endangered, and loggerhead (*Caretta caretta*, Casale & Tucker 2017), olive ridley (*Lepidochelys olivacea*, Abreu-Grobois & Plotkin 2008) and leatherback (*Dermochelys olivacea*, Wallace et al. 2013) turtles as vulnerable. Flatback turtles (*Natator depressus*), on the other hand, are not listed due to lack of data (Red List Standards & Petitions Subcommittee 1996). At a global scale, populations of green, loggerhead, leatherback, hawksbill and olive ridley turtles are declining. Population assessments for green, Kemp's ridley and flatback turtles are, however, at least 14 years out of date and need updating.

For all species, population declines are due to numerous factors, including, but not restricted to, direct exploitation, habitat degradation both in land and at sea, climate change and fisheries bycatch, with the latter thought to be the greatest threat to sea turtles around the world (Hamann et al. 2010, Wallace, Lewison, et al. 2010, Rees et al. 2016). More recently, however, it was suggested that assessing species at the subpopulation level is more appropriate to account for variation within and between regions, leading to the implementation of Regional Management Units (RMUs; Wallace, DiMatteo, et al. 2010) and Distinct Population Segments (DPS; Seminoff et al. 2015).

The Mediterranean Sea is frequented by five of the seven species of sea turtles. Only a limited number of leatherback (Casale et al. 2003), olive ridley (Revuelta et al. 2015) and Kemp's ridley (Tomás et al. 2008, Carreras et al. 2014) turtles enter the basin, while green and loggerhead turtles are abundant, including some individuals of non-Mediterranean origin (Carreras et al. 2011, 2014). Individuals of the latter two species, which have hatched on Mediterranean beaches, complete their entire life-cycle in the region, with loggerhead turtles being the most abundant of the two species (Casale & Heppell 2016, Casale et al. 2018). Despite juvenile loggerhead turtles of Atlantic and Mediterranean origin sharing common foraging grounds for a part of their life-cycle (Carreras et al.

2011), Mediterranean subpopulations of green and loggerhead turtles are considered genetically distinct (Carreras et al. 2011, Bradshaw et al. 2018), leading to their classification as separate RMU/DPS (Wallace, DiMatteo, et al. 2010, Seminoff et al. 2015). The subpopulations of the two species have experienced severe declines as a result of historical direct take, fisheries bycatch and coastal development (Casale et al. 2010, 2018). As such, both RMU/DPS have been described under high threat, while the green turtle subpopulation is also considered under high risk due to its restricted range (Wallace, DiMatteo, et al. 2010). While green turtles are endangered globally (Seminoff 2004) and in the Mediterranean Sea (Seminoff et al. 2015), loggerhead turtles are classified as vulnerable (Casale & Tucker 2017), with the Mediterranean RMU considered as least concern (Casale 2015). The conservation status of Mediterranean loggerhead turtles, however, is entirely conservation dependent and could be negatively impacted should intensive, long-term conservation action cease (Casale 2015).

Life cycle

Although inter-specific variation in life-history patterns exist among sea turtle species, green and loggerhead turtles exhibit a similar pattern (discussed in Chapter 2; Bolten 2003a). In the Mediterranean, the life cycle of green turtles is the least well understood of the two species (Casale et al. 2018), while loggerhead turtles are thought to have a more flexible life-history pattern compared to other loggerhead turtle subpopulations (Casale et al. 2008).

As for all sea turtle species, when Mediterranean green and loggerhead turtle hatchlings emerge from their nest, they crawl down the beach, entering into a “swimming frenzy” (Wyneken & Salmon 1992). Individuals become post-hatchlings, by definition, when they enter the oceanic zone (defined by the 200m isobath) and begin feeding (Bolten 2003b). Post-hatchlings are assumed to spend the next few years in oceanic nursery areas, although these locations are largely unknown for both Mediterranean species.

Particle distribution numerical simulations suggest that the Levantine basin and the Ionian, south-central Mediterranean and Adriatic Seas may host nurseries for Mediterranean loggerhead turtles (reviewed in Casale et al. 2018).

For this subpopulation, this first life-stage is thought to be very short, with individuals being constrained to oceanic zone due to their limited diving capacity. As individuals grow and diving capacity increases (Mori 2002), larger individuals may move between oceanic and neritic zones located in the Adriatic and Aegean Seas, as well as off the coast of Cyprus, Egypt, Greece, Italy, Libya, Spain, Tunisia and Turkey (reviewed in Casale et al. 2018). This movement may be associated with a dietary shift, with individuals transitioning from the strict consumption of epipelagic prey-items to foraging throughout the water column (Casale et al. 2008). In contrast, this second life-stage is believed to be much longer than the first stage, with no evidence of a strict neritic phase for Mediterranean loggerhead turtles (Casale et al. 2008).

The juvenile life-stages of Mediterranean green turtles, on the other hand, are poorly understood as of yet. Post-hatchlings, juveniles and adults are supposed to remain within the Levantine basin, with foraging grounds off the coast of Albania, Cyprus, Egypt, Greece, Israel, Libya, Syria, Tunisia and Turkey (reviewed in Casale et al. 2018). Small Mediterranean green turtles forage on a mixed diet similar to that of loggerhead turtles, before becoming primarily herbivorous as large juveniles and adults (Godley et al. 1998, Cardona et al. 2010, Lazar et al. 2010).

Individuals of both species remain at sea until they reach sexual maturity. Average age at sexual maturity has been estimated at 25 years for Mediterranean loggerhead turtles, while it is yet to be determined for the green turtle subpopulation (Casale et al. 2018). Once mature, adults of both sexes embark on periodic migrations between foraging and breeding/nesting grounds, showing fidelity to these locations (Bradshaw et al. 2018, reviewed in Casale et al. 2018).

Mediterranean adult loggerhead turtles are characterised by their smaller size in comparison to other populations around the world (Dodd 1988, Tiwari & Bjorndal 2000, Kamezaki 2003), with those nesting in Cyprus being the smallest of the species (Broderick & Godley 1996). Loggerhead turtles nest throughout the Mediterranean basin, with the majority (96 %) of clutches laid in Cyprus, Greece, Libya and Turkey (reviewed in Casale et al. 2018). Similarly, Mediterranean adult green turtles are towards the lower end of the range of body sizes for the species globally (Seminoff et al. 2015), with nesting sites restricted to the Levantine basin. Most nesting for this species occurs in Cyprus, Syria and

Turkey, with lower nesting levels in Egypt, Israel and Lebanon (Stokes et al. 2015, Casale et al. 2018). Remigration interval, i.e. the number of years elapsed between consecutive breeding seasons, varies between species, sexes and subpopulations within the Mediterranean, ranging from one year for male and female loggerhead turtles breeding in Cyprus and Greece (Broderick et al. 2003, Hays et al. 2010), to up to 10 and 14 years for loggerhead and green turtles respectively nesting in Cyprus (Chapter 3). Clutch size is highly variable within and between species, and among nesting aggregations in the region (Casale et al. 2018), being correlated with female body size (e.g. Broderick et al. 2003) and influenced by the foraging area frequented (Zbinden et al. 2011, Cardona et al. 2014, Patel et al. 2015). Females of both species lay between 1 and 6 clutches per season (Broderick et al. 2003, Stokes et al. 2014) before they return to their respective foraging grounds, where they remain for a variable period of time to accumulate sufficient resources to repeat the process (Broderick et al. 2001). In the meantime, eggs are left to incubate on their own for 45 to 70 days on average depending on temperature (reviewed in Casale et al. 2018), after which hatchlings may emerge from their nest. Thereafter, the whole life-cycle begins once again.

Population abundance and trend

Estimating population abundance for sea turtles is challenging as only adult females are readily accessible at nesting beaches. Nevertheless, it has been estimated that the total Mediterranean loggerhead turtle population size ranges between 1.20 and 2.36 million individuals, whereas between 0.26 and 1.25 million green turtles are thought to inhabit the region (Casale & Heppell 2016). Of these individuals, only a small proportion are adults, with between 1,806 and 6,222 loggerhead turtle and between 457 and 1,243 green turtle females thought to nest annually (Casale & Heppell 2016). All values presented above, however, should be interpreted with caution as they are based on numerous assumptions.

A comparison of past and present clutch counts revealed positive population trends at the basin-wide scale for both species (Casale 2015, Casale et al. 2018). Such trends, however, may not be representative of the whole

subpopulations as only part of the nesting activity is being recorded in the region and monitored beaches may have benefitted from long-term conservation actions (Casale et al. 2018).

Estimating life-history parameters

Although loggerhead turtles have been classified as an indicator species by the Bern Convention, it was highlighted that there is a need for a better knowledge of the demography of the species to do accurate population models. This was reiterated in a recent review of Mediterranean sea turtles, which emphasised the necessity of high quality data on demographic parameters, particularly for the less studied green turtles (Casale et al. 2018). While some life-history parameter estimates need to be improved or updated, others are currently lacking altogether for Mediterranean sea turtles, such as adult annual survival estimates, for example (Casale et al. 2018, Pfaller et al. 2018).

In the present thesis '**Investigating life-history traits of adult Mediterranean sea turtles**', throughout five chapters, written as independent units of study, I challenge and advance current knowledge and theories surrounding key life-history parameters, providing new data for the species globally. I focus on green and loggerhead turtles, which nest sympatrically at Alagadi Beach in North Cyprus (see Figure 1), an index nesting site where comprehensive monitoring and saturation tagging have been undertaken since 1993. Alagadi represents the second largest green turtle rookery in North Cyprus (Casale et al. 2010), hosting 30 % of all clutches laid in North Cyprus (Broderick et al. 2002), and less than 10 % of those laid in the region (Casale et al. 2018). Yearly nesting abundance is highly variable for this species at this study site, ranging from 8 to 306 clutches, with a mean of 95 clutches laid between 1993 and 2018 (Chapter 6). Alagadi Beach also represents an important nesting beach for loggerhead turtles, although to a lesser extent. Loggerhead turtle clutches also show interannual variation at this study site (mean: 59; range: 28-108; time period: 1993-2018, Chapter 6). Approximately 10 % of North Cyprus nesting occurs at Alagadi Beach (Broderick et al. 2002), representing less than 1 % of the regional nesting (Casale et al. 2018).

In **Chapter 2: 'Growth rates of adult sea turtles'**, I review the state of knowledge of growth rates of adult sea turtles from the onset of sexual maturity onwards, as well as potential life-history trade-offs. Although captive studies have provided insight into life-history trade-offs and the shape of growth curves, I highlight the lack of data on wild animals regarding temporal changes in post-maturity growth rates and reproductive output. I emphasise the need for such data both to further our understanding of ageing and population dynamics in sea turtles and to assess the status of species.

In **Chapter 3: 'Determinate or indeterminate growth? Revisiting the growth strategy of sea turtles'**, I investigate temporal variation in post-maturity growth rates of green and loggerhead turtles to determine whether sea turtles are determinate or indeterminate growers. I discuss which growth curve best describes that of sea turtles, collating data from published studies across sea turtle species globally. I underline that newer and clearer definitions of determinate and indeterminate growth, that fit each growth pattern exclusively, are required. I highlight that such long-term data are necessary both to refine life-history models and to further our understanding of ageing and longevity of wild sea turtles for conservation.

In **Chapter 4: 'The effect of biologging systems on reproduction, growth and survival of adult sea turtles'**, I examine the impacts of biologging systems on life-history traits of green and loggerhead turtles. I explore whether device attachment leads to biased estimates of life-history traits of individuals following device attachment. I call for other similar studies elsewhere to examine the effects of biologging devices at a broader scale and highlight the value of long-term individual-based monitoring to do so.

In **Chapter 5: 'The importance of passive integrated transponder (PIT) tags for measuring life-history traits of sea turtles'**, I describe flipper and PIT tag loss in green and loggerhead turtles using continuous functions, and assess whether the use of PIT tags has improved our estimates of reproductive longevity, reproductive periodicity, annual survival and flipper tag loss. I emphasise the importance of PIT tags for long-term monitoring to provide more accurate and robust estimates of life-history traits and population parameters necessary for the species' conservation.

In **Chapter 6: 'Investigating differences in population recovery rates of two sympatric sea turtle species'**, I explore long-term population trends for the two species at Alagadi Beach, focussing primarily on loggerhead turtles, for which the life-cycle is better understood in the region. I use different matrix model projection scenarios to examine which life-history trait(s) drive(s) the difference in recovery rates between the two species. I provide estimates of population growth rates and adult population sizes for the two species using a Bayesian state-space model. I also highlight the importance of long-term monitoring datasets to provide high-quality data on demographic parameters, and to assess population trends and temporal changes in population vital rates.

Finally, in **Chapter 7**, I provide a synthesis and evaluate the findings from this thesis. These will feed into population dynamic models essential to conservation and will also be used in both the regional and IUCN Red List assessments.

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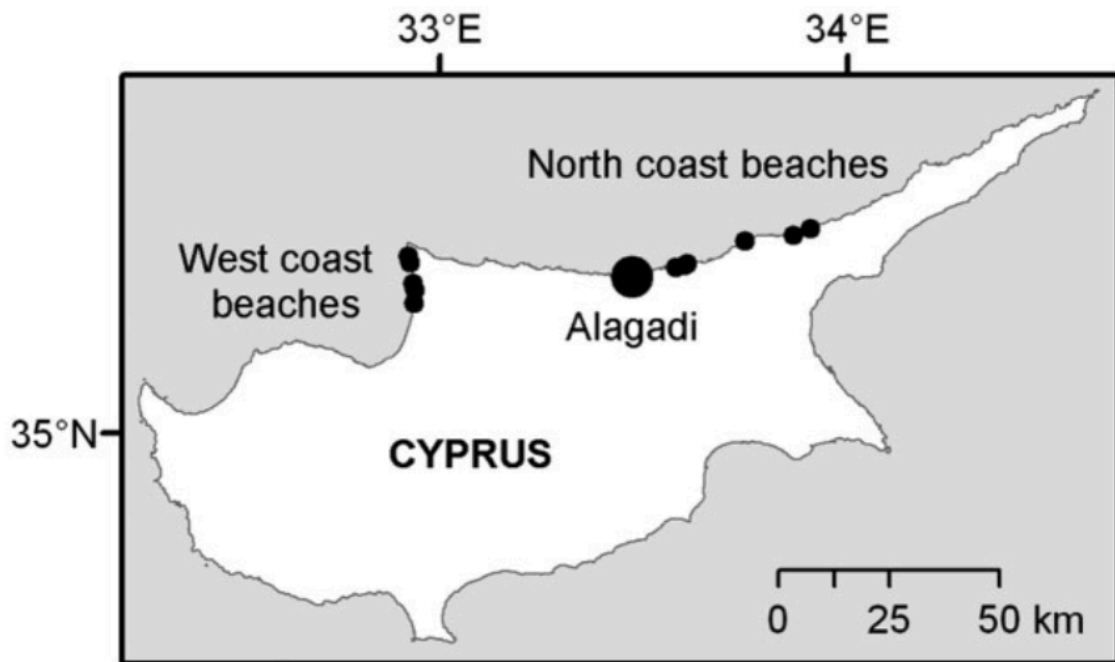


Figure 1. Monitored core nesting beaches in North Cyprus for green and loggerhead turtles. Alagadi Beach, shown by the larger dot, represents the main index beach. The North and West coast beaches refer to those discussed in Chapter 6. Map produced by Kimberley L. Stokes, originally published in Stokes et al. 2014. Permission granted from author.

CHAPTER 2: GROWTH RATES OF ADULT SEA TURTLES

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Abstract

Indeterminate growth, i.e., growth that persists throughout life, is common in long-lived reptiles. Because fecundity and body size tend to be correlated in such species, individuals face a life-history trade-off at sexual maturity. Saturation tagging and intensive monitoring at nesting grounds can potentially provide opportunities to accumulate data on individual measurements and reproductive output. Until recently, however, shortcomings from these methods have prevented the testing of theories on resource allocation between growth and reproduction at sexual maturity in wild populations of sea turtles. Here, we review the state of knowledge of growth rates in adult sea turtles and potential life-history trade-offs. We found that post-maturity growth rates varied among ocean basins. They appeared highest in the Atlantic Ocean for both green turtles *Chelonia mydas* and hawksbill turtles *Eretmochelys imbricata*, and highest in the Mediterranean Sea for loggerhead turtles *Caretta caretta*. For other species, there are too few studies at present to allow for intraspecific comparison. Additionally, we found no significant difference in mean female compound annual growth rates among species and ocean basins. Although captive studies have provided great insight into changes in energy allocation at sexual maturity and life-history trade-offs, this review highlights the lack of data on wild animals regarding changes in post-maturity growth rates and reproductive output over time. Such data are desirable to further our understanding of energy allocation, growth and ageing in wild sea turtles. They are further required to assess the status of species and to understand population dynamics for both conservation and management.

Introduction

Organisms need to partition finite resources among competing needs, such as somatic maintenance, growth and reproduction throughout life (Gadgil & Bossert 1970). Trade-offs occur so that fitness of any one trait cannot be maximised without leading to a cost in others (Stearns 1989). Sexual maturity represents the age, size or stage at which individuals can reproduce (Bernardo 1993). As somatic maintenance has priority over competing needs (Zera & Harshman 2001), maturation requires a change in resource allocation from growth to reproduction (Bernardo 1993). In contrast to species with determinate growth, where growth halts at sexual maturity, growth persists throughout life in species with indeterminate growth (Kozłowski 1996), as demonstrated in fish (Charnov & Berrigan 1991), clams (Heino & Kaitala 1996), freshwater turtles (Congdon et al. 2013) and desert tortoises (Nafus 2015). The Von Bertalanffy growth curve (von Bertalanffy 1957) is believed to be the best approximation of growth, defined as the increase in skeletal size, in indeterminate growers. It assumes that no maximum size exists and that growth rates decay with age.

Because fecundity and body size tend to be correlated in indeterminate growers (Olsson & Shine 1996), individuals face a life-history trade-off at sexual maturity (Heino & Kaitala 1999). Indeed, sexual maturity represents a balance between the benefits and costs associated with early versus late age at maturation and is influenced by growth rates during development (Stearns 1989). The most common maturation norm is one in which, when growth is rapid, organisms mature early at a large size, whereas, when growth is slow, sexual maturity is delayed and a smaller size at sexual maturity (SSM) is reached (Stearns & Koella 1986). In contrast, a less common maturation norm describes an inverse relationship between growth rates during development and age at sexual maturity (ASM; Stearns & Koella 1986, Day & Rowe 2002), such that either: (1) when growth is rapid, organisms mature early, benefit from increased survival to first reproduction and decreased generation time, at the cost of a smaller body size (Bernardo 1993), which is likely to lead to a reduction of lifetime reproductive output (Shine 1980), or (2) when growth is slow, individuals mature late, benefit from increased body size and competitive ability (Bernardo 1993), at the cost of a decrease in survival probability to first reproduction (Gadgil &

Bossert 1970). Finally, a rare maturation norm is one in which maturation is the result of a genetically determined size or age threshold (Bernardo 1993).

Carry-over effects are considered drivers of fitness differences (reviewed in Harrison et al. 2011). They occur as a result of changes in extrinsic factors between 2 time periods affecting an individual's body condition and therefore its fitness. Capital breeders, such as species that undergo long migrations to breed or species that provide parental care, fuel reproduction using resources accumulated during non-breeding years (Jönsson 1997, Price 2017). In such species, the cost of reproduction is high and individuals can skip reproduction in a given year in order to increase future reproduction (Harris & Ludwig 2004, Rivalan et al. 2005, Rideout & Tomkiewicz 2011). Kozłowski (1996) proposed that, in seasonal environments, indeterminate growth is the optimal strategy, allowing individuals to alternate allocation of resources in excess of somatic maintenance between growth and reproduction, such that reproduction is maximised over time. Thus, post-maturity growth phases are expected to vary temporally (e.g. Harris & Ludwig 2004, Baron et al. 2013, Folkvord et al. 2014), declining with age and occurring straight after breeding events in order to increase future reproduction (Heino & Kaitala 1996, Kozłowski 1996).

ASM and SSM inherently result from the interaction of intrinsic and extrinsic factors influencing somatic growth prior to sexual maturity (Bernardo 1993). Although empirical evidence (e.g. Choat et al. 2006, Armstrong & Brooks 2013, Tucek et al. 2014) suggests that sexual maturity is frequently the result of a genetically determined size threshold (Roff 2000), differences in growth curves, SSM and ASM are likely to arise between individuals (Bernardo 1993). Indeed, enormous variation in both ASM and SSM can be observed within and among species (e.g. Miaud et al. 1999, Madsen & Shine 2006, Bjorndal et al. 2013a, 2014, Campos et al. 2013, Folkvord et al. 2014, Avens et al. 2015, 2017). As males are less readily accessible to study, knowledge of reproductive biology in sea turtles remains highly female-biased (Rees et al. 2016). Whilst little is known about the maturation process of males (Blanvillain et al. 2008, Ishihara & Kamezaki 2011, Arendt et al. 2012, Avens et al. 2015), post-maturity growth rates (Avens et al. 2015), estimates of ASM (Schwanz et al. 2016; however, see Avens et al. 2017 for absence of a difference in ASM) and life-history trade-offs, as a consequence of sexual selection (Adler & Bonduriansky 2014), are likely to be sex-specific.

ASM and SSM are fundamental life-history parameters needed to assess the status of species and to understand population dynamics for both conservation and management (Chaloupka & Musick 1997, Heppell et al. 2003). Sea turtles are an excellent study system in which to investigate post-maturity growth rates and life-history trade-offs, being slow-growing with a 'bet-hedging' life-history strategy (Avens et al. 2015) and delaying sexual maturity for decades (Van Houtan et al. 2014, 2016). However, most work investigating growth rates in sea turtles has focussed on early-life stages prior to sexual maturity (Bjorndal et al. 2000b, 2016, Casale et al. 2009, Kubis et al. 2009, Sampson et al. 2015). Estimates of ASM have been generated by parametric growth curves (e.g. von Bertalanffy, logistic and Gompertz) using juvenile and sub-adult somatic growth data and estimates of SSM derived from mean female size at nesting grounds (reviewed in Avens & Snover 2013). Sea turtles, however, exhibit sex-specific growth functions as a result of sexual dimorphism, with males showing slower growth rates than females, resulting in differences in SSM, with mature males being on average smaller (Chaloupka & Limpus 1997, Limpus & Chaloupka 1997, Diez & van Dam 2002, Godley et al. 2002a, Chaloupka et al. 2004; see Table 1; but see Dodd 1988 and Kamezaki 2003 for larger SSM of males; see Avens et al. 2015 for faster growth in sub-adult and adult male loggerhead turtles and larger SSM; see Avens et al. 2017 for absence of a difference in SSM).

Sea turtle research has primarily been focussed at nesting beaches (Schroeder & Murphy 1999). Although saturation tagging and intensive monitoring at nesting grounds provide the perfect opportunity to accumulate data on individual measurements and reproductive output, such methods have shortcomings which, until recently, have prevented testing, for example, of theories on resource allocation between growth and reproduction at the onset of sexual maturity in wild populations of sea turtles (Bjorndal et al. 2013a, Avens et al. 2015, 2017). Indeed, despite being relatively inexpensive compared to in-water surveys, such programmes remain costly, labour intensive, logistically challenging and difficult to maintain for sufficiently long periods of time to be able to follow individuals throughout their reproductive lifespans (Sims et al. 2008). In addition, their effectiveness decreases as population size increases unless the study area ranges widely (Witt et al. 2009) to encompass flexibility in natal homing (Lee et al. 2007, Nishizawa et al. 2011, Lohmann et al. 2013, Brothers & Lohmann 2015) and nest site fidelity (Tucker 2010, Weber et al. 2013). Although

some populations are recovering (da Silva et al. 2007, Bellini et al. 2013, Weber et al. 2014, García-cruz et al. 2015), sea turtles remain conservation-dependent and require intensive management (Wallace et al. 2011, Casale & Heppell 2016). Hamann et al. (2010) highlight that reproductive biology and population ecology are 2 priority research categories for sea turtles, and these require methods to accurately age individuals and determine ASM. Additionally, Rees et al. (2016) reiterate that there is still much to be done in this regard.

This comprehensive review explores the state of knowledge of growth rates in adult sea turtles from the onset of sexual maturity as well as potential life-history trade-offs. Although some researchers consider ASM, age at first mating and age at first reproduction identical, it is possible for females to start reproducing 2-4 yr after reaching sexual maturity (Limpus 1990, Rostal 2005, Caillouet et al. 2011; some individuals in Bjorndal et al. 2013a, 2014). However, for the purpose of this review, ASM and age at first observed nesting are considered to be the same.

We searched for peer-reviewed literature on ISI Web of Knowledge and Google Scholar for the terms growth, growth rates, maturity, age, adult, survival, survivorship, nesting, reproductive output and trade-off. Along with each search term was included the word 'turtle'. Additionally, we searched for publications in the Marine Turtle Newsletter (<http://www.seaturtle.org/mtn/>, last accessed January 2016), Synopses of Biological Data for marine turtles (<http://www.fao.org/fishery/org/fishfinder/3,5/en>) and Proceedings of the Annual Symposia on Sea Turtle Biology and Conservation (<http://www.internationalseaturtlesociety.org/#/Proceedings>, last accessed January 2016). This review is structured in 6 major sections: life-history dichotomies, age-size trade-off, energy allocation shift, post-maturity growth rates, breeding frequency and population recovery.

Life-history dichotomies

Sea turtles are highly mobile and juveniles may move among multiple foraging habitats before reaching sexual maturity (Bolten 2003b, McClellan & Read 2007, Fukuoka et al. 2015). Environmental differences between foraging habitats will influence habitat use and foraging strategies of individuals and may, in turn, result in differential growth, survival, SSM and ASM (Peckham et al. 2011). While movement between alternative habitats may incur physiological, morphological and behavioural costs as individuals adapt to their new environment, these may be outweighed by the benefits associated with more suitable environmental conditions (Werner & Gilliam 1984, Bolten 2003b). Juveniles that move between habitats might benefit from higher growth rates due to higher food availability and quality and thus larger SSM (Werner & Gilliam 1984, Bolten 2003a, Snover et al. 2010). Although Gross (1984) argued that, for evolutionary strategies to be stable, fitness of alternative strategies should be equivalent, with reproductive output being positively correlated with SSM in sea turtles (Van Buskirk & Crowder 1994), life-history dichotomies may ultimately result in differential fecundity both within and between populations and species (Hatase et al. 2013, Ceriani et al. 2015).

Inter-specific differences in developmental life-history patterns exist within the sea turtles (reviewed in Bolten 2003b). Whereas flatback turtles (*Natator depressus*) develop entirely in neritic waters (Walker & Parmenter 1990), leatherback (*Dermochelys coriacea*) and many populations of olive ridley (*Lepidochelys olivacea*) turtles complete their development entirely in oceanic waters (Bolten 2003b). In contrast, green (*Chelonia mydas*), loggerhead (*Caretta caretta*), hawksbill (*Eretmochelys imbricata*), Kemp's ridley (*Lepidochelys kempii*) and remaining populations of olive ridley turtles generally exhibit an intermediate life-history pattern (Bolten 2003b). Hatchlings and small juveniles from the latter species inhabit oceanic waters for an undetermined period of time, feeding on nutrient-poor epipelagic prey and experiencing relatively slow growth (Bjorndal et al. 2000b, Bolten 2003a). Upon reaching a size threshold (Bjorndal et al. 2000b, Bolten 2003b), large juveniles undergo what was long thought to be a marked, non-reversible ontogenetic shift to neritic waters, feeding on more abundant, nutrient-rich benthic prey (Hawkes et al. 2006, Snover et al. 2010). Although this

change of environment may come at the cost of an increase in predation risk (Bolten 2003b), it could result in as much as a 30 % increase in juvenile growth rates (Snover et al. 2010), thus appearing highly advantageous. Recent studies, however, suggest that the ontogenetic shift is both facultative, with some individuals remaining in oceanic waters throughout their life-cycle (Hatase et al. 2002, Hawkes et al. 2006, Ramirez et al. 2015), and reversible, with some individuals returning to oceanic waters (McClellan & Read 2007, McClellan et al. 2010, Ramirez et al. 2015).

The decision to transition from oceanic to neritic waters is likely to result from a combination of body size, metabolic rate and density-dependent effects on food availability and growth rates (Olsson et al. 2006). Smaller individuals experiencing higher growth rates in oceanic waters are believed to remain there until they reach sexual maturity, whereas larger individuals with higher metabolic rates and low growth rates would disperse to neritic water in search of better growth conditions (Bjorndal et al. 2000b, Hawkes et al. 2006, Hatase et al. 2010). In turn, these individuals would compensate for previously low growth conditions by performing catch-up growth (Bjorndal et al. 2003, Roark et al. 2009, Bjorndal & Bolten 2010; but see Snover et al. 2007b for absence of compensatory growth). Smaller individuals, however, are potentially constrained to oceanic waters due to their size, which limits their diving capacity (Mori 2002, Hawkes et al. 2006). Thus, life-history dichotomies are maintained through differences in body size, which, in turn, influence habitat use and foraging strategy, leading to differences in SSM (e.g. Hatase et al. 2010, 2013, Peckham et al. 2011).

Age-size trade-off

Rare are the studies that observe wild individuals of known age due to the challenges associated with studying sea turtles throughout their lifecycle and ageing individuals (e.g. Bell et al. 2005, Caillouet et al. 2011, Tucek et al. 2014, Rees et al. 2016). To overcome this problem, a number of studies have investigated growth rates using captive individuals of known age (e.g. Jones et al. 2011, Bjorndal et al. 2013a, 2014). Unlike wild individuals, captive individuals can be measured at regular time intervals both before and after sexual maturity. Such studies have investigated how growth rates vary over the course of an individual's lifetime, providing great insight into life-history trade-offs and the shape of growth curves (e.g. Bjorndal et al. 2013a, 2014).

Captive individuals reared under similar conditions exhibit a wide range of age, size, mass and body condition at sexual maturity (Bjorndal et al. 2013a, 2014). Whilst a study of 47 captive green turtles *Chelonia mydas* found no evidence for an age-size trade-off, as the 2 individuals that matured at the greatest age had both the largest and second to smallest SSM (Bjorndal et al. 2013a), this trade-off was observed in a study of 14 captive Kemp's ridley turtles *Lepidochelys kempii*, potentially as a result of a greater variation in ASM in the latter species (Bjorndal et al. 2014). Additionally, the detection of an age size trade-off in green turtles could have been hampered by the mixed genetic origin of individuals (Bjorndal et al. 2013a) and group feeding of a high quality diet (Bjorndal et al. 2013a, 2014).

Within-species variation in SSM in wild individuals is greater than that observed in captive species (Witzell 1983, Dodd 1988, Marquez 1994, Hirth 1997, Tiwari & Bjorndal 2000, Caillouet et al. 2011, Avens et al. 2015, 2017; see Table 2), potentially due to greater variation in juvenile growth rates within and between populations and species (Chaloupka & Limpus 1997, Kubis et al. 2009, Bell & Pike 2012, Avens et al. 2017). Carry-over effects resulting from early environmental conditions, such as those associated with differences in habitat use or productivity at foraging grounds, have been speculated to be linked to differences in juvenile growth rates within and among populations and thus differences in SSM (Eder et al. 2012).

In contrast, data on variation in ASM in wild populations are scarce (Caillouet et al. 2011, Avens et al. 2015, 2017) and whether an age-size trade-off would be observed remains to be shown. The authors are aware of only one study in a wild population of loggerhead turtles *Caretta caretta* (Tucek et al. 2014) which found no evidence for such a trade-off. Variation in juvenile growth rates could be dampened if individuals performed compensatory growth – which in some cases they appear to do (e.g. Bjorndal et al. 2003, Roark et al. 2009, but see Snover et al. 2007b) – or if slow-growing individuals experienced increased mortality pressures as they remain in the vulnerable size classes for longer (Bjorndal et al. 2013a, 2014). This, in turn, would reduce the variation in ASM and SSM, which could hamper the detection of an age-size trade-off in wild populations.

Energy allocation shift

The onset of vitellogenesis occurs a few years prior to reaching sexual maturity (Saka et al. 2014) and requires some energy to be diverted away from somatic growth towards follicular development until breeding occurs (Kawazu et al. 2015). Using ultrasonography, Kawazu et al. (2015) observed a reduction of growth just after the onset of vitellogenesis in captive hawksbill turtles *Eretmochelys imbricata*. Similarly, pre-maturity growth rates were negatively correlated with ASM in both captive green (*Chelonia mydas*) and Kemp's ridley (*Lepidochelys kempii*) turtles (Bjorndal et al. 2013a, 2014). In both species, whereas one group of individuals shifted to negligible growth the same year as they reached sexual maturity, the other group shifted to negligible growth at least 2 yr prior to laying their first clutch (Bjorndal et al. 2013a, 2014). This, coupled with changes in pre-maturity growth rates, suggests that the shift in energy allocation occurs a few years prior to reaching sexual maturity.

The delay observed when captive individuals shift to negligible growth and first reproduction could result from turtles being less efficient at shifting resources away from skeletal and mass growth towards reproduction (Bjorndal et al. 2013a) or could result from individuals in poorer condition delaying reproduction to accumulate sufficient resources to exceed a certain threshold (Kwan 1994). The decision to nest in a given year is likely to result from the combination of an assessment of body condition and favourable environmental conditions (e.g. Baron et al. 2013). For example, annual breeding probability is correlated with sea surface temperatures (Chaloupka 2001, Saba et al. 2007, Mazaris et al. 2009, del Monte-Luna et al. 2012), which may correlate with favourable conditions.

Whilst the shift in energy allocation starts a few years prior to sexual maturity, it persists for an unknown number of years after. Changes in energy allocation can be inferred from changes in post-maturity growth rates. In both Bjorndal et al. studies (2013a, 2014), growth rates in the first 3 to 4 yr after sexual maturity were higher than those averaged throughout post-maturity years, regardless of SSM. This, coupled with the abrupt decrease in spacing of lines of arrested growth (LAG) in bone cross sections in females of known history (Avens et al. 2015), supports the idea that, once females reach sexual maturity,

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resources are gradually diverted from growth towards reproduction (Hatase et al. 2004).

Post-maturity growth

Skeletochronology and capture-mark-recapture (CMR) studies have provided estimates of post-maturity growth rates for wild populations, which are summarised in Table 1. Although skeletochronology derives growth rates from estimates of female length from humerus diameter (reviewed in Avens & Snover 2013), comparison of lengths and growth rates obtained from such a technique and those collected and calculated at nesting beaches proves skeletochronology to be a powerful technique to estimate growth rates (Snover et al. 2007a, Goshe et al. 2010, Avens et al. 2015, 2017).

Growth rates (Table 1) ranged from 0.20 to 0.42 cm yr⁻¹ for green turtles *Chelonia mydas* and appeared higher in the Atlantic Ocean than in the Mediterranean Sea and Pacific Ocean. Similarly, growth rates appeared higher in the Atlantic Ocean than in the Pacific Ocean for hawksbill turtles *Eretmochelys imbricata*, ranging from 0.17 to 0.30 cm yr⁻¹. For loggerhead turtles *Caretta caretta*, growth rates ranged from 0.20 to 0.47 cm year⁻¹ and appeared higher in the Mediterranean Sea than in the Atlantic Ocean and Pacific Ocean. It should be noted, however, that growth rates for the Atlantic Ocean (0.20 cm yr⁻¹ in Bjorndal et al. 2013b; 0.47 cm yr⁻¹ in Avens et al. 2015) are not included in Table 1 and Fig.1 because they are averages from 10 cm bins, which can include both large juveniles and adults, assuming that females are sexually mature at >80 cm straight carapace length (SCL). Data are lacking altogether for olive ridley turtles *Lepidochelys olivacea* and only one growth measurement was available for leatherback (*Dermochelys coriacea*; 0.20 cm yr⁻¹), flatback (*Natator depressus*; 0.012 cm yr⁻¹) and Kemp's ridley turtles (*Lepidochelys kempii*; 0.6 cm yr⁻¹; Avens et al. 2017). Again, it should be noted that the value for Kemp's ridley turtles is not included in Table 1 and Fig.1 as it is an average from 10 cm bins, which can include both large juveniles and adults, assuming that females are sexually mature at >60 cm SCL (Caillouet et al. 2011).

Post-maturity growth rates in sea turtles are low regardless of ocean basin or species in both captive and wild populations (Table 1) and were correlated with neither SSM, ASM nor body condition in captive species (Bjorndal et al. 2013a, 2014). As expected under indeterminate growth, in the first 3 to 4 yr following sexual maturity, individuals grew more rapidly before growth decreased and

became negligible (Bjørndal et al. 2013a, 2014; Table 1). Similar temporal analyses of post-maturity growth rates are needed in wild populations, as all studies reporting post-maturity growth rates have averaged values across years without taking into account factors such as years since first reproduction. Additionally, differences in resource use between oceanic and neritic foragers are likely to lead to foraging ground specific growth curves and post-maturity growth rates.

In order to be better able to compare growth rates across populations and species and to account for individuals maturing at different sizes, female compound annual growth rates were calculated from Table 1 for wild populations and for each species as a percentage of body size per year. When comparing hawksbill, green and loggerhead turtles for which there are more than one data point, there is no significant difference in mean female compound annual growth rates among species (Kruskal-Wallis, $H_{10} = 10$, $p > 0.05$) or ocean basins (Kruskal-Wallis, $H_2 = 1.35$, $p > 0.05$). Regardless of the large variation in SSM at nesting beaches, post-maturity growth rates appear to follow a similar pattern among species (Fig.1). This would support findings from both captive and wild studies that suggest that post-maturity growth rates are correlated neither with SSM, ASM nor body condition (Bjørndal et al. 2013a, 2014, Avens et al. 2015). However, Avens et al. (2015) found lifetime mean growth rates to be correlated with both ASM and SSM in wild loggerhead turtles. Additionally, although sample size is very small, like juvenile growth rates, post-maturity growth rates appear to be sex-specific in green turtles, with males exhibiting lower growth rates than females (Table 1; but see Avens et al. 2015 for faster growth in sub-adult and adult male loggerhead turtles). More data for wild individuals, however, are needed, both across species and sex, to further investigate both of these emerging trends.

Inter-individual differences in responses to seasonality play a role in the duration of both nesting seasons and time spent at foraging grounds (Chaloupka 2001). Vitellogenesis and follicular development are seasonal, occurring around 8-10 mo prior to the breeding season (Rostal et al. 1998) and happen in parallel with lipid deposition (reviewed in Hamann et al. 2003). With reproduction occurring every 2-4 yr (Miller 1997), individuals that remigrate sooner would have a shorter interval to partition resources between growth and restoring body condition. Although delaying reproduction in a given year to invest in growth

should be advantageous and individuals with longer remigration intervals should exhibit higher growth rates, data from leatherback turtles *Dermochelys coriacea* show no such trade-off (Price et al. 2004). Changes in energy allocation appear independent of reproduction.

Seasonality might also help explain some of the variation in post-maturity growth rates. Whereas some individuals remain in colder waters throughout colder months, others migrate into warmer waters (Hawkes et al. 2007). At temperatures below 15°C, individuals in some populations have been observed to rest on the sea floor for extended periods of time, increasing their dive duration as sea surface temperatures decrease (Godley et al. 2002b, Hochscheid et al. 2005, Broderick et al. 2007). Resting dives allow individuals to conserve large amounts of energy (Hays et al. 2000), which could then be partitioned between growth and restoring body condition. In contrast, individuals that migrate out of colder waters might incur greater energetic costs, which could lead to reduced energy available for growth and restoring body condition. However, Hawkes et al. (2007) suggest that those individuals acquire sufficient energy to counteract such costs and that neither strategies confer a significant advantage with regards to reproduction. Nevertheless, as growth and temperature are inversely correlated (Balazs & Chaloupka 2004, Richard et al. 2014), individuals that do not migrate during colder months and reside in highly seasonal environments would be expected to exhibit lower post-maturity growth rates.

Breeding frequency

The amount of resources invested in post-maturity growth decreases over time after sexual maturity, freeing increasing proportions of surplus energy available to maximise lifetime reproductive output (Kozłowski 1996, Rideout & Tomkiewicz 2011, Bjorndal et al. 2013a, 2014). Changes in reproductive efficiency or capacity with age have often been used to explain the difference in reproductive output between new and returning females (Stokes et al. 2014) and have been reported in multiple populations (e.g. Tucker & Frazer 1991, Hawkes et al. 2005, Beggs et al. 2007). Satellite tracking of both new and returning females, however, suggests that low site fidelity of new females is more likely to explain this pattern (Tucker 2010).

With migration being costly, females that delay reproduction should accumulate larger fat stores than females that remigrate sooner. In turn, those females would use a smaller proportion of their fat stores while migrating, which could result in increased clutch size or frequency (number of clutches per season) (Price et al. 2004). While data from leatherback turtles *Dermochelys coriacea* showed that females with longer remigration intervals do not have a greater reproductive output in a given season (Price et al. 2004), Stokes et al. (2014) found that female green turtles *Chelonia mydas* in Cyprus with remigration intervals of less than 3 yr laid 25 % fewer clutches in a given season. These contradictory findings could result from variation in how clutch frequency was estimated or from geographical differences in resources availability (Tucker 2010, Weber et al. 2013). Indeed, the Mediterranean Sea is characterised by low levels of nutrients (Sarà 1985), which may constrain clutch frequencies when remigration intervals are shorter. Similarly, climatic variability is likely to dramatically change resources availability from year to year (Barber et al. 1996, Hays et al. 2005), resulting in both changes in remigration interval and clutch frequency (Broderick et al. 2001, Saba et al. 2007, Neeman et al. 2015).

While changes in energy allocation could help explain the variation in reproductive output over time, individual physiological differences and environmental factors might play a larger role. Indeed, increased energy assimilation efficiency, coupled with increased food availability and quality at foraging grounds, should result in a decrease in remigration interval (Hays 2000,

Price et al. 2004, Ceriani et al. 2015). Similarly, should all foraging grounds be of equal quality, females with a shorter migration between foraging and breeding grounds will require shorter periods to acquire sufficient energy (Price et al. 2004).

Body size can influence foraging habitat use, which in turn influences remigration intervals and breeding frequency (Hawkes et al. 2006, Ceriani et al. 2015; Fig.2). Adult female loggerhead turtles in Japan exhibit size-related differences in foraging habitat use, with smaller females foraging on nutrient-poor planktonic items in oceanic waters, requiring more time to accumulate sufficient resources (Hatase et al. 2004). In contrast, not only do larger females have a shorter interbreeding interval, they also lay a greater number of larger clutches (Hatase et al. 2013). Although similar foraging dichotomies have been documented in other populations and species (Hatase et al. 2006, Hawkes et al. 2006, Seminoff et al. 2008, Reich et al. 2010, Watanabe et al. 2011), they appear to be facultative. For example, telemetry studies in Cyprus showed that nearly all loggerhead turtles are neritic foragers despite their unusual small size (Snape et al. 2016).

Exactly why life-history dichotomies have evolved in sea turtles remains unclear, as they do not appear to be evolutionarily stable. Indeed, settling in oceanic, rather than in neritic, waters appears to be suboptimal for reproducing females as explained above. Eder et al. (2012) speculated that life-history dichotomies have arisen because of immature juveniles settling opportunistically in previously encountered foraging grounds close to their natal beaches (Bowen et al. 2005, Casale et al. 2008), rather than in the best available ones, maturing there and returning to these same foraging grounds with high fidelity as adults (Broderick et al. 2007, Marcovaldi et al. 2010). In turn, differences in settlement locations would lead to differences in growth rates and thus differences in SSM and, ultimately, fitness between oceanic and neritic foragers.

Population recovery

Many maturity threshold studies have focussed on exploited fish stocks where both ASM and SSM were observed to vary with fisheries intensity and ASM and SSM of fish targeted (e.g. Ernande et al. 2004, Dieckmann & Heino 2007). As fish stocks were exploited, ASM and/or SSM decreased (Folkvord et al. 2014). Overexploitation of sea turtles likely resulted in the release of intraspecific competition pressures which allowed individuals to exhibit higher growth rates and thus to mature at a larger size and potentially younger age if sexual maturity resulted from a size threshold (Bernardo 1993). However, it is unlikely that individuals matured at a younger age, as data currently available suggest that sexual maturity is not the result of a size threshold (Caillouet et al. 2011, Bjorndal et al. 2013a, 2014, Avens et al. 2015, 2017).

In contrast, population recovery and its associated density-dependent effects are likely to influence ASM and SSM through increased intraspecific competition for limited resources and habitat availability at foraging grounds. This, in turn, would lead to slower growth rates (Bjorndal et al. 2000a, Balazs & Chaloupka 2004), thus decreasing both SSM and mass at sexual maturity and, increasing ASM (Heppell et al. 2007, Chaloupka et al. 2008), potentially explaining the observed decrease in mean female size at nesting grounds in a number of recovering populations (e.g. da Silva et al. 2007, Bellini et al. 2013, Weber et al. 2014).

Additionally, the reduction in mean SSM observed at nesting beaches could result from selection pressures on larger individuals as a result of fisheries interactions. For example, survival probabilities of loggerhead turtles *Caretta caretta* worldwide are higher for oceanic than for neritic juveniles (Casale et al. 2015, Casale & Heppell 2016). This, coupled with the higher levels of predation in neritic habitats (Bolten 2003b), could help explain the decrease in mean SSM observed at nesting beaches (e.g. da Silva et al. 2007, Bellini et al. 2013, Weber et al. 2014) and is likely to lead to a temporal variation in mean SSM. Whether ASM would follow a similar pattern seems unlikely as oceanic and neritic foragers appear to reach sexual maturity at similar ages (Hatase et al. 2010).

Conclusion

Despite the need to refine population models and the long-term emphasis on obtaining life-history parameters for wild populations in order to assess the conservation status of sea turtles (Rees et al. 2016), unanswered questions remain. The cryptic life-history of sea turtles makes the necessary data difficult to obtain and most studies have therefore relied on indirect methods to estimate these parameters.

Captive studies (e.g. Bjorndal et al. 2013a, 2014) have provided great insight into life-history trade-offs and the shape of growth curves of some, but not all, individuals. They have shown changes in energy allocation to occur a few years prior to sexual maturity and to persist for an unknown number of years after. As expected under indeterminate growth, regardless of size at sexual maturity, captive individuals grow more rapidly in the first few years following sexual maturity before growth decreases and becomes negligible. Similar temporal analyses of post-maturity growth rates for wild populations and for both sexes are needed to refine existing growth curves, estimates of ASM and population dynamic models.

Furthermore, life-history dichotomies have been linked to differences in SSM as well as fitness differences in wild populations. However, it is yet to be demonstrated why these have evolved as they do not appear to be evolutionary stable. Additionally, mean SSM has decreased in recovering populations potentially as a result of a combination of selection pressures imposed by fisheries interaction as well as density-dependent effects associated with population recovery and habitat loss. Whether the observed decrease in mean SSM is due to younger and smaller females entering an older, stable nesting female size distribution due to population protection and recovery over several decades remains to be shown.

Finally, theories on resource allocation and life-history trade-offs from the onset of sexual maturity need to be tested in wild populations. Indeed, it is unclear whether captive species exhibit an age-size trade-off and whether such a trade-off would be observed in wild populations. We have yet to find a non-lethal method that can be used to accurately age all species of sea turtles and determine ASM. Such data are desirable to further our understanding of energy

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allocation, growth and ageing in wild sea turtles. Furthermore, they are required to assess the status of species and to understand population dynamics for both conservation and management.

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Table 1. Summary of published studies of wild male and female post-maturity growth rates per species and ocean basin. No data available for Kemp's ridley and olive ridley turtles. Curved carapace length (CCL): mean \pm SD (range). Estimated clutch frequency: mean \pm SD (range; n). CMR: capture-mark-recapture. Interbreeding interval: mean \pm SD (range; n). CCL growth rates: mean \pm SD (range; n). N/A: not applicable. ¹Broderick et al. (2003); ^{2*} oceanic foragers, Hatase et al. (2013); ^{2**} neritic foragers Hatase et al. (2013); ³Hatase et al. (2004); ⁴Goshe et al. (2010); ⁵Bjorndal et al. (1999); ⁶Troëng & Chaloupka (2007); ⁷Carr & Goodman (1970); ⁸Chaloupka & Limpus (1997); ⁹Limpus (1993); ¹⁰Limpus (1979); ¹¹Santidrián Tomillo et al. (2009); ¹²Santidrián Tomillo et al. (2007); ¹³Price et al. (2004); ¹⁴Dobbs et al. (1999); ¹⁵Bell & Pike (2012); ¹⁶Bjorndal et al. (1985); ¹⁷Snover et al. (2013); ¹⁸Pilcher & Ali (1999); ¹⁹Limpus (2007); ²⁰Limpus et al. (1984); ²¹Parmenter & Limpus (1995)

Species	Ocean basin and study area	Year of study	CCL (cm)	Method	Estimated clutch frequency	Inter-breeding interval (yr)	CCL growth rates (cm yr ⁻¹)
<i>Caretta caretta</i>	Mediterranean Sea ♀ E Mediterranean (N Cyprus)	1992-2000	73.6 \pm 4.6 (63-87)	CMR nesting beach	1.9 \pm 1.2 (168)	2 (median) (1-6; 44)	0.36 \pm 0.57 (-1.0-1.8; 38) ¹
	Pacific Ocean ♀ NW (Minabe, Japan)	1992-2001	(79.3-102.3) ^a	CMR nesting beach	3.6 \pm 1.0 (1-5; 31) ^{2*} 4.3 \pm 1.2 (1-6; 229) ^{2**}	2.7 \pm 1.0 (1-6; 78)	0.27 (-1.89-1.57; 78) ^{3,9}
<i>Chelonia mydas</i>	Atlantic Ocean ♀ NW (Virginia to Florida, USA)	N/A	(106.1-110.0) ^{b,c}	Skeletochronology	N/A	N/A	0.30 (0-1.75; 9) ^{4,9}
	♀ Caribbean Sea (Limón, Costa Rica)	1956-1968	106.1 \pm 5.3 (76.9-126.7) ^d	CMR nesting beach	2.8 (1-6) ⁵	2.95 \pm 0.88 (1-6) ⁶	0.42 (179) ^{7,9}

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	Mediterranean Sea						
	♀ E Mediterranean (N Cyprus)	1992-2000	91.5 ± 6.3 (77-106)	CMR nesting beach	3.0 ± 1.4 (97)	3 (median) (2-6; 46)	0.11 ± 0.46 (-1.0-1.3;51) ¹
	Pacific Ocean						
	♀ Coral Sea (Qld, Australia)	1974-1991	(100-105)	CMR, laparoscopy at foraging grounds	N/A	N/A	0.12 ± 0.04 (± SE) ⁸
	♂	1974-1991	(95-99)	CMR foraging grounds	N/A	N/A	0.07 ± 0.02 (± SE) ⁸
	♂ Coral Sea (Heron Island and Wistari Reefs, Qld, Australia)	N/A	(90-102)	CMR foraging grounds	N/A	2.08 ± 1.14 (1-5; 24) ⁹	0.14 ± 0.11 (-0.3-2.6; 12) ¹⁰
<i>Dermochelys coriacea</i>	Pacific Ocean						
	♀ NE (Guanacaste, Costa Rica)	1993-2002	147.0 ± 5.9 (133-165)	CMR nesting beach	9.45 ± 1.63 (61) ¹¹	3.7 ± 0.2 (1-9) ¹²	0.2 ± 0.05 (-1.5-2.0; 152) ¹³
<i>Eretmochelys imbricata</i>	Atlantic Ocean						
	♀ Caribbean Sea (Limón, Costa Rica)	1955-1977	82.0 ± 3.9 (72.4-94.0)	CMR nesting beach	2.1	3.0 (3-6; 4)	0.3 ± 0.3 (-0.9-2.7; 4) ¹⁶
	Pacific Ocean						
	♀ SW (Milman Island, Qld, Australia)	1991-1995	81.6 (63.5-91.9)	CMR nesting beach	2.54 ± 1.44 (1-7; 1525)	3.4 ± 0.62 (22)	0.27 ± 0.19 (0.0-0.7; 22) ¹⁴
	♀ Coral Sea (Qld, Australia)	1997-2008	>80	CMR, laparoscopy at foraging grounds	N/A	N/A	0.17 (-0.9-2.7; 45) ¹⁵
	♀ N (Hawaii, USA)	N/A	> 86.5 ^{d,e}	Skeletochronology	N/A	N/A	0.30 (9) ^{17,g}

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<i>Natator depressus</i>	♀ NW (Sabah, Malaysia)	1985-1997	82.1 ^d	CMR nesting beach	2.7	1.84	0.24 ^{18,g}
	Pacific Ocean						
	♀ SW (Peak Island, Qld, Australia)	1980-1991	94.0 ± 2.60 (85.5-100.0) ¹⁹	CMR nesting beach	2.84 ± 0.78 (1-4; 43) ²⁰	2.2 ± 0.44 (1-5; 215)	0.012 ± 0.009 (± SE; 440) ²¹

^aConverted from straight carapace length (SCL) using equation in Peckham et al. (2011). ^bConverted using equation in Goshe (2009). ^cAdult green turtles nesting at an average of 99.1 cm SCL (105.2 cm CCL) (Van Buskirk & Crowder 1994). ^dConverted using equation in Bjorndal et al. (2008). ^eAdult hawksbill turtles nesting at an average of 82.3 cm SCL (89 cm CCL) (Seitz et al. 2012). ^fThree females and 6 individuals of unknown sex. ^gConverted from original straight carapace length growth values.

Table 2. Summary of captive studies of female post-maturity growth rates per species and ocean basin. No data available for loggerhead, leatherback, olive ridley and flatback turtles. Curved carapace length (CCL): mean \pm SD (range; n). CCL growth rates: mean \pm SD (range; n). CMR: capture-mark-recapture. ¹Bjorndal et al. (2013a); ²Kawazu et al. (2015); ³Bjorndal et al. (2014); ⁴Marquez (1994).

Species	Ocean basin and study area	Origin of individuals	CCL (cm)	Method	CCL growth rates (cm yr ⁻¹)
<i>Chelonia mydas</i>	Atlantic Ocean				
	Caribbean Sea (Grand Cayman, UK) ¹	Derived from eggs collected at Ascension Island, Suriname and Tortuguero, Costa Rica between 1968 and 1972	101.8 \pm 7.1 (87.6-119.4; 33)	CMR	0.94 \pm 0.73 (0-3.81; 33) ^a 0.38 \pm 0.21 (0.13-0.95; 31) ^b
<i>Eretmochelys imbricata</i>	Pacific Ocean NW (Okinawa, Japan) ²	Derived from eggs collected at Zamami Island between 1993 and 1994	84.0 \pm 3.3 (79.2-90.3; 23) ^c	Ultrasonography	1.08 (23) ^{d,i}
<i>Lepidochelys kempii</i>	Atlantic Ocean				
	Caribbean Sea (Grand Cayman, UK) ³	Derived from eggs collected at Tamaulipas, Mexico in 1979	55.2 \pm 3.7 (47.0-61.0; 12)	CMR	0.4 \pm 0.4 (0-1.3; 12) ^e 0.3 \pm 0.2 (0-0.5; 10) ^f
	Gulf of Mexico (Mexico) ^{4,g}	Unknown	66.6 \pm 2.4 (63.7-71.1; 11) ^h	CMR	0.96 (-2.35-6.32; 11) ⁱ

^aFour-year duration after first nesting. ^bAverage across ages (9-20 yr duration after first nesting). ^cThree-year duration after the onset of follicular development. ^dConverted from straight carapace length using equation in Bjorndal et al. (2008). ^eThree-year

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duration after first nesting. ^fAverage across ages (6-11 yr duration after first nesting). ^gExtracted from Table 15 in Marquez (1994), excluding females with recapture interval of < 11 mo (n = 2). ^hConverted using equation in Snover et al. (2007b). ⁱConverted from original straight carapace length growth values.

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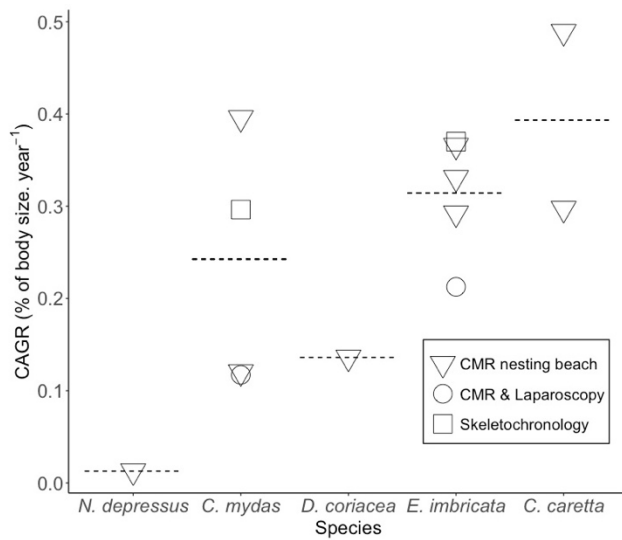


Figure 1. Female compound annual growth rates (CAGR) for wild populations. Dashed lines represent the mean for each species. CAGR were calculated from values presented in Table 1. The arithmetic mean of range values was used when mean CCL was not available. CMR: capture-mark-recapture. See Table 1 for genus names.

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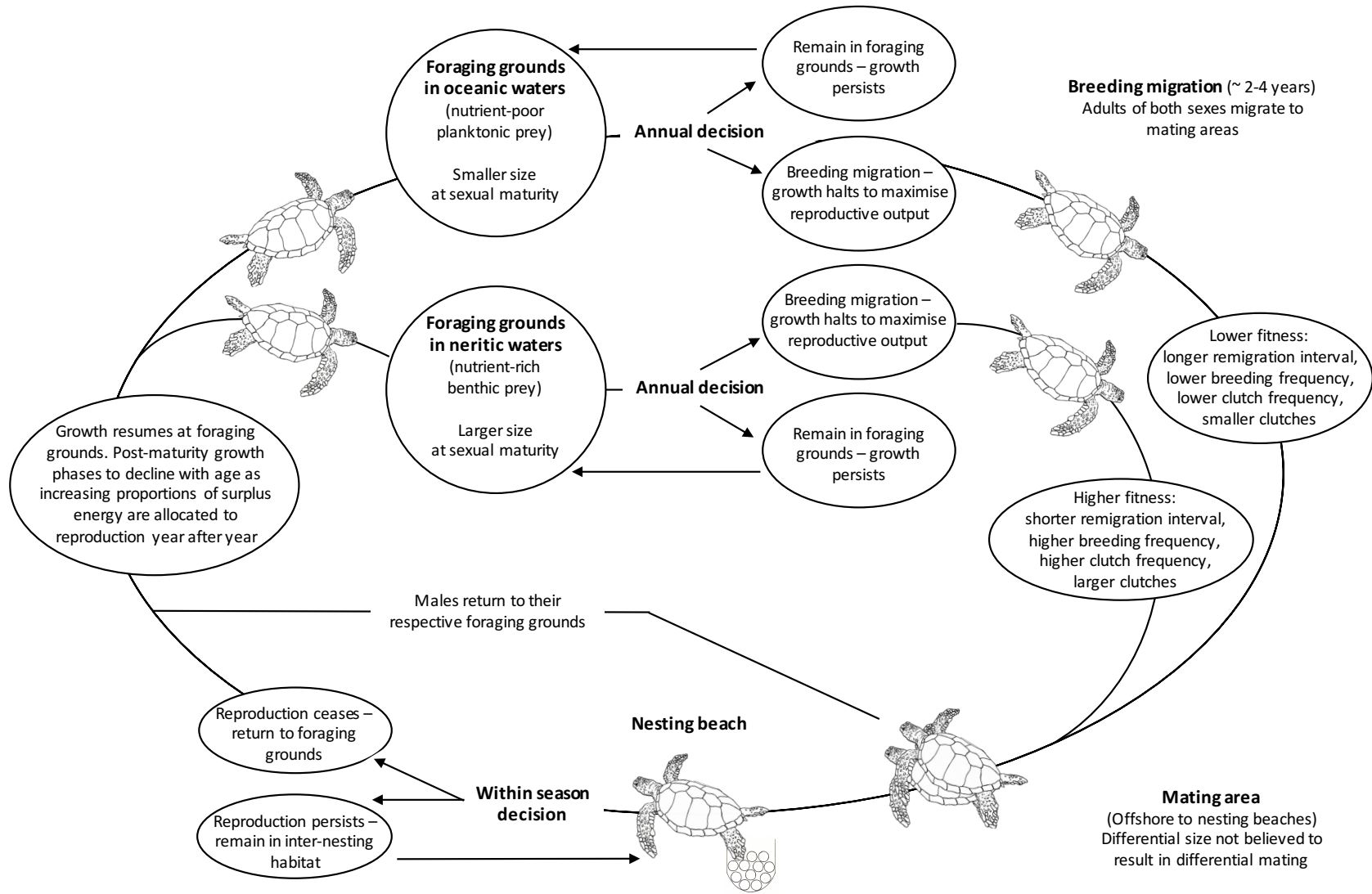


Figure 2. Dichotomous adult life-cycle for loggerhead, green, hawksbill, Kemp’s ridley and olive ridley turtles.

CHAPTER 3: DETERMINATE OR INDETERMINATE GROWTH? REVISITING THE GROWTH STRATEGY OF SEA TURTLES

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Abstract

Traditionally, growth can be either determinate, ceasing during the natural lifespan of individuals, or indeterminate, persisting throughout life. Although indeterminate growth is a widely accepted strategy and believed to be ubiquitous among long-lived species, it may not be as common as previously thought. Sea turtles are believed to be indeterminate growers despite the paucity of long-term studies into post-maturity growth. In this study, we provide the first temporal analysis of post-maturity growth rates in wild living sea turtles, using 26 yr of data on individual measurements of females nesting in Cyprus. We used generalised additive/linear mixed models to incorporate multiple growth measurements for each female and model post-maturity growth over time. We found post-maturity growth to persist in green *Chelonia mydas* and loggerhead *Caretta caretta* turtles, with growth decreasing for approximately 14 yr before plateauing around zero for a further decade solely in green turtles. We also found growth to be independent of size at sexual maturity in both species. Additionally, although annual growth and compound annual growth rates were higher in green turtles than in loggerhead turtles, this difference was not statistically significant. While indeterminate growth is believed to be a key life-history trait of ectothermic vertebrates, here, we provide evidence of determinate growth in green and loggerhead turtles and suggest that determinate growth is a life-history trait shared by cheloniid species. Our results highlight the need for long-term studies to refine life-history models and further our understanding of ageing and longevity of wild sea turtles for conservation and management.

Introduction

Traditionally, growth, defined as the increase in skeletal size, can be either determinate or indeterminate. These 2 growth strategies were first coined by Lincoln et al. (1982), who defined determinate growth as growth that ceases during an individual's natural lifespan after it has reached its final body size, whereas under indeterminate growth, individuals retain the ability to grow throughout their life and age and body size are correlated. Growth strategies can be further categorised into 7 basic growth curves, which are variations on attenuating or asymptotic growth that is genetically or environmentally determined (Sebens 1987, Fig. 1, Table 1).

The key difference between determinate and indeterminate growth strategies lies in the growth trajectories themselves rather than the attainment of a final body size (Sebens 1987). Whereas growth trajectories under determinate growth are set during ontogeny, after which large changes in trajectory are not possible, growth trajectories of indeterminate growers are far less constrained (Sebens 1987). Indeed, indeterminate growers retain the ability to grow and to match their growth rates to their environment throughout their life, such that an individual's asymptotic body size is reversible and not confounded with its final body size (Sebens 1987).

Age at sexual maturity (ASM) and size at sexual maturity (SSM) are key life-history parameters which result from an individual's growth strategy (Bernardo 1993). The 2 most common maturation norms depict an inverse relationship between growth rates during development and ASM and an inverse or positive relationship between growth rates and SSM (Stearns & Koella 1986). Individuals can mature at either a large or a small SSM under both growth scenarios, but individuals tend to mature early when growth is rapid and late when growth is slow. Rarely is sexual maturity the result of a genetically determined age or size threshold (Bernardo 1993).

Because organisms have finite resources to partition between competing needs (Gadgil & Bossert 1970), maturation requires a change in resource allocation from growth towards reproduction (Bernardo 1993), leading to a reduction of growth rates prior to sexual maturity (Kozłowski 1996). Although sexual maturity is often considered a turning point during which growth should cease under determinate growth, growth can persist after sexual maturity for a

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number of years in both determinate and indeterminate growers (Sebens 1987, Karkach 2006). However, because fecundity tends to increase with body size in indeterminate growers (Olsson & Shine 1996), such a growth strategy would be selected if post-maturity growth leads to a larger body size that confers a fitness advantage (Kingsolver & Pfennig 2004).

Indeterminate growth is believed to be ubiquitous among ectothermic vertebrates despite the lack of evidence to support this theory (Congdon et al. 2013, Lee et al. 2013). Indeed, because ectothermic vertebrates tend to be long-lived, longitudinal studies are rare yet are needed to accumulate such evidence (Tinkle 1979). Such studies, however, tend to be logistically challenging to maintain over sufficiently long periods of time to encompass the natural lifespan of individuals.

Nevertheless, recent work suggests that indeterminate growth might not be as common as previously thought. Osteohistological analysis of both extinct and extant species believed to be indeterminate growers has revealed growth to cease entirely during their natural lifespan (e.g. Erickson 2014, Werning & Nesbitt 2016, Wilkinson et al. 2016, Company & Pereda-Suberbiola 2017, Frydlova et al. 2017). In addition, results from capture–mark–recapture (e.g. Bjorndal et al. 2013, 2014, Congdon et al. 2013, Nafus 2015, Plummer & Mills 2015) and skeletochronological studies (e.g. Chaloupka & Zug 1997, Limpus & Chaloupka 1997, Zug et al. 2002, Avens et al. 2013, 2015, 2017) of testudine species suggest that some individuals may cease growing during their natural lifespan. Whether this reflects evidence to support determinate growth in these species requires further research.

Although growth in sea turtles is widely accepted to be indeterminate (Shine & Iverson 1995), post-maturity growth rates are considered overall to be negligible once individuals reach sexual maturity (Omeyer et al. 2017). No study has looked at the long-term temporal variation of post-maturity growth rates in wild individuals to determine whether sea turtles are truly indeterminate growers. Two captive studies have found, however, that individuals grew more rapidly in the first 3 to 4 yr following sexual maturity than across all post-maturity years before growth became negligible. This pattern was not age or size related, nor was it linked to body condition at sexual maturity (Bjorndal et al. 2013, 2014). Additionally, a marked decrease in growth rates around sexual maturity has been observed in skeletochronological studies, with post-maturity growth rates

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becoming negligible and with size-at-age curves suggesting a possible cessation of growth altogether (e.g. Chaloupka & Zug 1997, Limpus & Chaloupka 1997, Zug et al. 2002, Casale et al. 2011b, Avens et al. 2013, 2015, 2017). Together these lines of evidence would suggest that growth is potentially determinate in sea turtles.

In this study, we describe post-maturity growth in wild loggerhead *Caretta caretta* and green *Chelonia mydas* turtles nesting sympatrically over a 26 yr period and provide the first temporal analysis of post-maturity growth in wild living sea turtles. We sought to answer 4 questions: (1) Does growth persist after sexual maturity in wild individuals? (2) If so, how does it vary over time? (3) Is post-maturity growth size dependent? (4) Is growth determinate or indeterminate in green and loggerhead turtles in the Mediterranean?

Materials and methods

Study site

Data were collected at Alagadi beach, Cyprus (35° 33' N, 33° 47' E), between 1992 and 2017. Alagadi Beach consists of 2 coves, 0.8 and 1.2 km in length, separated by a rocky headland (Broderick et al. 2002).

Data collection

The beach was monitored between 21:00 and 06:00 h each night throughout the nesting seasons (late May to mid-August) of 1993 to 2017 and from July to mid-August in 1992. Females were externally tagged using plastic (1992 to 1998), titanium (1998 to 2012 and 2014 to 2017) and Inconel (2013 and 2017) flipper tags and were also injected with passive integrated transponder (PIT) tags (Godley et al. 1999) from 1997 onwards. Curved carapace length (CCL) notch to notch (see Bolten 1999 for further details) was used as the proxy for skeletal size (i.e. carapace size without the keratinous scutes). Three CCL measurements were taken by 1 observer at each laying event for each female using a flexible tape measure and a mean calculated. Mean size for each female was then calculated for each nesting season. The measurement protocol was kept consistent throughout the study period, and new tape measures were used each season to avoid error associated with stretching. CCL measurement error within a nesting season was calculated as 0.5 cm for both green and loggerhead turtles. Although loggerhead turtles, in particular, often carry a heavy and variable load of epibiota, females nesting in Cyprus are relatively free of epibiota. If epibiota distribution influenced CCL measurements, these measurements were removed from the dataset. Remigration interval (RI) was calculated as the number of years elapsed between consecutive breeding years. Annual growth was calculated for each female at each recapture interval as:

$$\frac{(CCL_n - CCL_{n-1})}{RI}$$

(1)

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where n represents the capture number. To account for females recruiting to the nesting population at different sizes, compound annual growth rate (CAGR), expressed as a percentage of body size per year, was calculated as follows:

$$\left(\left(\frac{CCL_n}{CCL_{n-1}} \right)^{\left(\frac{1}{RI} \right)} - 1 \right) \times 100 \quad (2)$$

Data analysis

Generalised additive mixed models (GAMMs) were used to model non-linear relationships between covariates and growth and incorporated multiple growth measurements for each female. Generalised linear mixed models (GLMMs) were subsequently used if relationships were found to be linear.

Annual growth models included 3 covariates (mean CCL, RI and years since first capture/nesting), and CAGR models included 2 covariates (RI and years since first capture/nesting). Mean CCL between captures was used because it is believed to be the best approximation of the individual's size for which growth was calculated, assuming linear growth within the recapture interval. RI was also included in the models to account for any bias introduced by variable lengths of recapture intervals. Years since first capture/nesting was calculated as the number of years elapsed since recruitment to the nesting population, with first-time nesters being given year 0, to investigate temporal variability of annual growth.

Two datasets were used to analyse the data: a dataset that comprised all growth records from 1992 onwards and a restricted dataset from 2000 onwards. The restricted dataset was used to increase the accuracy of neophyte classification following 1 breeding cycle after the introduction of PIT tagging in 1997. Flipper tag loss prior to 1997 may have reduced recaptures, whereas PIT tag loss is negligible (e.g. Braun-McNeill et al. 2013). Thus, we distinguish between years since first capture for the analysis of the complete dataset and year since first nesting for the analysis of the restricted dataset.

Because of the inherent time-dependent sampling design of capture-mark-recapture studies, all models included mean year as a random effect, which was calculated as the midpoint of the recapture interval. All models also included

female ID as a random effect to account for pseudoreplication of repeat captures. Negative and zero growth values were included in the analyses to avoid systematic bias. These could result from measurement error, leading to overestimation of growth if removed (e.g. Bjorndal & Bolten 1988, Chaloupka & Limpus 1997, Bjorndal et al. 2000), from carapace abrasion rates exceeding growth later in life (Bell & Pike 2012) or from a loss of body condition leading to shrinkage, as previously observed in tortoises (Loehr et al. 2007).

All models were implemented using the `gamm4`, `nlme` and `mgcv` packages (Wood 2006, Pinheiro et al. 2013, Wood & Scheipl 2014) in the statistical program R (R Core Team 2014). GAMM models incorporated an identity link function, a robust quasi-likelihood function and flexible cubic smoothing splines. Stepwise removal of covariates in subsequent models was conducted, and Akaike's information criterion values were evaluated for each model fit. GLMM models incorporated an identity link function. Models were fitted by stepwise model simplification, and significance of removed terms was assessed by likelihood ratio tests using maximum likelihood estimates in order of least significance with a threshold of $p = 0.05$ (Crawley 2007). Finally, model residuals were checked for over-dispersion, normality and homoscedasticity.

Results

Dataset and basic parameters

The complete dataset comprised 339 growth records for 147 green turtles and 158 growth records for 85 loggerhead turtles, and the restricted dataset comprised 174 growth records for 104 green turtles and 69 growth records for 45 loggerhead turtles (see Table S1 in the Supplement at www.int-res.com/articles/suppl/m596p199_supp.pdf for further details).

Capture histories were longer for green turtles than for loggerhead turtles in both datasets (Fig. 2). The median length of capture histories was 6 yr (complete dataset) or 5 yr (restricted dataset) for green turtles and 4 yr (both datasets) for loggerhead turtles (Table 2).

At first nesting, green turtles measured on average 86.5 cm CCL (SD: ± 5.5), whereas loggerhead turtles measured 72.3 cm CCL (SD: ± 3.6 ; Table 2). The median RI for both species was 3 yr for both datasets (Table 2). Mean annual growth rates and mean CAGR were higher in green turtles (0.4 ± 0.6 cm yr⁻¹ and 0.4 ± 0.7 % of body size yr⁻¹, respectively) than in loggerhead turtles (0.2 ± 0.6 cm yr⁻¹ and 0.3 ± 0.5 % of body size yr⁻¹, respectively; Table 2). However, both mean annual growth rates and mean CAGR were higher in the restricted dataset than in the complete dataset for both species (see Table 2).

Green turtles

Complete dataset

Results of the GAMM analyses for green turtles for both annual growth and CAGR are summarised in Tables S2 & S3 in the Supplement.

We found that initial annual growth at first capture averaged 0.7 cm yr⁻¹, with growth decreasing for approximately 14 yr before plateauing around zero (Fig. S1a in the Supplement). Similarly, CAGR averaged 0.8 % of body size yr⁻¹ at first capture, decreasing for approximately 12 yr before plateauing around zero (Fig. 3a). We also found that annual growth significantly decreased with increasing mean CCL (Fig. S2a in the Supplement). However, using CAGR models, we found that growth significantly decreased, independently of SSM (Fig.

3a). Furthermore, we found RI not to have a significant effect on annual growth or CAGR.

Restricted dataset

Results of the GLMM analyses for both annual growth and CAGR on the restricted dataset are similar to those conducted on the complete dataset. Indeed, we found that both annual growth ($\chi^2_{(1)} = 18.44$, $p < 0.0001$; Fig. S1b in the Supplement) and CAGR ($\chi^2_{(1)} = 33.94$, $p < 0.0001$; Fig. 3b) decreased significantly over time. Note that initial annual growth (1.0 cm yr^{-1}) and initial CAGR (1.1% of body size yr^{-1}) values at first nesting were higher than initial values calculated from the complete dataset (respectively 0.7 cm yr^{-1} and 0.8% of body size yr^{-1}). Similarly to the complete dataset, annual growth significantly decreased with increasing mean CCL ($\chi^2_{(1)} = 9.52$, $p = 0.002$; Fig. 4a) and RI was found not to have a significant effect on annual growth ($\chi^2_{(1)} = 0.79$, $p = 0.38$) or CAGR ($\chi^2_{(1)} = 0.53$, $p = 0.47$).

Loggerhead turtles

Complete dataset

In contrast with green turtles, results of the GLMM analyses for loggerhead turtles indicated that neither annual growth nor CAGR were influenced by years since first capture (annual growth: $\chi^2_{(1)} = 1.92$, $p = 0.17$, Fig. S1c in the Supplement; CAGR: $\chi^2_{(1)} = 2.13$, $p = 0.14$, Fig. 3c), mean CCL (annual growth: $\chi^2_{(1)} = 0.73$, $p = 0.39$; Fig. S2b in the Supplement) or RI (annual growth: $\chi^2_{(1)} = 0.03$, $p = 0.86$; CAGR: $\chi^2_{(1)} = 0.02$, $p = 0.89$).

Restricted dataset

Results from the restricted database, however, were similar to green turtles, in that we found that both annual growth ($\chi^2_{(1)} = 4.43$, $p = 0.04$; Fig. S1d in the Supplement) and CAGR ($\chi^2_{(1)} = 4.14$, $p = 0.04$; Fig. 3d) significantly decreased with years since first nesting. However, initial annual growth (0.5 cm yr^{-1}) and initial CAGR (0.7% of body size yr^{-1}) values for loggerhead turtles were lower than for green turtles (respectively 1.0 cm yr^{-1} and 1.1% of body size yr^{-1}) for the restricted dataset. Additionally, there was no significant difference in

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growth curves between the 2 species (annual growth: $\chi^2_{(1)} = 3.19$, $p = 0.07$; CAGR: $\chi^2_{(1)} = 1.24$, $p = 0.27$). Furthermore, neither mean CCL (annual growth: $\chi^2_{(1)} = 1.04$, $p = 0.31$; Fig. 4b) nor RI (annual growth: $\chi^2_{(1)} = 0.92$, $p = 0.34$; CAGR: $\chi^2_{(1)} = 1.06$, $p = 0.30$) had significant effects on annual growth or CAGR. Although annual growth decreased with mean CCL for green turtles but not for loggerhead turtles, this difference was not significant ($\chi^2_{(1)} = 0.76$, $p = 0.38$). The smaller sample size for loggerhead turtles due to lack of recaptures likely prevented the detection of this trend.

Discussion

Based on Lincoln et al.'s (1982) definitions of both determinate and indeterminate growth, our results would suggest that green and loggerhead turtles nesting in Cyprus are determinate growers. Indeed, our analysis showed post-maturity growth to persist in both species, significantly decreasing for over a decade, before individuals reached an asymptotic body size solely in green turtles. Indeterminate growth in sea turtles is widely accepted; however, we believe that results from both captive (Bjorndal et al. 2013, 2014) and skeletochronological (e.g. Chaloupka & Zug 1997, Limpus & Chaloupka 1997, Zug et al. 2002, Avens et al. 2013, 2015, 2017) studies would support our findings suggesting that sea turtles are in fact determinate growers, although variation in growth strategy within and between populations and species might occur. While longevity of sea turtles remains unknown, it is unlikely that captive individuals reached their asymptotic body size outside of their natural lifespan, as captive individuals tend to mature earlier and therefore reach their asymptotic body size earlier than their wild counterparts (Bjorndal et al. 2013).

Under Lincoln et al.'s (1982) indeterminate growth definition, age and body size are expected to be correlated such that the largest individuals would be the oldest. Although investigating the age-size trade-off was outside the scope of this study, 3 studies have done so, providing inconclusive results (Bjorndal et al. 2013, 2014, Tucek et al. 2014). Indeed, while such a trade-off was observed in 14 captive Kemp's ridley turtles (*Lepidochelys kempii*; Bjorndal et al. 2014), it was not observed in 47 captive green turtles (Bjorndal et al. 2013) or 137 wild loggerhead turtles (Tucek et al. 2014), suggesting that age and body size are unlikely to be correlated at sexual maturity in adult sea turtles, such as in a species of freshwater turtles (Congdon et al. 2001). Even though size and age are found to be highly correlated, although with large variation, in juvenile sea turtles in skeletochronological studies (e.g. Avens et al. 2013, 2015, Ramirez et al. 2017), with growth ceasing around sexual maturity, such a correlation would be expected to weaken and possibly disappear as individuals age. Thus, it would appear that the growth strategy of sea turtles does not match either part of Lincoln et al.'s (1982) definition of indeterminate growth. Regarding Sebens' (1987) 7 basic growth curves (see Fig. 1 and Table 1 for more details), the growth strategy of green turtles in this study and of other species in captive (Bjorndal et al. 2013,

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2014) and skeletochronological (e.g. Chaloupka & Zug 1997, Limpus & Chaloupka 1997, Zug et al. 2002, Avens et al. 2013, 2015, 2017) studies seems to more closely resemble that of determinate growth types I and II (asymptotic growth). Using results from this study alone, however, we cannot exclude indeterminate growth type I (asymptotic growth), in which the asymptotic body size is not confounded with an individual's final body size and is reversible, should environmental conditions change. On the other hand, determinate growth types III and IV (attenuating growth) and indeterminate growth types II and III (exponential and attenuating growth, respectively) can be excluded. Indeed, growth ceased in green turtles in this study as well as in captive studies (Bjorndal et al. 2013, 2014), and size-at-age curves from skeletochronology studies (e.g. Chaloupka & Zug 1997, Limpus & Chaloupka 1997, Zug et al. 2002, Avens et al. 2013, 2015, 2017) suggest cessation of growth after sexual maturity. Additionally, sea turtles are not modular animals.

Sea turtles are characterised by a large variation in SSM across both nesting rookeries and species (Van Buskirk & Crowder 1994). Using captive individuals, studies have recently suggested that the variation in SSM observed within and among rookeries is due to variation in juvenile growth rates rather than post-maturity growth (Bjorndal et al. 2013, 2014). Indeed, even when raised under identical conditions, individuals of the same genetic stock showed a large variation in SSM (Bjorndal et al. 2014). In addition, our CAGR models showed post-maturity growth to decrease in a similar manner across individuals regardless of SSM in both species. The smallest individuals at sexual maturity did not invest more in growth than the largest ones, as observed in captive individuals (Bjorndal et al. 2013), and individuals with larger RIs did not invest more in growth, as observed in wild leatherback turtles (*Dermochelys coriacea*; Price et al. 2004), although the latter study was based on single growth rates and RIs. Together, these results allow us to exclude determinate type I (genetically determined asymptotic growth) and partially exclude indeterminate type I (asymptotic growth with reversible asymptotic body size). Indeed, sexual maturity does not appear to result from a genetically determined size threshold, and large changes in post-maturity growth trajectories appear unlikely.

In addition, growth trajectories of juvenile sea turtles appear more constrained than previously thought. Indeed, it was believed that the reversible and facultative ontogenetic shift between oceanic and neritic waters allowed

juveniles to compensate for low growth conditions by performing catch-up growth (Bjørndal et al. 2003, Roark et al. 2009, Bjørndal & Bolten 2010, but see Snover et al. 2007 for absence of compensatory growth), leading to differences in growth trajectories and SSM between oceanic and neritic foragers (Hatase & Tsukamoto 2008, Peckham et al. 2011). However, Ramirez et al. (2017) showed that although this habitat shift does result in higher growth rates, this increase is short lived (1 to 2 yr) and growth trajectories of oceanic and neritic foragers remain similar. This would further support determinate growth type II (habitat-dependent asymptotic growth with non-reversible asymptotic body size) in sea turtles rather than indeterminate growth type I (habitat-dependent asymptotic growth with reversible asymptotic body size), as large changes in growth trajectories both during development and after sexual maturity do not seem possible, which would suggest that the asymptotic body size reached by individuals might be confounded with their final body size.

Osteohistological analysis and, more precisely, the presence of an external fundamental system (EFS) could be used to determine whether skeletal maturity is ever reached in sea turtles. An EFS is a tightly spaced set of lines of arrested growth (LAG), which is thought to be characteristic of determinate growers, as it marks the attainment of a final non-reversible body size. It has been observed in a number of reptile species previously thought to be indeterminate growers (e.g. Wilkinson et al. 2016, Frydlova et al. 2017). Although an EFS has not been documented yet in sea turtles, evidence from skeletochronological studies would suggest that it might have been observed. Indeed, the term LAG rapprochement, used in sea turtle studies (e.g. Snover et al. 2013, Avens et al. 2015, 2017, Petit et al. 2015), appears to resemble an EFS. It corresponds to an abrupt decrease in the spacing of LAGs, associated with the decrease in growth rates once individuals reach sexual maturity, and has been used to estimate SSM (Table 3). Osteohistological analysis of large specimens is needed to investigate the presence or absence of an EFS to determine whether sea turtles are truly determinate growers.

Furthermore, it appears that indeterminate growth is unlikely to have been selected in sea turtles. Indeed, indeterminate growth should be selected if post-maturity growth leads to a larger body size that confers a fitness advantage, resulting in higher lifetime reproductive output through either increased survival or fecundity (Kingsolver & Pfennig 2004). In our study, we found that an average

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green turtle would reach sexual maturity having grown 96 % of its asymptotic body size and would grow just under 3.5 cm over the next decade. This equates to the differences in size between neophyte and remigrant females at this nesting ground (Stokes et al. 2014). However, measurement error could have biased these estimates. Such an increase in size would result in females laying on average 8 additional eggs per clutch, after having grown for over a decade (Broderick et al. 2003), although this is a potential underestimate, as it was calculated using values from the complete dataset. Additionally, focussing on changes in body mass rather than body size might be more informative in terms of fitness advantages, for both survival and fecundity. In a similar manner, we extracted from the literature values for SSM and asymptotic body size for 6 of the 7 species of sea turtles (Table 3). From this table, we calculated that, on average, sea turtles reach sexual maturity having grown 85 % of their asymptotic body size, with loggerhead and hawksbill turtles maturing having grown less of their asymptotic body size (80 % and 83 % respectively) than green turtles (85 %), Kemp's ridley turtles (88 %) and leatherback and olive ridley turtles (90 %). With on average only 15 % of their asymptotic body size remaining to grow after sexual maturity, it appears unlikely that post-maturity growth would lead to large increases in fecundity across species and, thus, that indeterminate growth would have been selected for in sea turtles, as has also been found in the freshwater Blanding's turtle (*Emydoidea blandingii*; Congdon et al. 2001). Delaying sexual maturity would be expected to be more advantageous, as it would allow individuals to reach a larger SSM and therefore asymptotic body size when growth rates are still relatively high. Captive studies suggest that even when fed ad libitum, rather than investing in post-maturity growth, after sexual maturity, resources were better invested into maximising lifetime reproductive output by increasing clutch frequency and decreasing the interval between breeding years (Bjorndal et al. 2013).

Finally, as highlighted by Sebens (1987), many growth patterns do not exclusively fit either of Lincoln et al.'s (1982) definitions. For example, the definition of indeterminate growth more closely resembles determinate growth type III (genetically determined attenuating growth) rather than any indeterminate growth curves (Sebens 1987, see Table 1 and Fig. 1). In a review of animal growth, Karkach (2006) suggested to redefine these 2 growth strategies around life-history traits rather than around sexual maturity and the attainment of an

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asymptotic body size. He proposed 2 definitions centred around mortality and reproduction, such that individuals would be determinate growers if they reach their asymptotic body size either when many individuals from their cohort were still alive or when individuals had most of their reproductive lifespan ahead of them. Here, we estimated that individuals would reach their asymptotic body size just over a decade after first nesting, which seems realistic, as growth was found to persist for up to 18 yr after LAG rapprochement in other studies (Avens et al. 2015, Petit et al. 2015). Using skeletochronology, Snover et al. (2013) suggested that reproductive longevity post-LAG rapprochement ranged between 4 and 49 yr, with an average of 19 yr. This would imply that sea turtles might reach their asymptotic body size at the end of their reproductive lifespan, making them indeterminate growers. However, because knowledge of reproductive longevity is currently limited for sea turtles (Seminoff 2004, Casale 2015, Rees et al. 2016), determining the growth strategy of sea turtles under such a definition will require further research. On the other hand, based on the survival hypothesis, because survival probability to adulthood is extremely low (Frazer 1986, Chaloupka & Limpus 2005, Casale et al. 2015), sea turtles would be considered indeterminate growers. These contradictory results highlight the need for newer, clearer definitions of both determinate and indeterminate growth which fit basic growth patterns exclusively.

In conclusion, while sea turtles were long thought to be indeterminate growers (Shine & Iverson 1995), in this study, we challenge this idea, provide evidence for determinate growth in green and loggerhead turtles nesting in Cyprus and suggest that determinate growth is a life-history trait shared by cheloniid species. Indeed, we showed that growth persisted after sexual maturity in both wild green and loggerhead turtles, decreasing for approximately a decade in both species before reaching an asymptote solely in green turtles. We also showed, using CAGR models, that post-maturity growth decreased in a similar manner across individuals regardless of SSM in both species. We suggest that the asymptotic body size is likely to be confounded with an individual's final body size and that growth trajectories of sea turtles are relatively constrained after an initial growth period preceding their ontogenetic shift from oceanic to neritic habitats. Such a growth strategy most closely resembles Sebens' (1987) determinate growth type II, in which growth is asymptotic and habitat dependent, leading to small variation in SSM and asymptotic body size. Although results from

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captive (Bjørndal et al. 2013, 2014) and skeletochronology studies (e.g. Chaloupka & Zug 1997, Limpus & Chaloupka 1997, Zug et al. 2002, Avens et al. 2013, 2015, 2017) would support our findings, similar temporal analyses of post-maturity growth and osteohistological studies are needed to further explore the growth strategy of sea turtles and to determine whether variation within and between populations and species occurs. Such studies will help refine life-history models and further our understanding of ageing and longevity of wild sea turtles for both conservation and management.

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- Zug GR, Parham JF (1996) Age and growth in leatherback turtles, *Dermochelys coriacea* (Testudines: *Dermochelyidae*): a skeletochronological analysis. *Chelonian Conserv Biol* 2:244–249

Chapter 3: Determinate or indeterminate growth?

Table 1. Summary of Sebens' (1987) 7 basic growth curves and Lincoln et al.'s (1982) determinate and indeterminate definitions, providing evidence (√) for and against (×) each growth strategies or definitions. ?: inconclusive, more research needed.

Growth Reference	Definition	This study	Other studies
Determinate			
(Lincoln et al. 1982)	Growth ceases during an individual's natural lifespan after it has reached its final body size	√	√ Asymptotic growth in captive green ^a and Kemp's ridley ^b turtles √? Skeletochronology suggests individuals may reach skeletal maturity ^{c,d,e,f}
(Sebens 1987)	Type I: Asymptotic growth, genetically determined with little environmental variation	√	√ Asymptotic growth in captive green ^a and Kemp's ridley ^b turtles √? Skeletochronology suggests individuals may reach skeletal maturity ^{c,d,e,f} × Sexual maturity not genetically determined in captive green ^a and Kemp's ridley ^b turtles
	Type II: Asymptotic growth, habitat dependent	√	√ Asymptotic growth in captive green ^a and Kemp's ridley ^b turtles √ Constrained growth trajectories both during ontogeny and post-maturity ^{a,b,g,h} √ Large variation in size at sexual maturity observed within and among rookeries and species ^l √? Skeletochronology suggests individuals may reach skeletal maturity ^{c,d,e,f}
	Type III: Attenuating growth, genetically determined with little environmental variation	×	× Asymptotic growth in captive green ^a and Kemp's ridley ^b turtles × Sexual maturity not genetically determined in captive green ^a and Kemp's ridley ^b turtles
	Type IV: Attenuating growth, habitat dependent	×	× Asymptotic growth in captive green ^a and Kemp's ridley ^b turtles

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Indeterminate

(Lincoln et al. 1982)	Individuals retain the ability to grow throughout life and age and body size are correlated	×	×	Cessation of growth around sexual maturity in captive green ^a and Kemp's ridley ^b turtles
			×?	Skeletochronology suggests individuals may reach skeletal maturity ^{c,d,e,f}
			×	Age and body size unlikely to be correlated throughout life
(Sebens 1987)	Type I: Asymptotic growth, habitat dependent. Asymptotic size is reversible and not confounded with an individual's final body size	√	√	Asymptotic growth in captive green ^a and Kemp's ridley ^b turtles
			×	Constrained growth trajectories both during ontogeny and post-maturity ^{a,b,g,h}
			×?	Skeletochronology suggests individuals may reach skeletal maturity ^{c,d,e,f}
	Type II: Exponential growth (modular animals)	×	×	Asymptotic growth in captive green ^a and Kemp's ridley ^b turtles
	Type III: Attenuating growth. Individuals can match their growth rates to their environment throughout life	×	×	Asymptotic growth in captive green ^a and Kemp's ridley ^b turtles

^aBjorndal et al. (2013); ^bBjorndal et al. (2014); ^cSnover et al. (2013); ^dAvens et al. (2015); ^ePetit et al. (2015); ^fAvens et al. (2017); ^gRamirez et al. (2017); ^hTable 3 of this study; ⁱVan Buskirk & Crowder (1994).

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Table 2. Summary of basic parameters for both green and loggerhead turtles for both datasets. Annual growth: mean \pm SD (range, n). CAGR (compound annual growth rates): mean \pm SD (range, n). RI (remigration interval): median (interquartile range, range, n). Years since first capture/nesting: median (interquartile range, range, n). Average curved carapace length (CCL) at first nesting: mean \pm SD (range, n), only calculated for the restricted dataset (2000 to 2017) due to the increased accuracy of neophyte classification. na: not applicable.

Dataset Turtle species	Annual growth (cm yr ⁻¹)	CAGR (% of body size yr ⁻¹)	RI (yr)	Years since first capture/nesting	CCL at first nesting (cm)
1992 – 2017					
Green	0.4 \pm 0.6 (-1.0 to 2.6, 339)	0.4 \pm 0.7 (-1.0 to 3.1, 339)	3.0 (2.0 to 4.0, 1.0 to 14.0, 339)	6.0 (4.0 to 9.0, 2.0 to 24.0, 147)	na
Loggerhead	0.2 \pm 0.6 (-2.0 to 2.3, 158)	0.3 \pm 0.8 (-2.5 to 3.2, 158)	3.0 (2.0 to 4.0, 1.0 to 10.0, 158)	4.0 (3.0 to 8.0, 1.0 to 25.0, 85)	na
2000 – 2017					
Green	0.7 \pm 0.7 (-0.6 to 2.6, 174)	0.7 \pm 0.7 (-0.7 to 3.1, 174)	3.0 (2.0 to 4.0, 1.0 to 14.0, 174)	5.0 (4.0 to 7.0, 2.0 to 16.0, 104)	86.5 \pm 5.5 (73.5 to 103.0, 104)
Loggerhead	0.3 \pm 0.5 (-0.9 to 2.0, 69)	0.5 \pm 0.7 (-1.2 to 2.6, 69)	3.0 (2.0 to 4.0, 1.0 to 10.0, 69)	4.0 (3.0 to 5.8, 1.0 to 16.0, 45)	72.3 \pm 3.6 (64.5 to 80.2, 45)

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Table 3. Summary of published studies for which both L_{α} and L_{∞} could be extracted. L_{α} represents size at sexual maturity and L_{∞} represents asymptotic size. Both size measurements are straight carapace length measurements. L_{α} and L_{∞} : mean (range; n); Unk: unknown; Sk: skeletochronology; FmvBGF: Faben’s modified von Bertalanffy growth function; AS: age-at-size method; GR: growth rate method; LGM: logistic growth model; CMR: capture-mark-recapture; SvBGF: seasonalised von Bertalanffy growth function; vBGF: von Bertalanffy growth function.

Species	Ocean basin, Sex & Study area	Year	Method	L_{α} (cm)	L_{∞} (cm)	L_{α}/L_{∞}	Reference	
<i>Caretta caretta</i>	Atlantic Ocean							
	♀	NW (Atlantic coast, USA)	1999–2011	Sk, FmvBGF	90.5 (75.0–101.3, 32) ^a	110.7 (110.2–110.9, 32)	0.82	Avens et al. (2015)
	♂	NW (Atlantic coast, USA)	1999–2011	Sk, FmvBGF	95.8 (80.6–103.8, 27) ^a	114.0 (113.7–114.1, 27)	0.84	Avens et al. (2015)
	♀♂	NW (Georgia, USA)	1979–1993	Sk, vBGF	92.0 ^b	95.4 (26) ^c	0.96	Parham and Zug (1997)
	Mediterranean Sea							
	♀♂	W (Lampedusa Island, Italy)	2001–2007	Sk, vBGF, AS	72.6 ^{d,e}	103.9 (55) ^{e,f}	0.70	Casale et al. (2011a)
♀♂	W (Lampedusa Island, Italy)	2001–2007	Sk, vBGF, GR	72.6 ^{d,e}	119.3 (55) ^{e,f}	0.61	Casale et al. (2011a)	
♀♂	W (Italy)	1986–2007	CMR, vBGF	72.6 ^{d,e}	84.8 (38) ^e	0.86	Casale et al. (2009)	
<i>Chelonia mydas</i>	Atlantic Ocean							
	♀♂	NW (Atlantic coast, USA)	1991–2007	Sk, LGM	96.7 (89.7–101.5, 4) ^a	104.7 (85)	0.92	Goshe et al. (2010)
	Mediterranean Sea							
♀	E (North Cyprus)	1992–2016	CMR	81.1 (68.8–96.9, 104) ^g	84.4 (72.1–100.1, 147) ^g	0.96	This study	

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	Pacific Ocean							
	♀♂	NE (Mexico)	2000–2003	CMR, SvBGF	77.3 ^h	101.0 (39) ^f	0.77	Koch et al. (2007)
	♀♂	NE (San Diego Bay, USA)	1990–2010	CMR, FmvBGF	77.3 ^h	101.8 (99.9–103.9, 52)	0.76	Eguchi et al. (2012)
<i>Dermochelys coriacea</i>	Atlantic Ocean							
	♀♂	NW (Atlantic coast, USA)	2001–2008	Sk, vBGF	141.1 ^{i,j,k}	164.7 (158.7–185.6, 41) ^{j,k}	0.86	Avens et al. (2009)
	♀♂	NW (British Virgin Islands, UK)	1934–2006	Sk, vBGF	121.0 ^{k,l}	142.7 ^k	0.85	Jones et al. (2011)
	Pacific Ocean							
	♀♂	SE (Peru)	Unk	Sk, vBGF	140.6 ^{i,m}	143.6 (16) ^{j,k}	0.98	Zug and Parham (1996)
<i>Eretmochelys imbricata</i>	Pacific Ocean							
	♀♂	NE (Hawaii, USA)	Unk	Sk, vBGF	78.6 ⁿ	94.8 (83.9–105.7, 40)	0.83	Snover et al. (2012)
<i>Lepidochelys kempii</i>	Atlantic Ocean							
	♀♂	NW (Gulf of Mexico, USA)	1993–2010	Sk, FmvBGF	61.0 ^a	65.9 (55)	0.93	Avens et al. (2017)
	♀♂	NW (Florida, USA)	1986–1991	CMR, vBGF	64.2 (56.0–72.5, 468) ^o	72.5 (38)	0.89	Schmid and Witzell (1997)
	♀	NW (Gulf of Mexico, USA)	1982–1995	CMR, vBGF	61.8 (58.1–65.8, 49) ^p	64.1 (49)	0.96	Caillouet et al. (2011)
	♀♂	NW (Atlantic coast, USA)	Unk	Sk, vBGF	65.0 ^q	87.7 (69)	0.74	Zug et al. (1997)
<i>Lepidochelys olivacea</i>	Atlantic Ocean							
	♀♂	SW (Brazil)	2010–2012	CMR, vBGF	63.3 (56.1–68.6, 60) ^a	71.7 (68.1–76.3, 68)	0.88	Petit et al. (2015)

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♀	SW (Brazil)	2010–2012	CMR, vBGF	65.5 (60.8– 68.5, 17) ^a	71.7 (68.1– 76.3, 68)	0.91	Petit et al. (2015)
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^aSize at sexual maturity (SSM) estimated from size at lines of arrested growth rapprochement; ^bAssumed to be the SSM for this population; ^cConverted from original curved carapace length (CCL) measurements using the equation in Snover et al. (2010); ^dAssumed to be the SSM of Mediterranean loggerhead turtles (Casale et al. 2011a); ^eConverted from original CCL measurements using unpublished conversion equation for loggerhead turtles nesting in Cyprus, as no conversion equation is available for Italian loggerhead turtles; ^fExtrapolated outside the range of sizes recorded during the study; ^gConverted from original CCL measurements using unpublished conversion equation for this population; ^hAverage size of nesting females in the East Pacific (Seminoff 2004); ⁱAverage size at first nesting (Stewart et al. 2007); ^jConverted from original CCL measurements using the equation in Avens et al. (2009); ^kIncludes captive individuals; ^lMinimum SSM rather than mean; ^mAverage size of nesting females; ⁿAverage size of adult female hawksbill turtles globally (Van Buskirk & Crowder 1994); ^oAverage size of nesting females (Schmid & Witzell 1997); ^pAverage size of neophyte nesters that were head-started and released and recaptured in the Gulf of Mexico; ^qAverage size of nesting females (Marquez 1994)

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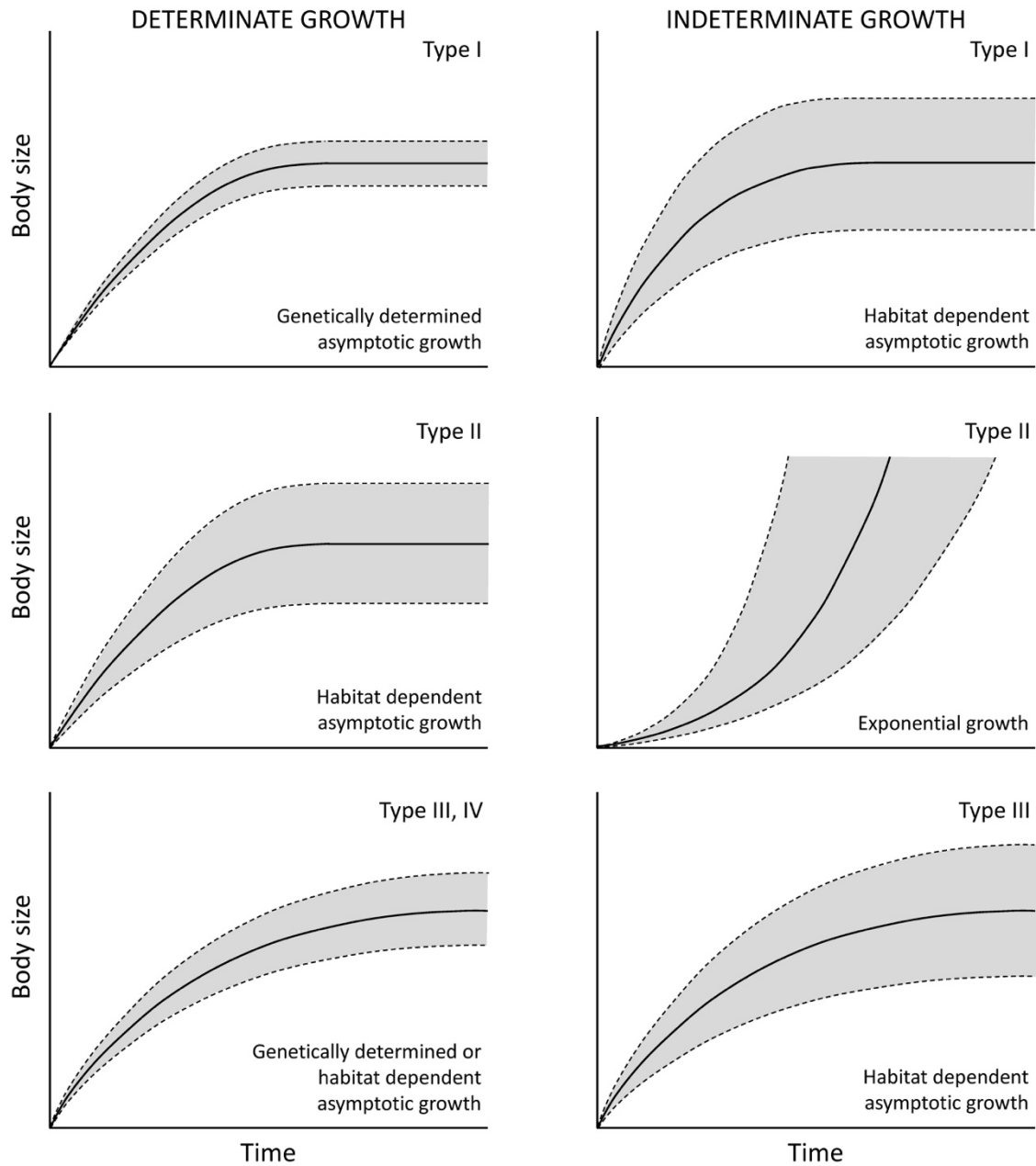


Figure 1. Growth trajectories under determinate growth types I-IV and indeterminate growth types I-III according to Sebens (1987). Figure is adapted from Figure 1 in Sebens (1987). The grey shaded area represents possible growth trajectories under different environmental conditions.

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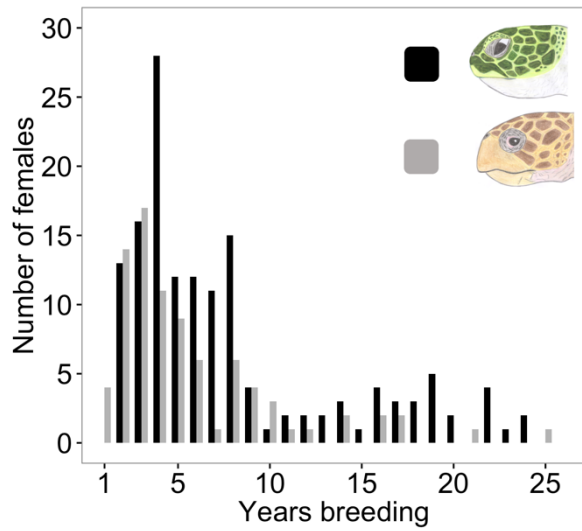


Figure 2. Frequency distribution of capture histories for green (black bars) and loggerhead (grey bars) turtles for the 1992 – 2017 dataset. Note that each female is only represented once.

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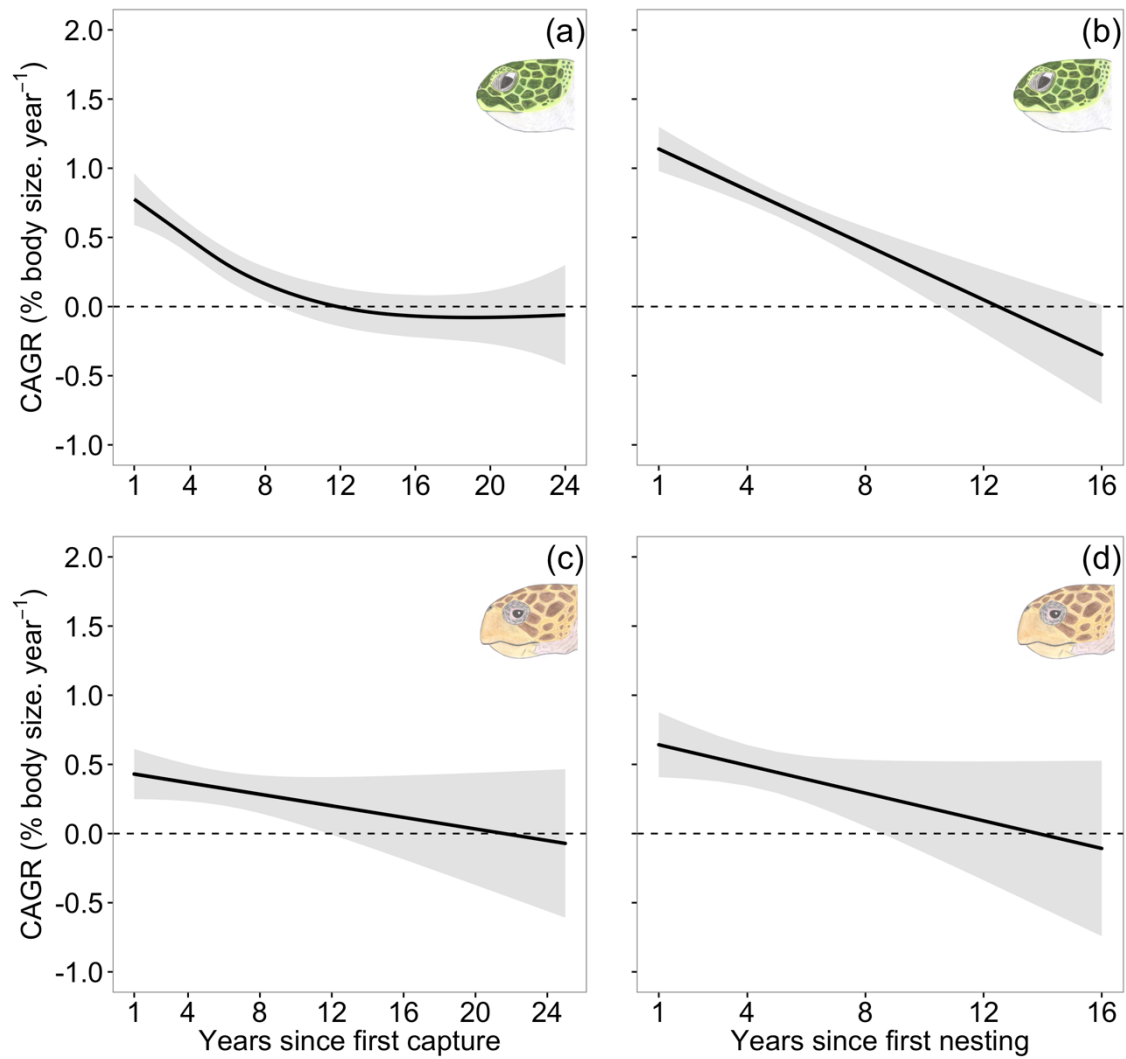


Figure 3. Summary of (a) generalised additive mixed model and (b-d) generalised linear mixed model analyses of compound annual growth rates (CAGR) as a function of years since first capture/nesting for (a-b) green and (c-d) loggerhead turtles for the (a, c) 1992 – 2017 and (b, d) 2000 – 2017 datasets. The response variables are shown on the y-axis, shifted by the intercept for ease of visualisation. Grey areas indicate 95 % CIs. Dashed lines represent the absence of growth.

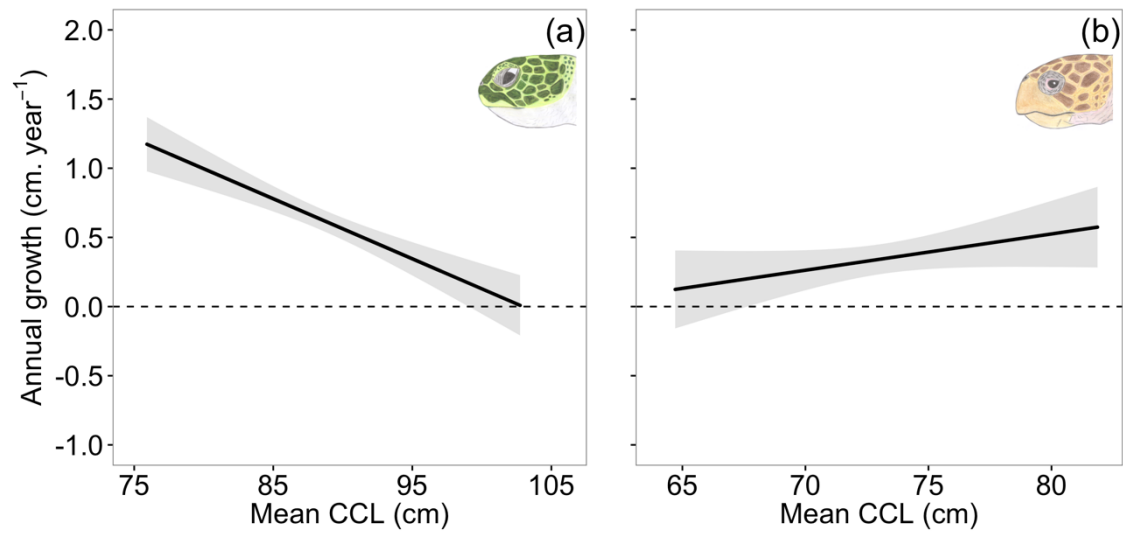


Figure 4. Summary of generalised linear mixed model analyses for annual growth as a function of mean curved carapace length (CCL) for (a) green and (b) loggerhead turtles for the 2000 – 2017 dataset. The response variables are shown on the y-axis, shifted by the intercept for ease of visualisation. Grey areas indicate 95 % CIs. Dashed lines represent the absence of growth.

Supplementary information

Table S1. Breakdown of the datasets for both species. n: number of females.

Growth records	1992 – 2017		2000 – 2017	
	Green turtles (n = 147)	Loggerhead turtles (n = 85)	Green turtles (n = 104)	Loggerhead turtles (n = 45)
1	147	85	104	45
2	76	30	42	13
3	50	18	18	5
4	28	12	7	4
5	18	6	2	1
6	14	3	1	1
7	5	2	0	0
8	1	2	0	0
Total	339	158	174	69

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Table S2. Statistical output from generalised additive mixed models (GAMM) to investigate the potential influence of different covariates on annual growth response of green turtles. YearsSFC: years since first capture; CCL: curved carapace length; RI: remigration interval; AIC: Akaike's information criterion; Edf: estimated degrees of freedom; SE: standard error.

Model	Adj r ²	AIC	Variable	Edf	F	Prob(F)	Variable	Estimate	SE	t
GAMM _{YearsSFC+MeanCCL+RI}	0.24	499.14	YearsSFC	2.77	15.58	<0.0001	Intercept	0.32	0.05	7.28
			MeanCCL (cm)	1.00	19.70	<0.0001				
			RI (yr)	1.00	0.43	0.51				
GAMM _{YearsSFC+MeanCCL}	0.24	495.00	YearsSFC	2.82	17.57	<0.0001	Intercept	0.32	0.04	7.30
			MeanCCL (cm)	1.00	19.51	<0.0001				
GAMM _{YearsSFC+RI}	0.16	510.91	YearsSFC	2.90	27.61	<0.0001	Intercept	0.30	0.05	5.95
			RI (yr)	1.00	0.16	0.69				
GAMM _{MeanCCL+RI}	0.18	526.84	MeanCCL (cm)	1.00	51.86	<0.0001	Intercept	0.36	0.04	8.63
			RI (yr)	1.00	5.09	<0.05				
GAMM _{YearsSFC}	0.16	506.57	YearsSFC	2.93	30.27	<0.0001	Intercept	0.30	0.05	5.97
GAMM _{MeanCCL}	0.17	527.27	MeanCCL (cm)	1.00	53.65	<0.0001	Intercept	0.36	0.04	8.64
GAMM _{RI}	0.02	567.66	RI (yr)	1.00	6.39	<0.05	Intercept	0.37	0.05	7.57

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Table S3. Statistical output from generalised additive mixed models (GAMM) to investigate the potential influence of different covariates on compound annual growth rates response of green turtles. YearsSFC: years since first capture; RI: remigration interval; AIC: Akaike's information criterion; Edf: estimated degrees of freedom; SE: standard error.

Model	Adj r ²	AIC	Variable	Edf	F	Prob(F)	Variable	Estimate	SE	t
GAMM _{YearsSFC+RI}	0.17	609.50	YearsSFC	2.94	28.35	<0.0001	Intercept	0.35	0.06	5.99
			RI (yr)	1.00	0.17	0.68				
GAMM _{YearsSFC}	0.16	506.57	YearsSFC	2.93	30.27	<0.0001	Intercept	0.30	0.05	5.97
GAMM _{RI}	0.02	567.66	RI (yr)	1.00	6.39	<0.05	Intercept	0.37	0.05	7.57

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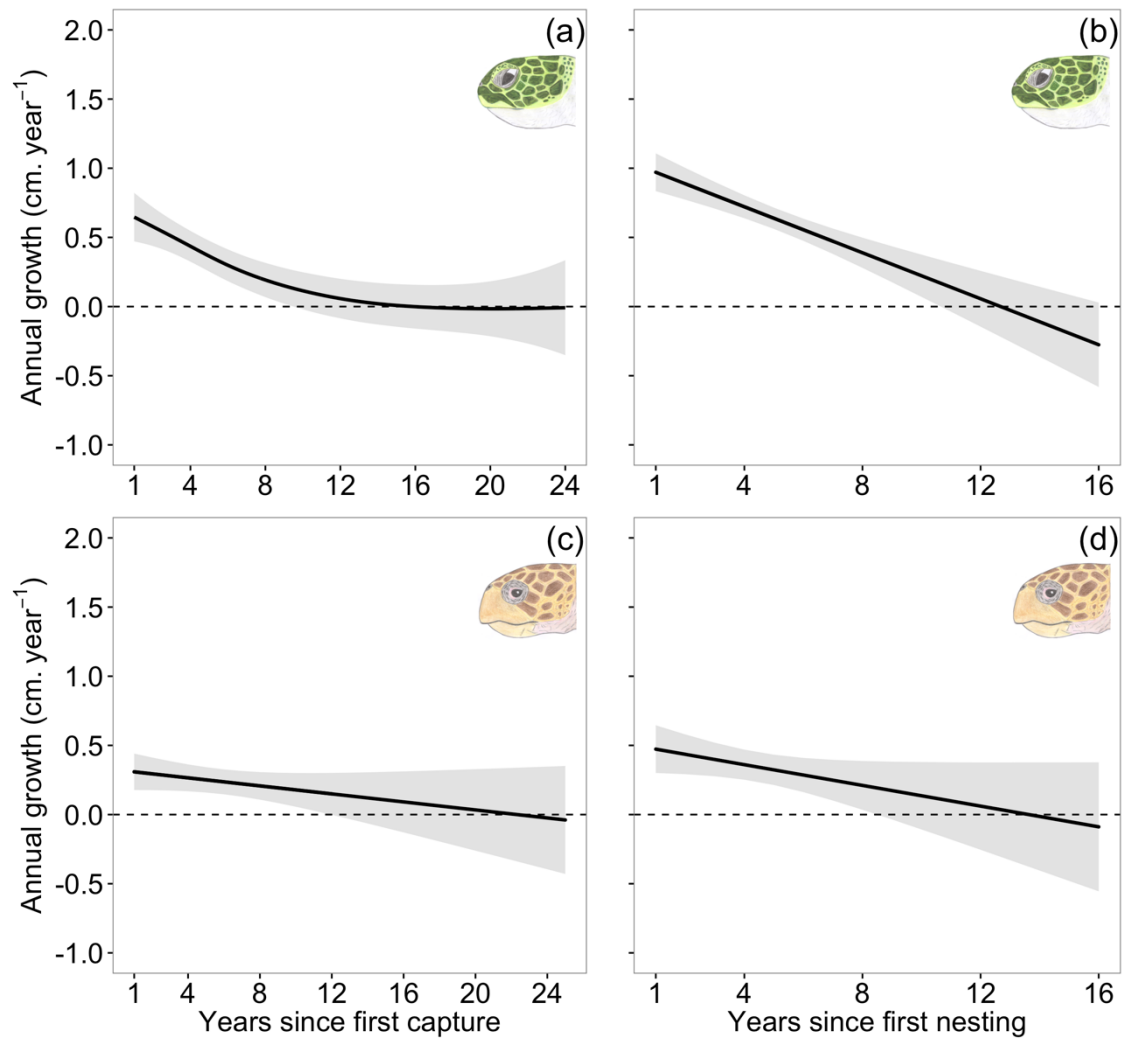


Figure S1. Summary of (a) generalised additive mixed model and (b-d) generalised linear mixed models analyses of annual growth for (a-b) green and (c-d) loggerhead turtles for the (a, c) 1992 – 2017 and (b, d) 2000 – 2017 datasets. The response variables are shown on the y-axis, shifted by the intercept for ease of visualisation. Grey areas indicate 95 % CIs. Dashed lines represent the absence of growth.

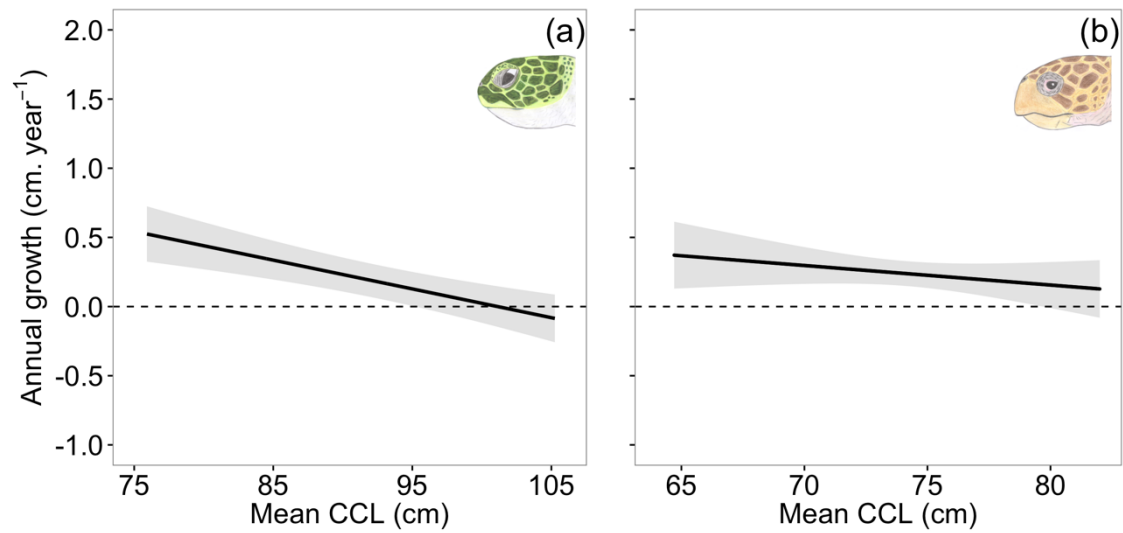


Figure S2. Summary of (a) generalised additive mixed model and (b) generalised linear mixed model analyses for annual growth as a function of mean curved carapace length (CCL) for (a) green and (b) loggerhead turtles for the 1992 – 2017 dataset. The response variables are shown on the y-axis, shifted by the intercept for ease of visualisation. Grey areas indicate 95 % CIs. Dashed lines represent the absence of growth.

CHAPTER 4: THE EFFECT OF BIOLOGGING SYSTEMS ON REPRODUCTION, GROWTH AND SURVIVAL OF ADULT SEA TURTLES

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Abstract

Background: Telemetry and biologging systems, ‘tracking’ hereafter, have been instrumental in meeting the challenges associated with studying the ecology and behaviour of cryptic, wide-ranging marine mega-vertebrates. Over recent decades, globally, sea turtle tracking has increased exponentially, across species and life-stages, despite a paucity of studies investigating the effects of such devices on study animals. Indeed, such studies are key to informing whether data collected are unbiased and, whether derived estimates can be considered typical of the population at large.

Methods: Here, using a 26-year individual-based monitoring dataset on sympatric green (*Chelonia mydas*) and loggerhead (*Caretta caretta*) turtles, we provide the first analysis of the effects of device attachment on reproduction, growth and survival of nesting females.

Results: We found no significant difference in growth and reproductive correlates between tracked and non-tracked females in the years following device attachment. Similarly, when comparing pre- and post-tracking data, we found no significant difference in the reproductive correlates of tracked females for either species or significant carry-over effects of device attachment on reproductive correlates in green turtles. The latter was not investigated for loggerhead turtles due to small sample size. Finally, we found no significant effects of device attachment on return rates or survival of tracked females for either species.

Conclusion: While there were no significant detrimental effects of device attachment on adult sea turtles in this region, our study highlights the need for other similar studies elsewhere and the value of long-term individual-based monitoring.

Background

Telemetry and biologging systems, 'tracking' hereafter, have been instrumental in meeting the challenges associated with studying the ecology and behaviour of cryptic, wide-ranging marine mega-vertebrates [1]. Such systems have evolved greatly, particularly over the last two decades, becoming smaller, with increased storage capacity. Thus, they have provided scientists with a powerful tool, with which to obtain key information not previously available [2]. Technological advancements have permitted the tracking of smaller animals [3 – 5], across multiple life stages [6] and around the world [7, 8]. Although tracking has greatly furthered our understanding of the natural world, it is key to determine whether the data collected are unbiased and whether derived estimates can be considered typical of the population at large.

Although benign in some instances [9 – 12], device attachment does not always come free of cost to study animals. For example, it can lead to increased energy expenditure [13 – 15], influence reproductive success [16 – 18] as well as alter natural behaviours [19 – 22]. Device improvements have led to the tracking of animals over extensive periods of time [23 – 25], which may have physiological implications [26], with potential carry-over effects [27, 28]. In addition, a recent meta-analysis on birds highlights that these effects may be cumulative, such that, for example, effects on annual survival could also impact reproduction [29]. Therefore, assessing the effects of device attachment on the overall fitness of study animals, in both the short- and long-term, focussing on multiple traits [29], is crucial to mitigate against potential deleterious effects in the future.

Over the years, tracking has increased exponentially, worldwide, across species and life-stages in sea turtles [30, 31], contributing widely to priority research questions [32]. It has allowed researchers to explore migration patterns [33], diving behaviours [34 – 36] and foraging strategies of sea turtles [37, 38], as well as providing improved estimates of sea turtle abundance [39, 40]. Despite this increase in use, the number of studies that consider ethical or welfare issues associated with device attachment is low [20 %; 31], and the number of studies that investigate welfare issues as their main theme is even lower [2 %; 31]. Device attachment has been modelled as increasing drag and energy expenditure [15, 41], potentially influencing reproductive correlates and survival of study animals.

Empirically, differences in swimming efficiency and diving capacities, as well as differences in data quality, have been reported in leatherback turtles (*Dermochelys coriacea*) based on attachment methods alone [20, 21]. Such studies highlight the need for an evaluation of the effects of device attachment on life-history traits and survival of study animals, as well as the need to compare data between tracked and non-tracked individuals.

Here, we provide the first long-term analysis of the effects of device attachment on reproduction, growth and annual survival of green (*Chelonia mydas*) and loggerhead (*Caretta caretta*) turtles nesting sympatrically, using a 26-year individual-based monitoring dataset, with devices first attached in 1997. We compare differences in reproductive correlates, growth and annual survival, both between tracked and non-tracked females, and pre- and post-tracking of individual females.

Methods

Further details for each corresponding section can be found in the Additional file A for this article.

Study site and data collection

Data were collected at Alagadi Beach, Northern Cyprus (35°33 N, 33°47 E) between 1992 and 2017, where intensive night-time monitoring and tagging programmes have been carried out (see [42] for detailed methods). Female identification was based on flipper tags and passive integrated transponder tags (PIT tags [43]). Curved carapace length (CCL) notch to notch was used as a measure of female size. Growth was calculated from CCL measurements (see [44] for further details). Due to the intensive nature of the monitoring carried out at Alagadi, very few nests per year cannot be attributed to individual females [45]. However, when a missed nest was apparent (i.e. intervals of > 18 days observed between two clutches), clutch frequency was adjusted and referred to as ECF (estimated clutch frequency) hereafter (see [42, 45] for further details). Mean clutch size and ECF were calculated for each individual, each nesting season. Remigration interval (RI) was calculated as the number of years elapsed between two nesting seasons. Date of first nest was determined as the day of the year (d.o.y) the female was first observed laying. ECF and date of first nest were not calculated in 1992 due to incomplete survey effort.

Device attachment

A variety of devices (Table 1) were attached to nesting females between 1997 and 2017, following the protocol outlined by Godley et al. [46]. Satellite transmitters (PTTs: platform terminal transmitters) were attached for studies of migration, whereas all other devices were designed to be recovered within a breeding season to investigate inter-nesting behaviours. Given that all devices were attached in a similar manner and were of similar magnitude, we consider animals with any devices attached as 'tracked', irrespective of device type. In

some instances, multiple devices of the same type were attached within a breeding season using the same attachment base. For the analysis, however, we focussed only on the last attached device. Note that attaching multiple devices of the same type to the same base attachment platform is no different to attaching one device early in the nesting season, which is not retrieved between clutches. Although some females were fitted simultaneously with two devices, not all females returned to foraging grounds with both devices attached (Table 1). Except for PTTs, whenever possible, devices were retrieved, leaving behind the attachment base, except in 1997, when the base was also removed. Individuals for which the base was removed were included in this analysis of return rates but were excluded for the remainder of the analysis. Females that returned to foraging grounds without any devices attached were included in the analysis because, although the attachment base was shaped to reduce drag, it could not be excluded that it did not affect individuals. We distinguish between ‘tracked’ females with a device attached (hereafter referred to as ‘device attached’) and females for which only the attachment base remained (hereafter referred to as ‘attachment base only’).

Statistical analysis – Return rates

Fisher’s exact tests were used to calculate differences in return rates among groups, looking at differences between ‘tracked’ and ‘non-tracked’ as well as within ‘tracked’ groups.

Odds ratios were used as a measure of effect size. Females that were not resighted were assumed to be dead, although it is possible that individuals migrated to other nesting beaches which are not monitored during the night.

Statistical analysis – Among-female differences

To investigate differences between ‘tracked’ and ‘non-tracked’ females, ‘initial year’, i.e. year of device attachment for ‘tracked’ females, was determined as the first year of capture for ‘non-tracked’ neophyte (first time nesters) females and was randomly generated for other ‘non-tracked’ females for which three or

more captures were available. This means that the analysis only included females for which two or more captures were available.

One-way analysis of variance and linear models were used to compare differences in body size and reproductive correlates among groups. The analysis was conducted in R version 3.2.3. Models were fitted by stepwise model simplification and significance of removed terms was assessed with a threshold of $P = 0.05$ [47]. We checked for over-dispersion, normality, homoscedasticity and homogeneity of variance. Female size and 'year' were included as fixed effects to control for larger females laying larger clutches [42] and to investigate whether differences were due to annual effects. Partial omega squared ω_p^2 was used as a measure of effect size. Tukey post-hoc tests were used to look at pairwise comparisons, using the package multcomp [48]. Furthermore, we looked at the interactions between growth covariates and device attachment to investigate whether device attachment influenced growth of 'tracked' females (see [44] for further details).

Statistical analysis – Within-female differences

Generalised linear mixed models (GLMM) and generalised least squares (GLS) were used to investigate within-female differences in reproduction between pre- and post-tracking years. To detect small non-significant effects of device attachment, a systematic analysis was used to look at seasonal (mean clutch size*ECF) and annual reproductive output (seasonal reproductive output/RI). Models were implemented using nlme and mgcv packages [49, 50] and included female identity as a random effect and 'year' as a fixed effect. CCL was also included in models of mean clutch size and seasonal/annual reproductive output. Models were fitted as explained in the previous section.

Statistical analysis – Carry-over effects

To investigate whether device attachment had any carry-over effects, GLMM and GLS were used on a subset dataset that included only females for which two pre- (including year of device attachment) and two post-tracking

seasons were available. This restricted the analysis to nine green turtle females, with 'attachment base only' and 'device attached' groups pooled. Sample size was too small for loggerhead turtles ($n = 4$). Models were fitted as explained in the previous section.

Statistical analysis – Survivorship estimates

Encounter histories were created based on successful nesting attempts. Survival probability was estimated using the multi-state model in the programme MARK [51], assuming a breeding state (B; observable state) and a non-breeding state (NB; unobservable state). The parameters estimated were survival probability (S), encounter probability (p) and transition probabilities between states ($\psi_{B \rightarrow NB}$ and $\psi_{NB \rightarrow B}$). Goodness of fit was assessed using the programme U-CARE [52]. In particular, test component 3G.SR was used to evaluate the effect of presumed transient individuals on survival probabilities and test component M.ITEC was used to test for trap-dependence. Transient individuals are individuals that are caught, marked and released but never recaptured. Such individuals can be considered in transit and therefore have a zero probability of recapture although they are alive. Model selection was based on the lowest $qAIC_c$ value (corrected quasi-likelihood Akaike information criterion). Parameters were estimated using the Markov chain Monte Carlo method in MARK. Parameter estimates were based on posterior distributions and 95 % highest posterior density credibility intervals were reported.

Results

Return rates

A total of 170 devices (Table 1) were attached to 51 green and 50 loggerhead turtle females between 1997 and 2017. Of these females, 13 green and 9 loggerhead turtle females had devices attached in two different years and 3 green turtle females had devices attached in three different years. However, the remainder of the analysis focussed on females that had devices attached in a single year.

Almost all green turtles (93 %) and just under three quarters of loggerhead turtles (70 %) that had devices attached in a single year were resighted within a maximum of 15 years (Table 2). Of the females that had devices attached in a single year, 17 % of green and 48 % of loggerhead turtles were neophyte females. For both species, there was no significant difference in return rates between groups (Table 2 and Additional file 1: Table S1). Based on the odds ratios, 'tracked' neophyte females were no more or less likely to be resighted than 'non-tracked' neophyte females or 'tracked' remigrant females (Additional file 1: Table S1). Similarly, 'attachment base only' females were no more or less likely to be resighted than 'device attached' females (Additional file 1: Table S1).

Among-female differences

The basic parameters for each group and species are summarised in Additional file 1: Table S2.

Green turtles

For green turtles, there was a large significant difference in body size in the year of device attachment among groups ($F_{2,125} = 9.30$, $P < 0.001$, $\omega_p^2 = 0.115$, Fig.1a), with 'device attached' females being on average 6.0 cm (95 % CI: 2.6 – 9.4, $P_{adj} < 0.001$, $n = 20$) larger than 'non-tracked' females ($n = 94$). There was, however, no significant difference in body size between 'device attached'

and ‘attachment base only’ females ($P_{\text{adj}} = 0.416$) and between ‘non-tracked’ and ‘attachment base only’ females ($P_{\text{adj}} = 0.176$, $n = 14$).

In addition, there was no significant difference in mean clutch size ($F_{2,125} = 2.92$, $P = 0.058$, $\omega_p^2 = 0.029$, Fig.1b), RI ($F_{2,125} = 0.65$, $P = 0.586$, $\omega_p^2 < 0.001$, Fig.1d) and date of first nest ($F_{2,125} = 3.00$, $P = 0.053$, $\omega_p^2 = 0.030$, Fig.1e) among groups in the years following device attachment. Observed differences in mean clutch size ($F_{1,126} = 5.68$, $P = 0.019$, $\omega_p^2 = 0.037$, Fig.1b) and date of first nest ($F_{1,126} = 12.26$, $P < 0.001$, $\omega_p^2 = 0.065$, Fig.1e) were due to annual effects rather than device attachment.

However, there was a significant difference in ECF among groups in the years following device attachment ($F_{2,126} = 6.528$, $P = 0.002$, $\omega_p^2 = 0.085$, Fig.1c), which could not be explained by annual effects ($F_{1,125} = 1.09$, $P = 0.297$, $\omega_p^2 = 0.006$). ‘Attachment base only’ females laid on average 1.10 (0.29 – 1.91) clutches more and ‘device attached’ females laid on average 0.63 (-0.07 – 1.33) clutches more than ‘non-tracked’ females ($P_{\text{adj}} = 0.005$ and $P_{\text{adj}} = 0.084$ respectively). There was, however, no significant difference in ECF between ‘device attached’ and ‘attachment base only’ females ($P_{\text{adj}} = 0.492$). Finally, device attachment did not have a significant effect on post-maturity growth or compound annual growth rates (Fig.2ab, Additional file 1: Table S3).

Loggerhead turtles

For loggerhead turtles, there was no significant difference in size ($F_{2,61} = 1.58$, $P = 0.215$, $\omega_p^2 = 0.018$, Fig.1a), mean clutch size ($F_{2,61} = 0.63$, $P = 0.534$, $\omega_p^2 = 0.012$, Fig.1b), RI ($F_{2,61} = 0.64$, $P = 0.532$, $\omega_p^2 = 0.012$, Fig.1d) and date of first nest ($F_{2,61} = 1.27$, $P = 0.289$, $\omega_p^2 = 0.008$, Fig.1e) between ‘attachment base only’ ($n = 6$), ‘device attached’ ($n = 8$) and ‘non-tracked’ ($n = 50$) females in the year of device attachment for female size and in the years following device attachment for reproductive correlates. Observed differences in date of first nest were due to annual effects rather than device attachment ($F_{1,63} = 5.98$, $P = 0.017$, $\omega_p^2 = 0.073$, Fig.1e).

However, there was a large significant difference in ECF among groups in the years following device attachment ($F_{2,61} = 5.06$, $P = 0.009$, $\omega_p^2 = 0.121$, Fig.1c), which could not be explained by annual effects ($F_{2,60} = 0.76$, $P = 0.386$,

$\omega_p^2 = 0.016$). ‘Attachment base only’ females laid on average 1.47 (0.09 – 2.85) clutches more and ‘device attached’ females laid on average 1.20 (0.03 – 2.37) clutches more than ‘non-tracked’ females ($P_{adj} = 0.035$ and $P_{adj} = 0.044$ respectively). There was no significant difference in ECF between the ‘device attached’ and ‘attachment base only’ females ($P_{adj} = 0.921$). Finally, device attachment did not have a significant effect on post-maturity growth or compound annual growth rates (Fig.2cd, Additional file 1: Table S3).

Within-female differences

For both species, there was no significant difference in all reproductive correlates between pre- and post-tracking years (Fig.3, Additional file 1: Table S4). Observed differences in mean clutch size and date of first nest for both species, and in seasonal reproductive output for green turtles between pre- and post-tracking years for particular groups were due to annual effects (Fig.3, Additional file 1: Table S4). To further explore whether RI increased between pre- and post-tracking years, we looked at pairs of randomly generated consecutive RIs for ‘non-tracked’ females. We found that RI did not significantly increase between pairs for both species (green turtles: $F_{1,64} = 1.64$, $P = 0.205$; loggerhead turtles: $F_{1,30} = 0.07$, $P = 0.798$).

Carry-over effects

For green turtles, there were no significant carry-over effects of device attachment on mean clutch size ($\chi^2_1 = 0.10$, $P = 0.756$, Fig.4a), ECF ($\chi^2_1 = 0.22$, $P = 0.639$, Fig.4b), date of first nest ($\chi^2_1 = 1.56$, $P = 0.212$, Fig.4d), seasonal reproductive output ($\chi^2_1 = 0.002$, $P = 0.963$, Fig.4e) and annual reproductive output ($\chi^2_1 = 2.84$, $P = 0.092$, Fig.4f). However, RI significantly increased by 0.67 year over the course of 4 breeding events, with device attachment occurring on the second breeding event ($\chi^2_1 = 3.93$, $P = 0.048$, Fig.4c). This increase in RI was not due to annual effects ($\chi^2_1 = 1.88$, $P = 0.171$). To further explore this result, we compared RI of eight non-tracked females with similar histories across

the same time frame and also found RI to increase in a similar manner ($\chi^2_1 = 6.44$, $P = 0.011$).

Survivorship

Because no estimates are available for these two populations, we had to estimate annual survival for both 'tracked' and 'non-tracked' females. Goodness of fit results and model output tables (Additional file 1: Tables S5-S8) can be found in the supplemental material for this article. All parameter estimates for both species and groups can be found in Additional file 1: Table S9.

For green turtles, annual survival was 0.91 (0.88 – 0.94) for 'non-tracked' females and 0.97 (0.95 – 0.99) for 'tracked' females. Confidence intervals were higher for 'tracked' females than for 'non-tracked' females for green turtles.

For loggerhead turtles, annual survival was 0.44 (0.30 – 0.61) for transient 'non-tracked' females, 0.83 (0.77 – 0.88) for remigrant 'non-tracked' females and 0.82 (0.73 – 0.90) for 'tracked' females. Estimates for 'tracked' and 'non-tracked' remigrant loggerhead turtles were similar, with overlapping confidence intervals.

Discussion

Here, we provide the first analysis of the effects of device attachment on life-history traits of sea turtles. We found no evidence of deleterious effects of device attachment on reproduction, growth and annual survival of green and loggerhead turtles nesting sympatrically.

The most important effect of device attachment has been suggested to be the increase in energy expenditure, as a result of increased drag [15, 41, 53]. Sea turtles are capital breeders [54 – 56], meaning that the decision to nest in a given year results from the combination of an assessment of body condition and favourable environmental conditions [57]. Thus, an increase in energy expenditure during non-breeding years could have knock-on effects on the breeding phenology of study animals. Indeed, if device attachment results in reduced locomotor capacity through reduced swim speed, individuals fitted with devices at nesting grounds could arrive later at foraging grounds, but also at breeding grounds, if devices remain attached throughout the RI, which is not uncommon. In this study, as well as in previous studies [58, 59], females have been resighted at breeding grounds with devices still attached. Despite this, we found no evidence of a delayed arrival of ‘tracked’ females when subsequently returning to nest, both compared to the population at large, as well as within ‘tracked’ females. Similarly, no evidence of a delay in return rates has been observed for male loggerhead turtles [60]. In all instances, date of first nest was influenced by annual effects for both species, with first, median and final lay date having shifted towards earlier nesting over the study period [61]. Similar shifts in the breeding phenology of sea turtles have been observed in a number of populations, as a result of climate change [62 – 65].

In addition, device attachment could result in females requiring more time to accumulate sufficient resources to initiate reproduction [15, 20, 41, 66]. Indeed, if swimming efficiency and foraging ability are impaired by device attachment [20, 21], later arrival at foraging grounds could result in longer RIs. However, Benson et al. [67] noted that ‘tracked’ individuals arrived presumably on time at foraging grounds and we found no evidence for longer RIs in ‘tracked’ females. Although RI appeared to increase post-tracking, the magnitude of the effect was small and not significant (Fig.3). Likewise, RI did not increase when comparing pairs of

consecutive recaptures for 'non-tracked' females, suggesting that device attachment is unlikely to be the cause of the increase observed in 'tracked' females. The small sample size in this study, however, may have prevented the detection of such a trend, as a power analysis showed that a sample size of more than 400 would be needed to detect a small significant effect of device attachment on RI with a 0.8 probability. Furthermore, while RI appeared to increase with years since device attachment in green turtles, we found a similar significant increase for eight 'non-tracked' females with similar capture histories across the same time frame. This suggests that device attachment is unlikely to have had carry-over effects on RI of green turtles. Due to the scaling of the effects of drag on swim speed, the impacts of device attachment might be heightened in pursuit predators, such as penguins [68], and lessened in herbivores and benthic feeders, such as adult green and loggerhead turtles [69], which could explain the absence of an effect on RI. Despite the absence of a baseline for 'non-tracked' individuals, it is possible that changes in behaviour and swimming efficiency could have offset the effects of device attachment. Indeed, tracked females have been observed to forage 'en route' back to their over-wintering sites, travelling at depths and speeds which minimise drag [46, 70, 71] and thus, minimising the cost of migration and potentially device attachment.

Increased energy expenditure associated with device attachment may negatively influence reproductive output of study animals. Indeed, as females have to balance a tight energy budget, attaching devices during the inter-nesting period could have knock-on effects on their seasonal reproductive output [53]. Similarly, to overcome the increase in drag, when returning to nest, study animals either can (1) reduce their swim speed and arrive later at breeding grounds than the rest of the population, which does not appear to be the case or, (2) increase their power output thus decreasing the proportion of energy reserves available to fuel reproduction [53]. Here, we found no evidence for impaired reproductive output for either species, suggesting that females were not energetically compromised in the year of device attachment, as well as in subsequent breeding seasons. However, we cannot entirely exclude that some effects of device attachment on reproduction may have been masked by environmental effects, by the use of estimated reproductive correlates and by the targeted sampling of

remigrant females, with high nest site fidelity, which can explain the differences in ECF among groups.

The cost of device attachment during the inter-nesting period will not be uniform across study animals, potentially preventing the detection of within-season effects on reproduction. While some females remain close to the nesting beach, resting on the sea floor and not actively foraging [34, 72, 73], others forage [72 – 74] and commute between beaches, and at times, countries, to lay their eggs [24, 39, 40]. Although it appears highly unlikely that device attachment will result in females laying fewer clutches, as improved estimates of clutch frequency have been obtained using this method, [39, 40], it will be hard to determine whether device attachment results in females laying smaller clutches due to increased energy expenditure. Depletion of resources, as shown by haematological data, is more likely to trigger the need for individuals to forage and therefore to cease reproduction [56, 75 – 77].

Due to the partitioning of finite resources [78], attaching devices to animals could compromise their growth, especially in juveniles, as growth is negligible in adults [44]. Nevertheless, Seney et al. [79] found no effect of device attachment on growth of captive reared juvenile individuals. Similarly, we found no evidence for such an effect in wild adult nesting green and loggerhead turtles. The significant difference in size at device attachment among groups for green turtles is likely due to targeted sampling of remigrant females in preference for some studies. Indeed, remigrant females are known to be significantly larger than neophyte nesters at Alagadi beach [44, 45] and represented the vast majority (92 %) of tracked green turtles. By contrast, sampling for loggerhead turtles aimed to target females across a range of sizes [24], which resulted in a more even ratio (almost 1:1 ratio) of neophyte to remigrant nesters and can explain the absence of a significant difference in body size at device attachment among groups.

Ultimately, determining whether device attachment influences annual survival of study animals is crucial. Although device attachment has been suggested to influence return rates in some species [19, 80, 81], potentially due to increased energetic expenditure [82], we found no significant effects of device attachment on return rates or survival of 'tracked' females for either species.

Annual survival estimates for green turtles are not available for the Mediterranean [69], however, estimates calculated here for ‘non-tracked’ females (0.91, CI: 0.88 – 0.94) fall within the predictions for green turtle populations around the world (0.88, CI: 0.80 – 0.93). Annual survival estimates for ‘tracked’ green turtle females were higher, with non-overlapping confidence intervals, than those for ‘non-tracked’ females, which was likely due to targeted sampling of remigrant females, with higher nest site fidelity. For loggerhead turtles, our estimates for ‘non-tracked females’ (0.83, CI: 0.77 – 0.88) also fall within those predicted by Pfaller et al.’s [83] for loggerhead turtles around the world (0.82, CI: 0.79 – 0.85), are comparable to previous estimates calculated for loggerhead turtles in the Mediterranean [84, 85] and were similar to those of ‘tracked’ females in our study.

These estimates suggest that device attachment does not result in reduced annual survival in sea turtles and highlight yet again the heterogeneity of annual survival between green and loggerhead turtles worldwide, with loggerhead turtle estimates being consistently lower than those of green turtles [83]. The relatively low estimates for loggerhead turtles are thought to be linked to anthropogenic mortality, in particular bycatch, levels of which are unsustainable in the Mediterranean [86]. Finally, although annual survival estimates are prone to problems associated with tag loss [83], in this study, female identification was based on a combination of both flipper and PIT tag readings, making estimates more robust to tag loss, as PIT tag loss is thought to be negligible [87].

Conclusion

We provide the first analysis of the effects of device attachment on life-history traits of adult sea turtles, as well as the first estimates of annual survival for green turtles in the Mediterranean. Although we cannot entirely exclude that small sample size, individual variation and climate change prevented the detection of an effect, device attachment was found to have no significant detrimental effects on adult sea turtles. Nevertheless, in all instances, device attachment should aim to minimise device size and drag, using low profile tags for example [88]. Finally, this study highlights the need for other similar studies elsewhere and the value of long-term individual-based monitoring.

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Table 1. Devices attached to nesting females.

Device type	Device weight (g; range)	Green turtles (n = 51)	Loggerhead turtles (n = 50)	References
PTT	275 – 750	26	25	[24,46,70,89–91]
i-gotU® data loggers	37	24	33	[92]
GLS	48	20	13	[93]
TDR	16 – 200	16	5	[72,73,94–96]
PTT & GLS	162 – 275	4 ^a	2 ^b	[93]
GLS & Camera	700	2	0	[97]
Total	na	92	78	na

This table includes females that had devices attached in multiple years as well as within the same breeding season. PTT: platform terminal transmitter; GLS: global location sensing; TDR: time depth recorder; na: not applicable. ^a Female was fitted with one PTT and 3 GLS during the nesting season and returned to foraging grounds with both devices attached; ^b Female returned to foraging grounds with both devices attached.

Table 2. Returns rates for tracked and non-tracked females.

Species Groups	Non-tracked			Tracked		
	≤ 5 yr	≤ 10 yr	≤ 15 yr	≤ 5 yr	≤ 10 yr	≤ 15 yr
Green turtles						
All females	na	na	na	76 % (n = 45)	86 % (n = 43)	93 % (n = 40)
Neophytes	39 % (n = 236)	51 % (n = 197)	53 % (n = 189)	63 % (n = 8)	75 % (n = 8)	86 % (n = 7)
Remigrants	na	na	na	78 % (n = 37)	89 % (n = 35)	94 % (n = 33)
'Attachment base only'	na	na	na	84 % (n = 19)	89 % (n = 19)	89 % (n = 19)
'Device attached'	na	na	na	69 % (n = 26)	83 % (n = 24)	95 % (n = 21)
Loggerhead turtles						
All females	na	na	na	47 % (n = 30)	50 % (n = 28)	70 % (n = 20)
Neophytes	21 % (n = 387)	29 % (n = 325)	34 % (n = 274)	33 % (n = 9)	38 % (n = 8)	60 % (n = 5)
Remigrants	na	na	na	52 % (n = 21)	55 % (n = 20)	73 % (n = 15)
'Attachment base only'	na	na	na	100 % (n = 6)	100 % (n = 6)	100 % (n = 6)
'Device attached'	na	na	na	33 % (n = 24)	36 % (n = 22)	57 % (n = 14)

Percentage of females resighted after 5, 10, 15 or less years after device attachment or for non-tracked females for both green and loggerhead turtles. All of the resighted females were resighted within a maximum of 15 years. na: not applicable.

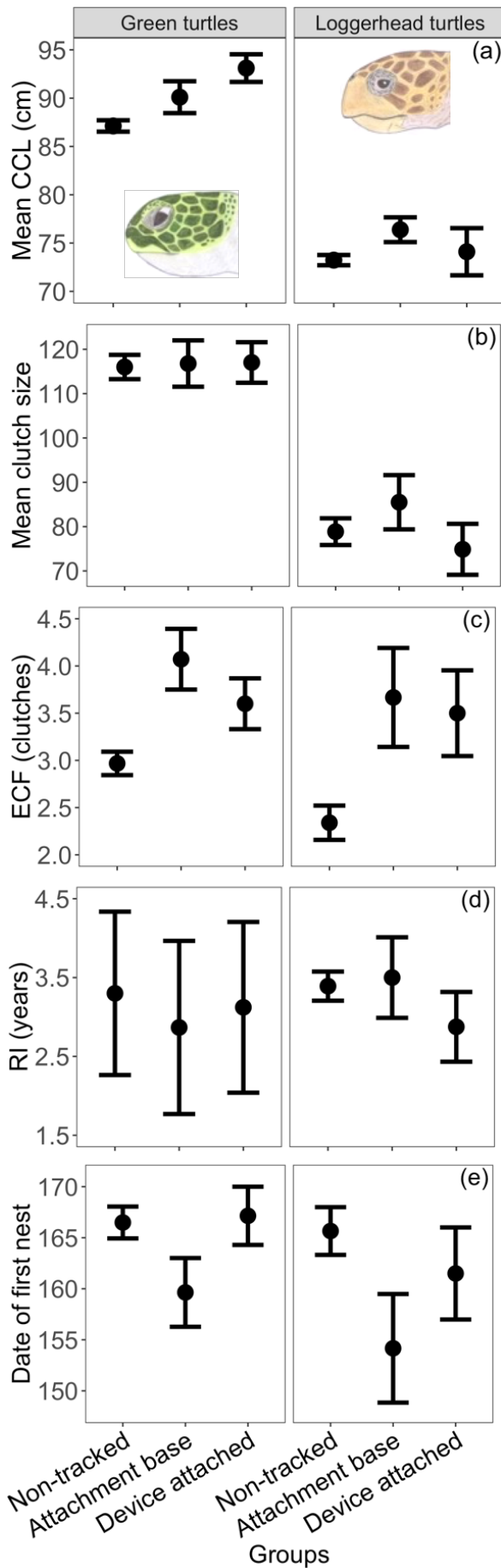


Figure 1. Effects on reproduction among females. Differences in female size (a) in the year of device attachment and reproductive correlates in the year following device attachment (b-e) for groups of females. For ‘non-tracked’ females, year(s) of and following device attachment represent randomly generated following recaptures. Observed differences in mean clutch size (eggs) for green turtles and in date of first nest (d.o.y) for both species were due to annual effects rather than device attachment (see main text). Mean \pm SE. CCL: curved carapace length; ECF: estimated clutch frequency; RI: remigration interval; d.o.y: day of the year.

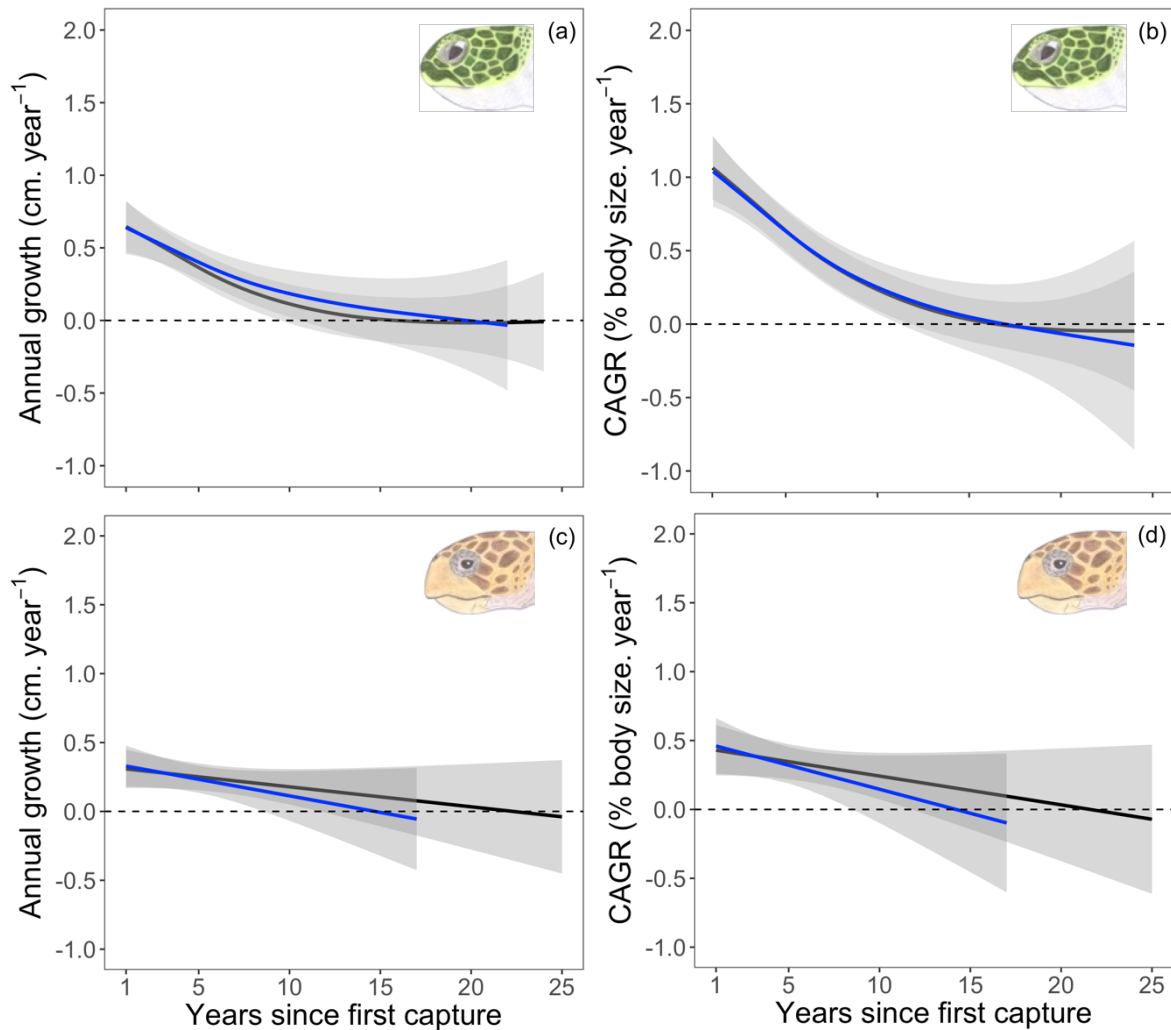


Figure 2. Effects on growth. Summary of (a, b) generalised additive mixed model and (c, d) generalised linear mixed model analyses of annual growth and compound annual growth rates (CAGR) for (a, b) green and (c, d) loggerhead turtles for the complete dataset (1992 – 2017) mentioned in Omeyer et al. [44]. The response variables are shown on the y axis, shifted by the intercept for ease of visualisation. Grey shaded area represents 95 % confidence intervals. Dashed lines represent the absence of growth. The black lines represent the model outputs for growth records of ‘non-tracked’ and ‘tracked’ females pooled and represent the model outputs presented in Omeyer et al. [44]. The blue lines represent the model outputs for ‘non-tracked’ females and for ‘tracked’ females up until year of device attachment.

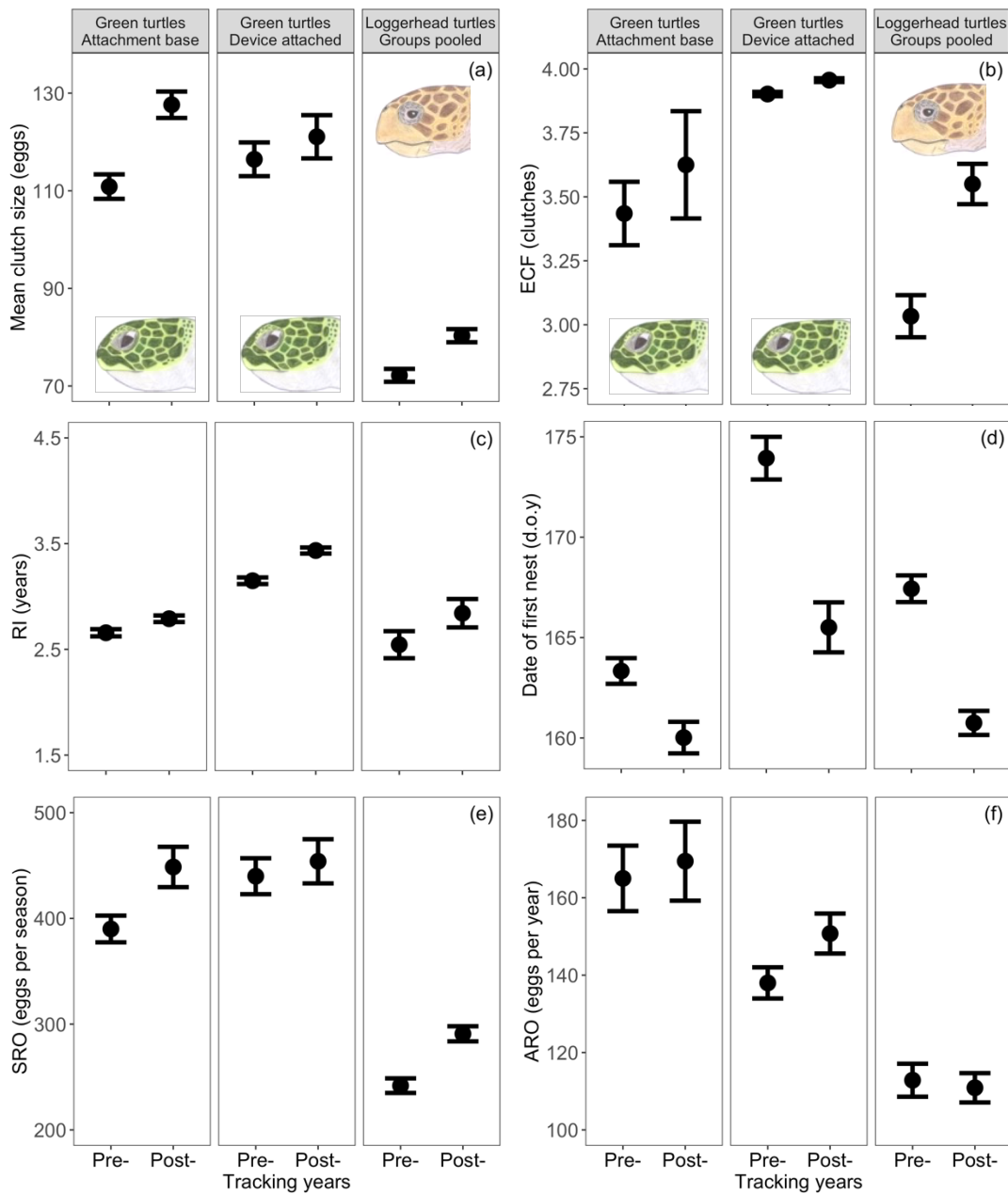


Figure 3. Effects on reproduction within females. Differences in mean clutch size (a), estimated clutch frequency (ECF, b), remigration interval (RI, c), date of first nest (d.o.y: day of the year, d), seasonal reproductive output (SRO, e) and annual reproductive output (ARO, f) between pre- and post-tracking years for the different groups and species. Pre-tracking years include all years including year of device attachment. Observed difference in mean clutch size ('attachment base only' group for green turtles and pooled group for loggerhead turtles), date of first nest (for all groups) and seasonal reproductive output ('attachment base only' for green turtles) between pre- and post-tracking years for particular groups were due to annual effects rather than device attachment (see Table 5). Mean \pm SE.

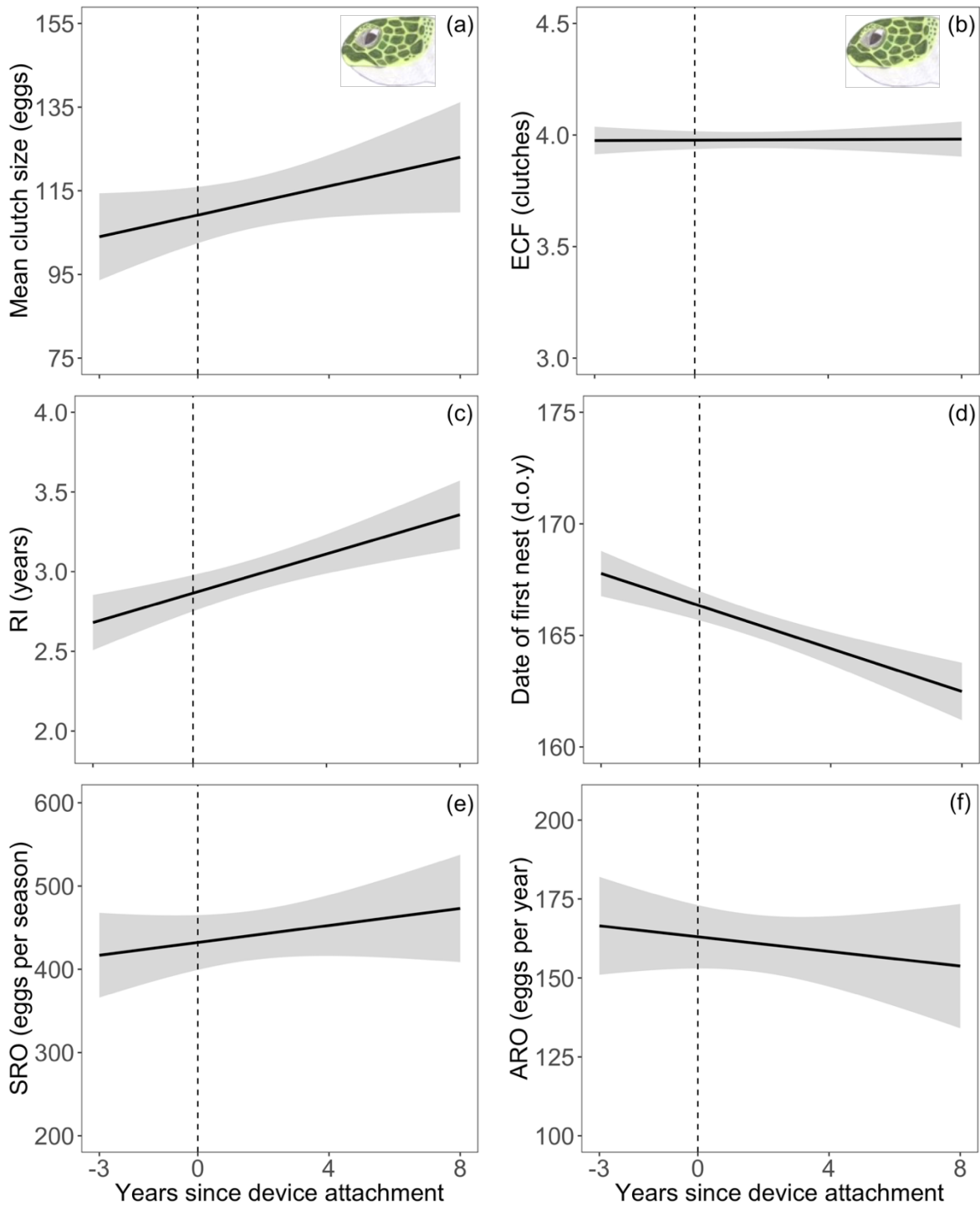


Figure 4. Carry-over effects on reproduction. Variation in mean clutch size (a), estimated clutch frequency (ECF, b), remigration interval (RI, c), date of first nest (d.o.y: day of year, d), seasonal reproductive output (SRO, e) and annual reproductive output (ARO, f) as a function of years since device attachment for green turtles, with year 0 being year of device attachment. The vertical dashed line represents year of device attachment. Grey shaded area represents 95 % confidence intervals.

Supplementary information

Methods

Statistical analysis – Among-female differences

Female size (curved carapace length: CCL) at device attachment or size at initial year was used to compare differences in size between ‘tracked’ and ‘non-tracked’ females. RI was calculated as the number of years elapsed between year of device attachment or initial year and the following capture. Mean clutch size, ECF and date of first nest were extracted from the following capture, i.e. post-tracking or post-initial year.

To determine whether device attachment influenced post-maturity growth, we looked at differences in curves between growth records pooled (‘tracked’ and ‘non-tracked’ females) and ‘non-tracked’ growth records, i.e. all growth records for ‘non-tracked’ females as well as growth records for ‘tracked’ females up until year of device attachment.

Statistical analysis – Within-female differences

To investigate within-female differences, capture histories were divided in pre- (including year of device attachment) and post-tracking years and subsequently separated in ‘attachment base only’ (n = 9) and ‘device attached’ (n = 12) groups for green turtles. Both groups were pooled (n = 10) for loggerhead turtles due to smaller sample size. If females had devices attached in more than one year, we compared the years prior and post first device attachment only. Because RI could not be calculated for pre-tracking years for females that were neophytes at device attachment, the analysis of RI and annual reproductive output only included remigrant females.

Statistical analysis – Carry-over effects

We included the first pre-tracking season as a baseline because devices were attached at variable points during the breeding season, which could possibly have influenced estimates of mean clutch size and ECF in the year of device attachment. We removed females that had devices attached in years following first device attachment.

Statistical analysis – Survivorship

Encounter histories were created for each female based on annual flipper and PIT tag re-sightings. Females were recorded as either present or absent based on successful nesting attempts. Although encounter histories are available from 1992 onwards, survey effort in 1992 was incomplete. We decided to use 1995 as the start date for the analysis of 'non-tracked' females as this represents three years after the beginning of the saturation tagging programme, which is equivalent to the average remigration interval for these two populations [1 – 3]. We therefore removed encounter histories for females that were first observed nesting prior to 1995 and after 2014 as these females will have had three or less years to potentially return to nest.

For the analysis of 'tracked' females, encounter histories were truncated such that the first year females were observed nesting was equivalent to the year of device attachment. This was done to avoid biasing survivorship estimates as females which had devices attached as remigrants would have a survivorship equal to 1 prior to device attachment. Survivorship estimates for 'tracked' females will therefore reflect survival for the 'tracked' period rather than survival for their entire encounter history. As for 'non-tracked' females, we removed encounter histories for females that had devices attached after 2014. All 'tracked' females were included in the analysis, as females that had devices attached in multiple years will have had to have survived previous device attachments.

Survival probability was assumed to be equal in both states because separating survival probabilities between the two states would require additional data collected at foraging grounds. Encounter probability in the non-breeding

state was fixed at 0. Transition probability $\psi_{B \rightarrow NB}$ was held constant for green turtles as only one female was observed nesting in consecutive years at Alagadi.

Goodness of fit (GoF) was assessed using the programme U-CARE [4]. The \hat{c} (c-hat) estimate (quasi-likelihood over-dispersion coefficient) was calculated using U-CARE and used to adjust the model selection metric: qAIC_c (quasi-likelihood Akaike's Information Criterion corrected for small sample size). Any estimates of $\hat{c} \leq 3.0$ are considered acceptable and suggest a reasonable fit of the model to the data [5].

We used the Markov chain Monte Carlo method to estimate parameters because it produces unbiased estimates compared to the maximum likelihood estimation method [6]. We simulated 10 chains with 4,000 tuning samples and a burn-in period of 1,000 samples. We used 10,000 samples from the Markov chain to generate posterior distributions. We assumed prior distributions to be normal (0, 1.75) on a logit scale.

Green turtles

The GoF tests indicated a lack of fit of the data to the global models for 'non-tracked' and 'tracked' green turtle datasets ($\chi^2_{73} = 149.95$, $P < 0.0001$ and $\chi^2_{44} = 94.46$, $P < 0.0001$ respectively). Results from test components 3G.SR ('non-tracked': $\chi^2_{14} = 18.28$, $P = 0.194$; 'tracked': $\chi^2_5 = 4.77$, $P = 0.444$) and M.I TEC ('non-tracked': $\chi^2_{19} = 54.66$, $P < 0.0001$, 'tracked': $\chi^2_{16} = 44.57$, $P < 0.0001$) indicated evidence of immediate trap-dependence, which can be interpreted as non-random temporary emigration [4]. A time-since-marking model structure was therefore used to estimate encounter probabilities for transient and remigrant individuals for both datasets. The over-dispersion coefficient \hat{c} was calculated as 2.05 for the 'non-tracked' dataset and as 2.15 for the 'tracked' dataset.

Loggerhead turtles

The GoF tests did not indicate a lack of fit of the data to the global models for 'non-tracked' and 'tracked' loggerhead turtle datasets ($\chi^2_{65} = 70.39$, $P = 0.302$ and $\chi^2_{31} = 34.70$, $P = 0.296$ respectively). Results from test components 3G.SR ('non-tracked': $\chi^2_{17} = 21.67$, $P = 0.198$; 'tracked': $\chi^2_7 = 2.98$, $P = 0.887$) and

M.ITEC ('non-tracked': $\chi^2_{19} = 22.26$, $P = 0.272$; 'tracked': $\chi^2_{12} = 18.58$, $P = 0.099$) did not indicate any evidence of transience or trap dependence. The over-dispersion coefficient \hat{c} was calculated as 1.08 for the 'non-tracked' dataset and as 1.12 for the 'tracked' dataset.

Results

Survivorship

Green turtles

The dataset comprised 224 encounter histories for ‘non-tracked’ green turtles and 46 encounter histories for ‘tracked’ green turtles. For both ‘non-tracked’ and ‘tracked’ datasets, the lowest $qAIC_c$ ranking models estimated a single survival probability, a single recapture probability for transient and remigrant individuals and single transition probabilities. Although test components 3G.SR were not significant, we tested the most parsimonious models with a time-since-marking model structure in survival to estimate survival probabilities for transient and remigrant individuals. However, this did not result in a better fit to both datasets (see Table S5 and Table S6).

Loggerhead turtles

The dataset comprised 327 encounter histories for ‘non-tracked’ loggerhead turtles and 46 encounter histories for ‘tracked’ loggerhead turtles. Due to the small size of the ‘non-tracked’ loggerhead turtle dataset and the small number of females that returned to nest following device attachment, transition probabilities were held constant over time for the ‘non-tracked’ dataset. For both ‘tracked’ and ‘non-tracked’ datasets, the lowest $qAIC_c$ ranking models estimated a single survival probability, a single recapture probability and single transition probabilities. Although test components 3G.SR and M.I TEC were not significant, we tested the most parsimonious models with a time-since-marking model structure in survival and recapture probability to estimate probabilities for transient and remigrant individuals, as a large number of females nesting at Alagadi can be considered transients. The model accounting for transience only resulted in a better fit to the data than the other models for the ‘non-tracked’ dataset (see Table S7). However, it did not result in a better fit to the data for the ‘tracked’ dataset (see Table S8).

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Table S1. Significance results for return rate analysis.

Species	Time-frame	Test 1: tracked versus non-tracked neophytes		Test 2: tracked neophytes versus tracked remigrants		Test 3: 'attachment base only versus 'device attached' groups	
		p value	Odds ratio (95 % CI)	p value	Odds ratio (95 % CI)	p value	Odds ratio (95 % CI)
Green turtles	≤ 5 yr	0.271	0.383 (0.090 – 1.643)	0.382	0.460 (0.090 – 2.350)	0.310	0.403 (0.060 – 1.991)
	≤ 10 yr	0.282	0.344 (0.068 – 1.744)	0.574	0.387 (0.057 – 2.612)	0.678	0.595 (0.048 – 4.763)
	≤ 15 yr	0.127	0.187 (0.022 – 1.586)	1.000	0.387 (0.030 – 4.981)	0.596	2.304 (0.111 – 145.491)
Loggerhead turtles	≤ 5 yr	0.407	0.529 (0.130 – 2.163)	0.440	0.467 (0.059 – 2.930)	0.440	2.143 (0.341 – 16.895)
	≤ 10 yr	0.696	0.678 (0.159 – 2.895)	0.678	0.504 (0.061 – 3.452)	0.678	1.986 (0.290 – 16.454)
	≤ 15 yr	0.343	0.343 (0.056 – 2.086)	0.613	0.563 (0.044 – 9.110)	0.613	1.775 (0.110 – 22.859)

Test 1 investigates whether there is a significant difference between the number of resighted 'tracked' and 'non-tracked' neophyte (first-time nesters) females. Test 2 investigates whether there is a significant difference between the number of resighted 'tracked' neophyte and remigrant females. Finally, test 3 investigates whether there is a significant difference between the number of resighted 'attachment base only' and 'device attached' females. Odds ratio are used as a measure of effect size. CI: confidence intervals.

Table S2. Significance results looking at effects of device attachment on reproductive correlates among females.

Species Group	CCL (cm)	Mean clutch size (eggs)	ECF (clutches)	RI (years)	Date of first nest (day of year)
Green turtles					
'Non-tracked' (n = 94)	87.1 ± 5.7 (74.3 – 99.0)	115.9 ± 20.3 (69.0 – 184.0)	3.0 ± 1.3 (1.0 – 6.0)	3.7 ± 1.5 (2.0 – 9.0)	167.1 ± 14.6 (142.0 – 224.0)
'Attachment base only' (n = 14)	90.1 ± 6.2 (81.5 – 103.0)	116.8 ± 25.6 (72.0 – 162.0)	4.1 ± 1.0 (2.0 – 6.0)	3.4 ± 1.6 (2.0 – 8.0)	159.6 ± 7.1 (151.0 – 175.0)
'Device attached' (n = 20)	93.1 ± 6.4 (79.7 – 105.0)	117.0 ± 26.6 (62.0 – 154.0)	3.6 ± 0.9 (1.0 – 5.0)	3.9 ± 2.0 (2.0 – 10.0)	167.2 ± 10.8 (144.0 – 186.0)
Loggerhead turtles					
'Non-tracked' (n = 50)	73.2 ± 3.7 (65.4 – 82.0)	78.8 ± 15.9 (47.5 – 124.0)	2.3 ± 1.3 (1.0 – 5.0)	3.8 ± 2.0 (1.0 – 10.0)	165.7 ± 13.0 (147.0 – 198.0)
'Attachment base only' (n = 6)	76.4 ± 3.1 (72.5 – 81.2)	85.5 ± 10.3 (76.0 – 99.0)	3.7 ± 0.8 (3.0 – 5.0)	3.5 ± 0.8 (3.0 – 5.0)	154.2 ± 9.2 (143.0 – 170.0)
'Device attached' (n = 8)	74.1 ± 6.9 (67.5 – 87.2)	74.9 ± 10.7 (64.0 – 99.0)	3.5 ± 1.7 (1.0 – 6.0)	2.9 ± 1.0 (2.0 – 5.0)	161.5 ± 12.8 (142.0 – 187.0)

Differences in body size in the year of device attachment and reproductive correlates in the years following device attachment among groups of females. For 'non-tracked' females, the year(s) of and following device attachment represent randomly generated following recaptures. Mean ± SD (range). CCL: curved carapace length; ECF: estimated clutch frequency; RI: remigration interval.

Table S3. Significance results looking at growth covariates and device attachment.

Species	Model	Interaction	Coefficient (\pm SE)	t value	p value
Green turtles	Annual growth	Years since first capture : Tracking	0.002 \pm 0.014	0.167	0.867
		Mean CCL : Tracking	-0.002 \pm 0.002	-1.086	0.278
		RI : Tracking	0.029 \pm 0.043	0.660	0.510
	Compound annual growth rates	Years since first capture : Tracking	-0.013 \pm 0.014	-0.915	0.361
		RI : Tracking	0.025 \pm 0.042	0.590	0.556
Loggerhead turtles	Annual growth	Years since first capture : Tracking	0.013 \pm 0.031	0.422	0.674
		Mean CCL : Tracking	0.001 \pm 0.007	0.204	0.839
		RI : Tracking	-0.004 \pm 0.142	-0.026	0.980
	Compound annual growth rates	Years since first capture : Tracking	0.025 \pm 0.038	0.673	0.502
		RI : Tracking	0.012 \pm 0.127	0.097	0.923

Growth covariates are those used in Omeyer et al. [3] to investigate whether device attachment influenced post-maturity growth of 'tracked' females. SE: standard error; CCL: curved carapace length; CAGR: compound annual growth rates.

Table S4. Significance results of within-female differences in reproductive correlates between pre- and post-tracking years.

Species	Group	Significance: reproduction			Significance: annual effect	
		Reproductive correlate	χ^2_1	p value	χ^2_1	p value
Green turtles	'Attachment base only'	<i>Mean clutch size</i>	0.13	0.716	<i>11.24</i>	<i>< 0.0001</i>
		Estimated clutch frequency	0.87	0.351	0.03	0.861
		Remigration interval	0.31	0.579	0.66	0.415
		<i>Date of first nest</i>	0.19	0.662	<i>5.39</i>	<i>0.020</i>
		<i>Seasonal reproductive output</i>	0.99	0.320	<i>5.10</i>	<i>0.024</i>
		Annual reproductive output	1.41	0.235	0.04	0.844
	'Device attached'	Mean clutch size	0.01	0.927	1.63	0.202
		Estimated clutch frequency	0.07	0.789	0.05	0.821
		Remigration interval	0.03	0.867	1.77	0.184
		<i>Date of first nest</i>	< 0.001	0.987	<i>10.05</i>	<i>0.002</i>
		Seasonal reproductive output	0.10	0.755	0.83	0.361
		Annual reproductive output	0.64	0.425	0.01	0.909
Loggerhead turtles	Groups pooled	<i>Mean clutch size</i>	0.24	0.625	<i>4.72</i>	<i>0.030</i>
		Estimated clutch frequency	3.44	0.064	0.21	0.643
		Remigration interval	2.04	0.153	1.05	0.305
		<i>Date of first nest</i>	0.08	0.780	<i>7.69</i>	<i>0.006</i>
		Seasonal reproductive output	2.63	0.105	1.27	0.260
		Annual reproductive output	0.55	0.460	0.43	0.513

'Attachment base only' and 'device attached' groups were pooled for loggerhead turtles due to smaller sample size. Significant results are italicised.

Table S5. Summary of models analysed in MARK for ‘non-tracked’ green turtles.

Model	qAICc	Δ qAICc	AICc weights	Model likelihood
S(.) $p_B(\text{tsm}-./.)$ $p_{NB}(0)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(\cdot)$	445.57	0.00	0.999	0.999
S(tsm-./.) $p_B(\text{tsm}-./.)$ $p_{NB}(0)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(\cdot)$	459.43	13.87	0.001	0.001
S(.) $p_B(\text{tsm}-./t)$ $p_{NB}(0)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(\cdot)$	474.21	28.64	0.000	0.000
S(.) $p_B(\text{tsm}-./.)$ $p_{NB}(0)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(t)$	474.71	29.14	0.000	0.000
S(t) $p_B(\text{tsm}-./.)$ $p_{NB}(0)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(\cdot)$	481.29	35.72	0.000	0.000
S(.) $p_B(\text{tsm}-t/.)$ $p_{NB}(0)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(\cdot)$	484.88	39.32	0.000	0.000
S(.) $p_B(\text{tsm}-./t)$ $p_{NB}(0)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(t)$	504.89	59.32	0.000	0.000
S(t) $p_B(\text{tsm}-./t)$ $p_{NB}(0)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(\cdot)$	509.18	63.61	0.000	0.000
S(t) $p_B(\text{tsm}-./.)$ $p_{NB}(0)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(t)$	517.70	72.14	0.000	0.000
S(.) $p_B(\text{tsm}-t/t)$ $p_{NB}(0)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(\cdot)$	518.29	72.72	0.000	0.000
S(.) $p_B(\text{tsm}-t/.)$ $p_{NB}(0)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(t)$	519.67	74.10	0.000	0.000
S(t) $p_B(\text{tsm}-t/.)$ $p_{NB}(0)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(\cdot)$	526.50	80.94	0.000	0.000
S(t) $p_B(\text{tsm}-./t)$ $p_{NB}(0)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(t)$	552.70	107.13	0.000	0.000
S(.) $p_B(\text{tsm}-t/t)$ $p_{NB}(0)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(t)$	555.77	110.21	0.000	0.000
S(t) $p_B(\text{tsm}-t/.)$ $p_{NB}(0)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(t)$	569.71	124.15	0.000	0.000
S(t) $p_B(\text{tsm}-t/t)$ $p_{NB}(0)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(\cdot)$	574.13	128.56	0.000	0.000
S(t) $p_B(\text{tsm}-t/t)$ $p_{NB}(0)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(t)$	612.08	166.52	0.000	0.000

qAICc: quasi-likelihood Akaike’s information criterion corrected for small sample size; S: survival rate, assumed to be equal in the breeding and non-breeding state; p_B : probability of recapture in the breeding state; p_{NB} : probability of recapture in the non-breeding state, fixed at 0 throughout; $\psi_{B \rightarrow NB}$: breeding transition probability from the breeding to the non-breeding state, held constant as green turtles extremely rarely breed in consecutive years; $\psi_{NB \rightarrow B}$: breeding transition probability from the non-breeding to the breeding state; ‘t’ denotes that the parameter was time varying; ‘.’ denotes that the parameter was constant; ‘tsm’: time-since-marking model structure; ‘/’ separates age-classes (transients versus remigrants) for parameters with a time-since-marking model structure.

Table S6. Summary of models analysed in MARK for ‘tracked’ green turtles.

Model	qAIC _c	ΔqAIC _c	AIC _c weights	Model likelihood
S(.) p _B (tsm-./.) p _{NB} (0) ψ _{B→NB} (.) ψ _{NB→B} (.)	209.33	0.00	0.695	1.000
S(tsm-./.) p _B (tsm-./.) p _{NB} (0) ψ _{B→NB} (.) ψ _{NB→B} (.)	210.99	1.67	0.302	0.434
S(.) p _B (tsm-./t) p _{NB} (0) ψ _{B→NB} (.) ψ _{NB→B} (.)	221.92	12.60	0.001	0.002
S(.) p _B (tsm-t/t) p _{NB} (0) ψ _{B→NB} (.) ψ _{NB→B} (.)	221.92	12.60	0.001	0.002
S(.) p _B (tsm-t/.) p _{NB} (0) ψ _{B→NB} (.) ψ _{NB→B} (.)	225.42	16.09	0.000	0.000
S(.) p _B (tsm-./.) p _{NB} (0) ψ _{B→NB} (.) ψ _{NB→B} (t)	239.67	30.34	0.000	0.000
S(.) p _B (tsm-t/.) p _{NB} (0) ψ _{B→NB} (.) ψ _{NB→B} (t)	239.67	30.34	0.000	0.000
S(t) p _B (tsm-./.) p _{NB} (0) ψ _{B→NB} (.) ψ _{NB→B} (.)	251.96	42.64	0.000	0.000
S(t) p _B (tsm-t/.) p _{NB} (0) ψ _{B→NB} (.) ψ _{NB→B} (.)	251.96	42.64	0.000	0.000
S(.) p _B (tsm-./t) p _{NB} (0) ψ _{B→NB} (.) ψ _{NB→B} (t)	257.21	47.88	0.000	0.000
S(.) p _B (tsm-t/t) p _{NB} (0) ψ _{B→NB} (.) ψ _{NB→B} (t)	257.21	47.88	0.000	0.000
S(t) p _B (tsm-./t) p _{NB} (0) ψ _{B→NB} (.) ψ _{NB→B} (.)	272.73	63.41	0.000	0.000
S(t) p _B (tsm-./.) p _{NB} (0) ψ _{B→NB} (.) ψ _{NB→B} (t)	293.80	84.48	0.000	0.000
S(t) p _B (tsm-t/.) p _{NB} (0) ψ _{B→NB} (.) ψ _{NB→B} (t)	293.80	84.48	0.000	0.000
S(t) p _B (tsm-./t) p _{NB} (0) ψ _{B→NB} (.) ψ _{NB→B} (t)	321.36	112.04	0.000	0.000
S(t) p _B (tsm-t/t) p _{NB} (0) ψ _{B→NB} (.) ψ _{NB→B} (t)	321.36	112.04	0.000	0.000
S(t) p _B (tsm-t/t) p _{NB} (0) ψ _{B→NB} (.) ψ _{NB→B} (.)	327.22	117.89	0.000	0.000

qAIC_c: quasi-likelihood Akaike’s information criterion corrected for small sample size; S: survival rate, assumed to be equal in the breeding and non-breeding state; p_B: probability of recapture in the breeding state; p_{NB}: probability of recapture in the non-breeding state, fixed at 0 throughout; ψ_{B→NB}: breeding transition probability from the breeding to the non-breeding state, held constant as green turtles extremely rarely breed in consecutive years; ψ_{NB→B}: breeding transition probability from the non-breeding to the breeding state; ‘t’ denotes that the parameter was time varying; ‘.’ denotes that the parameter was constant; ‘tsm’: time-since-marking model structure; ‘/’ separates age-classes (individuals that become transient after device attachment and individuals that remain in the breeding population after device attachment) for parameters with a time-since-marking model structure.

Table S7. Summary of models analysed in MARK for ‘non-tracked’ loggerhead turtles.

Model	qAICc	Δ qAICc	AICc weights	Model likelihood
S(tsm-./.) $p_B(\cdot)$ $p_{NB}(0)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(\cdot)$	667.06	0.00	0.705	1.000
S(tsm-./.) $p_B(\text{tsm-./.})$ $p_{NB}(0)$ $\psi_{B \rightarrow B}(\cdot)$ $\psi_{NB \rightarrow B}(\cdot)$	669.11	2.05	0.253	0.359
S(.) $p_B(\cdot)$ $p_{NB}(0)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(\cdot)$	673.79	6.72	0.024	0.035
S(.) $p_B(\text{tsm-./.})$ $p_{NB}(0)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(\cdot)$	674.96	7.90	0.014	0.019
S(.) $p_B(t)$ $p_{NB}(0)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(\cdot)$	678.41	11.35	0.002	0.003
S(.) $p_B(\cdot)$ $p_{NB}(0)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(t)$	679.25	12.19	0.002	0.002
S(.) $p_B(\cdot)$ $p_{NB}(0)$ $\psi_{B \rightarrow NB}(t)$ $\psi_{NB \rightarrow B}(\cdot)$	691.29	24.23	0.000	0.000
S(t) $p_B(\cdot)$ $p_{NB}(0)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(\cdot)$	698.59	31.53	0.000	0.000
S(.) $p_B(t)$ $p_{NB}(0)$ $\psi_{B \rightarrow NB}(t)$ $\psi_{NB \rightarrow B}(\cdot)$	705.68	38.62	0.000	0.000
S(.) $p_B(t)$ $p_{NB}(0)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(t)$	705.73	38.66	0.000	0.000
S(.) $p_B(\cdot)$ $p_{NB}(0)$ $\psi_{B \rightarrow NB}(t)$ $\psi_{NB \rightarrow B}(t)$	712.35	45.29	0.000	0.000
S(t) $p_B(t)$ $p_{NB}(0)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(\cdot)$	714.38	47.32	0.000	0.000
S(t) $p_B(\cdot)$ $p_{NB}(0)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(t)$	716.21	49.14	0.000	0.000
S(t) $p_B(\cdot)$ $p_{NB}(0)$ $\psi_{B \rightarrow NB}(t)$ $\psi_{NB \rightarrow B}(\cdot)$	728.82	61.76	0.000	0.000
S(.) $p_B(t)$ $p_{NB}(0)$ $\psi_{B \rightarrow NB}(t)$ $\psi_{NB \rightarrow B}(t)$	736.28	69.21	0.000	0.000
S(t) $p_B(t)$ $p_{NB}(0)$ $\psi_{B \rightarrow NB}(t)$ $\psi_{NB \rightarrow B}(\cdot)$	744.28	77.21	0.000	0.000
S(t) $p_B(t)$ $p_{NB}(0)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(t)$	745.50	78.44	0.000	0.000
S(t) $p_B(\cdot)$ $p_{NB}(0)$ $\psi_{B \rightarrow NB}(t)$ $\psi_{NB \rightarrow B}(t)$	749.32	82.26	0.000	0.000
S(t) $p_B(t)$ $p_{NB}(0)$ $\psi_{B \rightarrow NB}(t)$ $\psi_{NB \rightarrow B}(t)$	773.14	106.08	0.000	0.000

qAICc: quasi-likelihood Akaike’s information criterion corrected for small sample size; S: survival rate, assumed to be equal in the breeding and non-breeding state; p_B : probability of recapture in the breeding state; p_{NB} : probability of recapture in the non-breeding state, fixed at 0 throughout; $\psi_{B \rightarrow NB}$: breeding transition probability from the breeding to the non-breeding state, held constant as green turtles extremely rarely breed in consecutive years; $\psi_{NB \rightarrow B}$: breeding transition probability from the non-breeding to the breeding state; ‘t’ denotes that the parameter was time varying; ‘.’ denotes that the parameter was constant; ‘tsm’: time-since-marking model structure; ‘/’ separates age-classes (transients versus remigrants) for parameters with a time-since-marking model structure.

Table S8. Summary of models analysed in MARK for ‘tracked’ loggerhead turtles.

Model	qAICc	Δ qAICc	AICc weights	Model likelihood
S(.) p_B (.) $p_{NB}(0)$ $\psi_{B \rightarrow NB}$ (.) $\psi_{NB \rightarrow B}$ (.)	152.56	0.00	0.414	1.000
S(tsm-./.) p_B (.) $p_{NB}(0)$ $\psi_{B \rightarrow NB}$ (.) $\psi_{NB \rightarrow B}$ (.)	152.89	0.32	0.352	0.850
S(.) p_B (tsm-./.) $p_{NB}(0)$ $\psi_{B \rightarrow NB}$ (.) $\psi_{NB \rightarrow B}$ (.)	154.89	2.33	0.129	0.312
S(tsm-./.) p_B (tsm-./.) $p_{NB}(0)$ $\psi_{B \rightarrow NB}$ (.) $\psi_{NB \rightarrow B}$ (.)	155.29	2.73	0.106	0.256
S(.) p_B (t) $p_{NB}(0)$ $\psi_{B \rightarrow NB}$ (.) $\psi_{NB \rightarrow B}$ (.)	188.90	36.34	0.000	0.000
S(t) p_B (.) $p_{NB}(0)$ $\psi_{B \rightarrow NB}$ (.) $\psi_{NB \rightarrow B}$ (.)	194.75	42.19	0.000	0.000
S(t) p_B (t) $p_{NB}(0)$ $\psi_{B \rightarrow NB}$ (.) $\psi_{NB \rightarrow B}$ (.)	275.30	122.74	0.000	0.000

Due to the small size of the dataset and the small number of females that returned to nest following device attachment, transition probabilities were held constant over time. qAICc: quasi-likelihood Akaike’s information criterion corrected for small sample size; S: survival rate, assumed to be equal in the breeding and non-breeding state; p_B : probability of recapture in the breeding state; p_{NB} : probability of recapture in the non-breeding state, fixed at 0 throughout; $\psi_{B \rightarrow NB}$: breeding transition probability from the breeding to the non-breeding state; $\psi_{NB \rightarrow B}$: breeding transition probability from the non-breeding to the breeding state; ‘.’ denotes that the parameter was constant; ‘tsm’: time-since-marking model structure; ‘/’ separates age-classes (individuals that become transient after device attachment and individuals that remain in the breeding population after device attachment) for parameters with a time-since-marking model structure.

Table S9. Summary of parameter estimates calculated using MARK for both species and groups.

Species Group	Survival	Recapture probability in the breeding state	Breeding transition probability between states
Green turtles			
'Non-tracked'	S = 0.91 (0.88 – 0.94)	p_B (transients) = 0.39 (0.02 – 0.89) p_B (remigrants) = 0.87 (0.70 – 1.00)	$\psi_{B \rightarrow NB}$ = 0.98 (0.95 – 1.00) $\psi_{NB \rightarrow B}$ = 0.22 (0.16 – 0.30)
'Tracked'	S = 0.97 (0.95 – 0.99)	p_B (transients) = 0.43 (0.01 – 0.93) p_B (remigrants) = 0.92 (0.79 – 1.00)	$\psi_{B \rightarrow NB}$ = 0.98 (0.96 – 1.00) $\psi_{NB \rightarrow B}$ = 0.35 (0.27 – 0.43)
Loggerhead turtles			
'Non-tracked'	S (transients) = 0.44 (0.30 – 0.61) S (remigrants) = 0.83 (0.77 – 0.88)	p_B = 0.55 (0.23 – 0.99)	$\psi_{B \rightarrow NB}$ = 0.89 (0.74 – 0.98) $\psi_{NB \rightarrow B}$ = 0.37 (0.11 – 0.73)
'Tracked'	S = 0.82 (0.73 – 0.90)	p_B = 0.78 (0.48 – 1.00)	$\psi_{B \rightarrow NB}$ = 0.94 (0.87 – 1.00) $\psi_{NB \rightarrow B}$ = 0.38 (0.20 – 0.60)

Survival, recapture probability and breeding transition probability: mean (95 % highest posterior density confidence intervals).

$\psi_{B \rightarrow NB}$: breeding transition probability from the breeding to the non-breeding state; $\psi_{NB \rightarrow B}$: breeding transition probability from the non-breeding to the breeding state.

CHAPTER 5: THE IMPORTANCE OF PASSIVE INTEGRATED TRANSPONDER (PIT) TAGS FOR MEASURING LIFE-HISTORY TRAITS OF SEA TURTLES

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Abstract

Capture-mark-recapture studies rely on the identification of individuals through time, using markers or tags, which are assumed to be retained. This assumption, however, may be violated, having implications for population models. In sea turtles, individual identification is typically based on external flipper tags, which can be combined with internal passive integrated transponder (PIT) tags. Despite the widespread and extensive use of flipper tags, few studies have modelled tag loss using continuous functions. Using a 26-year dataset for sympatrically nesting green (*Chelonia mydas*) and loggerhead (*Caretta caretta*) turtles, this study aims to assess how the use of PIT tags increases the accuracy of estimates of life-history traits. The addition of PIT tags improved female identification: between 2000 and 2017, 53% of green turtles and 29% of loggerhead turtles were identified from PIT tags alone. We found that flipper and PIT tag losses were best described by decreasing logistic curves with lower asymptotes. Excluding PIT tags from our dataset led to underestimation of flipper tag loss, reproductive periodicity, reproductive longevity and annual survival, and overestimation of female abundance and recruitment for both species. This shows the importance of PIT tags in improving the accuracy of estimates of life-history traits. Thus, estimates where tag loss has not been corrected for should be interpreted with caution and could bias IUCN Red List assessments. As such, long-term population monitoring programmes should aim to estimate tag loss and assess the impact of loss on life-history trait estimates, to provide robust estimates without which population models and stock assessments cannot be derived accurately.

Introduction

Population-based conservation is dependent on accurate estimates of life-history traits (Hernández-Camacho et al., 2015; Yokoi et al., 2017). Most population studies use capture-mark-recapture (CMR), which involves the release of tagged individuals and their subsequent recapture events over time. These studies rely on individual recognition to provide information about demography, behaviour and survival, assuming tags are correctly identified and retained over time (Pradel, 1996). This assumption, however, is often violated, having implications for the interpretation of demographic and survivorship data (Arnason and Mills, 1981; González-Vicente et al., 2012; Rotella and Hines, 2005). In CMR models, individuals having lost all tags are no longer identifiable and are indistinguishable from dead individuals, which can lead to the overestimation of population abundance and underestimation of survival (Arnason and Mills, 1981; Cowen and Schwarz, 2006; Laake et al., 2014).

CMR has been used extensively in sea turtle research to study behaviour (e.g. Lazar et al., 2004) and to estimate life-history traits (e.g. Stokes et al., 2014). Such studies generally rely on tagging individuals with two external flipper tags, reducing the probability of individual loss from the identifiable population. Double tagging also allows tag loss estimation, the rate of which may be influenced by tag type and size, species and tagger experience (Casale et al., 2017; Limpus, 1992).

Flipper tags can be combined with subcutaneously injected passive integrated transponder (PIT) tags which are thought to be more durable, cannot be lost through abrasion or during courtship and have higher readability and retention than flipper tags (Gibbons and Andrews, 2004; Godley et al., 1999; McNeill et al., 2013; Rivalan et al., 2005). Thus, individuals having lost all external tags may nevertheless be re-identified. Detection failure can occur, however, if tags are expelled from the body before wound healing (Feldheim et al., 2002; Godley et al., 1999), if tags migrate within the animal's tissue (Van Dam and Diez, 1999; Wyneken et al., 2010) or if tags become unreadable (McNeill et al., 2013; Van Dam and Diez, 1999). Whilst PIT tags have very little negative impact on animals overall (Gibbons and Andrews, 2004), their benefits may be outweighed by their higher financial cost. Furthermore, the availability and necessity of PIT

tag readers for tag detection (Gibbons and Andrews, 2004) may prohibit their use, especially when recapture probability is low or when non-project personnel, such as fishermen, encounter tagged animals.

Although tagging, and particularly flipper tagging, is considered standard practice in sea turtle research, few studies have estimated tag loss. Two approaches have been used to do so: proportion of tags lost (e.g. Bjørndal et al., 1996; Limpus, 1992) and, recently, modelling (e.g. Casale et al., 2017). Typically, individuals are tagged with two flipper tags and the shedding of one of the two tags is used to model tag loss using different scenarios. Only five studies have modelled flipper tag loss in such a manner at foraging (timeframe: 11 yr, McNeill et al., 2013, timeframe: 14 yr, Casale et al., 2017) and nesting (timeframe: 22 yr, Nishizawa et al., 2017; timeframe: 9 yr, Pfaller et al., 2019) grounds for loggerhead turtles (*Caretta caretta*), and only at nesting grounds for leatherback turtles (*Dermochelys coriacea*, timeframe: 7 yr, Rivalan et al., 2005). Tag loss was best described by a high initial loss before remaining constant thereafter (Casale et al., 2017; Nishizawa et al., 2017; Pfaller et al., 2019; Rivalan et al., 2005), except in McNeill et al. (2013), where it was constant over time. Only one study has used its findings to adjust survival estimates and to compare them to non-adjusted estimates (Nishizawa et al., 2017). Similarly, only one study has modelled PIT tag loss using continuous functions indicating that PIT tag loss is negligible in nesting loggerhead turtles (timeframe: 9 yr, Pfaller et al., 2019).

The need for more accurate data on life-history parameters for demographic models and population assessments has been highlighted as a research priority for sea turtles globally (Hamann et al., 2010; Rees et al., 2016) and, in particular, for green turtles (*Chelonia mydas*) in the Mediterranean (Casale et al., 2018). For example, although annual survival has been calculated for subset groups of green and loggerhead nesting females in the Mediterranean (Omeyer et al., 2019; Snape et al., 2016), no estimates are available for nesting populations as a whole in the region.

Saturation flipper tagging has been carried out since 1992 at Alagadi Beach, North Cyprus, and PIT tags were introduced in 1997. Using the resulting 26-year individual-based monitoring dataset for green and loggerhead turtles, this study aims (1) to accurately estimate long-term flipper and PIT tag loss for green and loggerhead turtles; and (2) to assess how the use of PIT tags has increased

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the accuracy of estimates of flipper tag loss, population abundance and recruitment, survival, and reproductive periodicity and longevity.

Material and methods

Data collection

Since 1992, sea turtle monitoring at Alagadi Beach has been carried out by the Marine Turtle Conservation Project (University of Exeter, UK), a collaboration between the Marine Turtle Research Group, the North Cyprus Department for Environmental Protection and the North Cyprus Society for the Protection of Turtles. Alagadi Beach, situated on the north coast of Cyprus (35°33' N, 33°47' E), consists of two coves of 0.8 and 1.2 km in length, separated by a rocky headland (Broderick and Godley, 1996). On average, 217 green and 65 loggerhead turtle clutches are laid annually (2014–2018). Satellite tracking of females of both species at this study site has revealed foraging sites in Syria, Egypt, Libya, Lebanon, Tunisia, Turkey and Cyprus (Bradshaw et al., 2017; Snape et al., 2016).

Data were collected between early May and mid-August (encompassing the entire nesting season) from 1993 to 2017, except in 1992 when monitoring began in early July. Flipper tags were fitted on the trailing edge of the fore-flippers between the proximal second and third scales during the covering phase, immediately after oviposition (Balazs, 1999). From 1992 to 1999, plastic flipper tags were used (1992–1994: Dalton Jumbotags®, 1994–1999: Dalton Supertag®; Dalton Tags, UK). Because these tags became unreadable after a few years, from 1999 to 2015, titanium Stockbrands® (Australia) flipper tags were used, except in 2013, where Inconel 681/C tags were used (National Band & Tag Company, Kentucky, USA). In 2016 and 2017, Inconel and titanium flipper tags were used because it was decided to stop using titanium tags when females reacted negatively to the new design. The estimation of Inconel flipper tag loss was not possible due to their recent introduction and the resultant low level of tag returns to date.

PIT tags were injected from 1997 onwards, as per Godley et al. (1999), to increase recapture rates of females having lost all flipper tags. Prior to 2014, Trovan microchips (11.50 x 2.12 mm, 0.10 g) were used, after which the newly available Trovan mini-transponders (8.00 x 1.40 mm, 0.06 g) were used due to their smaller, less invasive gauge needle. Until 2013, one PIT tag was given in

each shoulder where time permitted, whereas from 2014 onwards, only one PIT tag was given, in preference, in the right shoulder, both to reduce costs and limit the number of invasive procedures. Checks of both shoulders were nevertheless maintained as standard. Effects of flipper and PIT tagging have been investigated at Alagadi Beach, showing no significant effects on post-ovipositional behaviour and reproductive success (Broderick and Godley, 1999).

Data handling

Two datasets were compared to assess the error associated with tag loss and to determine whether the use of PIT tags resulted in more accurate estimates of life-history parameters and flipper tag loss. In the 'PIT tag' dataset, flipper and PIT tag readings were used, whereas, in the 'no PIT tag' dataset, PIT tags were omitted and female identification was based solely on flipper tags. In the 'no PIT tag' dataset, if a previously known female returned to nest and was identified by PIT tag(s) alone, having lost all flipper tags, she was given a new identification number and thus treated as a neophyte female (first-time nester). Reproductive periodicity and longevity were calculated for each new female, except for females that were identified by PIT tag(s) alone on their first recapture at their second nesting season, as these females will not have successfully completed one remigration interval with both flipper tags. A new encounter history was created for each female and the process was repeated each time females had lost both flipper tags, meaning that a known female could have multiple identification numbers and thus multiple encounter histories in the 'no PIT tag' dataset. Finally, for the tag loss analysis of the 'no PIT tag' dataset, tag histories in which all tags were lost were excluded, as these could not be determined without the use of PIT tags (TH20 and TH10, see section 5 for further details).

Reproductive periodicity and longevity

While reproductive periodicity is the number of years elapsed between two consecutive nesting seasons, reproductive longevity is the time span since recruitment (year of first capture) to the nesting population, with neophytes being given year 0. The annual number of neophyte females and the annual proportion

of misidentified remigrant females were calculated from 2000 onwards because of the increased accuracy of neophyte classification following one modal breeding cycle (3 yrs) after the introduction of PIT tags.

Linear models and generalised linear mixed effect models were used to determine whether PIT tags significantly improved estimates of reproductive longevity and periodicity respectively, using the package 'nlme' in R (R Core Team, 2018). Female ID was included to account for pseudoreplication and temporal effects were controlled for.

Annual survival

Encounter histories were created based on nesting events. Survival probability was estimated using the multi-state model in MARK (White and Burnham, 1999), assuming a breeding state (B; observable state) and a non-breeding state (NB; unobservable state). The parameters estimated were annual survival probability (S), encounter probability (p) and transition probabilities between states ($\psi_{B \rightarrow NB}$ and $\psi_{NB \rightarrow B}$). A 'time-since-marking' approach with two 'age' classes was used to allow survival the first year after initial tagging (hereafter S1) to differ from that in subsequent years (hereafter S2; Chaloupka and Limpus, 2002; Kendall et al., 2018; Pradel et al., 1997; Sasso et al., 2006). This allows us to account for imperfect fidelity, assuming that some neophytes are transient individuals, i.e. those being individuals that are never seen again after their initial capture. While S1 confounds permanent emigration and mortality, S2 is more likely to reflect true survival.

Goodness of fit was assessed using U-CARE (Choquet et al., 2005). Model selection was based on the lowest $qAIC_c$ value (corrected quasi-likelihood Akaike information criterion). Parameters were estimated using the Markov chain Monte Carlo method and were based on posterior distributions. 95% highest posterior density credibility intervals were reported (see supplementary material for further details).

Tag loss

Tag returns were ascribed to five types of tag histories (TH), using days as the unit, and were defined as follows: females released/resighted with two tags and resighted with both tags (TH22), with one tag (TH21) or with no tags (TH20); and, females released/resighted with one tag and resighted with one tag (TH11) or no tag (TH10). PIT tag(s) permitted the identification of females having lost both flipper tags and thus the calculation of TH20 and TH10. Tag histories can be combined such that a female released with two tags, resighted with two tags, and resighted again with no tags would have the following tag history: TH22+TH20.

Tag history probabilities were defined as per Casale et al. (2017), adapted to include TH20 and TH10. Maximum likelihood estimation was performed using the package 'bbmle'. The same five models as in Casale et al. (2017, see supplementary material for further details) were compared. Model selection was based on the lowest AIC_c (corrected Akaike Information Criterion) value.

The analysis was conducted separately for each tag type, species and dataset. Both types of plastic flipper tags and PIT tags were grouped due to small sample size. Because new tags were fitted if lost, the datasets included multiple tags per female.

Other studies

All previously published studies which calculated tag loss using continuous functions were reviewed and presented in Table 1 for comparison. Cumulative tag loss probabilities after 1 and 5 yr were calculated when absent from those original studies (see Table 1 for details).

Results

Population parameters at Alagadi Beach

Female identification

Of the females previously tagged with both flipper and PIT tags at Alagadi Beach, 53% of green turtles ($n = 305$) and 29% of loggerhead turtles ($n = 132$) were identified in subsequent nesting seasons by PIT tag(s) alone between 2000 and 2017, resulting in the overestimation of neophytes, particularly for green turtles (Fig. 1, Table S1). On average, over that period, without PIT tags, we would have assumed that 74% of green turtles ($n = 671$) and 78% of loggerhead turtles ($n = 492$) nesting were neophyte females, instead of the 44% and 69% respectively using PIT tags (Table S1). Simultaneously, nesting female abundance would have been overestimated by 37% for green turtles (2000–2017, PIT tags: $n = 389$, no PIT tags: $n = 533$) and 9% for loggerhead turtles (PIT tags: $n = 371$, no PIT tags: $n = 405$).

Reproductive periodicity

The median reproductive periodicity was 3.0 yr for both species at this study site, with a mean of 3.5 yr for green turtles and 3.0 yr for loggerhead turtles, and intervals of up to 12 and 10 yr for green and loggerhead turtles respectively (Fig. 2, Table S1). Omitting PIT tags resulted in less accurate estimates of reproductive periodicity, although not significantly, for both species (green turtles: $\chi^2_1 = 1.98$, $P = 0.159$; loggerhead turtles: $\chi^2_1 = 0.15$, $P = 0.701$). For green turtles, the median reproductive periodicity remained unchanged when omitting PIT tags, but the mean was slightly reduced to 3.2 yr, whereas, for loggerhead turtles, it resulted in underestimation of the median (2.0 yr) and the mean (2.8 yr; Fig. 2, Table S1). While PIT tags captured intervals of up to 12 yr, rarely were intervals of ≥ 5 yr captured using flipper tags only at this study site (Fig. 2).

Reproductive longevity

Median and mean reproductive longevity were 6.0 and 8.0 yr for green turtles and 4.0 and 5.5 yr for loggerhead turtles, with females breeding for up to 24 and 25 yr respectively at Alagadi Beach (Fig. 2, Table S1). Estimates of

reproductive longevity were significantly improved by PIT tags for green turtles ($F_{1,266} = 15.76$, $P < 0.0001$) but not for loggerhead turtles ($F_{1,182} = 1.25$, $P = 0.265$). Without PIT tags, the median and mean reproductive longevity were reduced by 2.0 and 2.7 yr respectively for green turtles (Table S1). For loggerhead turtles, the median reproductive longevity remained unchanged, whereas the mean was reduced by 1.0 yr without PIT tags (Table S1). While females remained identifiable for up to 25 yr after first nesting at this study site using both flipper and PIT tags, rarely were females of either species still identifiable after 10 yr of breeding using flipper tags only (Fig. 2).

Annual survival

Model results are summarised in Tables S2-5. Without PIT tags, some females would have been misidentified as up to six different females, therefore underestimating annual survival at Alagadi Beach (Table S6). Mean annual survival was 0.48 for the first year after initial capture and 0.84 thereafter for green turtles, instead of 0.66 and 0.97 respectively estimated using PIT tags. For loggerhead turtles, the difference was not as large: 0.36 instead of 0.44 for the first 'age' class and 0.76 instead of 0.83 for the second 'age' class.

Tag loss

Tag histories, tag retention and model results are summarised in Tables S7-10. Tag retention is illustrated in Fig. S1.

Loggerhead turtles at Alagadi Beach

Initial daily tag loss probability rapidly decreased before remaining constant 200 and 126 days after initial tagging for plastic and titanium flipper tags respectively for loggerhead turtles at Alagadi Beach (Table 1, Fig. S2). Projections indicated that over half of double-tagged females (58% and 56% respectively) had retained both of their plastic and titanium flipper tags after 1 remigration interval (3 yr), and over four-fifths of single-tagged females (83% and 81% respectively) had retained their only flipper tag (Fig. 3ab). Half of all tagged females had lost their flipper tag(s) and were no longer identifiable after ≤ 3 remigration intervals (~ 8 yr) for plastic flipper tags, and after just over 2

remigration intervals (~6.5 yr) for titanium flipper tags (Fig. 3ab). For both flipper tag types, daily tag loss probability was underestimated when PIT tag readings were omitted (Fig.S2), resulting in the overestimation of the proportion of females (single- or double-tagged) having retained their tag(s) over the course of the study period at this study site (Fig.3 ab).

Although initial daily tag loss probability was higher for PIT tags than for both flipper tag types, daily tag loss probability was lower for PIT tags once it plateaued for loggerhead turtles at Alagadi Beach (Fig.S3). Tag retention was higher for PIT tags than for both flipper tag types. After 1 remigration interval, 79% of double-tagged females had retained both PIT tags, and 95% of single-tagged females had retained their only PIT tag (Fig. 3c). Half of double-tagged females still retained both PIT tags 17 yr after initial tagging, and two-thirds of single-tagged females still retained their PIT tag 22 yr after initial tagging (Fig. 3c).

Green turtles at Alagadi Beach

Initial daily tag loss probability increased before remaining stable 9 yr after initial tagging for plastic flipper tags, whereas it rapidly decreased before remaining constant 192 days after initial tagging for titanium flipper tags for green turtles at Alagadi Beach (Table 1, Fig. S4). Whereas daily tag loss probability was higher in green turtles than in loggerhead turtles at this study site for plastic flipper tags, it plateaued around similar values for titanium flipper tags.

Projections indicated that half of double-tagged females (50% for both flipper tag types) had retained both of their plastic and titanium flipper tags after 1 remigration interval (3 yr), and three-quarters of single-tagged females (76% and 75% respectively) had retained their only flipper tag at Alagadi Beach (Fig. 3de). Half of all tagged females had lost their flipper tag(s) and were no longer identifiable after ≤ 2 remigration intervals (~5 yr) for plastic flipper tags, and after 2 remigration intervals (6 yr) for titanium flipper tags (Fig. 3de). Similarly to loggerhead turtles at this study site, the omission of PIT tags resulted in the underestimation of daily tag loss probability for green turtles and, therefore, the overestimation of the proportion of females having retained their flipper tags over the course of the study period, irrespective of tag type (Fig. 3de).

Although initial daily tag loss probability for PIT tags and titanium flipper tags were similar for green turtles at Alagadi Beach, daily tag loss probability was lower for PIT tags once it stabilised (Fig. S3). Tag retention 3 yr after initial tagging was much higher for PIT tags than for both flipper tag types, and was higher in green turtles than in loggerhead turtles at this study site. After 1 remigration interval, 91% of double-tagged females had retained both PIT tags, and 99% of single-tagged females had retained their only PIT tag (Fig. 3f). Only 5% of all tagged females were no longer identifiable using PIT tags 22 yr after initial tagging (Fig. 3f).

All studies

Table 1 compiles all previously published studies which estimate tag loss using continuous functions, including this study. Estimates for both flipper tag types at Alagadi Beach for green turtles were higher than those calculated in Malaysia for Inconel and titanium flipper tags. For loggerhead turtles, estimates at this study site were within the range of those previously reported for Inconel flipper tags in Italy and the USA. In contrast, the asymptotic values and the cumulative tag loss probabilities after 5 yr for PIT tags for the two species at Alagadi Beach were far lower than those corrected by the presence of PIT tags for all flipper tag types. Without accounting for non-independence of tag loss, on average, over a fifth (22%) of tagged individuals will have lost at least one flipper tag after 1 year and over half (58%) of tagged individuals after 5 yr across green and loggerhead turtle studies. In contrast, on average, 10% of tagged individuals will have lost at least one PIT tag after 1 yr and 14% after 5 yr.

Combination of annual survival and tag loss

Half of loggerhead turtles tagged at Alagadi Beach will still be identifiable with at least one tag upon recapture 2-3 yr after initial tagging using titanium flipper tags, and 3-4 yr after initial tagging using PIT tags (Fig. S5a). On average, irrespective of tag type, only 50% of loggerhead turtles will be identifiable upon recapture after 1 remigration interval only. In contrast, 50% of green turtles tagged at Alagadi Beach will still be identifiable using at least one tag upon

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recapture 3-5 yr after initial tagging using titanium flipper tags, and 16-21 yr after initial tagging using PIT tags (Fig. S5b).

Discussion

Here, we show the importance of PIT tags for the long-term population monitoring of two different sea turtle species. Combining flipper and PIT tagging at this study site allowed for greater female identification and thus more accurate estimates of tag loss, life-history traits and population parameters, in particular for green turtles.

Flipper tag loss

Variation in flipper tag loss can be observed across species, life-stages, sex, tag types and geographical locations (e.g. Bradshaw et al., 2000; Chambers et al., 2015; Hastings et al., 2018; Oosthuizen et al., 2010). For sea turtles, a pattern appears to be emerging, whereby flipper tag loss is best described by a decreasing logistic curve with a lower asymptote (Table 1). While flipper tag loss was found to increase with age due to individual growth in elephant seals for example (Oosthuizen et al., 2010), this was not observed in sea turtles, potentially because estimates were mainly from adults, which have negligible growth (Omeyer et al., 2017, 2018). The increase in tag loss found for plastic flipper tags in green turtles here is likely due to the writing on the tag fading rather than loss per se. In contrast, the constant tag loss for loggerhead turtles in McNeill et al. (2013) likely resulted from the lack of short-term recaptures, preventing the detection of high initial loss. Additionally, while tag loss may be influenced by interspecific behavioural differences and habitat effects, as observed in fur seals (Bradshaw et al., 2000) and previously described in sea turtles (Limpus, 1992), this was not apparent from Table 1, likely due to small sample size. Initial and asymptotic flipper tag loss across sea turtle studies remained within the same order of magnitude (Table 1), although care should be taken when drawing conclusions from such comparisons because of the inherent differences among studies (Casale et al., 2017; McNeill et al., 2013; Nishizawa et al., 2017; Pfaller et al., 2019; Rivalan et al., 2005).

Evidence is increasingly suggesting that loss is not independent between flipper tag pairs (Steller sea lions: Hastings et al., 2018; elephant seals: McMahan and White, 2009; Schwarz et al., 2012; sea turtles: McNeill et al., 2013; Nishizawa

et al., 2017; Pfaller et al., 2019; Rivalan et al., 2005). Not accounting for non-independence of tag loss overestimates loss for the first tag and largely underestimates loss for the second tag. Unfortunately, investigating this at Alagadi Beach was not possible because of the large number of researchers with varying tagging abilities involved over the study period, the inclusion of multiple tags per female and the relatively small cohort size. It has, nevertheless, been documented for leatherback (Rivalan et al., 2005), loggerhead (McNeill et al., 2013) and green (Nishizawa et al., 2017) turtles. While tissue necrosis was proposed to be the cause for leatherback turtles, it was suggested for the other two species to result from human error, also thought to be the cause of the high initial flipper tag loss in sea turtles (Table 1). Such a tagger effect on tag loss estimates has also been documented in fur seals (Bradshaw et al., 2000) and bluefin tuna (Chambers et al., 2015). Both of these emerging patterns – high initial loss and non-independence of flipper tag loss – suggest that thorough training of the tagging research staff is key to increasing long-term flipper tag retention across sea turtle studies (McNeill et al., 2013; Pfaller et al., 2019).

PIT tags

PIT tags have been proposed as permanent tags (Gibbons and Andrews, 2004) despite also being subject to loss (lemon sharks: Feldheim et al., 2002; salmon: Foldvik and Kvingedal, 2018; sea turtles: McNeill et al., 2013; Pfaller et al., 2019; spiny lobsters: O'Malley, 2008). In this study, for both species, PIT tag loss was found to be best described by a decreasing logistic curve with a lower asymptote, similarly to flipper tags (Table 1). The high initial loss is likely to be the result of faulty application or ejection from the body before wound healing, such as in lemon sharks (Feldheim et al., 2002) and loggerhead turtles (Pfaller et al., 2019). As opposed to fish (e.g. Onders et al., 2004) and moulting species (e.g. Frusher et al., 2009; González-Vicente et al., 2012), physical loss is highly unlikely in sea turtles once the insertion wound has healed (Pfaller et al., 2019). Once improperly applied tags have been shed, detection failure is more likely due to human error, although mechanical failure (i.e. failure in tag transmission or reader failure) and tag migration may also influence PIT tag detection (McNeill et al., 2013; Pfaller et al., 2019; Van Dam and Diez, 1999; Wyneken et al., 2010). Indeed, this can be seen in our data where PIT tags previously thought to be lost

are recorded at future recapture events. This phenomenon is bound to be exacerbated in females with multiple PIT tags in the same shoulder at this study site, in particular, if the research staff do not consistently search for the presence of more than one PIT tag. Similarly to flipper tags, short-term within-season PIT tag retention could be improved by providing adequate training to the tagging research staff (McNeill et al., 2013; Pfaller et al., 2019). Pfaller et al. (2019) also suggest the use of a temporary, fast-drying adhesive or patch at the tagging site as a method to reduce the likelihood of PIT tag expulsion before wound healing. While this suggestion could improve long-term PIT tag retention, it should not be seen as an alternative method to reducing high initial loss, but rather should be used in conjunction with thorough training of the tagging research staff. This additional step to the tagging procedure will require further training and will reduce within-season PIT tag loss only if performed correctly.

Nevertheless, PIT tag loss is substantially less than that of flipper tags for sea turtles (Table 1; Pfaller et al., 2019; Groom et al., 2017; Schäuble et al., 2006; Parmenter, 2003, 1993). While PIT tags are also subject to loss, Pfaller et al. (2019) tested the assumption that PIT tags can be used as permanent markers in nesting loggerhead turtles in the USA. Using genetic markers, they showed that flipper tag loss estimates were not substantially biased by PIT tag loss, although this should be tested at other locations. Such high retention has also been observed in salmon (Foldvik and Kvingedal, 2018) and sea lions (Chilvers and MacKenzie, 2010). PIT tag retention is, however, highly variable between species, ranging from 100% in lobsters (Frusher et al., 2009) to as low as 3% in paddlefish (Onders et al., 2004), and is likely to be impacted by species-specific life-history traits and behaviours. The interspecific differences in PIT tag retention at this study site are likely to be due to a combination of different factors. Indeed, the accuracy of PIT tag loss estimates for loggerhead turtles is likely to have been reduced by the lower return rates of this species linked to lower nest site fidelity compared to green turtles (Snape et al., 2018, 2016) thus, reducing sample size, as well as associated length of capture histories (Tables S7-S8, Fig. S1; Omeyer et al., 2019, 2018). Increasing PIT tag reporting rates at a basin-wide scale would improve, and likely reduce, long-term PIT tag loss estimates for loggerhead turtles but is dependent on the availability of PIT tag readers at other monitoring sites.

The rate at which flipper tags and other external tags are being lost in sea turtles, sea lions (Hastings et al., 2018) and spiny lobsters (González-Vicente et al., 2012) for example, is of concern for long-term individual-based population monitoring relying solely on one set of identification markers. The estimation of life-history traits and population parameters may, however, be improved by the use of additional identification methods, such as those making use of natural patterns (e.g. Smout et al., 2011), human-made marks (e.g. branding, Smout et al., 2011) or genetic markers (Pfaller et al., 2019). Here, results highlighted that the typical method used to estimate tag loss by quantifying the loss of one of the two tags in double-tagged individuals largely underestimated tag loss in the absence of PIT tags. As such, tag loss estimates which are not corrected for using at least one other identification method should be interpreted with caution.

PIT tags allowed for a larger number of individual females to be identified after a longer period of time compared to flipper tags, increasing the accuracy of life-history traits and population parameters, as also demonstrated in sea lions (Chilvers and MacKenzie, 2010; Hastings et al., 2018). As such, the use of PIT tags over flipper tags is far preferable for the long-term individual monitoring of turtles (Pfaller et al., 2019), and particularly for green turtles at this study site. Nevertheless, both types of tags are still being used at Alagadi Beach as the presence of flipper tags should also improve short-term identification of individual females at recapture opportunities elsewhere when PIT tag readers are not available, such as when individuals are bycaught. The difference in the efficacy of PIT tags was likely influenced by interspecific differences in nest site fidelity at this study site (Snape et al., 2018). Indeed, considering the high flipper tag loss observed at Alagadi Beach, the proportion of loggerhead turtle females identified by PIT tags alone, as well as the accuracy of parameter estimates for this species, would likely increase should return rates be higher.

Annual survival

The 'time-since-marking' modelling approach allowed the decoupling of annual survival estimates for sea turtles. Survival was lower the first year after initial tagging (S1) than in subsequent years (S2) and was likely underestimated as mortality and permanent emigration were confounded. However, there is

currently no way to assess permanent emigration given the coverage of CMR programmes in North Cyprus and in the Mediterranean. Although imperfect fidelity to our study site was accounted for by the modelling approach, the misclassification of remigrant nesters having nested undetected elsewhere as neophytes could have further influenced estimates.

While S1 estimates are low, S2 estimates are more likely to reflect true survival of remigrant females. Estimates calculated here highlight yet again the consistently lower estimates for loggerhead turtles globally compared to those of green turtles (Pfaller et al., 2018), which is thought to be the result of interspecific differences in foraging behaviour (Broderick et al., 2006). Apparent annual survival estimates for loggerhead turtles (0.83, CI: 0.78-0.87) are comparable to those of Casale et al. (2015, 2007) for large juveniles and adults in the Mediterranean, to those of adults from subset groups at this study site (Omeyer et al., 2019; Snape et al., 2016), and fall within the predictions for loggerhead turtles globally (0.82, 0.79-0.85; Pfaller et al., 2018). For green turtles, S2 estimates (0.97, CI: 0.95-0.99) are also comparable to those from subset groups at Alagadi Beach (Omeyer et al., 2019) and exceed the global predictions for green turtles (0.88, CI: 0.80-0.93; Pfaller et al., 2018). The difference in PIT tag loss estimates, combined with interspecific differences in annual survival, resulted in large differences in the proportion of individuals still alive and identifiable using PIT tags over time between the two species at this study site. It is, however, likely that the values presented here for loggerhead turtles are an underestimate due to low nest site fidelity (Snape et al., 2018, 2016).

Excluding PIT tags resulted in the underestimation of both S1 and S2 survival estimates. As Wilkinson et al (2011) highlighted for sea lions using branding marks, the presence of PIT tags allowed for more robust estimates of annual survival to be calculated at this study site. Because life-history data are often not available, sea turtle population assessments have been based on temporal changes in clutch counts rather than individual count. Therefore, providing new or improved estimates of life-history traits and population parameters, such as those calculated here, will be key in generating population models for IUCN Red List assessments for both species in the Mediterranean, which will contribute to the conservation of these threatened species. Indeed, such population models will inform our understanding of population demography and dynamics and can be used to identify life-history parameters at which to

target conservation actions (sea turtles: Casale and Heppell, 2016; Crouse et al., 1987; Crowder et al., 1994; Mazaris et al., 2005; spotted turtles: Enneson and Litzgus, 2008). However, these models are dependent on high-quality, long-term data on all life-stages to be accurately parametrised, yet they are necessary to avoid erroneous or detrimental management decision from being made (Hernández-Camacho et al., 2015; Winker and Sherley, 2019; Yokoi et al., 2017).

Future recommendations

Life-history data can be acquired using multiple techniques, however, the accuracy of parameter estimates is dependent on the inherent biases of each method as highlighted in this study. Therefore, data used for IUCN Red List assessments should systematically be updated for each species and sub-population when tag loss estimates become available. While we have shown how PIT tags have improved the accuracy of female identification and life-history and population parameter estimates at this study site, there is still scope in improving these estimates further. Indeed, for example, satellite tracking, which has been used extensively across marine megafauna to provide information on animal behaviour, distribution and movement (e.g. Hart et al., 2019; Heerah et al., 2019; Snape et al., 2018), could be used to refine estimates of clutch frequency at this study site without relying on tag returns. This would be particularly relevant for loggerhead turtles as they have been shown to nest in multiple countries within the same nesting season (Snape et al., 2018, 2016). Tracking devices, however, are costly, have a shorter lifespan compared to PIT tags especially (e.g. max < 2 yrs in Hart et al., 2019; and in Stokes et al., 2015), and therefore cannot be used to obtain individual-based long-term life-history data for the species.

While CMR programmes rarely set out to quantify tag loss, less invasive techniques, such as natural marks (sea turtles: Araujo et al., 2016; whale sharks: McCoy et al., 2018), human-made marks (hawksbill turtles: Richardson et al., 2006) or genetic markers (lemon sharks: Feldheim et al., 2002; sea turtles: Pfaller et al., 2019; giant salamanders: Unger et al., 2012), will be useful in further improving tag loss estimates and determining biological and physical factors driving this loss. Indeed, an improved understanding of flipper and PIT tag loss in sea turtles will help determine better tagging practices. Although photo-

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identification and genetic tagging can be used to track individuals through time (bottlenose dolphins: Diaz-Aguirre et al., 2018; short-finned pilot whales: Hill et al., 2018; whale sharks: McCoy et al., 2018), physical tags will currently remain necessary in the wild for sea turtles when individual-specific procedures are required, as neither method allows for near real-time individual identification. The CMR programme at Alagadi Beach currently lacks a photo-identification library, however, genetic samples of both species have been collected for almost two decades. Therefore, genetic tagging at this study site could be used to assess the accuracy of our PIT tag loss estimates, as per Pfaller et al. (2019), as well as estimates of life-history parameters (e.g. Shamblin et al., 2017).

Conclusion

In conclusion, we showed the importance of PIT tags for long-term individual-based population monitoring for two different sea turtle species. Permanent marks or long-lasting tags, such as PIT tags, are invaluable to provide more accurate estimates of tag loss and life-history parameters. Not accounting for tag loss has large implications for the interpretation of population demography, such as population abundance and recruitment. Thus, estimates where tag loss has not been corrected for should be interpreted with caution and could bias IUCN Red List assessments. Long-term population monitoring programmes should aim to estimate tag loss using continuous functions and multiple identification methods and assess its impact on life-history traits, in order to provide robust parameter estimates without which population models and stock assessments cannot be derived accurately.

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Table 1. Summary of published studies for which tag loss was estimated using tagging scenarios. Tag loss estimates are as follow: initial value, asymptotic value, cumulative probability of loss after 1 and 5 yr. If two values are presented in the same cell, these corresponds to estimates for the first and second tag. PIT tags: passive integrated transponder tags; CH: number of capture histories; n.a.: not applicable; ind./n-ind: (non)-independence of tag loss between tags. Presence (√) or absence (×) of PIT tags, with start date. Values in italic were not provided in the original article but were calculated here. ^a Model resulting in better fit to the data; ^b flipper tag loss estimates calculated for the ‘no PIT tag’ dataset in this study were included in this table to highlight the extent to which flipper tag loss is underestimated when based on one identification method only; ^c tag loss confirmed using genetic markers; ^d maximum likelihood parameter estimates; ^e Bayesian parameter estimates; ^f estimate after 2 yr; ^g tag loss confirmed using PIT tags.

Species Ocean basin and study area	Year	Tag type	PIT tags	Location	Shedding scenario and assumption	CH	Tag loss estimates				Reference
							Initial	Asymptote	1yr	5yrs	
<i>Dermochelys coriacea</i>											
Atlantic Ocean, French Guiana	1994- 2000	Monel 49	√ (1995)	Nesting beach	Decreasing logistic, n- ind.	1293	0.0037 n.a.	0.00028 0.00060	<i>0.24</i> <i>0.20</i>	<i>0.67</i> <i>0.67</i>	Rivalan et al. (2005)
<i>Chelonia mydas</i>											
Pacific Ocean, Malaysia	1993- 2014	Inconel 681	×	Nesting beach	Decreasing logistic, n- ind.	742	0.0025 0.0180	0.00028 0.00016	<i>0.23</i> <i>0.42</i>	<i>0.66</i> <i>0.63</i>	Nishizawa et al. (2017)

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Pacific Ocean, Malaysia	1993-2014	Inconel 681	×	Nesting beach	Decreasing logistic, ind. ^a	742	0.0028	0.00025	0.23	0.62	Nishizawa et al. (2017)
Pacific Ocean, Malaysia	1993-2014	Titanium Stockbrand	×	Nesting beach	Decreasing logistic, n-ind.	46	0.0150 0.1100	0.00016 0.00022	0.42 0.78	0.63 0.88	Nishizawa et al. (2017)
Pacific Ocean, Malaysia	1993-2014	Titanium Stockbrand	×	Nesting beach	Decreasing logistic, ind. ^a	46	0.0155	0.00019	0.40	0.66	Nishizawa et al. (2017)
Mediterranean Sea, N Cyprus	1992-2017	Plastic Jumbo and Supertags	×	Nesting beach	Constant, ind.	94	n.a.	0.00022	0.08	0.33 ^b	Present study
Mediterranean Sea, N Cyprus	1992-2017	Plastic Jumbo and Supertags	√ (1997)	Nesting beach	Increasing logistic, ind.	100	0.0004	0.00092	0.16	0.72 ^b	Present study
Mediterranean Sea, N Cyprus	1999-2017	Titanium Stockbrand	×	Nesting beach	Decreasing and increasing logistic, ind.	393	0.0022	0.00013	0.21	0.35 ^b	Present study
Mediterranean Sea, N Cyprus	1999-2017	Titanium Stockbrand	√ (1997)	Nesting beach	Decreasing logistic, ind.	426	0.0038	0.00057	0.25	0.67 ^b	Present study
Mediterranean Sea, N Cyprus	1997-2017	PIT	n.a.	Nesting beach	Decreasing logistic, ind.	317	0.0035	0.00002	0.07	0.10	Present study

Caretta caretta

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Atlantic Ocean, N Carolina (USA)	1989-2010	Inconel 681	√ (1995)	By-caught	Constant n-ind. ^a	618	n.a.	0.00033 0.00060	0.11 0.20	0.45 0.67	McNeill et al. (2013)
Atlantic Ocean, N Carolina (USA)	1989-2010	Inconel 681	√ (1995)	By-caught	Constant, ind. ^a	618	n.a.	0.00037	0.13	0.49	McNeill et al. (2013)
Atlantic Ocean, N Carolina (USA)	1989-2010	Inconel 681	√ First capture	By-caught	Constant and decreasing logistic, n-ind. ^a	585	n.a. 0.0367	0.00037 0.00044	0.13 0.80	0.49 0.94	McNeill et al. (2013)
Atlantic Ocean, N Carolina (USA)	1989-2010	Inconel 681	√ First capture	By-caught	Decreasing logistic, ind. ^a	585	0.0018	0.00034	0.25	0.72	McNeill et al. (2013)
Atlantic Ocean, Georgia (USA)	2008-2016	Inconel 681	√ First capture	Nesting beach	Decreasing logistic, n-ind.	186	0.0070 ^{c,d} 0.1160 ^{c,d}	0.00028 ^{c,d} 0.00009 ^{c,d}	~0.18 (0.22 ^{c,d,f})	0.38 ^{c,d}	Pfaller et al. (2019)
Atlantic Ocean, Georgia (USA)	2008-2016	Inconel 681	√ First capture	Nesting beach	Decreasing logistic, n-ind.	186	0.0029 ^e 0.0036 ^e	0.00029 ^e 0.00005 ^e	~0.17 (0.21 ^{c,e,f})	0.40 ^{c,e}	Pfaller et al. (2019)

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Atlantic Ocean, Georgia (USA)	2008-2016	Inconel 681	√ First capture	Nesting beach	Decreasing logistic, n-ind.	186	0.0060 ^d 0.0900 ^d	0.00028 ^d 0.00011 ^d	~0.17 (0.21 ^{d,f,g})	0.37 ^{d,g}	Pfaller et al. (2019)
Atlantic Ocean, Georgia (USA)	2008-2016	Inconel 681	√ First capture	Nesting beach	Decreasing logistic, n-ind.	186	0.0040 ^e 0.0034 ^e	0.00029 ^e 0.00006 ^e	~0.17 (0.21 ^{e,f,g})	0.39 ^{e,g}	Pfaller et al. (2019)
Atlantic Ocean, Georgia (USA)	2008-2016	PIT	n.a.	Nesting beach	Constant initial loss, null long-term loss, ind.	186	0.0010 ^d	~0.0000 ^d	0.06	0.06 ^{c,d}	Pfaller et al. (2019)
Atlantic Ocean, Georgia (USA)	2008-2016	PIT	n.a.	Nesting beach	Constant initial loss, null long-term loss, ind.	186	0.0007 ^e	~0.0000 ^e	0.07	0.07 ^{c,e}	Pfaller et al. (2019)
Mediterranean Sea, Italy	2002-2015	Inconel 681	×	Foraging area	Decreasing logistic, ind.	64	0.0058	0.00014	0.15	0.31	Casale et al. (2017)
Mediterranean Sea, N Cyprus	1992-2017	Plastic Jumbo and Supertags	×	Nesting beach	Decreasing logistic, ind.	84	0.0041	0.00008	0.11	0.21 ^b	Present study
Mediterranean Sea, N Cyprus	1992-2017	Plastic Jumbo and Supertags	√ (1997)	Nesting beach	Decreasing logistic, ind.	92	0.0043	0.00041	0.21	0.57 ^b	Present study

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Mediterranean Sea, N Cyprus	1999-2017	Titanium Stockbrand	×	Nesting beach	Decreasing logistic, ind.	177	0.0018	0.00022	0.11	0.36 ^b	Present study
Mediterranean Sea, N Cyprus	1999-2017	Titanium Stockbrand	√ (1997)	Nesting beach	Decreasing logistic, ind.	94	0.0019	0.00050	0.19	0.61 ^b	Present study
Mediterranean Sea, N Cyprus	1997-2017	PIT	n.a.	Nesting beach	Decreasing logistic, ind.	155	0.0066	0.00009	0.16	0.26	Present study

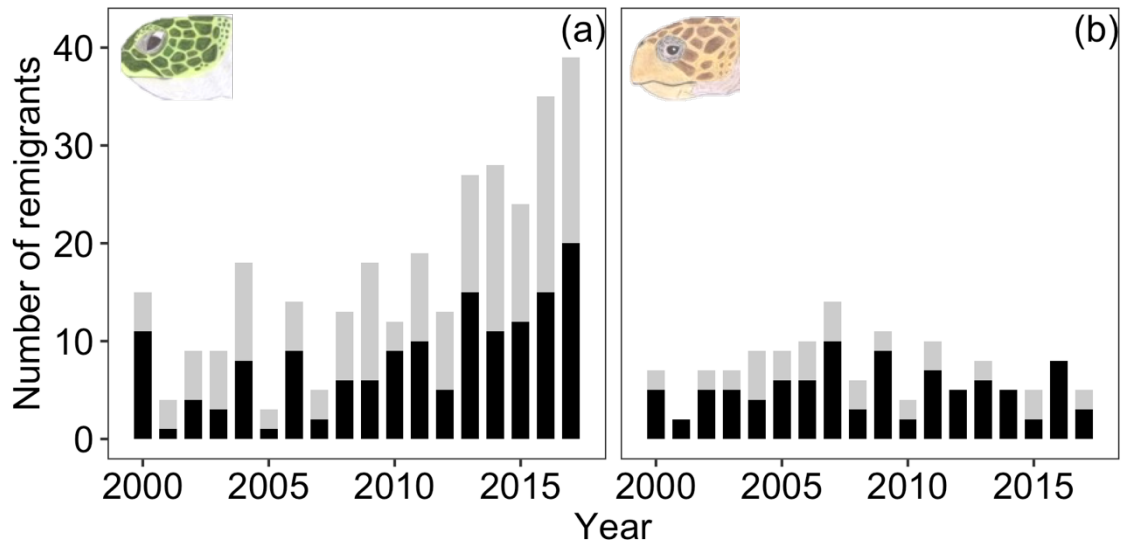


Figure 1. Misidentification of remigrants. Time series of the number of remigrant green (a) and loggerhead (b) turtles that left Alagadi Beach with both flipper and PIT tags and were subsequently identified by PIT tag(s) alone (grey bars) and by PIT and flipper tags or flipper tags alone (black bars). The grey bars show the number of remigrant females that would have been misidentified as neophyte females without the use of PIT tags.

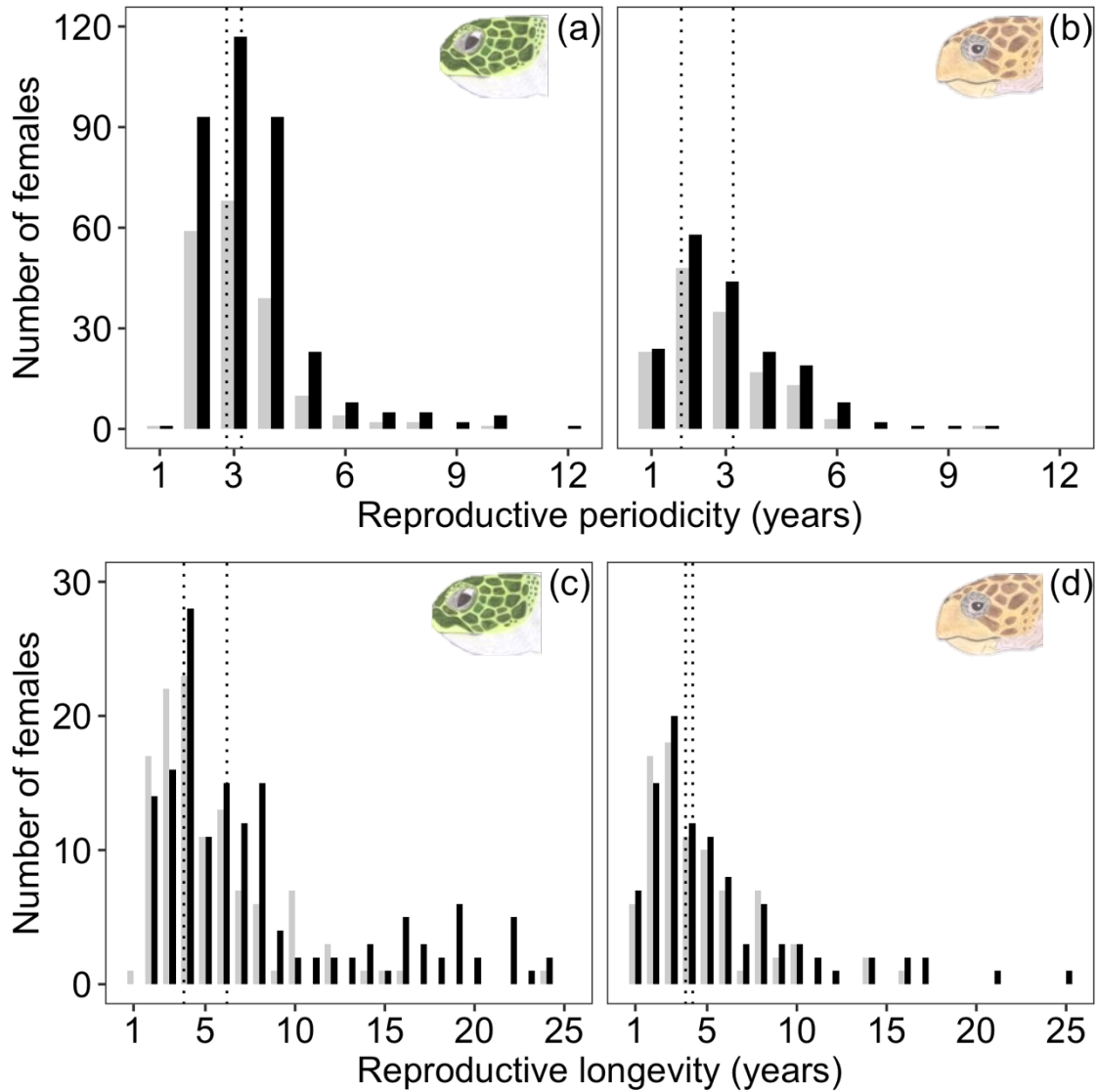


Figure 2. Accuracy of reproductive parameter estimates. Frequency distribution of reproductive periodicity (a-b) and longevity (c-d) for green (a, c) and loggerhead (b, d) turtles, as a function of female identification method. Identification based on flipper and PIT tag readings is shown in black and based on flipper tags only is shown in grey. Dotted lines are median values.

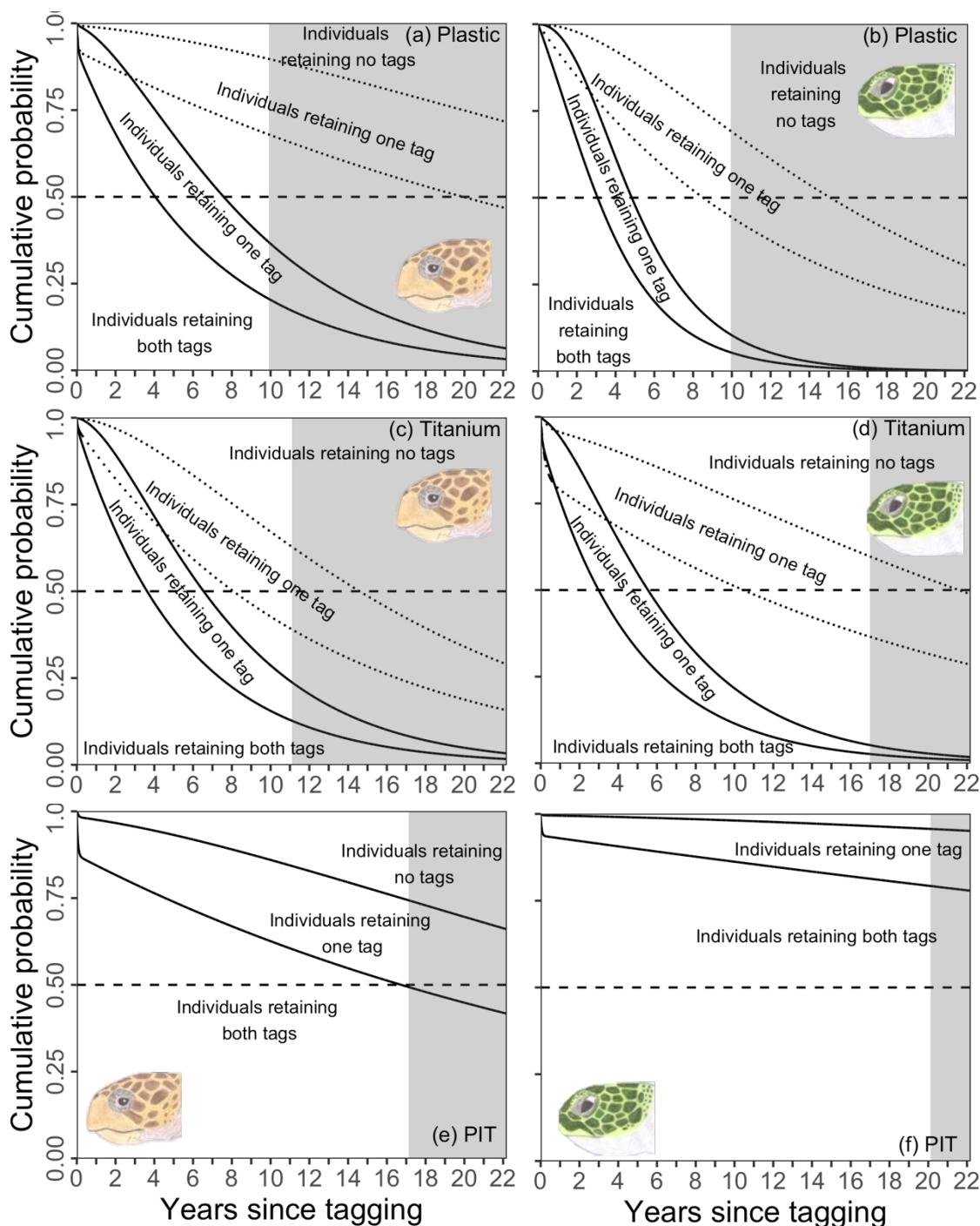


Figure 3. Tag loss. Estimated cumulative probabilities of individuals retaining two, one or no plastic (a,b), titanium (c,d) and PIT (e,f) tags, predicted by the models with the lowest AICc values, for loggerhead (a,c,e) and green (b,d,f) turtles, as a function of identification method ('PIT tag' dataset: solid curves; 'no PIT tag' dataset: dashed curves). The upper curve of each pair represents the probability that a single-tagged individual retains its tag, whereas the lower curve represents the probability that a double-tagged individual retains at least one tag. The horizontal dashed line represents 50% probability. The grey area shows extrapolation outside the range of the observed data.

Supplementary information

Material and methods – Survival

Encounter histories were created for each female based on tag returns. Females were recorded as either present or absent based on nesting events. Although encounter histories are available from 1992 onwards, survey effort in 1992 was incomplete. We decided to use 1995 as the start date for the survival analysis, as this represents three years after the beginning of the saturation tagging programme, which is equivalent to the median remigration interval for these two populations (Broderick et al., 2003; Omeyer et al., 2018; Stokes et al., 2014). We therefore removed encounter histories for females that were first observed nesting prior to 1995 and after 2014 as these females will have had three or less years to potentially return to nest.

Survival probability was assumed to be equal in both states because separating annual survival probabilities between the two states would require additional data collected at foraging grounds. Encounter probability in the non-breeding state was fixed at 0. Transition probability $\psi_{B \rightarrow NB}$ was held constant for green turtles as only one female was observed nesting in consecutive years at Alagadi.

Goodness of fit (GoF) was assessed using the programme U-CARE (Choquet et al., 2005). In particular, test component M.ITEC was used to test for trap-dependence. The \hat{c} (c-hat) estimate (quasi-likelihood over-dispersion coefficient) was calculated using U-CARE and used to adjust the model selection metric: $qAIC_c$ (quasi-likelihood Akaike's Information Criterion corrected for small sample size). Any estimates of $\hat{c} \leq 3.0$ are considered acceptable and suggest a reasonable fit of the model to the data (Lebreton et al., 1992).

We used the Markov chain Monte Carlo method to estimate parameters because it produces unbiased estimates compared to the maximum likelihood estimation method (Link et al., 2002). We simulated 10 chains with 4,000 tuning samples and a burn-in period of 1,000 samples. We used 10,000 samples from the Markov chain to generate posterior distributions. We assumed prior distributions to be normal (0, 1.75) on a logit scale.

Results – Survival

Green turtles

The 'PIT tag' and 'no PIT tag' datasets respectively comprised 265 and 405 encounter histories for green turtles. Results from test component M.ITEC (PIT tag: $\chi^2_{20} = 116.45$, $P < 0.0001$; no PIT tag: $\chi^2_{19} = 65.12$, $P < 0.0001$) indicated evidence of immediate trap-dependence for both datasets. A 'time-since-marking' model structure was therefore used to estimate annual survival and encounter probabilities using two 'age' classes to allow for each parameter to differ between the first year after initial tagging and subsequent years. The over-dispersion coefficient \hat{c} was calculated as 3.29 for the 'PIT tag' dataset and 2.08 for the 'no PIT tag' dataset. The lowest qAIC_c ranking models estimated single annual survival and recapture probabilities for each 'age' class, and single transition probabilities between states for both datasets (Tables S2, S4 and S6).

Loggerhead turtles

The 'PIT tag' and 'no PIT tag' datasets respectively comprised 372 and 407 encounter histories for loggerhead turtles. Results from test component M.ITEC (PIT tag: $\chi^2_{20} = 39.52$, $P = 0.006$; no PIT tag: $\chi^2_{20} = 36.99$, $P = 0.012$) indicated evidence of immediate trap-dependence for both datasets. Although the GoF test did not indicate evidence of a lack of fit of the data to the global model for the 'no PIT tag' dataset ($\chi^2_{72} = 90.06$, $P = 0.074$), the most parsimonious model with a 'time-since-marking' model structure in annual survival probability resulted in a better fit to the data (Table S5). Therefore, as for green turtles, a 'time-since-marking' structure was used to estimate annual survival and encounter probabilities for two 'age' classes. The over-dispersion coefficient \hat{c} was calculated as 1.48 for the 'PIT tag' dataset and 1.25 for the 'no PIT tag' dataset. The lowest qAIC_c ranking models estimated single annual survival and encounter probabilities for each 'age' class, and single transition probabilities between states (Tables S3 and S5-6).

Literature cited

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Table S1. Comparison of female identification and life-history estimates as a function of identification method for green and loggerhead turtles. Proportion of neophyte and remigrant females per year is only calculated from 2000 onwards (mean \pm SD, range). Reproductive periodicity and longevity: median (mean, interquartile range, range, n).

Species Dataset	Proportion of neophyte females per year	Proportion of remigrant females misidentified per year	Reproductive periodicity (years)	Reproductive longevity (years)
Green turtles				
'No PIT tag'	0.74 \pm 0.08 (0.55 – 0.86)	0.53 \pm 0.14 (0.25 – 0.75)	3.0 (3.2, 2.0 – 4.0, 1.0 – 10.0, 186)	4.0 (5.3, 3.0 – 6.0, 1.0 – 24.0, 115)
'PIT tag'	0.44 \pm 0.15 (0.17 – 0.68)	N.A.	3.0 (3.5, 2.0 – 4.0, 1.0 – 12.0, 352)	6.0 (8.0, 4.0 – 9.0, 2.0 – 24.0, 153)
Loggerhead turtles				
'No PIT tag'	0.78 \pm 0.09 (0.64 – 0.92)	0.29 \pm 0.19 (0.00 – 0.60)	2.0 (2.8, 2.0 – 3.0, 1.0 – 10.0, 140)	4.0 (4.5, 2.0 – 6.0, 1.0 – 16.0, 85)
'PIT tag'	0.69 \pm 0.11 (0.52 – 0.86)	N.A.	3.0 (3.0, 2.0 – 4.0, 1.0 – 10.0, 181)	4.0 (5.5, 3.0 – 7.0, 1.0 – 25.0, 99)

Table S2. Summary of models analysed in MARK for green turtles. Female identification was based on a combination of flipper and PIT tag readings.

Model	qAICc	Δ qAICc	AICc weights	Model likelihood
S(tsm – ./.) p _B (tsm – ./.) p _{NB} (0) $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(\cdot)$	442.35	0.00	1.00	1.00
S(tsm – ./.) p _B (tsm – ./t) p _{NB} (0) $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(\cdot)$	471.85	29.49	0.00	0.00
S(tsm – ./t) p _B (tsm – ./.) p _{NB} (0) $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(\cdot)$	473.74	31.39	0.00	0.00
S(tsm – ./.) p _B (tsm – ./.) p _{NB} (0) $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(t)$	474.00	31.64	0.00	0.00
S(tsm – t/.) p _B (tsm – ./.) p _{NB} (0) $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(\cdot)$	475.46	33.10	0.00	0.00
S(tsm – ./.) p _B (tsm – ./t) p _{NB} (0) $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(t)$	507.08	64.72	0.00	0.00
S(tsm – ./t) p _B (tsm – ./.) p _{NB} (0) $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(t)$	508.79	66.44	0.00	0.00
S(tsm – t/.) p _B (tsm – ./t) p _{NB} (0) $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(\cdot)$	509.12	66.77	0.00	0.00
S(tsm – ./t) p _B (tsm – ./t) p _{NB} (0) $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(\cdot)$	509.31	66.95	0.00	0.00
S(tsm – t/t) p _B (tsm – ./.) p _{NB} (0) $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(\cdot)$	510.30	67.95	0.00	0.00
S(tsm – t/.) p _B (tsm – ./.) p _{NB} (0) $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(t)$	510.41	68.06	0.00	0.00
S(tsm – ./.) p _B (tsm – t/.) p _{NB} (0) $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(\cdot)$	513.64	71.28	0.00	0.00
S(tsm – ./.) p _B (tsm – t/t) p _{NB} (0) $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(\cdot)$	514.76	72.40	0.00	0.00
S(tsm – t/.) p _B (tsm – t/.) p _{NB} (0) $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(\cdot)$	516.18	73.83	0.00	0.00
S(tsm – ./t) p _B (tsm – t/.) p _{NB} (0) $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(\cdot)$	516.79	74.44	0.00	0.00
S(tsm – ./.) p _B (tsm – t/.) p _{NB} (0) $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(t)$	517.28	74.93	0.00	0.00
S(tsm – t/.) p _B (tsm – ./t) p _{NB} (0) $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(t)$	548.05	105.69	0.00	0.00
S(tsm – ./t) p _B (tsm – ./t) p _{NB} (0) $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(t)$	548.36	106.00	0.00	0.00
S(tsm – t/t) p _B (tsm – ./.) p _{NB} (0) $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(t)$	549.26	106.90	0.00	0.00
S(tsm – t/t) p _B (tsm – ./t) p _{NB} (0) $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(\cdot)$	549.29	106.94	0.00	0.00
S(tsm – t/.) p _B (tsm – t/t) p _{NB} (0) $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(\cdot)$	550.48	108.13	0.00	0.00
S(tsm – ./.) p _B (tsm – t/t) p _{NB} (0) $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(t)$	554.00	111.65	0.00	0.00
S(tsm – t/t) p _B (tsm – t/.) p _{NB} (0) $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(\cdot)$	554.43	112.08	0.00	0.00
S(tsm – t/.) p _B (tsm – t/.) p _{NB} (0) $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(t)$	554.98	112.62	0.00	0.00
S(tsm – ./t) p _B (tsm – t/t) p _{NB} (0) $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(\cdot)$	555.82	113.46	0.00	0.00
S(tsm – ./t) p _B (tsm – t/.) p _{NB} (0) $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(t)$	555.89	113.54	0.00	0.00
S(tsm – t/t) p _B (tsm – ./t) p _{NB} (0) $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(t)$	592.72	150.37	0.00	0.00
S(tsm – t/.) p _B (tsm – t/t) p _{NB} (0) $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(t)$	593.48	151.12	0.00	0.00
S(tsm – t/t) p _B (tsm – t/t) p _{NB} (0) $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(\cdot)$	597.10	154.75	0.00	0.00
S(tsm – t/t) p _B (tsm – t/.) p _{NB} (0) $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(t)$	597.72	155.37	0.00	0.00
S(tsm – t/t) p _B (tsm – t/t) p _{NB} (0) $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(t)$	645.42	203.06	0.00	0.00

Chapter 5: The importance of PIT tags

qAIC_c: quasi-likelihood Akaike's information criterion corrected for small sample size; S: annual survival rate, assumed to be equal in the breeding and non-breeding state; p_B : probability of recapture in the breeding state; p_{NB} : probability of recapture in the non-breeding state, fixed at 0 throughout; $\psi_{B \rightarrow NB}$: breeding transition probability from the breeding to the non-breeding state, held constant as green turtles extremely rarely breed in consecutive years; $\psi_{NB \rightarrow B}$: breeding transition probability from the non-breeding state to the breeding state; 't' denotes that the parameter was time varying; '.' denotes that the parameter was constant; 'tsm': time-since-marking model structure, to allow for the parameter estimates to differ between the first year after initial tagging and subsequent years; '/' separates the two 'age' classes for parameters with a time-since-marking model structure.

Table S3. Summary of models analysed in MARK for loggerhead turtles. Female identification was based on a combination of flipper and PIT tag readings.

Model	qAICc	Δ qAICc	AICc weights	Model likelihood
S(tsm - ./.) p_B (tsm - ./.) $p_{NB}(0)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(\cdot)$	711.05	0.00	0.996	1.00
S(tsm - ./.) p_B (tsm - ./t) $p_{NB}(0)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(\cdot)$	722.36	11.31	0.003	0.0035
S(tsm - ./t) p_B (tsm - ./.) $p_{NB}(0)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(\cdot)$	729.08	18.03	0.0001	0.0012
S(tsm - ./.) p_B (tsm - ./.) $p_{NB}(0)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(t)$	731.33	20.28	0.00004	0.00004
S(tsm - ./.) p_B (tsm - ./.) $p_{NB}(0)$ $\psi_{B \rightarrow NB}(t)$ $\psi_{NB \rightarrow B}(\cdot)$	737.21	26.16	0.00	0.00
S(tsm - t/.) p_B (tsm - ./.) $p_{NB}(0)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(\cdot)$	737.48	26.43	0.00	0.00
S(tsm - ./.) p_B (tsm - t/.) $p_{NB}(0)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(\cdot)$	740.02	28.97	0.00	0.00
S(tsm - ./.) p_B (tsm - ./t) $p_{NB}(0)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(t)$	748.22	37.17	0.00	0.00
S(tsm - ./.) p_B (tsm - ./t) $p_{NB}(0)$ $\psi_{B \rightarrow NB}(t)$ $\psi_{NB \rightarrow B}(\cdot)$	750.57	39.52	0.00	0.00
S(tsm - ./t) p_B (tsm - ./t) $p_{NB}(0)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(\cdot)$	751.02	39.97	0.00	0.00
S(tsm - ./t) p_B (tsm - ./.) $p_{NB}(0)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(t)$	752.48	41.43	0.00	0.00
S(tsm - ./.) p_B (tsm - t/t) $p_{NB}(0)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(\cdot)$	753.08	42.03	0.00	0.00
S(tsm - ./.) p_B (tsm - ./t) $p_{NB}(0)$ $\psi_{B \rightarrow NB}(t)$ $\psi_{NB \rightarrow B}(\cdot)$	757.38	46.33	0.00	0.00
S(tsm - t/.) p_B (tsm - ./t) $p_{NB}(0)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(\cdot)$	757.79	46.75	0.00	0.00
S(tsm - t/t) p_B (tsm - ./.) $p_{NB}(0)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(\cdot)$	758.22	47.17	0.00	0.00
S(tsm - ./t) p_B (tsm - ./.) $p_{NB}(0)$ $\psi_{B \rightarrow NB}(t)$ $\psi_{NB \rightarrow B}(\cdot)$	759.15	48.10	0.00	0.00
S(tsm - ./.) p_B (tsm - t/.) $p_{NB}(0)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(t)$	761.35	50.30	0.00	0.00
S(tsm - ./t) p_B (tsm - t/.) $p_{NB}(0)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(\cdot)$	761.39	50.34	0.00	0.00
S(tsm - t/.) p_B (tsm - ./.) $p_{NB}(0)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(t)$	762.20	51.16	0.00	0.00
S(tsm - t/.) p_B (tsm - ./.) $p_{NB}(0)$ $\psi_{B \rightarrow NB}(t)$ $\psi_{NB \rightarrow B}(\cdot)$	768.54	57.49	0.00	0.00
S(tsm - t/.) p_B (tsm - t/.) $p_{NB}(0)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(\cdot)$	770.37	59.32	0.00	0.00
S(tsm - ./.) p_B (tsm - ./.) $p_{NB}(0)$ $\psi_{B \rightarrow NB}(t)$ $\psi_{NB \rightarrow B}(t)$	771.83	60.78	0.00	0.00
S(tsm - ./.) p_B (tsm - t/t) $p_{NB}(0)$ $\psi_{B \rightarrow NB}(t)$ $\psi_{NB \rightarrow B}(\cdot)$	774.15	63.10	0.00	0.00
S(tsm - ./t) p_B (tsm - t/.) $p_{NB}(0)$ $\psi_{B \rightarrow NB}(t)$ $\psi_{NB \rightarrow B}(\cdot)$	779.60	68.56	0.00	0.00
S(tsm - ./t) p_B (tsm - ./t) $p_{NB}(0)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(t)$	782.31	71.26	0.00	0.00
S(tsm - ./t) p_B (tsm - ./t) $p_{NB}(0)$ $\psi_{B \rightarrow NB}(t)$ $\psi_{NB \rightarrow B}(\cdot)$	782.33	71.28	0.00	0.00
S(tsm - ./.) p_B (tsm - t/t) $p_{NB}(0)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(t)$	783.51	72.47	0.00	0.00
S(tsm - ./t) p_B (tsm - t/t) $p_{NB}(0)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(\cdot)$	785.44	74.39	0.00	0.00
S(tsm - t/.) p_B (tsm - ./t) $p_{NB}(0)$ $\psi_{B \rightarrow NB}(t)$ $\psi_{NB \rightarrow B}(\cdot)$	786.58	75.53	0.00	0.00
S(tsm - t/.) p_B (tsm - ./t) $p_{NB}(0)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(t)$	786.64	75.59	0.00	0.00
S(tsm - ./.) p_B (tsm - ./t) $p_{NB}(0)$ $\psi_{B \rightarrow NB}(t)$ $\psi_{NB \rightarrow B}(t)$	787.75	76.70	0.00	0.00
S(tsm - ./.) p_B (tsm - t/.) $p_{NB}(0)$ $\psi_{B \rightarrow NB}(t)$ $\psi_{NB \rightarrow B}(t)$	787.85	76.80	0.00	0.00
S(tsm - ./t) p_B (tsm - t/.) $p_{NB}(0)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(t)$	788.78	77.73	0.00	0.00

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S(tsm – t/t) p_B (tsm – ./t) $p_{NB}(0)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(\cdot)$	788.93	77.88	0.00	0.00
S(tsm – t/.) p_B (tsm – t/.) $p_{NB}(0)$ $\psi_{B \rightarrow NB}(t)$ $\psi_{NB \rightarrow B}(\cdot)$	789.39	78.34	0.00	0.00
S(tsm – t/t) p_B (tsm – ./.) $p_{NB}(0)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(t)$	789.99	78.94	0.00	0.00
S(tsm – t/.) p_B (tsm – t/t) $p_{NB}(0)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(\cdot)$	794.53	83.48	0.00	0.00
S(tsm – t/t) p_B (tsm – ./.) $p_{NB}(0)$ $\psi_{B \rightarrow NB}(t)$ $\psi_{NB \rightarrow B}(\cdot)$	795.37	84.32	0.00	0.00
S(tsm – ./t) p_B (tsm – ./.) $p_{NB}(0)$ $\psi_{B \rightarrow NB}(t)$ $\psi_{NB \rightarrow B}(t)$	796.61	85.56	0.00	0.00
S(tsm – t/t) p_B (tsm – t/.) $p_{NB}(0)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(\cdot)$	797.88	86.83	0.00	0.00
S(tsm – t/.) p_B (tsm – t/.) $p_{NB}(0)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(t)$	799.24	88.19	0.00	0.00
S(tsm – ./.) p_B (tsm – t/t) $p_{NB}(0)$ $\psi_{B \rightarrow NB}(t)$ $\psi_{NB \rightarrow B}(t)$	807.40	96.35	0.00	0.00
S(tsm – t/.) p_B (tsm – ./.) $p_{NB}(0)$ $\psi_{B \rightarrow NB}(t)$ $\psi_{NB \rightarrow B}(t)$	807.51	96.46	0.00	0.00
S(tsm – ./t) p_B (tsm – t/t) $p_{NB}(0)$ $\psi_{B \rightarrow NB}(t)$ $\psi_{NB \rightarrow B}(\cdot)$	809.59	98.54	0.00	0.00
S(tsm – t/.) p_B (tsm – t/t) $p_{NB}(0)$ $\psi_{B \rightarrow NB}(t)$ $\psi_{NB \rightarrow B}(\cdot)$	814.52	103.47	0.00	0.00
S(tsm – ./t) p_B (tsm – t/.) $p_{NB}(0)$ $\psi_{B \rightarrow NB}(t)$ $\psi_{NB \rightarrow B}(t)$	818.59	107.54	0.00	0.00
S(tsm – t/t) p_B (tsm – t/.) $p_{NB}(0)$ $\psi_{B \rightarrow NB}(t)$ $\psi_{NB \rightarrow B}(\cdot)$	820.17	109.12	0.00	0.00
S(tsm – t/t) p_B (tsm – ./t) $p_{NB}(0)$ $\psi_{B \rightarrow NB}(t)$ $\psi_{NB \rightarrow B}(\cdot)$	821.54	110.49	0.00	0.00
S(tsm – ./t) p_B (tsm – t/t) $p_{NB}(0)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(t)$	821.83	110.78	0.00	0.00
S(tsm – t/t) p_B (tsm – ./t) $p_{NB}(0)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(t)$	824.12	113.07	0.00	0.00
S(tsm – t/.) p_B (tsm – t/.) $p_{NB}(0)$ $\psi_{B \rightarrow NB}(t)$ $\psi_{NB \rightarrow B}(t)$	826.86	115.81	0.00	0.00
S(tsm – ./t) p_B (tsm – ./t) $p_{NB}(0)$ $\psi_{B \rightarrow NB}(t)$ $\psi_{NB \rightarrow B}(t)$	828.09	117.04	0.00	0.00
S(tsm – t/.) p_B (tsm – t/t) $p_{NB}(0)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(t)$	828.49	117.44	0.00	0.00
S(tsm – t/t) p_B (tsm – t/t) $p_{NB}(0)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(\cdot)$	829.78	118.73	0.00	0.00
S(tsm – t/.) p_B (tsm – ./t) $p_{NB}(0)$ $\psi_{B \rightarrow NB}(t)$ $\psi_{NB \rightarrow B}(t)$	830.93	119.89	0.00	0.00
S(tsm – t/t) p_B (tsm – t/.) $p_{NB}(0)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(t)$	833.54	122.49	0.00	0.00
S(tsm – t/t) p_B (tsm – ./.) $p_{NB}(0)$ $\psi_{B \rightarrow NB}(t)$ $\psi_{NB \rightarrow B}(t)$	837.31	126.26	0.00	0.00
S(tsm – ./t) p_B (tsm – t/t) $p_{NB}(0)$ $\psi_{B \rightarrow NB}(t)$ $\psi_{NB \rightarrow B}(t)$	847.62	136.57	0.00	0.00
S(tsm – t/.) p_B (tsm – t/t) $p_{NB}(0)$ $\psi_{B \rightarrow NB}(t)$ $\psi_{NB \rightarrow B}(t)$	851.56	140.51	0.00	0.00
S(tsm – t/t) p_B (tsm – t/t) $p_{NB}(0)$ $\psi_{B \rightarrow NB}(t)$ $\psi_{NB \rightarrow B}(\cdot)$	854.61	143.56	0.00	0.00
S(tsm – t/t) p_B (tsm – t/.) $p_{NB}(0)$ $\psi_{B \rightarrow NB}(t)$ $\psi_{NB \rightarrow B}(t)$	866.27	155.22	0.00	0.00
S(tsm – t/t) p_B (tsm – t/t) $p_{NB}(0)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(t)$	871.04	159.99	0.00	0.00
S(tsm – t/t) p_B (tsm – ./t) $p_{NB}(0)$ $\psi_{B \rightarrow NB}(t)$ $\psi_{NB \rightarrow B}(t)$	875.65	164.60	0.00	0.00
S(tsm – t/t) p_B (tsm – t/t) $p_{NB}(0)$ $\psi_{B \rightarrow NB}(t)$ $\psi_{NB \rightarrow B}(t)$	898.46	187.41	0.00	0.00

qAIC_c: quasi-likelihood Akaike's information criterion corrected for small sample size; S: survival rate, assumed to be equal in the breeding and non-breeding state; p_B : probability of recapture in the breeding state; p_{NB} : probability of recapture in the non-breeding state, fixed at 0 throughout; $\psi_{B \rightarrow NB}$: breeding transition probability from the breeding to the non-breeding state; $\psi_{NB \rightarrow B}$: breeding transition probability from the non-breeding state to the breeding state;

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't' denotes that the parameter was time varying; '.' denotes that the parameter was constant; 'tsm': time-since-marking model structure, to allow for the parameter estimates to differ between the first year after initial tagging and subsequent years; '/' separates the two 'age' classes for parameters with a time-since-marking model structure.

Table S4. Summary of models analysed in MARK for green turtles. Female identification was based on flipper tag readings only.

Model	qAICc	Δ qAICc	AICc weights	Model likelihood
S(tsm – ./.) $p_{NB}(0)$ $p_B(\text{tsm} - ./.)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(\cdot)$	445.62	0.00	1.00	1.00
S(tsm – ./t) $p_{NB}(0)$ $p_B(\text{tsm} - ./.)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(\cdot)$	474.96	29.34	0.00	0.00
S(tsm – t/.) $p_{NB}(0)$ $p_B(\text{tsm} - ./.)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(\cdot)$	475.55	29.93	0.00	0.00
S(tsm – ./.) $p_{NB}(0)$ $p_B(\text{tsm} - ./t)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(\cdot)$	476.15	30.53	0.00	0.00
S(tsm – ./.) $p_{NB}(0)$ $p_B(\text{tsm} - ./.)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(t)$	480.74	35.12	0.00	0.00
S(tsm – ./.) $p_{NB}(0)$ $p_B(\text{tsm} - t/.)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(\cdot)$	489.44	43.82	0.00	0.00
S(tsm – t/.) $p_{NB}(0)$ $p_B(\text{tsm} - ./.)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(t)$	502.12	56.50	0.00	0.00
S(tsm – ./.) $p_{NB}(0)$ $p_B(\text{tsm} - ./t)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(t)$	503.66	58.04	0.00	0.00
S(tsm – ./t) $p_{NB}(0)$ $p_B(\text{tsm} - ./.)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(t)$	504.32	58.70	0.00	0.00
S(tsm – ./t) $p_{NB}(0)$ $p_B(\text{tsm} - ./t)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(\cdot)$	506.57	60.95	0.00	0.00
S(tsm – t/t) $p_{NB}(0)$ $p_B(\text{tsm} - ./.)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(\cdot)$	509.90	64.28	0.00	0.00
S(tsm – t/.) $p_{NB}(0)$ $p_B(\text{tsm} - ./t)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(\cdot)$	511.41	65.79	0.00	0.00
S(tsm – t/.) $p_{NB}(0)$ $p_B(\text{tsm} - t/.)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(\cdot)$	516.31	70.69	0.00	0.00
S(tsm – ./.) $p_{NB}(0)$ $p_B(\text{tsm} - t/.)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(t)$	518.96	73.34	0.00	0.00
S(tsm – ./.) $p_{NB}(0)$ $p_B(\text{tsm} - t/t)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(\cdot)$	518.98	73.36	0.00	0.00
S(tsm – ./t) $p_{NB}(0)$ $p_B(\text{tsm} - t/.)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(\cdot)$	522.66	77.04	0.00	0.00
S(tsm – ./.) $p_{NB}(0)$ $p_B(\text{tsm} - t/t)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(\cdot)$	523.38	77.76	0.00	0.00
S(tsm – ./t) $p_{NB}(0)$ $p_B(\text{tsm} - ./t)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(t)$	538.89	93.27	0.00	0.00
S(tsm – t/t) $p_{NB}(0)$ $p_B(\text{tsm} - ./.)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(t)$	542.15	96.53	0.00	0.00
S(tsm – t/.) $p_{NB}(0)$ $p_B(\text{tsm} - ./t)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(t)$	542.53	96.92	0.00	0.00
S(tsm – t/.) $p_{NB}(0)$ $p_B(\text{tsm} - t/.)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(t)$	546.79	101.17	0.00	0.00
S(tsm – t/t) $p_{NB}(0)$ $p_B(\text{tsm} - ./t)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(\cdot)$	549.70	104.08	0.00	0.00
S(tsm – t/t) $p_{NB}(0)$ $p_B(\text{tsm} - t/.)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(\cdot)$	551.76	106.14	0.00	0.00
S(tsm – t/.) $p_{NB}(0)$ $p_B(\text{tsm} - t/t)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(\cdot)$	552.69	107.07	0.00	0.00
S(tsm – ./t) $p_{NB}(0)$ $p_B(\text{tsm} - t/.)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(t)$	556.55	110.93	0.00	0.00
S(tsm – ./t) $p_{NB}(0)$ $p_B(\text{tsm} - t/t)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(\cdot)$	557.83	112.21	0.00	0.00
S(tsm – t/t) $p_{NB}(0)$ $p_B(\text{tsm} - ./t)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(t)$	586.22	140.61	0.00	0.00
S(tsm – t/t) $p_{NB}(0)$ $p_B(\text{tsm} - t/.)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(t)$	588.18	142.57	0.00	0.00
S(tsm – t/.) $p_{NB}(0)$ $p_B(\text{tsm} - t/t)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(t)$	588.49	142.87	0.00	0.00
S(tsm – t/t) $p_{NB}(0)$ $p_B(\text{tsm} - t/t)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(\cdot)$	592.13	146.51	0.00	0.00
S(tsm – ./t) $p_{NB}(0)$ $p_B(\text{tsm} - t/t)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(t)$	595.21	149.59	0.00	0.00
S(tsm – t/t) $p_{NB}(0)$ $p_B(\text{tsm} - t/t)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(t)$	636.31	190.69	0.00	0.00

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qAIC_c: quasi-likelihood Akaike's information criterion corrected for small sample size; S: survival rate, assumed to be equal in the breeding and non-breeding state; p_B : probability of recapture in the breeding state; p_{NB} : probability of recapture in the non-breeding state, fixed at 0 throughout; $\psi_{B \rightarrow NB}$: breeding transition probability from the breeding to the non-breeding state, held constant as green turtles extremely rarely breed in consecutive years; $\psi_{NB \rightarrow B}$: breeding transition probability from the non-breeding state to the breeding state; 't' denotes that the parameter was time varying; '.' denotes that the parameter was constant; 'tsm': time-since-marking model structure, to allow for the parameter estimates to differ between the first year after initial tagging and subsequent years; '/' separates the two 'age' classes for parameters with a time-since-marking model structure.

Table S5. Summary of models analysed in MARK for loggerhead turtles. Female identification was based on flipper tag readings only.

Model	qAICc	Δ qAICc	AICc weights	Model likelihood
S(tsm - ./.) $p_{NB}(0)$ $p_B(\text{tsm} - ./.)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(\cdot)$	659.70	0.00	0.993	1.000
S(.) $p_{NB}(0)$ $p_B(\text{tsm} - ./.)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(\cdot)$	669.45	9.76	0.008	0.008
S(.) $p_{NB}(0)$ $p_B(\text{tsm} - ./.)$ $\psi_{B \rightarrow NB}(t)$ $\psi_{NB \rightarrow B}(\cdot)$	685.29	25.59	0.00	0.00
S(.) $p_{NB}(0)$ $p_B(\text{tsm} - ./.)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(t)$	685.76	26.06	0.00	0.00
S(.) $p_{NB}(0)$ $p_B(\text{tsm} - ./t)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(\cdot)$	688.75	29.05	0.00	0.00
S(t) $p_{NB}(0)$ $p_B(\text{tsm} - ./.)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(\cdot)$	694.46	34.76	0.00	0.00
S(.) $p_{NB}(0)$ $p_B(\text{tsm} - t/.)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(\cdot)$	699.17	39.47	0.00	0.00
S(.) $p_{NB}(0)$ $p_B(\text{tsm} - t/.)$ $\psi_{B \rightarrow NB}(t)$ $\psi_{NB \rightarrow B}(\cdot)$	700.33	40.63	0.00	0.00
S(.) $p_{NB}(0)$ $p_B(\text{tsm} - ./t)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(t)$	708.75	49.05	0.00	0.00
S(.) $p_{NB}(0)$ $p_B(\text{tsm} - ./t)$ $\psi_{B \rightarrow NB}(t)$ $\psi_{NB \rightarrow B}(\cdot)$	712.40	52.70	0.00	0.00
S(.) $p_{NB}(0)$ $p_B(\text{tsm} - ./.)$ $\psi_{B \rightarrow NB}(t)$ $\psi_{NB \rightarrow B}(t)$	716.90	57.20	0.00	0.00
S(t) $p_{NB}(0)$ $p_B(\text{tsm} - ./t)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(\cdot)$	718.03	58.33	0.00	0.00
S(.) $p_{NB}(0)$ $p_B(\text{tsm} - t/.)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(t)$	719.34	59.64	0.00	0.00
S(t) $p_{NB}(0)$ $p_B(\text{tsm} - ./.)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(t)$	720.81	61.11	0.00	0.00
S(t) $p_{NB}(0)$ $p_B(\text{tsm} - ./.)$ $\psi_{B \rightarrow NB}(t)$ $\psi_{NB \rightarrow B}(\cdot)$	721.44	61.74	0.00	0.00
S(.) $p_{NB}(0)$ $p_B(\text{tsm} - t/t)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(\cdot)$	722.30	62.61	0.00	0.00
S(t) $p_{NB}(0)$ $p_B(\text{tsm} - t/.)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(\cdot)$	729.55	69.85	0.00	0.00
S(.) $p_{NB}(0)$ $p_B(\text{tsm} - t/.)$ $\psi_{B \rightarrow NB}(t)$ $\psi_{NB \rightarrow B}(t)$	732.12	72.42	0.00	0.00
S(.) $p_{NB}(0)$ $p_B(\text{tsm} - t/t)$ $\psi_{B \rightarrow NB}(t)$ $\psi_{NB \rightarrow B}(\cdot)$	737.00	77.30	0.00	0.00
S(t) $p_{NB}(0)$ $p_B(\text{tsm} - t/.)$ $\psi_{B \rightarrow NB}(t)$ $\psi_{NB \rightarrow B}(\cdot)$	741.98	82.28	0.00	0.00
S(.) $p_{NB}(0)$ $p_B(\text{tsm} - ./t)$ $\psi_{B \rightarrow NB}(t)$ $\psi_{NB \rightarrow B}(t)$	745.72	86.03	0.00	0.00
S(t) $p_{NB}(0)$ $p_B(\text{tsm} - ./t)$ $\psi_{B \rightarrow NB}(t)$ $\psi_{NB \rightarrow B}(\cdot)$	745.79	86.09	0.00	0.00
S(.) $p_{NB}(0)$ $p_B(\text{tsm} - t/t)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(t)$	746.57	86.87	0.00	0.00
S(t) $p_{NB}(0)$ $p_B(\text{tsm} - ./t)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(t)$	746.84	87.14	0.00	0.00
S(t) $p_{NB}(0)$ $p_B(\text{tsm} - ./.)$ $\psi_{B \rightarrow NB}(t)$ $\psi_{NB \rightarrow B}(t)$	751.23	91.53	0.00	0.00
S(t) $p_{NB}(0)$ $p_B(\text{tsm} - t/t)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(\cdot)$	757.28	97.59	0.00	0.00
S(.) $p_{NB}(0)$ $p_B(\text{tsm} - t/t)$ $\psi_{B \rightarrow NB}(t)$ $\psi_{NB \rightarrow B}(t)$	759.63	99.94	0.00	0.00
S(t) $p_{NB}(0)$ $p_B(\text{tsm} - t/.)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(t)$	760.13	100.43	0.00	0.00
S(t) $p_{NB}(0)$ $p_B(\text{tsm} - t/.)$ $\psi_{B \rightarrow NB}(t)$ $\psi_{NB \rightarrow B}(t)$	771.74	112.04	0.00	0.00
S(t) $p_{NB}(0)$ $p_B(\text{tsm} - ./t)$ $\psi_{B \rightarrow NB}(t)$ $\psi_{NB \rightarrow B}(t)$	779.91	120.22	0.00	0.00
S(t) $p_{NB}(0)$ $p_B(\text{tsm} - t/t)$ $\psi_{B \rightarrow NB}(t)$ $\psi_{NB \rightarrow B}(\cdot)$	784.55	124.86	0.00	0.00
S(t) $p_{NB}(0)$ $p_B(\text{tsm} - t/t)$ $\psi_{B \rightarrow NB}(\cdot)$ $\psi_{NB \rightarrow B}(t)$	792.15	132.46	0.00	0.00
S(t) $p_{NB}(0)$ $p_B(\text{tsm} - t/t)$ $\psi_{B \rightarrow NB}(t)$ $\psi_{NB \rightarrow B}(t)$	809.85	150.16	0.00	0.00

qAIC_c: quasi-likelihood Akaike's information criterion corrected for small sample size; S: survival rate, assumed to be equal in the breeding and non-breeding state; p_B : probability of recapture in the breeding state; p_{NB} : probability of recapture in the non-breeding state, fixed at 0 throughout; $\psi_{B \rightarrow NB}$: breeding transition probability from the breeding to the non-breeding state; $\psi_{NB \rightarrow B}$: breeding transition probability from the non-breeding state to the breeding state; 't' denotes that the parameter was time varying; '.' denotes that the parameter was constant; 'tsm': time-since-marking model structure, to allow for the parameter estimates to differ between the first year after initial tagging and subsequent years; '/' separates the two 'age' classes for parameters with a time-since-marking model structure.

Table S6. Estimated parameters of annual survival probability (S) for the two ‘age’ classes, recapture probability in the breeding state (p_B) for the two ‘age’ classes and breeding transition probabilities between states, calculated using MARK, for both species, based on female identification method. The first ‘age’ class (denoted ‘1’ in this table) represents the first year after initial capture, whereas the second ‘age’ class (denoted ‘2’) represents the remaining capture history. All parameters: mean (95% highest posterior density confidence intervals). $\psi_{B \rightarrow NB}$: breeding transition probability between the breeding and non-breeding state; $\psi_{NB \rightarrow B}$: breeding transition probability between the non-breeding and the breeding state.

Species Identification method	Survival	Recapture probability in the breeding state	Breeding transition probability between states
Green turtles			
‘PIT tag’	S1 = 0.66 (0.58 – 0.75)	$p_{B1} = 0.51$ (0.10 – 0.99)	$\psi_{B \rightarrow NB} = 0.99$ (0.97 – 1.00)
	S2 = 0.97 (0.95 – 0.99)	$p_{B2} = 0.94$ (0.85 – 1.00)	$\psi_{NB \rightarrow B} = 0.30$ (0.26 – 0.36)
‘No PIT tag’	S1 = 0.48 (0.36 – 0.61)	$p_{B1} = 0.47$ (0.06 – 0.96)	$\psi_{B \rightarrow NB} = 0.98$ (0.96 – 1.00)
	S2 = 0.84 (0.79 – 0.89)	$p_{B2} = 0.88$ (0.71 – 1.00)	$\psi_{NB \rightarrow B} = 0.30$ (0.21 – 0.40)
Loggerhead turtles			
‘PIT tag’	S1 = 0.44 (0.33 – 0.55)	$p_{B1} = 0.54$ (0.16 – 0.97)	$\psi_{B \rightarrow NB} = 0.88$ (0.73 – 0.96)
	S2 = 0.83 (0.78 – 0.87)	$p_{B2} = 0.70$ (0.38 – 0.99)	$\psi_{NB \rightarrow B} = 0.40$ (0.20 – 0.72)
‘No PIT tag’	S1 = 0.36 (0.26 – 0.48)	$p_{B1} = 0.46$ (0.11 – 0.91)	$\psi_{B \rightarrow NB} = 0.85$ (0.69 – 0.95)
	S2 = 0.76 (0.70 – 0.82)	$p_{B2} = 0.72$ (0.43 – 0.99)	$\psi_{NB \rightarrow B} = 0.43$ (0.22 – 0.72)

Table S7. Summary of tag histories for each tag type and for both species as a function of identification method. The use of flipper tags in combination with PIT tags ensures a greater chance of female identification and permitted the calculation of TH10 and TH20. n represents the number of females. PIT: passive integrated transponder. na: not applicable. The total for each column is shown in italics.

Species	'PIT tag'			'No PIT tag'	
	Plastic flipper tag	Titanium flipper tag	PIT tag	Plastic flipper tag	Titanium flipper tag
Loggerhead turtles	(n=69)	(n=116)	(n=116)	(n=66)	(n=110)
TH10	4	6	12	na	Na
TH11	17	41	91	29	63
TH11+TH10	12	22	3	na	Na
TH20	4	11	7	na	Na
TH21	4	6	4	6	8
TH21+TH10	2	2	0	na	Na
TH21+TH11	2	1	3	5	2
TH21+TH11+TH10	3	1	0	na	Na
TH22	33	54	26	40	63
TH22+TH20	7	9	4	na	Na
TH22+TH21	1	4	1	1	4
TH22+TH21+TH10	0	0	0	na	Na
TH22+TH21+TH11	1	15	3	3	20
TH22+TH21+TH11+TH10	2	5	1	na	Na
	<i>92</i>	<i>177</i>	<i>155</i>	<i>84</i>	<i>94</i>

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Green turtles	(n=63)	(n=232)	(n=244)	(n=63)	(n=227)
TH10	5	16	14	na	Na
TH11	12	71	215	40	136
TH11+TH10	28	65	6	na	Na
TH20	1	17	4	na	Na
TH21	0	2	0	1	4
TH21+TH10	1	2	0	na	Na
TH21+TH11	0	9	8	4	14
TH21+TH11+TH10	4	5	0	na	Na
TH22	21	110	66	35	172
TH22+TH20	14	62	0	na	Na
TH22+TH21	0	9	0	5	13
TH22+TH21+TH10	5	4	0	na	Na
TH22+TH21+TH11	0	31	4	9	54
TH22+TH21+TH11+TH10	9	23	0	na	Na
	<i>100</i>	<i>426</i>	<i>317</i>	<i>94</i>	<i>393</i>

Table S8. Summary of the number of tags fitted per individuals over the course of the study period and tag retention (i.e. the number of days tags were observed still in place) for all tag types and for both species. Tags fitted: median (IQR, range, n). Tag retention: median (IQR, maximum, n). PIT tags: passive integrated transponder tags.

Species	Tag	Tags fitted	Proportion of females fitted with more than 2 tags	Tag retention (days)	
				Double tagged	Single tagged
Loggerhead turtles	Plastic	2 (2 – 2, 1 – 6, 69)	0.22	39 (20 – 739, 2150, 44)	36 (14 – 739, 2223, 29)
	Titanium	2 (2 – 2, 1 – 10, 116)	0.24	28 (17 – 46, 2548, 87)	40 (25 – 1127, 4055, 63)
	PIT	2 (1 – 2, 1 – 5, 116)	0.15	1125 (41 – 1862, 6247, 34)	707 (27 – 1826, 6235, 94)
Green turtles	Plastic	2 (2 – 4, 1 – 5, 63)	0.30	38 (28 – 54, 2200, 49)	39 (25 – 860, 3633, 40)
	Titanium	2 (2 – 4, 1 – 10, 232)	0.42	31 (21 – 42, 4412, 239)	26 (19 – 43, 4386, 136)
	PIT	1 (1 – 2, 1 – 6, 244)	0.10	1872 (1453 – 2927, 7333, 70)	1098 (27 – 2186, 7345, 221)

Table S9. Results for the five models of daily tag loss probability ranked in ascending order of AICc values for the different tag types fitting n individual tag histories for loggerhead and green turtles in the Mediterranean, with female identification based on flipper and PIT tag readings. $a_0 - a_4$: model parameters; c : daily tag loss probability in models where probability is constant (model I) or nearly constant (range of values 1×10^{-8}). n represents the number of tag histories used to estimate tag loss.

Species	Model		df	AICc	Δ AICc	Akaike weight	a_0	a_1	a_2	a_3	a_4	c
Tag	Description											
Loggerhead turtles												
Plastic ($n=92$)	II	Decreasing curve	3	854.71	0.00	0.94	-4.9824×10^{-2}	-1.1029×10^2	NA	NA	4.1480×10^{-4}	NA
	IV	Decreasing and increasing curve	5	860.44	5.73	5.38×10^{-2}	-1.7426×10^{-2}	-9.0246×10^1	9.7214×10^{-4}	9.9324×10^1	5.8841×10^{-4}	NA
	I	Constant p	1	868.09	13.38	1.17×10^{-3}	NA	NA	NA	NA	NA	5.0391×10^{-4}
	III	Increasing curve	3	872.01	17.30	1.65×10^{-4}	8.9585×10^{-5}	9.9706×10^1	NA	NA	9.7049×10^{-4}	NA
	V	Increasing and decreasing curve	5	886.18	31.47	1.39×10^{-7}	4.1767×10^{-4}	-9.0079×10^1	-3.0346×10^{-2}	9.9032×10^1	5.4819×10^{-4}	NA
Titanium ($n=177$)	II	Decreasing curve	3	1571.25	0.00	0.61	-5.0066×10^{-2}	-1.3078×10^2	NA	NA	5.0234×10^{-4}	NA
	I	Constant p	1	1572.70	1.45	0.30	NA	NA	NA	NA	NA	5.3867×10^{-4}

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PIT (n=155)	IV	Decreasing and increasing curve	5	1576.07	4.82	5.49 $\times 10^{-2}$	-2.1454 $\times 10^{-2}$	-1.0641 $\times 10^2$	1.7042 $\times 10^{-4}$	1.1390 $\times 10^2$	9.2273 $\times 10^{-4}$	NA	
	III	Increasing curve	3	1576.84	5.59	3.74 $\times 10^{-2}$	8.6149 $\times 10^{-9}$	1.0965 $\times 10^2$	NA	NA	1.0771 $\times 10^{-3}$	5.3855 $\times 10^{-4}$	
	V	Increasing and decreasing curve	5	1625.62	54.37	9.55 $\times 10^{-13}$	2.5442 $\times 10^{-4}$	-8.9585 $\times 10^1$	-1.7774 $\times 10^{-2}$	9.8711 $\times 10^1$	6.2235 $\times 10^{-4}$	NA	
	II	Decreasing curve	3	758.72	0.00	0.99	-4.9731 $\times 10^{-2}$	-9.9961 $\times 10^1$	NA	NA	9.1215 $\times 10^{-5}$	NA	
	IV	Decreasing and increasing curve	5	767.34	8.62	1.32 $\times 10^{-2}$	-1.4038 $\times 10^{-2}$	-8.8366 $\times 10^1$	6.9481 $\times 10^{-1}$	1.0083 $\times 10^2$	7.4233 $\times 10^{-5}$	NA	
	V	Increasing and decreasing curve	5	773.26	14.54	6.86 $\times 10^{-4}$	1.9999 $\times 10^0$	-1.5637 $\times 10^2$	-4.4790 $\times 10^{-1}$	2.2155 $\times 10^1$	8.6003 $\times 10^{-5}$	NA	
	I	Constant p	1	816.98	58.26	2.20 $\times 10^{-13}$	NA	NA	NA	NA	NA	1.8115 $\times 10^{-4}$	
	III	Increasing curve	3	821.14	62.42	2.75 $\times 10^{-14}$	5.7961 $\times 10^{-10}$	1.0025 $\times 10^2$	NA	NA	3.6280 $\times 10^{-4}$	1.8140 $\times 10^{-4}$	
	Green turtles												
	Plastic (n=100)	III	Increasing curve	3	1468.87	0.00	0.88	1.7004 $\times 10^{-3}$	1.0971 $\times 10^2$	NA	NA	9.2018 $\times 10^{-4}$	NA
IV		Decreasing and increasing curve	5	1473.07	4.20	0.11	-4.1063 $\times 10^{-2}$	-9.8223 $\times 10^1$	1.7566 $\times 10^{-3}$	1.0852 $\times 10^2$	9.0849 $\times 10^{-4}$	NA	
I		Constant p	1	1476.88	8.01	1.59 $\times 10^{-2}$	NA	NA	NA	NA	NA	6.7969 $\times 10^{-4}$	
II		Decreasing curve	3	1481.13	12.26	1.90	-5.0051	-3.2474	NA	NA	6.7993	6.799	

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	V	Increasing and decreasing curve	5	1583.45	114.58	1.15×10^{-25}	2.0000×10^0	-8.2067×10^1	-2.0782×10^{-2}	6.4605×10^1	5.8214×10^{-4}	NA
Titanium (n=426)	II	Decreasing curve	3	4784.19	0.00	0.61	-5.0051×10^{-2}	-1.1349×10^2	NA	NA	5.7476×10^{-4}	NA
	IV	Decreasing and increasing curve	5	4785.09	0.90	0.39	-1.5487×10^{-2}	-8.8530×10^1	4.2141×10^{-3}	1.0083×10^2	6.1137×10^{-4}	NA
	I	Constant p	1	4829.04	44.85	1.11×10^{-10}	NA	NA	NA	NA	NA	6.6016×10^{-4}
	III	Increasing curve	3	4833.10	48.91	1.46×10^{-11}	1.6495×10^{-10}	1.0021×10^2	NA	NA	1.3196×10^{-3}	6.5980×10^{-4}
	V	Increasing and decreasing curve	5	4867.18	82.99	5.82×10^{-19}	4.9155×10^{-9}	-9.0641×10^1	-2.1812×10^{-2}	9.9467×10^1	9.1320×10^{-4}	NA
PIT (n=317)	II	Decreasing curve	3	721.24	0.00	0.9991	-5.5970×10^{-2}	-9.9957×10^1	NA	NA	2.2911×10^{-5}	NA
	IV	Decreasing and increasing curve	5	735.29	14.05	8.89×10^{-4}	-1.8013×10^{-2}	-1.0460×10^2	4.9227×10^{-1}	1.1291×10^2	1.9326×10^{-5}	NA
	I	Constant p	1	803.58	82.34	1.32×10^{-18}	NA	NA	NA	NA	NA	5.5371×10^{-5}
	III	Increasing curve	3	807.66	86.42	1.71×10^{-19}	1.2605×10^{-9}	1.0981×10^2	NA	NA	1.1075×10^{-4}	5.5375×10^{-5}
	V	Increasing and decreasing curve	5	875.34	154.1	3.45×10^{-34}	1.3885×10^{-9}	-9.0821×10^1	-5.0393×10^{-2}	9.9651×10^1	2.1347×10^{-5}	NA

Table S10. Results for the five models of daily tag loss probability ranked in ascending order of AICc values for the different tag types fitting n individual tag histories for loggerhead and green turtles in the Mediterranean, with female identification based on flipper tag readings only, meaning that TH10 and TH20 were not included in the analyses. $a_0 - a_4$: model parameters; c : daily tag loss probability in models where probability is constant (model I) or nearly constant (range of values 1×10^{-8}). n represents the number of tag histories used to estimate tag loss.

Species Tag	Model Description	df	AICc	Δ AICc	Akaike weight	a_0	a_1	a_2	a_3	a_4	c	
Loggerhead turtles												
Plastic ($n=84$)	II	Decreasing curve	3	248.64	0.00	0.99995	-4.9633×10^{-2}	-1.1019×10^2	NA	NA	8.3916×10^{-5}	NA
	I	Constant p	1	268.90	20.26	3.99×10^{-5}	NA	NA	NA	NA	NA	1.9980×10^{-4}
	IV	Decreasing and increasing curve	5	271.89	23.25	8.94×10^{-6}	-4.4724×10^{-2}	-9.0217×10^1	5.7825×10^{-10}	1.0002×10^2	3.1737×10^{-4}	NA
	III	Increasing curve	3	273.20	24.56	4.64×10^{-6}	2.2831×10^{-9}	1.0110×10^2	NA	NA	3.9991×10^{-4}	1.9996×10^{-4}
	V	Increasing and decreasing curve	5	276.15	27.51	1.06×10^{-6}	2.8867×10^{-10}	-8.9670×10^1	-4.5458×10^{-2}	9.8205×10^1	4.5922×10^{-5}	NA
Titanium ($n=160$)	II	Decreasing curve	3	578.40	0.00	0.63	-5.3882×10^{-2}	-1.1908×10^2	NA	NA	2.2498×10^{-4}	NA
	IV	Decreasing and increasing curve	5	580.00	1.60	0.28	-1.3869×10^{-2}	-1.0327×10^2	1.9999×10^0	1.0880×10^2	1.4194×10^{-4}	NA

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	I	Constant p	1	582.63	4.23	7.61 $\times 10^{-2}$	NA	NA	NA	NA	NA	2.7344 $\times 10^{-4}$
	III	Increasing curve	3	586.79	8.39	9.51 $\times 10^{-3}$	2.1224 $\times 10^{-10}$	1.0970 $\times 10^2$	NA	NA	5.4698 $\times 10^{-4}$	2.7349 $\times 10^{-4}$
	V	Increasing and decreasing curve	5	613.63	35.23	1.41 $\times 10^{-8}$	4.9857 $\times 10^{-10}$	-8.9999 $\times 10^1$	-4.5109 $\times 10^{-2}$	9.9583 $\times 10^1$	1.0611 $\times 10^{-4}$	NA
Green turtles												
Plastic (n=94)	I	Constant p	1	334.06	0.00	0.82	NA	NA	NA	NA	NA	2.2305 $\times 10^{-4}$
	II	Decreasing curve	3	337.97	3.91	0.12	-8.5033 $\times 10^{-2}$	-9.2929 $\times 10^1$	NA	NA	2.1631 $\times 10^{-4}$	NA
	III	Increasing curve	3	339.52	5.46	5.33 $\times 10^{-2}$	4.6021 $\times 10^{-3}$	1.0952 $\times 10^2$	NA	NA	2.6935 $\times 10^{-4}$	NA
	IV	Decreasing and increasing curve	5	342.29	8.23	1.33 $\times 10^{-2}$	-3.1991 $\times 10^{-2}$	-9.8922 $\times 10^1$	1.0867 $\times 10^{-1}$	1.1018 $\times 10^2$	2.3140 $\times 10^{-4}$	NA
	V	Increasing and decreasing curve	5	370.39	36.33	1.06 $\times 10^{-8}$	2.6558 $\times 10^{-9}$	-7.7360 $\times 10^1$	-4.7243 $\times 10^{-2}$	5.2852 $\times 10^1$	2.4865 $\times 10^{-4}$	NA
Titanium (n=393)	IV	Decreasing and increasing curve	5	1349.64	0.00	0.997	-1.3608 $\times 10^{-2}$	-8.8218 $\times 10^1$	1.7076 $\times 10^{-9}$	1.0192 $\times 10^2$	2.6365 $\times 10^{-4}$	NA
	II	Decreasing curve	3	1361.17	11.53	3.13 $\times 10^{-3}$	-5.5352 $\times 10^{-2}$	-1.0567 $\times 10^2$	NA	NA	2.2205 $\times 10^{-4}$	NA
	V	Increasing and decreasing curve	5	1381.61	31.97	1.14 $\times 10^{-7}$	6.1544 $\times 10^{-10}$	-9.3778 $\times 10^1$	-1.3032 $\times 10^{-2}$	8.3504 $\times 10^1$	1.3967 $\times 10^{-4}$	NA

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I	Constant p	1	1401.33	51.69	5.95×10^{-12}	NA	NA	NA	NA	NA	3.1992×10^{-4}
III	Increasing curve	3	1405.39	55.75	7.81×10^{-13}	1.2140×10^{-11}	1.0031×10^2	NA	NA	6.3984×10^{-4}	3.1992×10^{-4}

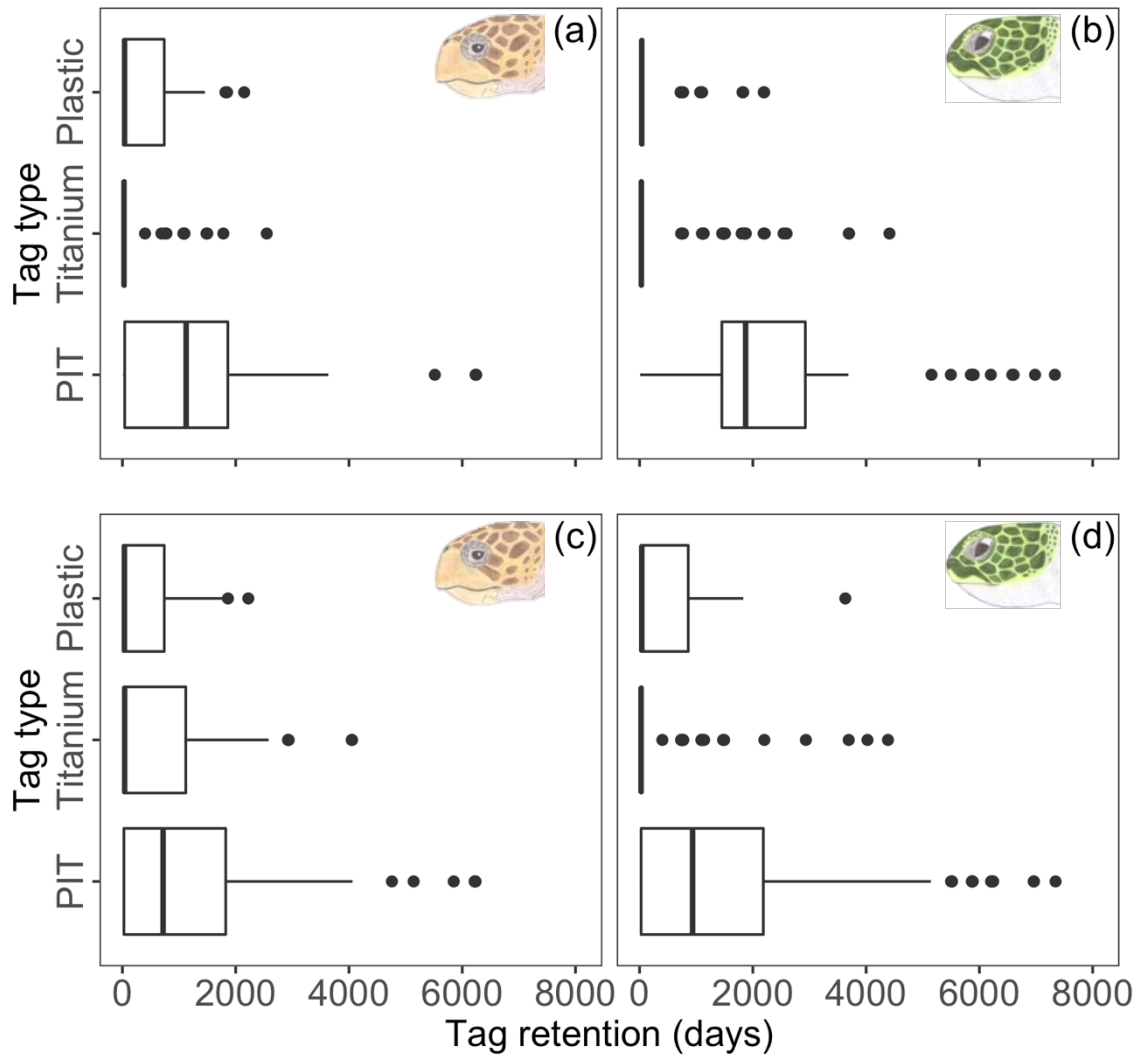


Figure S1. Tag retention (i.e. the number of days tags were observed still in place) for double- (a-b) and single-tagged (c-d) individuals as a function of tag type and species. Loggerhead turtles are shown in panels a and c and green turtles in panels b and d. Median, interquartile range, range and outliers shown. PIT tags: passive integrated transponder tags.

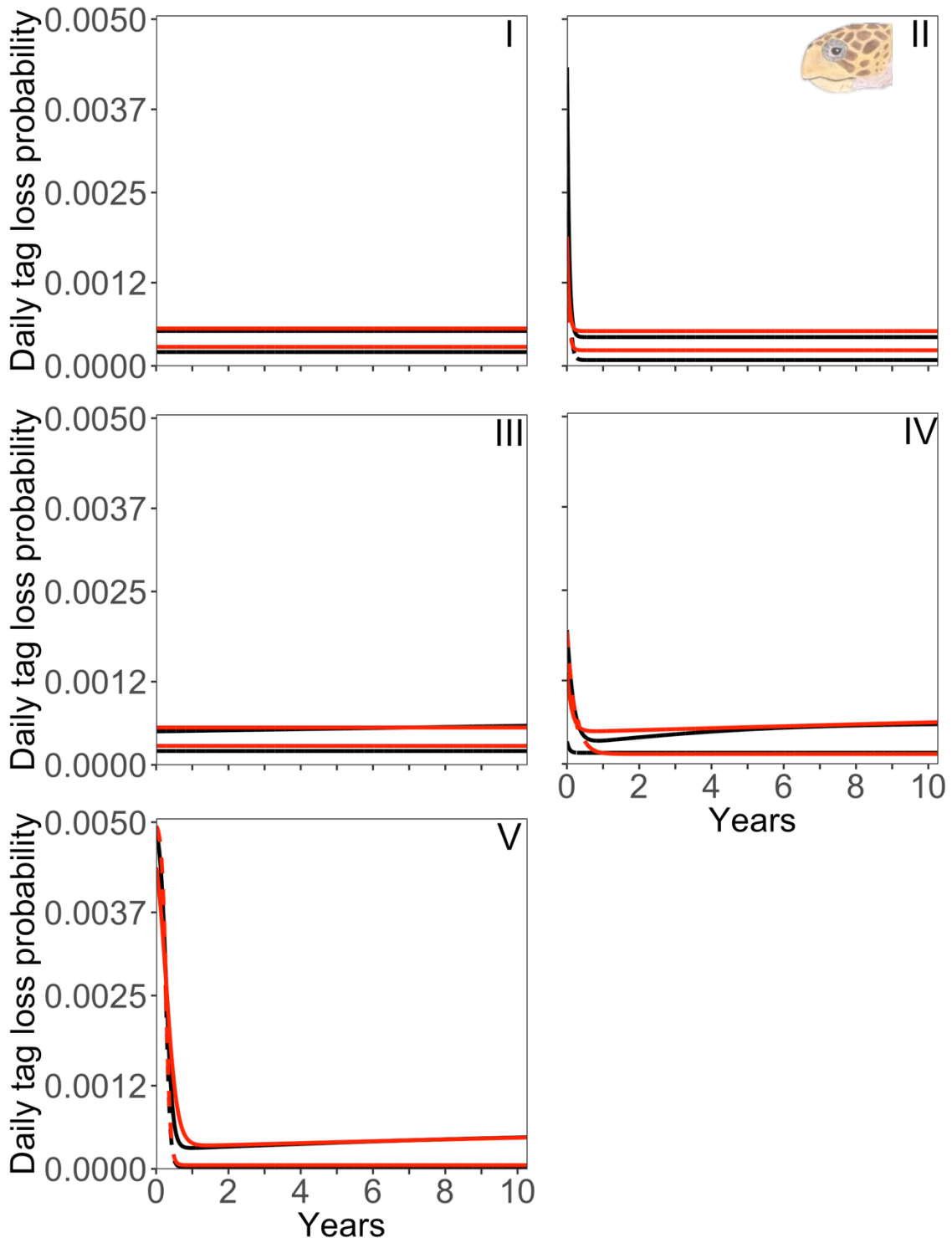


Figure S2. Five models of daily tag loss probability for plastic (black) and titanium (red) flipper tags for the 'PIT tag' (solid line) and 'no PIT tag' (dashed line) datasets for loggerhead turtles nesting at Alagadi beach.

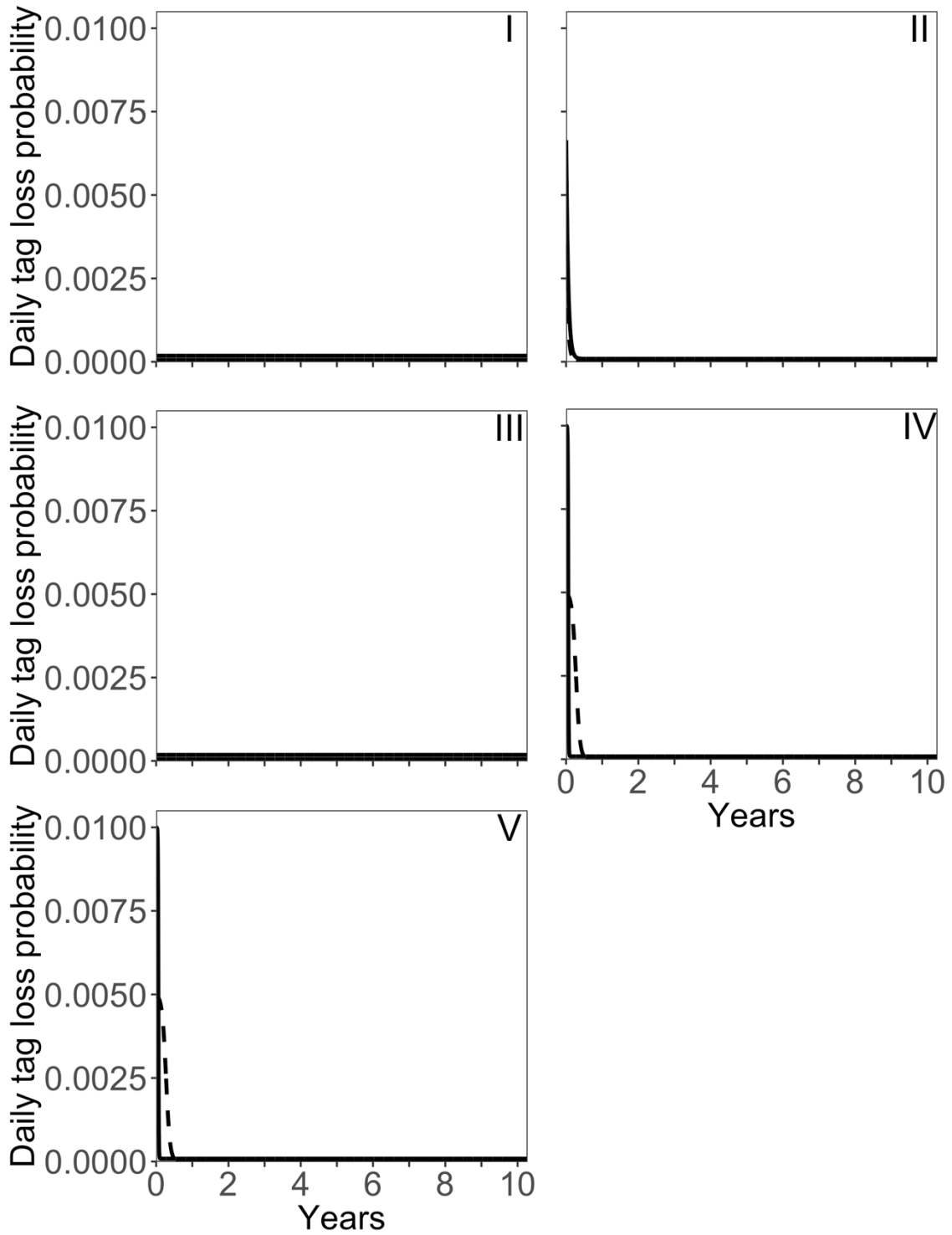


Figure S3. Five models of daily tag loss probability for PIT tags for loggerhead (solid line) and green (dashed line) turtles nesting at Alagadi beach.

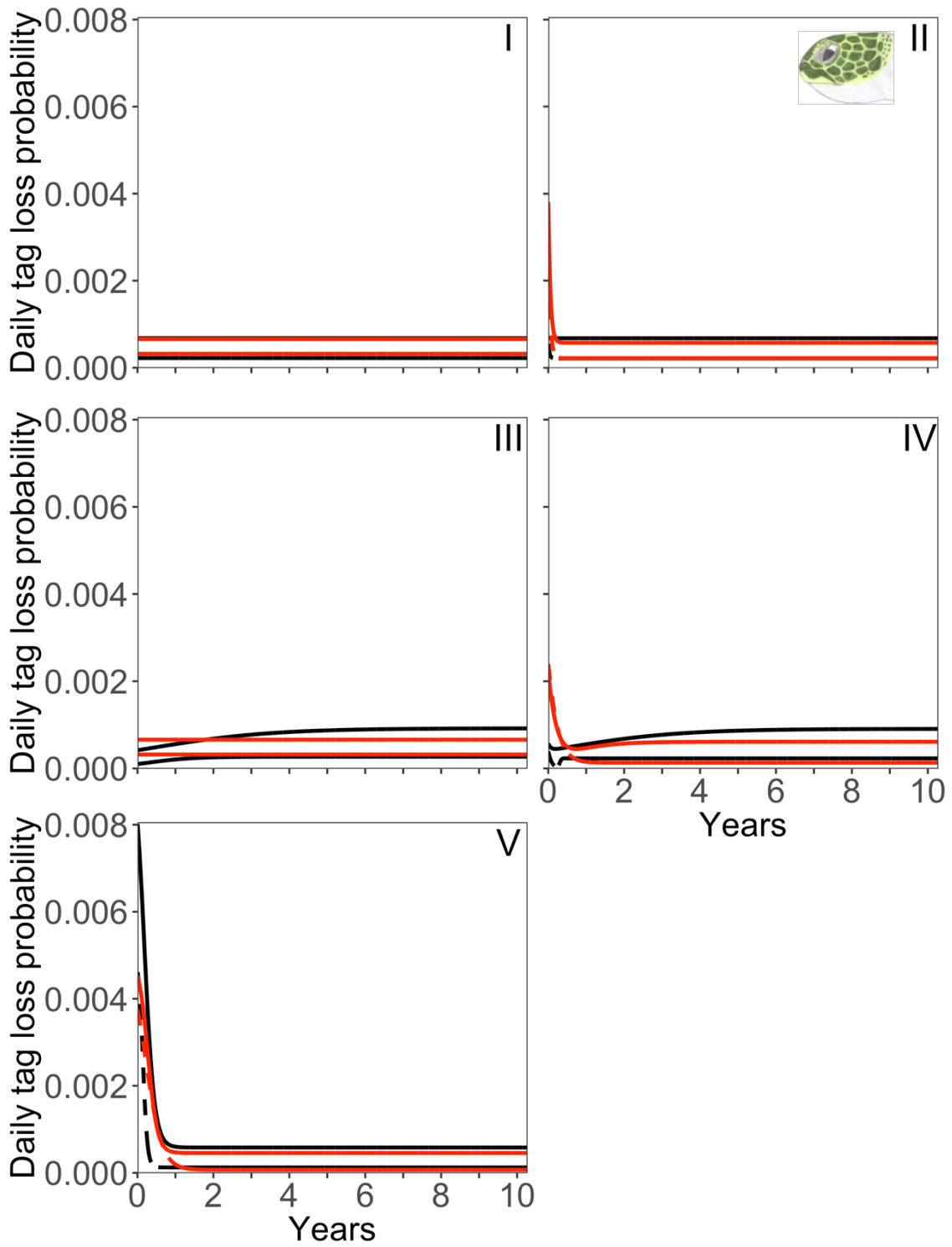


Figure S4. Five models of daily tag loss probability for plastic (black) and titanium (red) flipper tags for the 'PIT tag' (solid line) and 'no PIT tag' (dashed line) datasets for green turtles nesting at Alagadi beach.

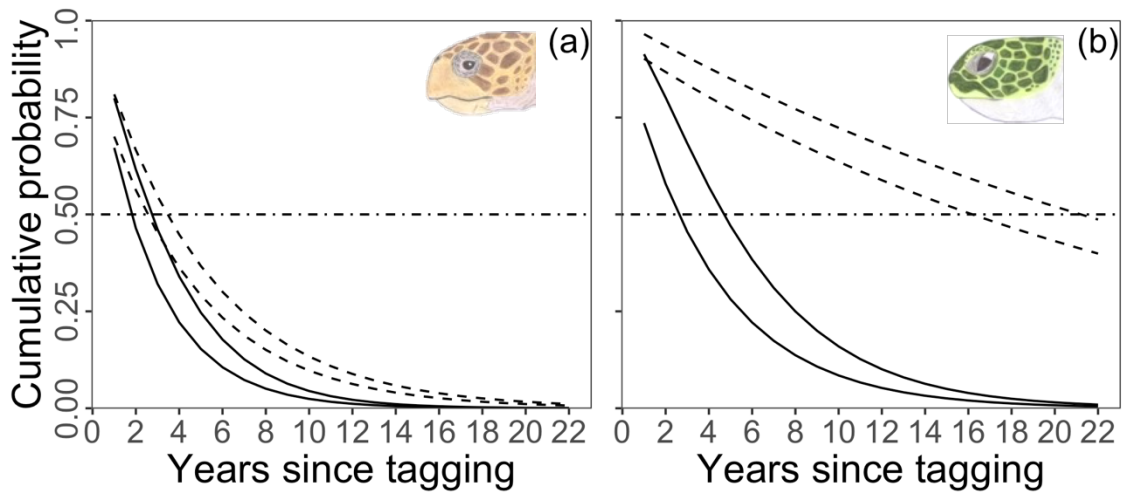


Figure S5. Estimated cumulative probabilities of loggerhead (a) and green (b) turtles double-tagged (upper curves) and single-tagged (lower curves) with titanium (solid lines) and PIT (dashed lines) tags still alive and still identifiable (retention of at least one tag) after x years. Estimates of apparent survival in the second age class (S2) were used for both species (Table S6). The horizontal dot-dashed line represents 50% probability.

CHAPTER 6: INVESTIGATING DIFFERENCES IN POPULATION RECOVERY RATES OF TWO SYMPATRIC SEA TURTLES SPECIES

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Abstract

Estimating life-history traits and understanding their variation underpins the management of long-lived, migratory species. Understanding recovery dynamics can aid and inform management of conservation dependent species such as sea turtles. Using life-history data collected since 1933, we explore the different drivers underlying contrasting population recovery rates of sympatric nesting green (*Chelonia mydas*) and loggerhead (*Caretta caretta*) turtles in North Cyprus. At Alagadi Beach in North Cyprus, where long-term individual-based monitoring has been undertaken since 1993, nest counts for loggerhead turtles have decreased slightly (-7%) between 1993 and 2018, while green turtle nest counts grew by 393% for green turtles. Using a Bayesian state-space model, we show that nesting female green turtle abundance increased annually at almost four times the rate of that of loggerhead turtles at this nesting beach. Meanwhile, across all core beaches (including Alagadi Beach) monitored consistently since 1995, nest counts increased by 52 % and 233 % for loggerhead and green turtles respectively. Loggerhead turtles nesting at Alagadi Beach have stable reproductive parameters and average adult survival for the species. Recruitment of first-time nesters underpins the observed increase in female abundance and the interannual variation in nesting numbers solely for green turtles at Alagadi Beach. Using multiple matrix model scenarios, we propose that bycatch-driven mortality of all age-classes, rather than lower reproductive output, is impeding the recovery of loggerhead turtles. While the increase of green turtles is encouraging, the recovery of loggerhead turtles is likely to be compromised until bycatch in the region is addressed. As sea turtle population numbers are driven by at-sea survival of immature individuals, more importance should be placed on management at pelagic and neritic foraging areas. Understanding threats faced by immature life-stages will be crucial to accurately derive population models and to target conservation actions for long-lived marine vertebrates.

Introduction

Although global declines in marine megafauna have occurred in the past and are continuing apace (McCauley et al. 2015), there are conservation success stories, with some populations now showing signs of recovery (Lotze, Coll, Magera, et al. 2011, Magera et al. 2013, Valdivia et al. 2018). It has been suggested that long-lived, wide-ranging, migratory species with slow life-histories are particularly at risk of extinction (Hutchings et al. 2012; Lewison et al. 2004) because they will encounter a multitude of diverse threats throughout their life (Lascelles et al. 2014). These species often require long-term, sustained, international conservation management, which is usually most successful when informed by an understanding of specific life-history traits and their variation (Ward-Paige et al. 2012, Dulvy et al. 2014).

Sea turtle populations have suffered severe declines in the past and have, in many cases, been reduced to a fraction of their historical abundance in many locations (McClenachan et al. 2006, Kittinger et al. 2013, Van Houtan & Kittinger 2014). Basic protective measures at nesting beaches have resulted in significant recovery trends in nesting numbers for many subpopulations (Broderick et al. 2006, Chaloupka et al. 2008, Mazaris et al. 2017, Valdivia et al. 2018, Colman et al. 2019). The simultaneous reduction in human overexploitation of individuals at sea has also contributed to population recoveries (Kittinger et al. 2013, Van Houtan & Kittinger 2014, Weber et al. 2014). Nonetheless, many populations remain at low levels and are under threat of extirpation (Mazaris et al. 2017, Valdivia et al. 2018). Exactly why this is remains unclear for some populations.

Matrix population models can inform our understanding of population demography and dynamics and have been used to identify the life-history parameters at which to target management in sea turtles (Crouse et al. 1987, Heppell 1998, Mazaris et al. 2005, Mazaris et al. 2005, Casale & Heppell 2016). These models require high-quality, long-term data on all life-stages, which is challenging to obtain for this taxon (Hamann et al. 2010, Rees et al. 2016), particularly as the juvenile life-stage remains understudied (Wildermann et al. 2018). From available modelling, it is apparent that immature individuals are the most abundant life-stage, with adults representing only 1 % of sea turtle populations (Heppell 1998, Casale & Heppell 2016). While the removal of nesting

females and their eggs can undeniably cause populations to collapse (Tomillo et al. 2008), at-sea protection is also key to population recovery (Crouse et al. 1987, Crowder et al. 1994, Mazaris et al. 2005, Casale & Heppell 2016).

In the Mediterranean, both loggerhead turtle (*Caretta caretta*) and green turtle (*Chelonia mydas*) populations have declined due to commercial exploitation, fisheries interactions, coastal development and elevated predation of nests and hatchlings (Casale, Margaritoulis, et al. 2010, Casale et al. 2018). Loggerhead turtles, the more abundant species in the Mediterranean, nest predominantly in Greece, Turkey, Cyprus and Libya, with lower levels of nesting occurring on the Levant coast and sporadic nesting occurring in some Western Mediterranean countries (Casale et al. 2018). In contrast, green turtle nesting sites are predominantly in Cyprus, Turkey and Syria, with minor aggregations in Egypt, Israel and Lebanon (Casale et al. 2018).

Both subpopulations are considered independent regional management units (RMUs; Wallace, DiMatteo, et al. 2010) and show clear genetic structuring within both RMUs (Carreras et al. 2006, Tikochinski et al. 2018). The two subpopulations are described as under high threat, with the green turtle RMU also considered to be under high risk because of its restricted range (Wallace et al. 2011). Globally, green and loggerhead turtles are classified as endangered (Seminoff 2004) and vulnerable (Casale & Tucker 2017) respectively under the International Union for the Conservation of Nature (IUCN) Red List of Threatened Species respectively. The Mediterranean loggerhead turtle subpopulation is assessed separately as least concern (Casale 2015), owing to recent increases in nesting abundance recorded at a basin-wide scale (Casale 2015, Casale et al. 2018). However, this subpopulation is considered conservation dependent, meaning that the population would decline again should nest protection efforts cease (Casale 2015).

Sea turtle bycatch rates in the Mediterranean are among the highest in the world and are likely unsustainable (Wallace, Lewison, et al. 2010, Lewison et al. 2014, Casale & Heppell 2016). Bycatch predominantly impacts post-pelagic individuals of relatively high reproductive value (Wallace et al. 2008), which is of concern for population stock maintenance and recovery (Casale 2011, Snape et al. 2013, Levy et al. 2015, Casale & Heppell 2016).

Chapter 6: Investigating differences in population recovery rates

Consistent and in-depth monitoring of sea turtle nesting beaches in North Cyprus has been undertaken since 1993, with an intensive night-time monitoring and tagging programme concentrated at Alagadi Beach but with other core nesting beaches monitored annually. Here we investigate the difference in population recovery rates between green and loggerhead turtles in North Cyprus. As the encouraging recovery of green turtles was analysed in depth by Stokes et al. (2014), we focus primarily on loggerhead turtles, exploring the population trend and the temporal variation in reproductive parameters. Using a Bayesian state-space model, we estimate population growth rates and use stochastic matrix model projections to explore the drivers of these contrasting recovery patterns.

Materials and methods

1. Data collection

1.1. *Alagadi Beach – individual-based monitoring*

Between 1993 and 2018, surveys were conducted every night at Alagadi Beach during the turtle nesting and nest hatching season (May to September) once the first nests of the season were confirmed (see Stokes et al. 2014 for beach location, and see Figure 1 in Chapter 1). Intensive monitoring and tagging were carried out each night to encounter all nesting females (Broderick & Godley 1996, Broderick et al. 2002, 2003). Identification was based on flipper and passive integrated transponder (PIT) tag readings (Omeyer et al. 2019). Neophyte (i.e. first-time nester) classification was determined from 2000 onwards, one modal breeding cycle (3 years) after the introduction of PIT tags (Omeyer et al. 2019). Recruitment was calculated as the proportion of nesters that are 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 inter-nesting intervals of ≥ 20 days were observed (Broderick et al. 2002). Remigration interval of uniquely identified females were calculated as the number of years elapsed between two consecutive nesting seasons.

1.2. *Other beaches*

During the same period, daytime surveys were conducted every 1–3 days at other core beaches on the North and West coasts of Cyprus. All nesting activities were examined and nests confirmed by the presence of eggs.

1.3. *All locations*

Clutches laid in suboptimal sites at all beaches were translocated to safer locations (supporting information 2.1. and 2.2) and all nests were protected from predation by dogs and foxes using wire-mesh screens. 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 (hatched eggs) and unhatched eggs upon excavation (Broderick et al. 2003). Only nests with hatchling tracks present were excavated before 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 as the proportion of emergent hatchlings per clutch (see supporting information).

2. Population trends and reproductive parameters

To avoid including temporally biased estimates in the matrix models, we explored the temporal variation in the reproductive parameters collected at Alagadi Beach for loggerhead turtles. Statistical modelling was carried out using R v.3.5.1 (R Core Team 2018) and the 'nlme' (Pinheiro et al. 2013), 'lme4' (Bates et al. 2015) and 'mgcv' (Wood 2004) packages. Tests of correlation were performed using Spearman's rank order correlation coefficient. Generalised least squares (GLS) modelling, generalised linear modelling (GLM), and generalised linear and additive mixed modelling (GLMM and GAMM respectively) were used to analyse trends in the data (supporting information).

3. Matrix model

We used an age-classified, female-only, post-breeding, birth-pulse, stochastic projection matrix with an annual time step (supporting information). We based our matrix model on the loggerhead turtle life-cycle because it is the better understood of the two species in the region (see supporting information for further details). We defined the following age classes: (1) eggs/neonates (one age class); (2) epipelagic juveniles <25 cm CCL (two age classes); (3) benthic juveniles >25 cm CCL (21 age classes); and, (4) adults (one age class).

Populations at the end of each year were calculated based on class-specific annual survival estimates, with surviving females in each class moving to a higher class until they reached the final adult age class where they remained. Only adults were assumed to reproduce. To introduce the stochasticity, we ran each matrix model over 5,000 iterations, replacing some life-history parameter estimates with a random draw from an appropriate distribution on each iteration (supporting information). Several matrix models were derived from the initial matrix model by varying one or multiple parameter estimates to explore their contribution to the contrasting recovery rates. On each iteration, we calculated the finite growth rate (λ) under stable-stage-distribution over the study period as the dominant eigen value. We report the mean ($\bar{\lambda}$) \pm 95% quantiles from all iterations for each model.

4. State-space model

To calculate the observed λ based on our female count data and to estimate female population sizes, we implemented a Bayesian state-space model in JAGS (v.4.3.0) via the “jagsUI” library (v.1.5.0, Kellner 2018) for R. We assume the underlying trend in our count data followed a conventional exponential growth model (supporting information). The model was fitted by running three Monte Carlo Markov chains (MCMC) for 300,000 iterations, with a burn-in of 100,000 and a thinning rate of 10. The Brooks-Gelman-Rubin diagnostic tool was used to confirm successful chain convergence (all \hat{R} values $<$ 1.01). We report $\lambda = \exp(\bar{r}) \pm 95\%$ Bayesian credible intervals (BCI) and compare this with the $\bar{\lambda}$ estimates derived from the different matrix model scenarios.

Results

1. Population trends

1.a. Nest counts

For both species, 2018 saw record numbers of nests across all core beaches on the North and West coasts, including Alagadi Beach (loggerhead turtles: $n = 469$, green turtles: $n = 418$), in addition to which a further 95 loggerhead and 664 green turtle nests were recorded across the Karpaz peninsula.

For loggerhead turtles, nest counts remained stable and low at Alagadi Beach over the study (autocorrelation: $\chi^2_1 = 3.50$, $P = 0.062$, linear slope: $\beta = -3.61 \pm 1.40$, quadratic: $\beta = 0.14 \pm 0.05$ (SE), $\phi = -0.29$, $\chi^2_1 = 6.54$, $P = 0.011$, Fig.1a), whereas nesting numbers for green turtles at Alagadi Beach have grown exponentially (autocorrelation: $\chi^2_1 = 12.01$, $P < 0.001$, linear slope: $\beta = -11.89 \pm 2.12$, quadratic slope: $\beta = 0.78 \pm 0.08$, $\phi = -0.56$, $\chi^2_1 = 31.52$, $P < 0.0001$, Fig.1b). When applying the IUCN Marine Turtle Specialist Group (MTSG) Red List assessment method which compares change between the oldest and most recent 3-5 yr averages, nest counts decreased by 7% for loggerhead turtles at Alagadi Beach, while they increased by 393% for green turtles (Table S1).

Across all core beaches, nest counts for both species showed clear positive quadratic trajectories (loggerhead turtles – autocorrelation: $\chi^2_1 = 11.81$, $P = 0.001$, linear slope: $\beta = -8.83 \pm 3.62$, quadratic slope: $\beta = 0.52 \pm 0.13$, $\phi = -0.67$, $\chi^2_1 = 13.54$, $P < 0.001$, Fig.1c; green turtles – autocorrelation: $\chi^2_1 = 4.74$, $P = 0.029$, linear slope: $\beta = -19.15 \pm 4.07$, quadratic slope: $\beta = 1.14 \pm 0.16$, $\phi = -0.33$, $\chi^2_1 = 22.86$, $P < 0.0001$, Fig.1d). Compared to the earliest period, nesting numbers for loggerhead turtles increased by 52% and 233% for loggerhead and green turtles respectively across core beaches (Table S1).

1.b. Female abundance

At Alagadi Beach, loggerhead turtle nester abundance remained stable (autocorrelation: $\chi^2_1 = 3.78$, $P = 0.052$, linear slope: $\beta = -1.07 \pm 0.69$, quadratic slope: $\beta = 0.06 \pm 0.03$, $\phi = -0.31$, $\chi^2_1 = 4.57$, $P = 0.033$, Fig.2a). Based on

observed female counts (Fig.2a), adult population size of this species increased by 2.2% annually ($\lambda = 1.022 \pm 0.034$ (mean \pm SD), 95% quantiles: 0.962–1.101), with no clear change since 2000 (1.019 ± 0.014 , 0.992–1.047; Fig.3). Using IUCN past and recent periods, nester abundance at Alagadi Beach increased by 27% (Table S1) from 26 (mean, 1993–1997) to 33 (2014–2018) nesting females. In contrast, the state-space model estimated female abundance increased from 20 (mean, 95% BCI: 11–29) to 34 (22–50) nesting females over the same time period, corresponding to a mean increase of 51 (-15–154)% (Fig.3, Table S1).

Female abundance for green turtles showed a clear positive quadratic trajectory (autocorrelation: $\chi^2_1 = 9.18$, $P = 0.003$, linear slope: $\beta = -3.51 \pm 0.76$, quadratic slope: $\beta = 0.25 \pm 0.03$, $\phi = -0.48$, $\chi^2_1 = 27.91$, $P < 0.0001$, Fig.2b), and increased at almost four times the rate of that of loggerhead turtles over the same time period, increasing by 9.1% annually (1993–2018, 1.091 ± 0.078 , 0.929–1.256, Fig.3). The average rate of increase was higher from 2000 onwards (1.117 ± 0.034 , 1.056–1.189, Fig.3). Using IUCN past and recent periods, nester abundance for this species increased by 485% (Table S1) from 13 (1993–1997) to 76 (2014–2018) females (Fig.2b). In contrast, the state-space model estimated female abundance increased from 10 (5–30) to 74 (29–210) females over the same period, corresponding to a mean increase of 778 (111–2421)% using IUCN past and recent periods (Fig.3, TableS1).

1.c. Recruitment

At Alagadi Beach, nest counts and recruitment were strongly correlated for green turtles only (2000–2018; $\rho = 0.90$, $P < 0.001$; loggerhead turtles: $\rho = 0.02$, $P = 0.939$). While nester abundance remained stable for loggerhead turtles (1993–2018), the percentage of neophyte nesters has significantly increased by 20% since 2000 ($\phi = 0.19$, $t_{17} = 2.50$, $P = 0.023$, Fig.2a). The absence of an increase in nest counts despite recruitment for loggerhead turtles at Alagadi Beach is likely to be due to low nest site fidelity rather than a decrease in clutch frequency (supporting information) considering the increase in nesting numbers across monitored beaches for this species (Fig.1ac).

2. Matrix models

Chapter 6: Investigating differences in population recovery rates

Parameter estimates are summarised in Table S2. For loggerhead turtles, female body size, clutch size, clutch frequency and remigration interval remained stable over the study period, while hatchling emergence success varied temporally due to changes in translocation practices (supporting information).

The finite population growth rate obtained from the initial matrix model was lower (0.944, 95% CI: 0.909–0.968) than that obtained from the state-space model (1.022, 95 % quantiles: 0.962–1.101) and suggested that the population should be decreasing by 5.6% annually. Increasing loggerhead clutch frequency to that of green turtles did not result in comparable λ estimates between loggerhead turtle models (scenarios 2–3, Table 1). Similarly, λ estimates were only slightly improved when both increasing clutch frequency and decreasing age at sexual maturity (scenarios 4–6, Table 1). Obtaining comparable λ estimates required a clutch frequency of 3, an age at sexual maturity of 21 years and a 5% increase in benthic juvenile survival (scenario 8, Table 1). For population growth rates to exceed those currently observed at Alagadi Beach for loggerhead turtles, survival needed to be increased by 5% across all age classes (scenarios 10–14, Table 1). Similarly, obtaining population growth rates that exceed those observed since 2000 for green turtles at Alagadi Beach required a 10% increase in survival across all age classes and an increase in HES (scenario 15, Table 1).

Compared to loggerhead turtles at this site, green turtles have higher adult survival and lay more and larger clutches with higher average HES (Table S2). Thus, green turtles produce more eggs and more emergent hatchlings (Figure 4 and supplemental material). Increasing loggerhead turtle reproductive output to mirror that of green turtles does not, however, result in comparable λ estimates between species (scenarios 16–19, Table 1). In contrast, increasing loggerhead turtle adult annual survival to equal that of green turtles results in comparable population growth rates between loggerhead turtle models; however, this scenario (scenario 20, Table 1) is unrealistic. Comparison of matrix model scenarios suggest that a discrepancy in survival is driving the difference in recovery rates between species.

Discussion

A quarter of a century after the commencement of intensive nest protection in North Cyprus and the interruption of legal trade globally, the two subpopulations have shown contrasting recovery rates. Five additional years have confirmed the suggestion by Stokes et al. (2014) that they recorded the initial recovery phase for green turtles. In contrast, loggerhead turtle nesting numbers have only slightly increased over the same period, which cannot be attributed to temporal changes in monitoring practices and reproductive parameters. It is, however, possible these two subpopulations are recovering from different levels of exploitation.

Neophyte recruitment, an indicator of population growth (Heppell et al. 2003, Richardson et al. 2006), drove the increase in nesting numbers solely for green turtles (Stokes et al. 2014) with differential recruitment among foraging areas; turtles foraging in Egypt's Lake Bardawil were the main drivers of population growth (Bradshaw et al. 2017). As satellite tracking of nesting females from North Cyprus revealed within-season multi-country nesting for loggerhead turtles (Snape et al. 2016), the high proportion of neophyte loggerhead turtles that were recorded laying only one clutch and that are never resighted raises two questions: are these females truly first-time nesters and/or to which rookery do these females belong? The coverage of capture-mark-recapture programmes in Cyprus and the Mediterranean currently prevent these questions from being answered, yet they are key to refining reproductive parameters and rookery-specific population sizes. High precision genetic markers (Komoroske et al. 2017) and laparoscopy (Dobbs et al. 2007), however, could possibly be used to answer these questions. Additionally, it suggests tag returns at nesting beaches likely overestimate remigration interval and underestimate clutch frequency (Pfaller et al. 2013, Tucker 2010, Weber et al. 2013), therefore influencing population size estimates (Esteban et al. 2017, Weber et al. 2013).

Given the interannual variation in sea turtle nesting numbers (Broderick et al. 2001, Limpus and Nicholls 2000, Monsinjon et al. 2019, Saba et al. 2007), long-term data series are required for meaningful population assessments (Mazaris et al. 2017, Valdivia et al. 2018). The IUCN MTSG Red List assessment method aims to provide a coarse measure of population trends by comparing

past and recent 5-yr time periods 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 and its sensitivity to small deviations resulted in opposing trends in nest counts for loggerhead turtles. Thus, when available, long-term time-series should be used to account for long-term fluctuations and to accurately reflect observed trends (D'Eon-Eggertson et al. 2015).

The difference in recovery rates between species in North Cyprus appears to be driven by differences in survival rather than reproductive output. As previously emphasised, population trends in sea turtles are largely driven by juvenile survival (Casale and Heppell, 2016; Crouse et al., 1987; Crowder et al., 1994; Mazaris et al., 2005). Therefore, the absence of clear signs of population recovery for loggerhead turtles at Alagadi Beach, despite stable reproductive parameters, average adult survival for the species (Pfaller et al., 2018, Omeyer et al. 2019) and neophyte recruitment, suggests juvenile mortality may be hindering the recovery of this subpopulation. Although the state-space model could not conclusively rule out a decline for this species (16.7% of λ values were <1), the contradicting population growth rates obtained from the two modelling approaches highlight the limitations of population modelling when key parameters are unknown. Indeed, while estimates used in the matrix models may be inaccurate for this subpopulation, accounting for potential biases in age at sexual maturity, clutch frequency and survival did not entirely explain the discrepancy between modelled growth rates. Unfortunately, age at sexual maturity and juvenile and adult survival estimates are scarce for Mediterranean loggerhead turtles (Casale et al., 2018) and obtaining population- and size-specific juvenile survival estimates is hindered by the current complicated geopolitical context of the region.

The successful recovery of green turtle subpopulations (e.g. Chaloupka et al., 2008; Mazaris et al., 2017; Valdivia et al., 2018) is thought to be facilitated by their highly localised inshore foraging and nesting grounds, which are more readily and effectively protected (Broderick et al., 2006). Loggerhead turtles, in contrast, generally have a complex movement pattern during (Snape et al., 2018, 2016; Tucker, 2010) and outside of the breeding season (Dujon et al., 2018; Haywood et al., In prep; Snape et al., 2016), which may make them particularly susceptible to bycatch (Wallace et al., 2010b, 2008). Additionally, incidental capture is highly variable within the basin (Casale, 2011) and is likely to impact

nesting aggregations differently based on the genetic origin of individuals in different fishing areas. For example, bycatch (Casale, 2011; Casale et al., 2010a; Nada and Casale, 2011; Turkozan et al., 2018) and intentional killing for meat (Nada and Casale, 2011) result in high mortality in the Adriatic Sea, Egypt, the Tunisian plateau and Turkey. All of these areas host foraging grounds for loggerhead (Bertuccio et al., 2019; Haywood et al., In Prep; Snape et al., 2016) and green turtles nesting in Cyprus (Bradshaw et al., 2017; Stokes et al., 2015), as well as for other populations and life-stages (Casale et al., 2018). Although North Cyprus is no exception in terms of high bycatch rates (Casale, 2011; Snape et al., 2016), it appears that small juvenile green turtles, which are likely to be from mixed stocks, are heavily impacted in the local area, while comparable young loggerhead turtles are rarely observed around the island or in the local small-scale fisheries (Snape et al., 2013).

For many marine vertebrate species, conservation actions have been focussed on land at breeding aggregations where individuals are readily accessible. While this has sufficed for some populations to recover, for others we may need to place more importance on distant management beyond breeding colonies. Indeed, mortality in juvenile life-stages has been shown to have important population-level effects in seabirds (Genovart et al., 2018; Sherley et al., 2017). For Mediterranean loggerhead and green turtles, we re-iterate the acute need to address bycatch as a priority to increase survival of post-pelagic individuals (Casale, 2011; Casale and Heppell, 2016; Levy et al., 2015; Snape et al., 2013; Wallace et al., 2008). While increasing reproductive success will undeniably be beneficial, 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 et al., 2018; Ward-Paige et al., 2012).

Concluding remarks

Although the increase in nesting numbers across North Cyprus for green turtles is encouraging, we cannot be complacent. Sustained 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 et al., 2018; Valdivia et al., 2018), however, the recovery of Mediterranean loggerhead turtles is likely to remain compromised until bycatch in the region is addressed in the long term. Extensive individual-based population monitoring datasets, such as the one used here, will be invaluable in assessing changes in population vital rates and population trends in the future. Nevertheless, more efforts need to be directed towards a better understanding of sea turtle juvenile abundance, distribution and survival (Casale et al., 2018; Hamann et al., 2010; Rees et al., 2016). Understanding threats faced by juveniles will be crucial to target conservation actions and to accurately parametrise population models necessary for the effective management of many threatened species.

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Table 1. Finite population growth rate (λ , mean and 95 % quantiles reported) estimates for loggerhead turtles calculated using the matrix model, with varying parameter estimates. The initial matrix model is shown in italics. HES (mean \pm SD, proportion): hatchling emergence success, PSR (mean \pm SE, proportion): primary sex ratios, S_{ej} (mean): epipelagic juvenile annual survival, S_{bj} (mean): benthic juvenile annual survival, ASM (mean, years): age at sexual maturity, S_a (mean \pm SD): adult annual survival, EPC (mean \pm SD, eggs): eggs per clutch, ECF (mean \pm SD, clutches): estimated clutch frequency, RI (mean \pm SD, years): remigration interval. 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 (1.022, 0.962–1.101).

Scenario	HES	PSR	S_{ej}	S_{bj}	ASM	S_a	EPC	ECF	RI	Lambda
1	<i>0.43\pm0.17^a</i>	<i>0.89\pm0.01^b</i>	<i>0.65^c</i>	<i>0.81^d</i>	<i>25^e</i>	<i>0.83\pm0.02^f</i>	<i>70\pm10^g</i>	<i>1.5\pm0.02^g</i>	<i>3.2\pm0.20^g</i>	<i>0.944 (0.909–0.968)</i>
2	-	-	-	-	-	-	-	3 ^h	-	0.964 (0.928–0.990)
3	-	-	-	-	-	-	-	5	-	0.980 (0.942–1.006)
4	-	-	-	-	21 ⁱ	-	-	-	-	0.958 (0.920–0.987)
5	-	-	-	-	21 ⁱ	-	-	3 ^h	-	0.981 (0.940–1.012)
6	-	-	-	-	21 ⁱ	-	-	5	-	1.001 (0.957–1.032)
7	-	-	0.70 ^j	-	21 ⁱ	-	-	3 ^h	-	0.993 (0.950–1.024)
8	-	-	-	0.86 ^j	21 ⁱ	-	-	3 ^h	-	1.018 (0.972–1.051)
9	-	-	-	-	21 ⁱ	0.88 ^j	-	3 ^h	-	0.997 (0.958–1.024)
10	-	-	0.70 ^j	0.86 ^j	21 ⁱ	0.88 ^j	-	3 ^h	-	1.044 (1.001–1.074)
11	0.56 \pm 0.17 ^k	-	0.70 ^j	0.86 ^j	21 ⁱ	0.88 ^j	-	3 ^h	-	1.056 (1.020–1.080)
12	-	-	0.72 ^l	0.88 ^l	21 ⁱ	0.90 ^l	-	3 ^h	-	1.069 (1.023–1.100)

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13	0.56±0.17 ^k	-	0.72 ^l	0.88 ^l	21 ⁱ	0.90 ^l	-	3 ^h	-	1.081 (1.045–1.106)
14	-	-	0.75 ^m	0.91 ^m	21 ⁱ	0.93 ^m	-	3 ^h	-	1.106 (1.059–1.138)
15	0.56±0.17 ^k	-	0.75 ^m	0.91 ^m	21 ⁱ	0.93 ^m	-	3 ^h	-	1.118 (1.079–1.144)
16	-	-	-	-	-	-	115 ⁿ	-	-	0.959 (0.925–0.983)
17	-	-	-	-	-	-	115 ⁿ	3 ^h	-	0.980 (0.944–1.005)
18	-	-	-	-	21 ⁱ	-	115 ⁿ	-	-	0.975 (0.934–1.003)
19	-	-	-	-	21 ⁱ	-	115 ⁿ	3 ^h	-	1.000 (0.957–1.029)
20	-	-	-	-	21 ⁱ	0.97 ^o	-	3 ^h	-	1.034 (1.005–1.056)

^a Because HES varied over the study period due to changes in translocation practices, a mean over the study period was used. ^b PSR were estimated from temperature dataloggers between 1997 and 2006 for this subpopulation (see Fuller et al. 2013 for further details). These were used here because looking at the temporal variation in PSR over the study period was outside the scope of this study. ^c Only one estimate of annual survival (mean: 0.05, 95 % CI: 0.003-0.200) was calculated for small juveniles (13.3-29.1 cm straight carapace length) in the Mediterranean (Abalo-Morla et al. 2018), however, it was extrapolated from 3 months of satellite tracking of 19 head-started individuals, originating from clutches laid in Spain, i.e. outside the species' known range (Casale et al. 2018). Additionally, because this annual survival estimate varied between individuals, was highly sensitive to small variations in daily survival and potentially confounded tag loss/malfunction with mortality, the mean annual survival estimate at age 2 for an ASM of 25 from Casale and Heppell's (2016) stationary age distribution model was used. ^d For benthic juveniles, the mean of four annual survival estimates (North and South Adriatic, North Ionian and Tunisian shelf) calculated by Casale et al. (2015) was used. ^e Although loggerhead turtles nesting in Cyprus are the smallest of the species (Broderick & Godley 1996), starting to reproduce at an average 72.3 cm CCL (Omeyer et al. 2018), the ASM estimates derived for the average SSM for Mediterranean loggerhead turtles were used, because studies on the age-size trade-off at sexual maturity provide

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inconclusive results (Bjorndal, Schroeder, et al. 2013, Bjorndal et al. 2014, Tucek et al. 2014, Omeyer et al. 2017). ^f Annual survival was calculated in Chapter 5 for this subpopulation, covering most of the study period. ^g Estimates calculated in this study. ^h Median ECF for remigrant green turtles (Stokes et al. 2014) and mean/median ECF for remigrant loggerhead turtles. ⁱ Lower end of ASM estimates for Mediterranean loggerhead turtles (Casale et al. 2018). ^j 5 % increase in annual survival. ^k Mean HES between 1997-2003, when more clutches were relocated. ^l 7 % increase in annual survival. ^m 10 % increase in annual survival. ⁿ Mean clutch size for green turtles (Broderick et al. 2003). ^o Adult annual survival for green turtles at this study site Chapter 5.

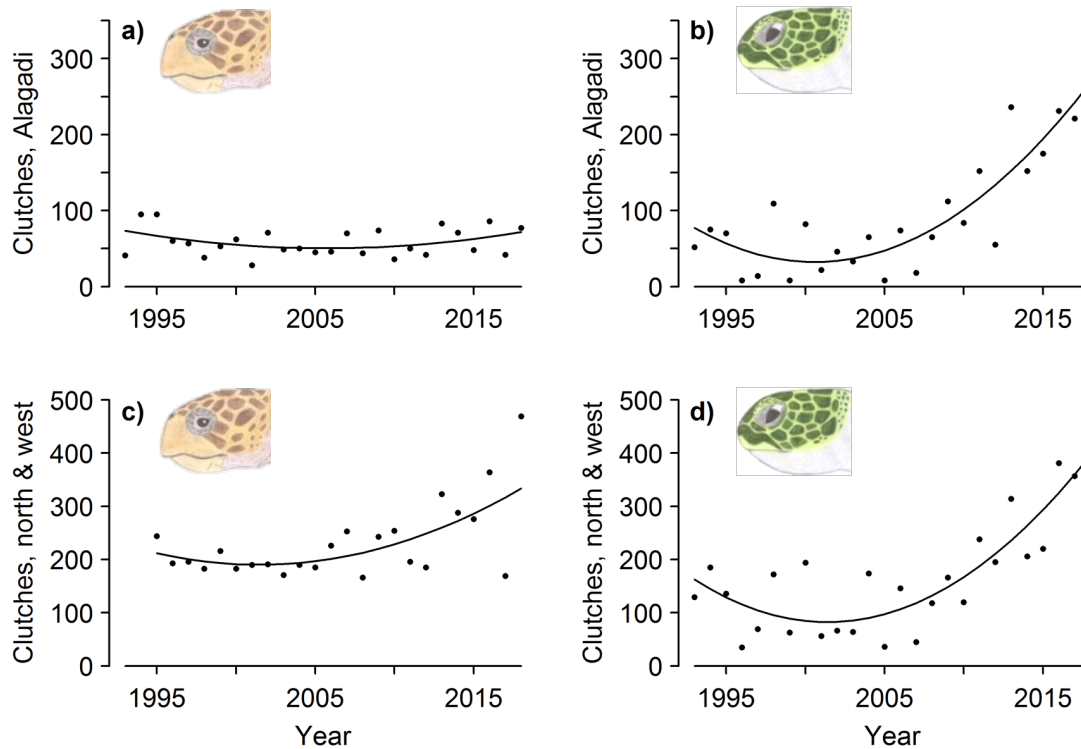


Figure 1. Loggerhead (a, c) and green turtle (b, d) clutches laid at Alagadi Beach (a-b) and across core nesting beaches on the North and West coasts of North Cyprus (c-d) over the study period 1993 to 2018. Note that Alagadi Beach is a core beach on the North coast, hence data from panels a) and b) are included in panels c) and d).

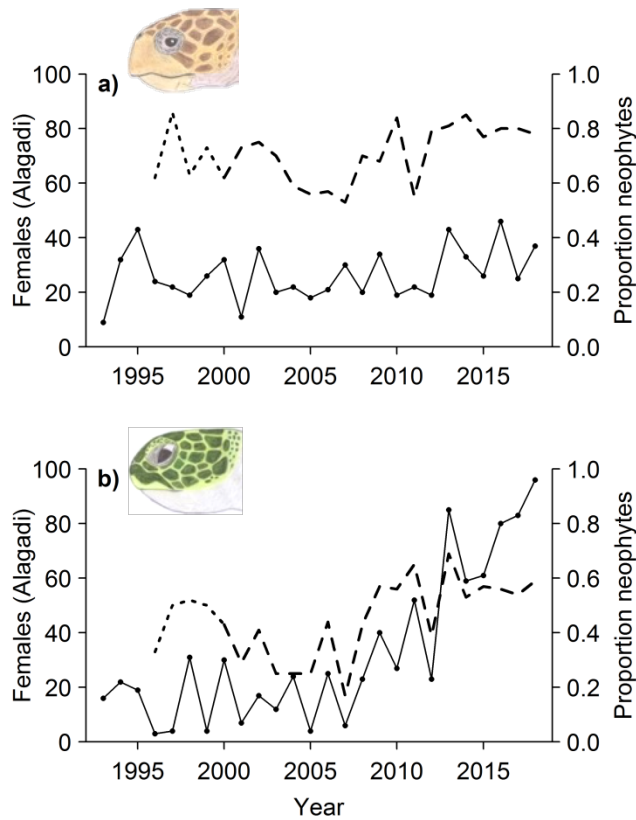


Figure 2. The number of (a) loggerhead and (b) green turtles nesting (solid lines) and the proportion of those that are neophytes/first time nesters (dashed lines) at Alagadi Beach over the study period 1993 to 2018. Dotted lines represent a period of lower certainty before the introduction of PIT tags in 1997.

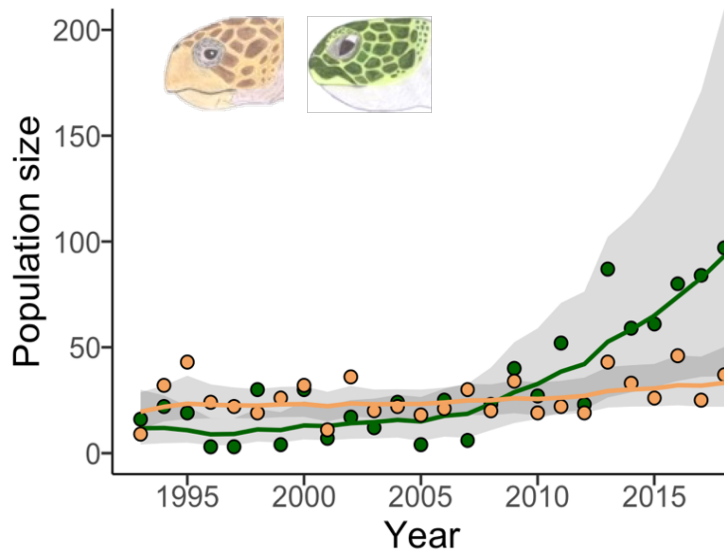


Figure 3. Female population size estimates for loggerhead (orange circles and trend line) and green (dark green circles and trend line) turtles, based on observed female counts (circles) at Alagadi Beach, calculated using the Bayesian state-space model. 95 % BCI shown as grey polygons for both species.

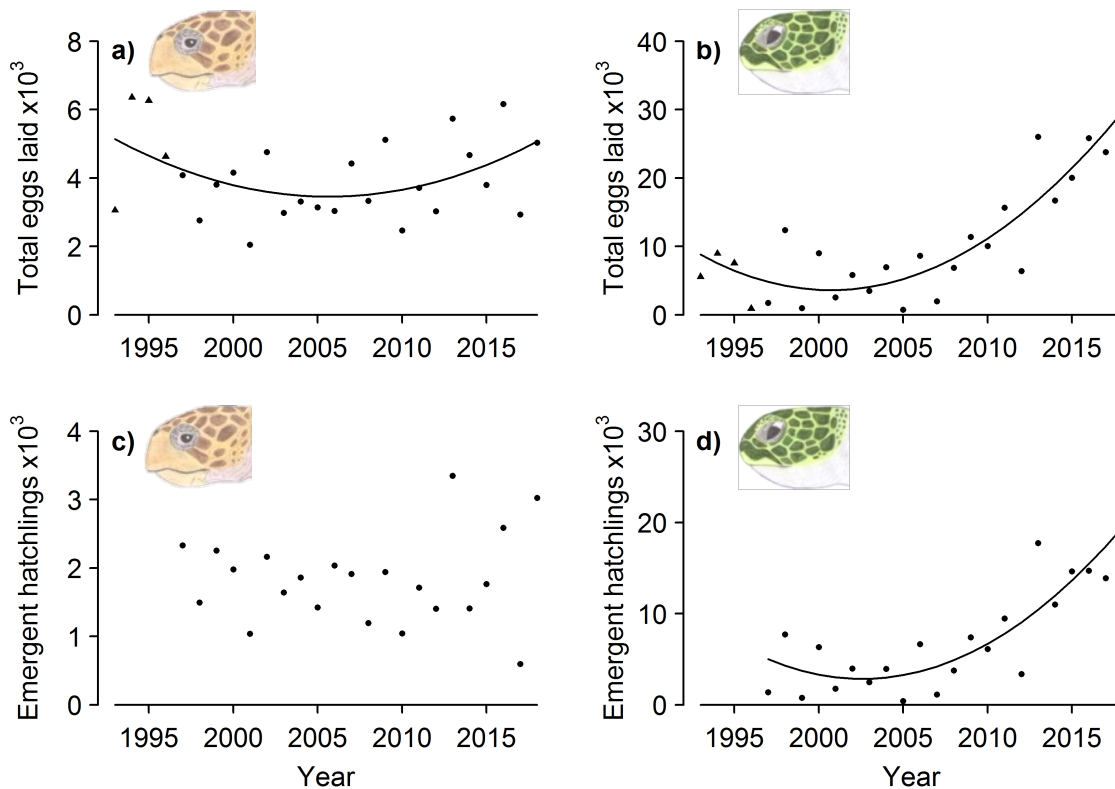


Figure 4. Estimated total number of eggs laid by (a) loggerhead and (b) green turtles at Alagadi Beach and resulting emergent hatchlings for each species respectively (c-d) between 1993 and 2018. The total number of eggs laid was estimated by replacing any missing clutch sizes (e.g. from nests lost to the sea) by the average clutch size over the study period for loggerhead turtles. Mean clutch size calculated in Broderick et al. (2003) was used for green turtles. Triangles in panels a) and b) denote period of high uncertainty in parameter estimate, as only nests that had visibly hatched were excavated between 1993 and 1996. For this same reason, analyses of emergent hatchlings were performed from 1997 onwards.

Supplementary information

Methods

1. Data collection

Split clutches, laid within a few days of one another, were counted as one to calculate OCF/ECF. From 1997 onwards, hatchling emergence success (HES), expressed as a proportion, was calculated as:

$$HES = \frac{H - D}{C}$$

(eqn S1)

where H is the number of hatched eggs, D the number of dead full-term hatchlings found in and around the nest, and C the clutch size (as defined above). Emergent hatchlings are those that have fully emerged from the nest (hatched eggs) or those found alive upon excavation.

2. Population trends and reproductive parameters

Person's chi-squared tests were used to explore differences in return rates. Nest counts, nester abundance, beach fidelity (expressed as the ratio of ECF and OCF), neophyte body size, total eggs laid at Alagadi Beach and total emergent hatchlings at Alagadi Beach were analysed using generalised least squares (GLS) modelling to account for temporal autocorrelation. In the absence of temporal autocorrelation, generalised linear modelling (GLM) was used. The total number of eggs laid at Alagadi Beach was estimated by replacing any missing clutch sizes (e.g. from nests lost to the sea) by the average clutch size over the study period for loggerhead turtles. Mean clutch size calculated in Broderick et al. (2003) was used for green turtles because looking at the temporal variation in clutch size at the population level for this species was outside the scope of this study.

Generalised additive mixed effect modelling (GAMM) was used to regress the following variables against time: (1) the proportion of total nests laid at Alagadi Beach, the proportion of nests attributed to individual females, the proportion of neophytes nesting at Alagadi Beach and the proportion of females recorded laying only one clutch – all using a binomial error structure and logit link function; (2) female body size at the population level, using a Gaussian error structure and identity link function; and (3) RI and OCF/ECF, using a negative binomial error structure and log link function. All models accounted for temporal autocorrelation and included a random effect to account for pseudoreplication if multiple measurements for individual females were included. GLMM was used if relationships were found to be linear. GAMM was also used to regress hatchling emergence success (HES) against time, clutch size, d.o.y (day of the year) and translocation (categorical; true or false), using a binomial error structure and logit link function, and accounting for temporal autocorrelation and individual pseudoreplication. Predated clutches as well as missed clutches for which d.o.y could not be determined were removed for this analysis.

To explore differences in body size (Gaussian error structure and identity link function) and OCF/ECF (negative binomial error structure and log link function) between neophyte and remigrant females from 2000 onwards, generalised linear mixed effect modelling (GLMM) was used, accounting for individual pseudoreplication and interannual variation in nesting numbers resulting from environmental stochasticity. Similarly, differences in RI between females that were recorded laying one or more clutches at first capture were explored using GLMM, with negative binomial error structure and log link function, accounting for individual pseudoreplication and temporal effects. OCF/ECF was also regressed against RI using GLMM with a negative binomial error structure and log link function, and accounting for individual pseudoreplication and interannual variation. Finally, GLMM was used to regress clutch size against time, CCL and d.o.y, using a negative binomial error structure and identity link function and accounting for temporal autocorrelation and pseudoreplication of individuals, as the GAMM model found relationships to be linear. Predated and split clutches were removed for this analysis. Clutches laid prior to 1997 were also removed to avoid introducing any potential bias resulting from only hatched nests being excavated in these early years.

3. Matrix model

The model was:

$$N_{t+1} = \mathbf{A}N_t \quad (\text{eqn S2})$$

where N_t is a vector holding the numbers in each stage at time t , and \mathbf{A} is the population projection matrix (equation S7).

This subpopulation is thought to have a flexible life-history strategy, with life stages centred around the habitats (epipelagic or benthic), rather than the oceanographic zones (oceanic or neritic), frequented (Casale et al. 2008). The strict oceanic/epipelagic stage is believed to be very short and restricted to very small dive-depth limited individuals (<25 cm CCL), after which individuals begin to forage throughout the entire water column on all trophic-level prey items (Casale et al. 2008, Lazar et al. 2008). Growth records for small Mediterranean juvenile loggerhead turtles suggest that it takes approximately 3 years for hatchlings to reach 25 cm CCL (Casale, Pino d'Astore, et al. 2009). By contrast, the transitional stage between oceanic and neritic waters is thought to be long, with no evidence of a strict neritic/benthic stage for this subpopulation (see Fig.4 in Casale et al. 2008). Using multiple growth models specific to Mediterranean loggerhead turtles (e.g. Casale, Mazaris, et al. 2009, Casale et al. 2011, Casale & Heppell 2016) and an average size at sexual maturity (SSM) of 80 cm CCL, age at sexual maturity (ASM) was estimated at 25 (mean; range: 21-34) years (reviewed in Casale et al. 2018).

To introduce the stochasticity, we ran each model for $i = 5,000$ iterations, replacing some life-history parameter estimates with a random draw from an appropriate distribution on each iteration. For HES, primary sex ratios (PSR) and adult survival, we took a random draw from a beta distribution (using the 'rbeta' function in R), parameterised using observed means (S_a) and standard deviations (SDs; σ_{S_a}) as (for example, for adult survival, S_a):

$$S_{a,i} = \text{Beta}(\alpha_i, \beta_i),$$

$$\alpha_i = \bar{S}_a \times \left(\frac{(\bar{S}_a \times (1 - \bar{S}_a))}{(\sigma_{S_a}^2) - 1} \right),$$

$$\beta_i = (1 - \overline{S_a}) \times \left(\frac{(\overline{S_a} \times (1 - \overline{S_a}))}{(\sigma_{S_a}^2) - 1} \right)$$

(eqn S3)

For clutch size and ECF, we used random draws from a normal distribution (using the 'rnorm' function in R), and for remigration interval (RI) we used draws from a gamma distribution (using the 'rgamma' function in R), parameterised via shape and rate parameters using the observed mean and SD as:

$$RI_i = \text{Gamma}(\alpha_i, \beta_i),$$

$$\alpha_i = \overline{RI}^2 / \sigma_{RI}^2,$$

$$\beta_i = \overline{RI} / \sigma_{RI}^2$$

(eqn S4)

The probability of a female hatchling surviving and successfully transitioning from the first to the second age class (S_h) was calculated as follows:

$$S_h = HES \times S_{ej} \times PSR$$

(eqn S5)

where S_{ej} the annual survival probability for epipelagic juveniles, which was included because individuals need to survive from hatching to the next calendar year, and PSR is primary sex ratio, which was included to only consider female hatchlings maturing and becoming epipelagic juveniles.

Fecundity (f) was calculated as the total number of female hatchlings produced per female per year using the following equation:

$$f = \frac{EPC \times ECF \times PSR}{RI}$$

(eqn S6)

where EPC is the number of eggs per clutch, ECF the estimated clutch frequency and RI the remigration interval. PSR was included to only consider female hatchlings. Fertility (F) was subsequently calculated by multiply the fecundity by adult annual survival.

The matrix model considering an average age at sexual maturity of 25 years had the following form:

Only one estimate of annual survival (mean: 0.05, 95% CI: 0.003-0.200) was calculated for small juveniles (13.3-29.1 cm straight carapace length) in the Mediterranean (Abalo-Morla et al., 2018), however, it was extrapolated from 3 months of satellite tracking of 19 head-started individuals, originating from clutches laid in Spain, i.e. outside the species' known range (Casale et al., 2018). Additionally, because this annual survival estimate varied between individuals, was highly sensitive to small variations in daily survival and potentially confounded tag loss/malfunction with mortality, the mean annual survival estimate at age 2 for an ASM of 25 from Casale and Heppell's (2016) stationary age distribution model was used.

4. State-space model

We assumed that the underlying trend in our count data (I_t) followed a conventional exponential growth model (e.g. Kery & Schaub 2012):

$$I_{t+1} = I_t \lambda_t \tag{eqn S8}$$

where λ_t is the growth rate in year t . State-space models decompose an observed time-series into two parts: a model for the process variation in the unobserved states (e.g. the population growth rate) and a stochastic model for the observation error. On the log scale, the state process model was:

$$\mu_{t+1} = \mu_t + r_t \tag{eqn S9}$$

where $\mu_t = \log(I_t)$ and $r_t = \log(\lambda_t)$ is the annual rate of change, with variations in log-growth rates given by $r_t \sim Normal(\bar{r}, \sigma_\eta^2)$, with the estimable process error variance σ_η^2 and the estimable mean population rate of change \bar{r} (i.e. the underlying trend). The observation process model was:

$$\log(y_t) = \mu_t + \epsilon_t, \tag{eqn S10}$$

where y_t is the count for year t and ϵ_t is the observation residual for year t , which is assumed to be normally distributed on log-scale $\epsilon_t \sim Normal(0, \sigma_\epsilon^2)$ as a function of the observation variance σ_ϵ^2 . The initial value for the first modelled count $I_{t=1}$ was drawn in log-space from a 'flat' normal distribution with the mean

equal to the log of the first observation $y_{t=1}$ and a standard deviation of 100. We used vague normal priors of $Normal(0,100)$ for \bar{r} , uniform priors of $Uniform(0,1)$ for both the observation and state process variance.

Results

1. Population trends

Both species showed synchrony in reproductive cycles across the two coasts. This was strongest in green turtles, for which nest counts were more strongly correlated (loggerhead turtles: $\rho = 0.41$, $P = 0.046$, green turtles: $\rho = 0.74$, $P < 0.0001$, between 1995–2018).

Of all the clutches laid at Alagadi Beach between 1993 and 2018, 12 % of loggerhead ($n = 1,513$) and 5 % of green ($n = 2,473$) turtle clutches had missing clutch size data, of which over half were laid prior to 1997 for each species (loggerhead turtles: $n = 186$, green turtles: $n = 122$). The total number of eggs laid for the two species show clear quadratic trajectories over the study period, although the increase is minimal for loggerhead turtles compared to green turtles (loggerhead turtles – autocorrelation: $\chi^2_1 = 3.44$, $P = 0.06$, linear slope: $\beta = -266.67 \pm 89.03$ (SE), quadratic slope: $\beta = 10.55 \pm 3.44$, $\phi = -0.28$, $\chi^2_1 = 8.06$, $P = 0.005$; green turtles – autocorrelation: $\chi^2_1 = 11.17$, $P < 0.001$, linear slope: $\beta = -1348.97 \pm 239.12$, quadratic slope: $\beta = 87.46 \pm 9.26$, $\phi = -0.55$, $\chi^2_1 = 30.91$, $P < 0.0001$; Fig.4ab).

The total number of emergent loggerhead turtle hatchlings has not shown a significant trend over time (autocorrelation: $\chi^2_1 = 8.68$, $P = 0.003$; $\phi = -0.60$, $\chi^2_1 = 0.10$, $P = 0.748$; Fig.4c; 1997–2018, mean \pm SD: $1,893 \pm 684$, range: 596–3,348) and has been affected by changes in relocation practices (see results in section below). On the other hand, the total number of emergent hatchlings has increased exponentially for green turtles over the same time period (autocorrelation: $\chi^2_1 = 14.44$, $P < 0.001$, linear slope: $\beta = -781.89 \pm 191.19$, quadratic slope: $\beta = 70.02 \pm 8.81$, $\phi = -0.67$, $\chi^2_1 = 26.31$, $P < 0.0001$, Fig.4d).

The absence of temporal trends in nest counts and nester abundance for loggerhead turtles at Alagadi Beach was not due to changes in survey effort,

detection probability (nests and females) or beach fidelity (Fig.S1). Although the percentage of total clutches laid at Alagadi Beach significantly decreased by 18 % since 1995 for loggerhead turtles ($\phi = -0.29$, $t_{22} = -3.34$, $P = 0.003$, Fig.S1b), the percentage of nests assigned to individual females at Alagadi significantly increased and stabilised around 87 % since 1997 ($\phi = -0.26$, $t_{24} = 2.43$, $P = 0.023$, Fig.S1a), with the low proportion of nests attributed to individual females prior to 1995 being due to lower surveying effort in the initial two years of monitoring. In addition, the ratio of ECF over OCF showed no temporal trend (autocorrelation: $\chi^2_1 = 0.24$, $P = 0.623$; $F_{1,687} = 1.54$, $P = 0.215$; Fig.S1c), indicating that female beach fidelity has not changed over the study period.

2. Reproductive parameters for loggerhead turtles

Nest counts at Alagadi Beach showed interannual variation typical of loggerhead turtles (mean \pm SD = 60 ± 20 , range: 28-108, 1993–2018), following a two- to three-year pseudo-cyclical pattern, with the coefficient of variation (CV = SD/mean: 0.34) lying within the range previously reported for this species (Broderick et al. 2001). Despite recruitment of neophyte nesters (see main text) and the significant difference in body size between neophyte and remigrant females (2000–2018; $\chi^2_1 = 22.63$, $P < 0.0001$; mean \pm SD for neophytes: 71.6 ± 4.0 cm CCL, $n = 345$; remigrants: 74.3 ± 4.0 cm CCL, $n = 141$; Fig.S2c), average female body size has remained stable around 72.3 ± 0.2 cm CCL at the population level (1993–2018; autocorrelation: $\phi = -0.66$, $\chi^2_1 = 19.17$, $P < 0.0001$; $\chi^2_1 = 1.96$, $P = 0.162$, $n = 649$, Fig.S2a). Similarly, there was no temporal trend in average neophyte body size since 2000 (71.6 ± 0.2 cm CCL; autocorrelation: $\chi^2_1 = 0.45$, $P = 0.502$; $\chi^2_1 = 0.87$, $P = 0.351$, $n = 345$, Fig.S2b). Likewise, despite clutch size significantly increasing with female body size ($\chi^2_1 = 79.44$, $P < 0.0001$, Fig.S3a) and decreasing over the course of the nesting season each year ($\chi^2_1 = 100.73$, $P < 0.0001$, Fig.S3c), average clutch size has remained stable around 70 ± 10 (\pm SD, range: 1-138) eggs per clutch since 1997 (autocorrelation: $\chi^2_1 = 0.35$, $P = 0.555$; $\chi^2_1 = 0.75$, $P = 0.388$, $n = 939$; Fig.S3b).

Over two-thirds (1994–2018: 70 %, 2000–2018: 71 %) of the females that returned to nest at Alagadi Beach did so within two to four years (1994–2018:

median = 3.0, IQR = 2-4, range = 1-10, n = 175 including individual pseudoreplication; 2000–2018: median = 3.0, IQR = 2-4, range = 1-10, n = 146 including individual pseudoreplication; Fig.S4a). However, of the females that first nested between 2000 and 2015, those that were recorded laying more than one clutch in their first nesting season were significantly more likely to be resighted than those that were recorded laying only one clutch ($\chi^2_1 = 37.02$, $P < 0.0001$), with only 11 % of females recorded laying one clutch (n = 80), compared with 44 % of females that were recorded laying more than one clutch (n = 203), being resighted. In addition, of these females, females that were recorded laying more than one clutch also had significantly shorter RIs on average than those that were recorded laying only one clutch in their first nesting season ($\chi^2_1 = 5.45$, $P = 0.019$, females recorded laying one clutch: 3.9 ± 1.8 yr (mean \pm SD), females recorded laying more than one clutch: 2.8 ± 1.5 yr, Fig.S5ab). The low incidence of unusually long RIs of 6 years or over (1994–2018: 7 %, 2000–2018: 8 %) is indicative of females with lower nest site fidelity nesting elsewhere, undetected. Furthermore, over half (60 %) of the females having nested at Alagadi Beach during three or more seasons varied their RI compared with their previous RI as a result of environmental stochasticity, with three-quarters (75 %) of these females varying their RI by 1 yr (Fig.S4b). Despite all these differences, the average RI has remained stable around 3.2 ± 0.2 (\pm SD) yrs since 2000 ($\phi = 0.51$, $t_{61} = 1.89$, $P = 0.063$, n = 146, Fig.S4c). The lower RIs at the start of the time series, resulting in a significant increase in the average RI over the study period ($\phi = 0.45$, $t_{78} = 3.22$, $P = 0.002$, n = 175, Fig.S4c), are a sampling artefact, whereby only females with lower than average RIs will have been re-encountered between 1993 and 1996.

In addition, RI was found to have a significant negative effect on clutch frequencies when all females were included (1994–2018, n = 177, OCF: $\chi^2_1 = 40.60$, $P < 0.0001$, Fig.S7a; ECF: $\chi^2_1 = 10.97$, $P = 0.001$, Fig.S7b). Removing females recorded laying on clutch with lower nest site fidelity, however, indicated that females with shorter RIs were no more or less likely to lay less clutches than those with longer RIs (1994–2018, n = 126, OCF: $\chi^2_1 < 0.01$, $P = 0.965$, Fig.S7a; ECF: $\chi^2_1 = 0.02$, $P = 0.886$, Fig.S7b). Similarly, the absence of correlations between median/mean clutch frequency estimates and nest counts suggest that females breeding in poor nesting seasons may not be in suboptimal condition

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compared to those nesting in good nesting years (1993–2018, median OCF: $\rho = -0.30$, $P = 0.136$; mean OCF: $\rho = -0.26$, $P = 0.206$; median ECF: $\rho = -0.14$, $P = 0.489$; mean ECF: $\rho = -0.17$, $P = 0.400$).

Of the clutches laid between 1997 and 2018 at Alagadi Beach for which hatchling emergence success could be calculated ($n = 1,118$), 20 % failed ($n = 219$), of which 79 % were clutches that remained in-situ ($n = 173$), and were inundated ($n = 96$, 44 %) or showed no visible sign of fertilisation ($n = 14$, 6 %). The remainder of clutches failed for unknown reasons ($n = 109$). For hatched nests, hatchling emergence success ranged from 1 % to 100 %, irrespective of whether nests remained in-situ or were translocated. Hatchling emergence success significantly decreased from 1997 before remaining stable around 40 % since 2007 (autocorrelation: $\phi = -0.04$, $t_{349} = 3.07$, $P = 0.002$, Fig.S8a). This decrease is due to changes in translocation practices over the study period, which resulted in the significant decrease in the proportion of translocated nests since 1997 (autocorrelation: $\phi = -0.21$, $t_{20} = 3.65$, $P = 0.002$, Fig.S8a), before increasing again in 2018 due to an experimental study. While hatching emergence success did not significantly vary with clutch size ($t_{349} = -0.51$, $P = 0.609$) or over the hatching season each year ($t_{349} = 1.74$, $P = 0.083$), translocating nests significantly influenced hatchling emergence success ($t_{349} = 25.60$, $P < 0.0001$, Fig.S8b), with translocated nests showing higher hatchling emergence success on average than those that remained in-situ (translocated nests (mean \pm SD): 0.63 ± 0.14 , $n = 252$; in-situ nests: 0.38 ± 0.14 , $n = 866$).

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Table S1. Applying the IUCN Marine Turtle Specialist Group Red List assessment method to obtain trends in female and nest abundance comparing two 5-yr time periods. Past and recent estimates are averages over the time periods. Change expressed as a percentage.

Species	Metric	Location	Data	Past time period	Past estimate	Recent time period	Recent estimate	Change
Loggerhead turtles	Nest counts	Alagadi	Time series data	1993–1997	70	2014–2018	65	- 7
	Nest counts	Core beaches	Time series data	1995–1999	206	2014–2018	313	+ 52
	Female counts	Alagadi	Time series data	1993–1997	26	2014–2018	33	+ 27
	Female counts	Alagadi	State-space model output	1993–1997	22	2014–2018	32	+ 45
Green turtles	Nest counts	Alagadi	Time series data	1993–1997	44	2014–2018	217	+ 393
	Nest counts	Core beaches	Time series data	1995–1999	95	2014–2018	316	+ 233
	Female counts	Alagadi	Time series data	1993–1997	13	2014–2018	76	+ 485
	Female counts	Alagadi	State-space model output	1993–1997	10	2014–2018	74	+ 640

Table S2. Comparison of life-history parameters of loggerhead and green turtles nesting at Alagadi Beach. CCL (cm): curved carapace length, EPC (eggs): eggs per clutch, OCF (clutches): observed clutch frequency, ECF (clutches): estimated clutch frequency, RI (years): remigration interval, S_a : adult annual survival, HES (proportion): hatchling emergence success, PSR (proportion): primary sex ratios, ASM (years): age at sexual maturity. Mean \pm SD (range, n) shown for CCL, EPC, HES and PSR. Mean \pm SD (median, IQR, range, n) shown for OCF, ECF, RI. Mean (95% highest posterior density confidence intervals, n) shown for S_a . Mean and range shown for ASM. Neophyte: first-time nester.

Species Group	CCL	EPC	OCF	ECF	RI	S_a	HES	PSR	ASM
Loggerhead turtles									
All females	72.3 \pm 0.2 (59.0-87.7, 649) ^{bc}	70 \pm 10 (1- 138, 939) ^{bd}	1.4 \pm 0.03 (1, 1-2, 1-6, 689) ^{be}	1.5 \pm 0.02 (1, 1-3, 1- 7, 689) ^{be}	3.2 \pm 0.2 (3, 2-4, 1-10, 146) ^{bf}	0.83 (0.78- 0.87, 265) ^{gh}	n.a.	n.a.	25 (21-34) ^k
Neophytes ^a	71.6 \pm 4.0 (59.0-87.7, 345) ^b	n.a.	1.5 \pm 0.9 (1, 1-2, 1-4, 369) ^b	1.6 \pm 1.0 (1, 1-2, 1-6, 369) ^b	n.a.	n.a.	n.a.	n.a.	n.a.
Remigrants ^a	74.3 \pm 4.0 (64.9-82.7, 141) ^b	n.a.	2.6 \pm 1.3 (3, 1-4, 1-6, 146) ^b	2.8 \pm 1.4 (3, 1-4, 1-6, 146) ^b	n.a.	n.a.	n.a.	n.a.	n.a.
Females recorded laying one clutch	n.a.	n.a.	n.a.	n.a.	3.9 \pm 1.8 (3, 3-5, 1-8, 29) ^b	n.a.	n.a.	n.a.	n.a.

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Females recorded laying more than one clutch	n.a.	n.a.	n.a.	n.a.	2.8±1.5 (2, 2-3, 1-9, 59) ^b	n.a.	n.a.	n.a.	n.a.
All clutches	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	0.43±0.17 (0-1.0, 1118) ^{di}	0.89±0.26 (0.0-1.0, 628) ^j	n.a.
In-situ clutches	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	0.38±0.14 (0.0-1.0, 866) ^d	n.a.	n.a.
Translocated clutches	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	0.63±0.14 (0.0-1.0, 252) ^d	n.a.	n.a.
<hr/>									
Green turtles									
All females	n.a.	115±27 (51-199, 277) ^{no}	2.9±1.3 (284) ^p	3.0±1.4 ⁿ (3, 1-4, 1-6, 485) ^l	3.5 (3, 2-4, 1-12, 352) ^{ef}	0.97 (0.95-0.99, 372) ^{fg}	n.a.	n.a.	34 (18-50) ^v
Neophytes	87.7±6.5 ^{lm}	n.a.	n.a.	(2, range: 1-6, 194) ^{lq}	n.a.	n.a.	n.a.	n.a.	n.a.
Remigrants	92.0±5.9 ^{lm}	n.a.	n.a.	(3, range: 1-6, 212) ^{lr}	n.a.	n.a.	n.a.	n.a.	n.a.
All clutches	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	0.66±0.28 (0.0-1.0, 2345) ^s	0.97±0.02 (0.9-1.0, 900) ^{tu}	n.a.

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In-situ clutches	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	0.67±0.28 (0.0-1.0, 2261) ^s	n.a.	n.a.
Translocated clutches	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	0.54±0.32 (0.0-1.0, 84) ^s	n.a.	n.a.

^a Time period: 2000-2018. ^b Estimates calculated in this study. Mean over the time series. ^c Time period: 1993-2018. ^d Time period: 1997-2018. ^e Time period: 1995-2018. ^f Time period: 2000-2018. ^g Extracted from Chapter 5. ^h Time period: 1995-2014. ⁱ Mean over the study period due to changes in relocation practices. All clutches included. ^j Extracted from Fuller et al. (2013). Clutches from multiple beaches across North Cyprus used. Time period: 1997-2006. ^k Extracted from Casale et al. (2018). Calculated using multiple growth models specific to Mediterranean loggerhead turtles and an average size at sexual maturity of 80 cm CCL (the average size of nesting females at the basin-wide scale). ^l Extracted from Stokes et al. (2014). ^m Time period: 1993-2013. ⁿ Extracted from Broderick et al. (2003). ^o Time period: 1995-2000. ^p Extracted from Broderick et al. (2002). ^q Time period: 2000-2013. ^r Time period: 1994-2013. ^s Calculated here. Time period: 1997–2018. ^t Extracted from Stokes et al. (In prep). ^u Time period: 1993–2012. Alagadi Beach only. ^v Extracted from Casale and Heppell (2016) for Mediterranean turtles.

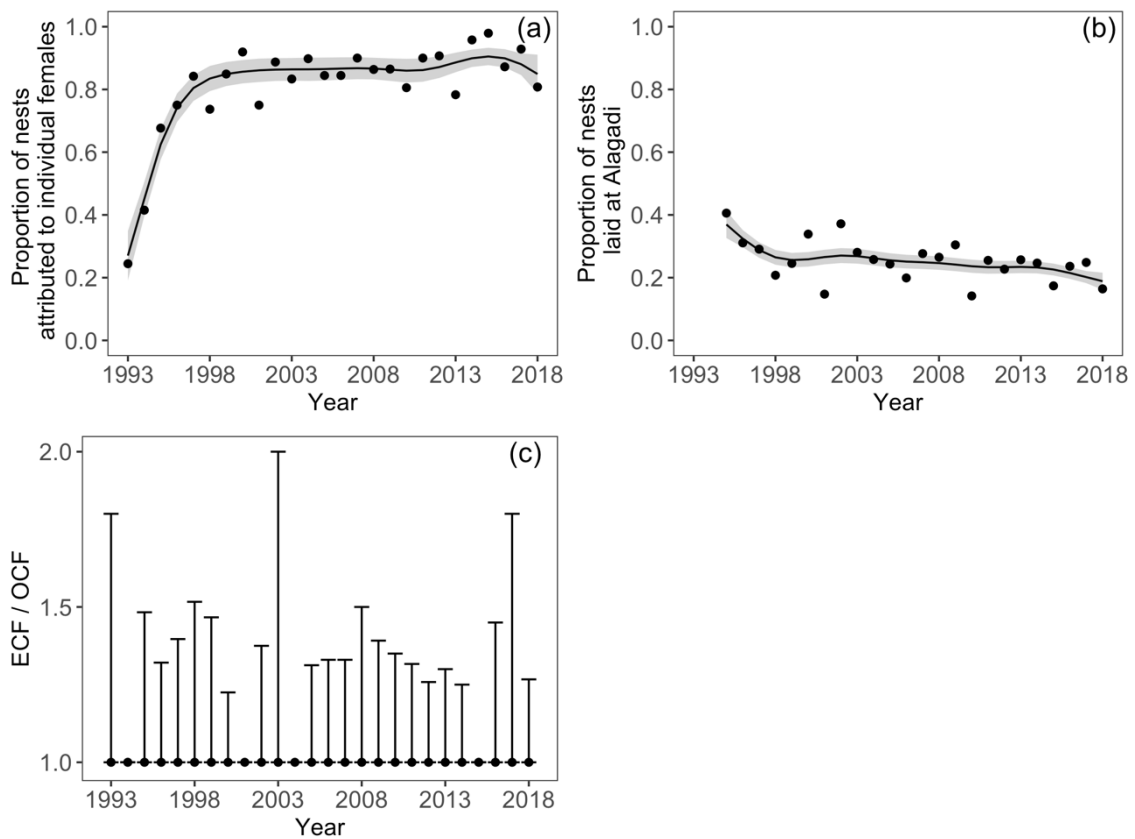


Figure S1. Trend in detection probability and detectability for loggerhead turtles. a) Proportion of clutches laid at Alagadi Beach that are not assigned to a particular female (through witnessing of oviposition). Grey area shows 95 % CI. b) Proportion of all clutches recorded across core beaches that are laid at Alagadi Beach. Grey area shows 95 % CI. c) Yearly median ratio of ECF:OCF (calculated for each individual female), with 5th - 95th percentiles displayed as error bars.

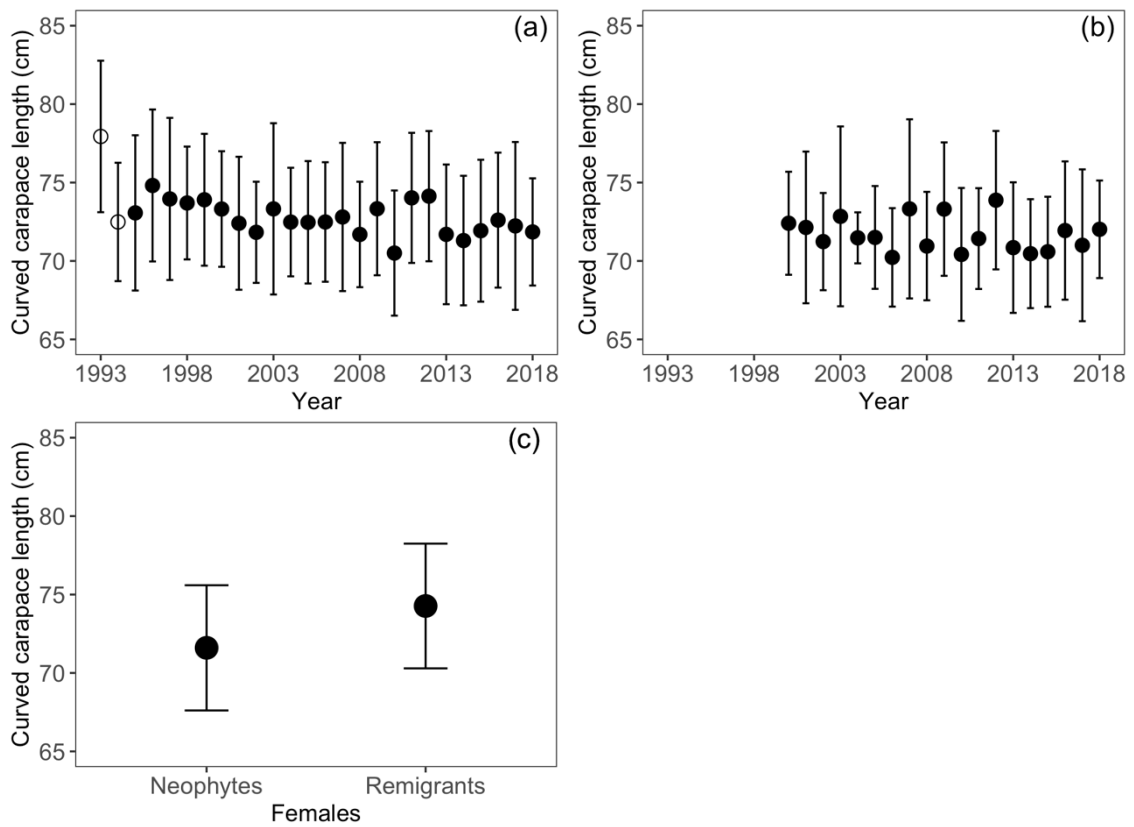


Figure S2. Female body size for loggerhead turtles. a) Temporal variation of female body size at the population level over the study period. Mean \pm SD for each year using the raw data. Open circles show period of lower certainty due to lower surveying efforts in the initial two years of monitoring. b) Temporal variation of neophyte female body size between 2000 and 2018. Mean \pm SD for each year using the raw data. c) Significant difference in body size between neophyte and remigrant females between 2000 and 2018. Mean \pm SD.

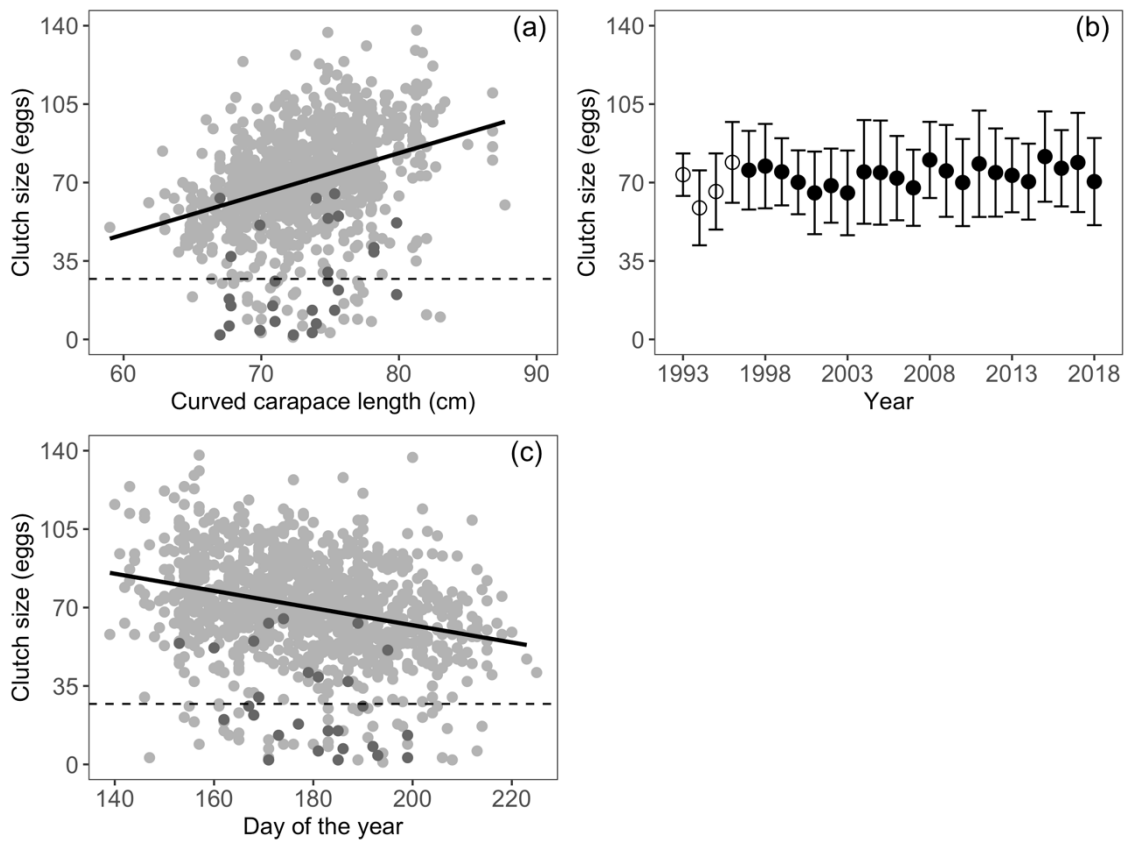


Figure S3. Clutch size for loggerhead turtles. a) Relationship between clutch size and female size ($y = 1.97 * CCL - 74.4$). b) Temporal variation of clutch size over the study period. Mean \pm SD for each year using the raw data. Open circles show period of lower certainty because only nests that had visibly hatched were excavated in those years. c) Relationship between clutch size and day of the year. All raw data (1993-2018) included in panels a) and c), with dark grey dots highlighting confirmed split clutches, which were removed for all analyses. In panels a) and c), the horizontal dashed line represents the average clutch size for confirmed split clutches. Note that predated clutches were not included in any panels.

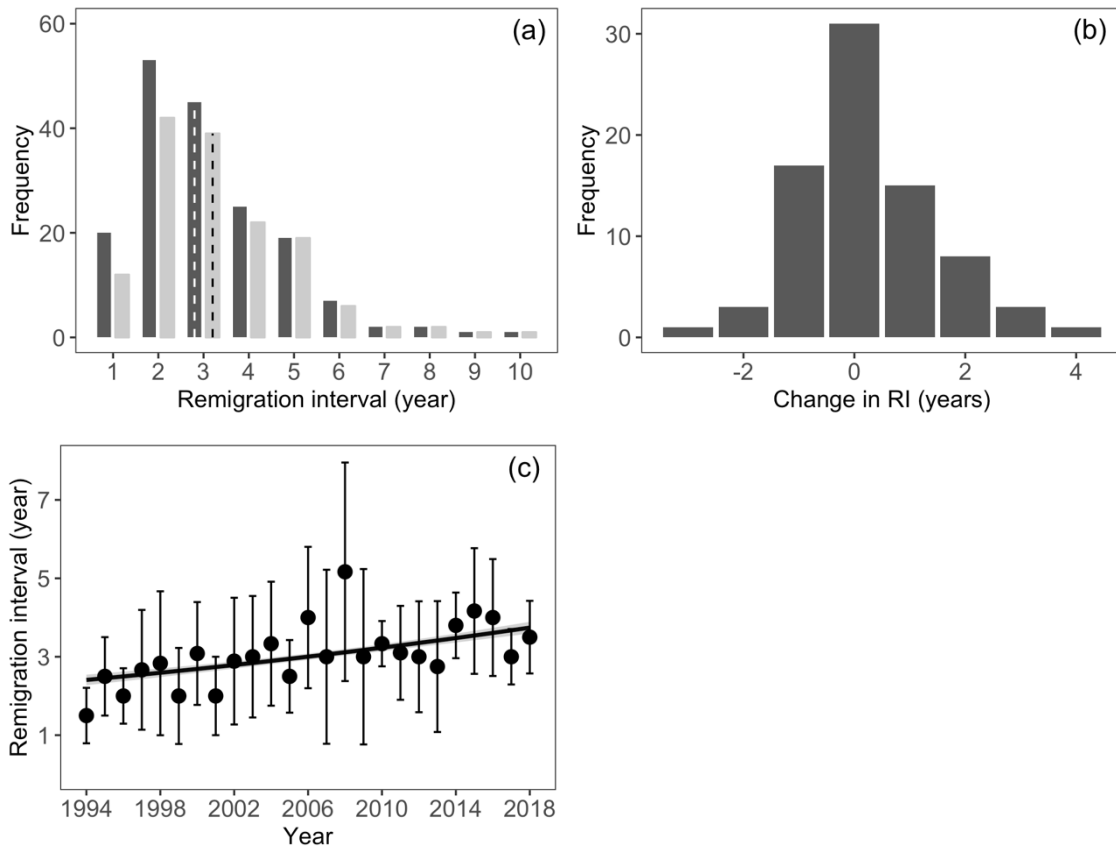


Figure S4. Remigration intervals (RIs) for loggerhead turtles. a) Frequency distribution of RIs over the study period (dark grey) and from 2000 onwards (light grey). Medians are shown by the dashed lines for each group. b) Frequency distribution of the change in RI for females nesting at Alagadi Beach during three or more seasons, expressed as the increase or decrease in RI compared with the previous RI recorded for individual females. c) Temporal variation of RI over the study period. 95 % CI shown in grey. Mean \pm SD for each year using the raw data.

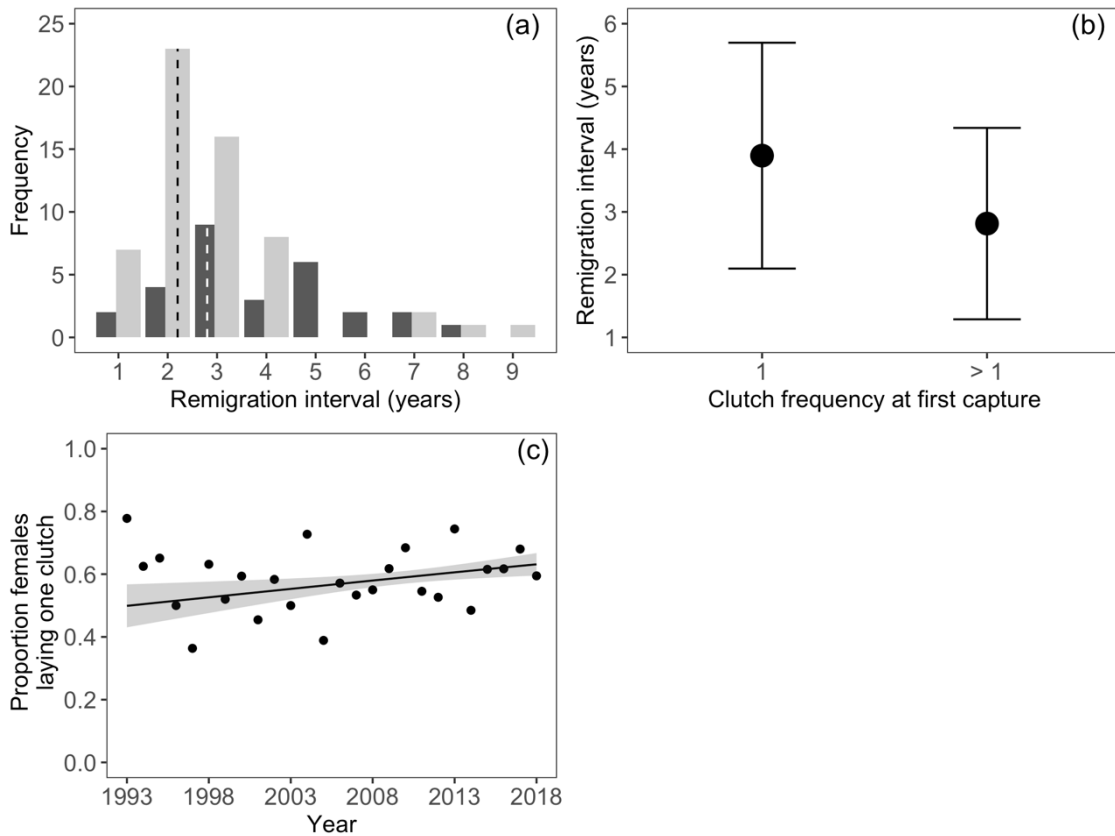


Figure S5. Loggerhead turtles recorded laying one clutch. a) Frequency distribution of RIs for females that first nested between 2000 and 2015 and laid only one clutch (light grey) and those that laid more than one clutch (dark grey). Medians are shown by the dashed lines. b) Difference in RI between females that first nested between 2000 and 2015 and were recorded laying only one clutch and those that were recorded laying more than one clutch. Mean \pm SD. c) Temporal variation of the proportion of females recorded laying one clutch. Model did not include 1993 and 1994 due to lower surveying effort.

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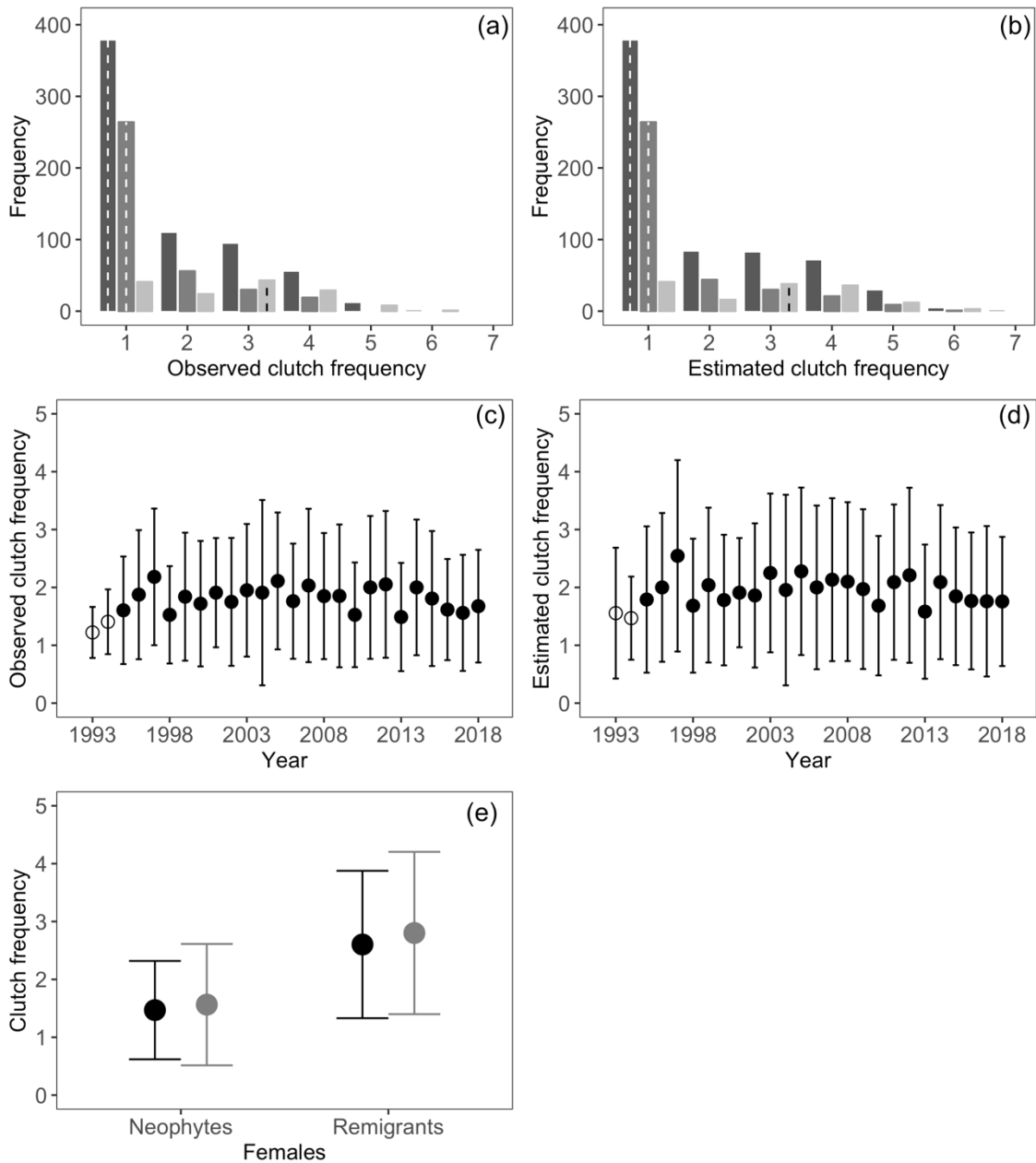


Figure S6. Observed and estimated clutch frequencies (OCF and ECF respectively) for loggerhead turtles. Frequency distribution of OCFs (a) and ECFs (b) at the population level (black), for neophyte females (dark grey) and for remigrant females (light grey). Medians are shown by the dashed lines. Temporal variation of OCF (c) and ECF (d) over the study period. 95 % CI shown in grey. Mean \pm SD for each year using the raw data. 1993 and 1994 were not included in the models due to lower surveying effort these years (open circles). E) Difference in OCF (black) ECF (grey) between neophyte and remigrant females between 2000 and 2018. Mean \pm SD.

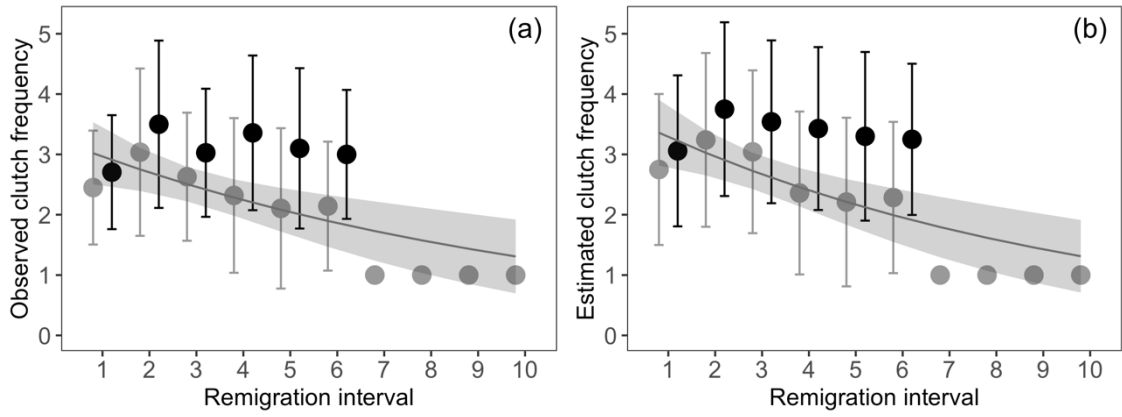


Figure S7. Relationship between observed (a) and estimated (b) clutch frequency and RI for loggerhead turtles. Results including all females are shown in grey, those only including females that were recorded laying more than one clutch in black. Mean \pm SD for each year using the raw data. 95 % CI shown in grey.

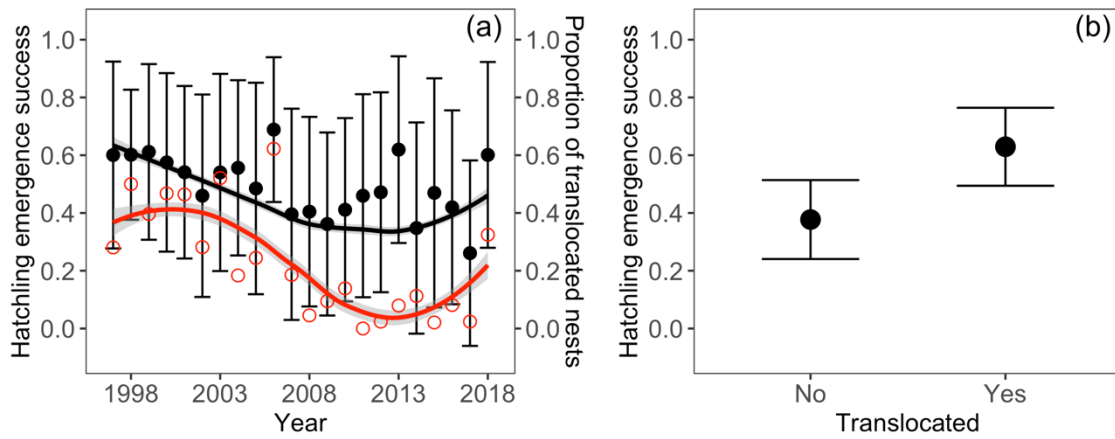


Figure S8. Hatchling emergence success for loggerhead turtles. a) Temporal variation of hatchling emergence success (black) and proportion of nests translocated (red) over the study period. 95 % CI shown in grey. Mean hatchling emergence success \pm SD for each year using the raw data. b) Difference in hatchling emergence success between translocated nests and those that remained in-situ. Mean \pm SD.

CHAPTER 7: GENERAL DISCUSSION

Overview

Throughout this thesis, I investigate life-history traits of adult sea turtles nesting in the Mediterranean and both further and challenge present knowledge and theories surrounding these life-history parameters. The key findings resulting from this thesis are that 1) there is a lack of data regarding the temporal variation in post-maturity growth rates in wild individuals (**Chapter 2**); 2) contrary to previous literature, sea turtles appear to have determinate growth after sexual maturity (**Chapter 3**); 3) biologging systems do not appear to have significant detrimental effects on reproduction, growth and annual survival of nesting females (**Chapter 4**); 4) PIT tags improve the accuracy of estimates of flipper tag loss, life-history traits and population parameters (**Chapter 5**); and lastly, 5) the contrasting recovery rates between the two species of sea turtles under consideration are likely to be due to bycatch-driven differences in annual survival of individuals of all life-stages rather than differences in reproductive output of nesting females alone (**Chapter 6**).

Post-maturity growth

Indeterminate growth is a widely-accepted strategy believed to be ubiquitous among long-lived species such as ectothermic vertebrates (Congdon et al. 2013, Lee & O'Connor 2013). Recently, however, the concept of indeterminate growth has been challenged and evidence has been accumulating suggesting that it might not be as common as previously thought (e.g. Erickson 2014, Werning & Nesbitt 2016, Wilkinson et al. 2016, Company & Pereda-Suberbiola 2017, Frydlova et al. 2017). In **Chapter 2**, I highlight that sea turtles are among these ectothermic vertebrates believed to be indeterminate growers despite the scarcity of studies investigating the temporal variation of post-maturity growth (e.g. Bjorndal et al. 2013, 2014). This forms the basis of **Chapter 3**, in which I found post-maturity growth to persist in both wild green and loggerhead

turtles, decreasing for approximately a decade before growth plateaued in green turtles. With this chapter, I provide the first analysis of post-maturity growth in wild rather than captive adult sea turtles. I suggest that this is evidence of determinate rather than indeterminate growth and propose that this growth strategy is a shared life-history trait of all cheloniid species.

It becomes apparent from **Chapter 3** that there is a need for new and more exact definitions of each growth strategy exclusively distinguishing determinate from indeterminate growth. Indeed, current definitions (Lincoln et al. 1982, Sebens 1987) and those more recently proposed (Karkach 2006) proved contradictory at this study site. Nevertheless, although variation in growth strategy within and among populations and species may occur, results from both captive (e.g. Bjorndal et al. 2013, 2014) and skeletochronological (e.g. Chaloupka & Zug 1997, Limpus & Chaloupka 1997, Zug et al. 2002, Avens et al. 2013, 2015, 2017) studies would support the finding from **Chapter 3**. Therefore, similar temporal analyses of post-maturity growth and osteohistological studies are needed to further explore the growth strategy of sea turtles and to refine existing growth curves and resulting ASM estimates.

Furthermore, this finding calls into question the thought that sea turtles have negligible senescence (Vaupel et al. 2004). Indeed, it has been suggested recently, despite scarce evidence, that species with indeterminate growth may be able to override actuarial and reproductive senescence (i.e. the decline in physiological functioning with age leading to reduced survival or reproductive output respectively; Williams 1957, Hamilton 1966) directly through enhanced fecundity at late ages or indirectly through increased survival, both as a result of continuous growth over time (Vaupel et al. 2004). However, because body size and reproductive output are correlated in sea turtles (Olsson & Shine 1996), with growth ceasing a few years after maturity, it would appear unlikely that this group of species would be able to escape senescence altogether, as shown in painted turtles (*Chrysemys picta*; Warner et al. 2016). Indeed, in **Chapter 3**, I calculate that the increase in adult body size for green turtles at this study site would only result in a slight increase in clutch size after a decade of growth. I therefore propose that post-maturity growth is unlikely to lead to large increases in fecundity across sea turtle species, as shown in the freshwater Blanding's turtles (*Emydoidea blandingii*; Congdon et al. 2001). This is also supported by captive studies which found that, even when fed ad libitum, rather than investing in post-

maturity growth, after sexual maturity energy resources were better invested into maximising lifetime reproductive output by increasing clutch frequency and decreasing length of breeding intervals (Bjorndal et al. 2013). Research into reproductive senescence is therefore necessary in sea turtles to further our understanding of ageing and longevity for the species' conservation.

Life-history parameter estimates

Estimating demographic parameters for population assessments is a research priority for sea turtles globally (Hamann et al. 2010, Rees et al. 2016), and, in particular, in the Mediterranean (Casale et al. 2018). Although sea turtle tracking has increased exponentially over the last 40 years, there is a paucity of studies investigating the effects of such devices on study animals (Jeffers & Godley 2016). Yet these studies are necessary both to inform whether data collected are unbiased and to determine whether derived estimates can be considered typical of the population at large. In **Chapter 4**, I establish that device attachment does not appear to have significant detrimental effects on reproduction, post-maturity growth rates (using the analysis from **Chapter 3**) and annual survival of nesting females. With this chapter, I provide the first long-term analysis of the effects of device attachment on adult sea turtles, indicating that life-history data collected from these females are not biased and can be used in future analyses. Nonetheless, it should be emphasised that, while I found no evidence of an effect in this region, it is essential that other studies do not simply use these findings to justify device attachment, but rather also quantify effects on their study animals. Indeed, it could not be excluded that numerous factors, such as small sample size, individual variation and climate change, prevented the detection of an effect at this study site in **Chapter 4**.

Central to capture-mark-recapture, which is extensively used in many branches of sea turtle research, is the assumption that all tags are retained and therefore that all individuals are correctly identified (Pradel 1996). However, in **Chapter 5**, I show that this assumption is violated in sea turtles by exploring flipper and PIT tag loss. I provide the first model of PIT tag loss in sea turtles, as well as the first estimates of apparent annual survival for nesting populations in the Mediterranean. PIT tags allow for improved and longer female identification

and lead to more accurate estimates of flipper tag loss, life-history traits and population parameters. On the other hand, the rate at which flipper tags are being lost across green and loggerhead turtle studies is of concern for long-term individual-based population monitoring and has important implications for the interpretation of demographic data. Therefore, estimates that do not account for tag loss should be interpreted with caution and could bias IUCN Red List assessments. The presence of a second type of tag with far higher and longer retention rates than flipper tags, such as PIT tags, is essential to provide high-quality, accurate data. Long-term population monitoring programmes should aim to estimate tag loss using continuous functions and multiple identification markers and assess the impact of identification loss on estimates of life-history traits and population parameters in order to revise current population assessments with robust estimates.

Furthermore, the analysis of the population vital rates for loggerhead turtles at Alagadi Beach in **Chapter 6** highlights that estimates of remigration intervals and clutch frequencies calculated from tag returns are likely to be biased, despite the use of two types of tags to identify nesting females. Indeed, the significantly lower return rates and longer remigration intervals of single-clutch neophytes raised multiple questions regarding their true classification as first-time nesters, especially when considering the multi-country nesting of females from Alagadi Beach uncovered by satellite tracking (Snape et al. 2016, 2018). In addition, it also raises the question as to which nesting aggregation single-clutch females belong to, which has implications for the estimation of rookery-specific population sizes derived from potentially shared nesting females.

Population assessment

Informing the management of species of conservation concern, such as sea turtles, requires a thorough understanding of their life-history traits and variation. Estimating apparent annual survival and assessing the accuracy of estimates of life-history traits and population parameters in **Chapter 4 and 5** were the first steps towards a better understanding of population trends for both species. In **Chapter 6**, I find that green turtle nesting numbers across monitored core beaches in North Cyprus are increasing exponentially, which can probably

be attributed to the intensive protection of nests against depredation by feral dogs and foxes, coupled with the interruption of legal trade globally. On the other hand, these measures do not seem to have been sufficient for loggerhead turtles in the area. Indeed, nesting numbers remain low, having only slightly increased over the same time period, despite evidence of recruitment to the nesting population. While the increase in neophyte abundance is a sign of population growth, the low number of females which return to nest at Alagadi Beach following their migration back to their foraging areas is of concern for population stocks considering the time required for individuals to reach sexual maturity.

Using multiple matrix model projection scenarios in **Chapter 6**, I suggest that the contrasting recoveries between the two species are due to bycatch-driven higher juvenile and adult mortality rates for loggerhead turtles than for green turtles of these nesting aggregations. Although challenging, at-sea conservation will be key for the species, as differences in foraging and nesting behaviours between the two species are thought to make carnivorous loggerhead turtles more at risk of incidental capture than herbivorous green turtles (Broderick et al. 2006). The recovery of loggerhead turtles is likely to be compromised until this threat is addressed in a long-term sustainable manner in the region. In addition, because juveniles are the most abundant and important life-stage (Heppell 1998, Casale & Heppell 2016), I re-iterate the need to gain a better understanding of this life-stage in sea turtles, without which population modelling will continue to be based on numerous simplifications and assumptions.

Furthermore, from work in **Chapter 6**, it becomes evident that the current assessment method used by the IUCN Marine Turtle Specialist Group underestimates population trends for sea turtles. The primary aim of the IUCN method is to provide a coarse measure of population increase or decrease by comparing past and recent 3-5 yr time periods, in particular for nesting sites for which long-term time-series data are unavailable. For the two species at Alagadi Beach, however, where long-term time-series data are available, such an approach was found to largely underestimate the rate of increase in nest and female abundance compared to population models which can account for long-term variations. In addition, the IUCN assessment method is too sensitive to large inter-annual variation within the 5-yr periods which results in contradictory trends for loggerhead turtles at this index nesting site. Therefore, when available, long-

term time-time series data should be used in their entirety to reflect observed trends.

Conclusion

To conclude, this thesis emphasises the importance of long-term studies to refine life-history models and provides new and improved data for Mediterranean adult sea turtles, which were previously lacking in the region, yet are essential for population modelling. As well as contributing to scientific knowledge and identifying knowledge gaps, findings from this thesis will be used in future regional and global IUCN Red List assessments of these two threatened species.

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