

Long-term growth and survival dynamics of green turtles (*Chelonia mydas*) at an isolated tropical archipelago in Brazil

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Abstract For effective management of species of conservation concern, knowledge of life history parameters is essential. Here, we present the results of one of the longest ongoing capture-mark-recapture studies of juvenile green turtles (*Chelonia mydas*) worldwide. From 1988 to 2013, 1,279 individual turtles were tagged in Fernando de Noronha, Brazil (3°51'S, 32°25'W). The size distribution at first capture varied between 27 and 87 cm (mean $\pm$ SD 47.9 $\pm$ 11.3 cm) curved carapace length (CCL). Median residence time was 2.4 year (with long-term residence of up to 11.2 year), with individuals exhibiting some site fidelity within the Archipelago. Turtles at this site are slow growing (mean 2.6 $\pm$ 1.6 cm year⁻¹; range -0.9 to 7.9 cm year⁻¹; $n = 1,022$), with a non-monotonic expected growth rate function and a peak in growth rates occurring at 50–60 cm CCL. At these rates, turtles in Fernando de

Noronha would need to spend ca. 22 years to grow from 30 to 87 cm CCL and even longer to reach minimum adult breeding size. A Cormack–Jolly–Seber model was used to estimate the apparent survival of the residents and recapture probabilities (2001–2012). The estimated annual abundance ranged from 420 to 1,148 individuals. Confidence around abundance estimates was low, and there was no significant trend over the period, despite steep recent increases at the major source rookery. Slow growth and stable stocking numbers may be suggestive of density-dependent regulation having taken place following initial population recovery that occurred prior to the current study.

Introduction

Management for the effective recovery of species of conservation concern depends on the knowledge of several demographic parameters, including recruitment, growth rates, survival probabilities and abundance (Lotze et al. 2011; Mills 2013). Long-term studies are key to informing these parameters and essential in assessing the status of populations and evaluating the effectiveness of conservation efforts (Brook et al. 2000; Magurran et al. 2010). In marine habitats, air-breathing vertebrates such as marine mammals, marine reptiles and fishes, such as tunas and sharks, are of particular concern, as they are typically slow growing, have late maturation and low reproductive capacity (Clapham et al. 1999; Musick et al. 2000; Bolten 2003; Fromentin and Powers 2005; Scott et al. 2012). This leads, consequently, to slow recovery rates and low resilience to disturbance such as direct (Jackson et al. 2001; Baum et al. 2003) or incidental take (Lewison et al. 2004; Zydelski et al. 2008; Soykan et al. 2008), highlighting the need for robust

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population models accounting for life stages to assess population sizes and trends in abundance.

Marine turtles are long-lived and slow-growing vertebrates that, although showing some diversity in developmental patterns, are believed to reach the open ocean as hatchlings after emerging from their nests, spending their first few years in an oceanic phase (Bolten 2003). The oceanic phase is thought to last ca. 3–5 years in the Greater Caribbean (Bjorndal et al. 2005; Reich et al. 2007; Goshe et al. 2010). As juveniles (ca. 20–35 cm carapace length), they recruit to one or a series of neritic foraging areas (Bolten 2003; Bjorndal et al. 2005) used as developmental habitats. They can remain within these areas for several years (Bjorndal et al. 2005) until reaching maturity, when they start periodic migrations between foraging areas, breeding grounds and nesting beaches (Bowen and Karl 2007; Arthur et al. 2008).

The green turtle (*Chelonia mydas*) has a pantropical distribution with regional population substructuring (Bowen et al. 1992). With a long history of overexploitation (Chaloupka et al. 2008), many green turtle populations are considered relictual (McClenachan et al. 2006). However, as a result of conservation efforts, the recovery of a number of populations has been observed (Broderick et al. 2006; Chaloupka et al. 2008). In this context, studies that provide information on demographic parameters for the different regional green turtle populations are highly valuable, as they contribute to our understanding of population dynamics and improve our capacity for managing sea turtle populations, e.g. in the light of ongoing direct (Humber et al. 2014) or incidental take (Alfaro-Shigueto et al. 2011).

In such a long-lived marine species, with life history traits such as wide-ranging dispersal and slow growth, unravelling population dynamics is complex and research has focused mainly on breeding adults on nesting beaches (Bjorndal 1999; Bjorndal et al. 2005). Although there has been relatively little research about juveniles, parameters such as growth rates have been estimated for green turtle populations in the western Atlantic (Mendonça 1981; Bjorndal and Bolten 1988; Boulon and Frazer 1990; Collazo et al. 1992; Bjorndal et al. 2000; Kubis et al. 2009; Torezani et al. 2010; Patrício et al. 2014), and less commonly, survival probabilities have been estimated in the Caribbean (Bjorndal et al. 2003; Patrício et al. 2011), Australia (Chaloupka and Limpus 2005) and Eastern Pacific (Seminoff et al. 2003; Eguchi et al. 2010). However, it is believed that variability among regions does exist, making comparison among sites valuable in understanding the structure of the different aggregations (Balazs and Chaloupka 2004; Kubis et al. 2009; Bjorndal et al. 2013a, b).

The Fernando de Noronha Archipelago, off the northeastern coast of Brazil, is a foraging ground for green

and also for hawksbill (*Eretmochelys imbricata*) turtles (Sanches and Bellini 1999). Genetic studies have shown that green turtles foraging at Fernando de Noronha are presumed to originate from Ascension Island, with additional probable contributions from the Greater Caribbean and West Africa (Bjorndal et al. 2006). The Archipelago also has a small green turtle nesting population (Bellini and Sanches 1996). A long-term capture-mark-recapture (CMR) study run by ProjetoTAMAR-ICMBio, the Brazilian sea turtle conservation programme, has existed since 1987 in Fernando de Noronha (Bellini and Sanches 1996). Using these long-term CMR data, we tested: (1) whether wide-scale recovery of this species in the Atlantic was reflected within the study population; (2) whether changes in population density affected the growth rates of individuals; and (3) whether CMR data could be used to construct a growth function for individuals and estimate age at maturity.

Methods

Study area

Fernando de Noronha is an offshore volcanic archipelago located 345 km off the northeastern Brazilian coast (Fig. 1a). It consists of one main island and approximately 18 small islets, encompassing a total land area of 26 km² (Garla et al. 2006). Part of the site is included in a National Marine Park (created by federal decree in 1988), and in addition, a sector on the main island where around 4,000 people live is an environmentally protected area (created in 1986). In 2001, the archipelago was declared a UNESCO (United Nations Educational, Scientific and Cultural Organisation) World Heritage Site, due to its importance for tropical seabirds, cetaceans, sharks, fish and marine turtles (UNESCO 2014). For comparisons among sites within the archipelago, the study area was divided into three sites, namely Mar de Dentro, Ilhas Secundárias and Sueste (Fig. 1b).

Capture of turtles

Green turtles were hand-captured by snorkelling or scuba diving at depths between 0.5 and 30 m. Snorkelling was used at most sites around the main island, with each bout taking ca. 1 h. Surveys consisted of groups of one to five people either departing from a beach or using a small boat as a platform. Scuba dives had a maximum duration of 50 min, as a function of dive depth, with an average time of 45 min. The surveyed sites were generally offshore and around the small adjacent islands that surround the archipelago, by arrangement with commercial diving operators. Scuba divers operated in groups of two to five people.

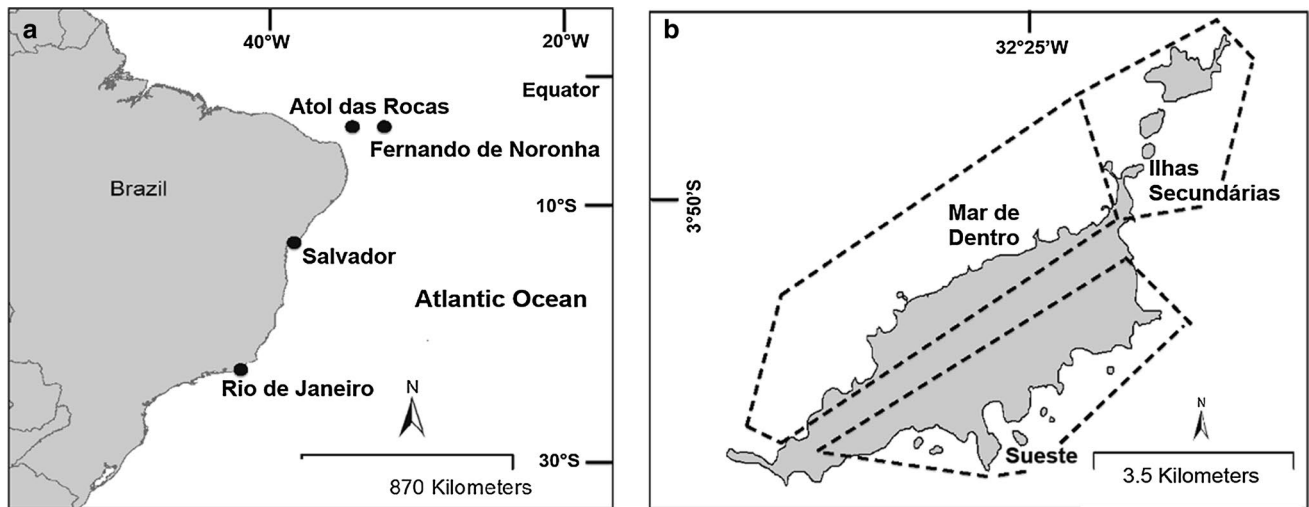


Fig. 1 Map of Brazil showing the location of Fernando de Noronha Archipelago (a) and map of the island showing the three main survey locations (Mar de Dentro, Ilhas Secundárias and Sueste) (b) (Source: programme Maptool at www.seaturtle.org)

Temporal patterns of the CMR programme

The sampling of turtles has not been homogeneous over the years, either spatially or temporally. Between 1988 and 1991, the survey locations were well distributed around the archipelago, but effort was generally lower than in subsequent years. From 1992, surveys were performed mainly at Baía do Sueste, although other places in the archipelago were also sampled. Between 1992 and 2011, there were surveys in at least 10 months of each year, except in 2006 and 2007, when surveys were performed for 7 and 6 months, respectively, while between 1988 and 1991 surveys covered from 4 to 9 months of each year. Between 2009 and 2012, surveys were performed 12 months per year.

Tagging and measurement

Turtles were tagged on both front flippers (Balazs 1999; Marcovaldi and Marcovaldi 1999) using monel tags until 1994 and inconel tags since 1995 (National Band and Tag Co., USA, style 681). Curved carapace length was measured with a flexible plastic measuring tape (precision 0.1 cm) following the methodology described in Marcovaldi and Marcovaldi (1999) and performed by Projeto TAMAR technical team since 1988 as part of the research programme in the area. Researchers were trained to check for tag scars, and individuals with scars signifying that both tags have been lost were found on 8 of 1,279 (0.6 %) untagged individuals. Records of tag replacement or of only a single tag being attached accounted for 9.4 % of all recaptures. Thus, we consider a conservative estimate of 10 % tag loss estimation in this study.

Data analysis

Size distribution

The size distribution of turtles was based on size at first capture ($n = 1,279$), which means that each turtle contributed to the distribution only once. Captured turtles were mostly immature, lacking external sexual dimorphism, and sex was not determined. A few adult-sized turtles (i.e. CCL > 94 cm; $n = 12$) were caught during the study period, but these were not considered in the analyses. Size distribution of the turtles was tested for possible differences among sites using a Kruskal–Wallis test. The variation of the CCL distribution of the turtles across years was analysed using a loess regression (with local quadratic fitting), where each individual contributed only once per year ($n = 2,455$). The 95 % pointwise confidence intervals for the regression curve were also computed using the loess method (Cleveland et al. 1993). All graphs were produced, and data analyses carried out using the software R 2.8.1 (R Core Team 2012). The significance level of the statistical tests was $\alpha = 0.05$. All data were checked for normality using the Shapiro–Wilk test, and when normality was not met, nonparametric statistical analyses were undertaken.

Median time of residency and distance between captures

The estimated time of residency within the area was calculated as the time interval in years between a turtle's first and last capture. This is a conservative estimate, as a turtle may have been present in our study site both before its first capture and after the last time it was caught, and not

detected. The minimum swimming distance between the most widely dispersed locations, resulting in maximal displacement, was estimated using Google Earth (Google Inc. 2009).

Growth rates

Growth rates (in centimetres per year; cm year^{-1}) were calculated for each turtle as: mean annual growth rate = $(\Delta\text{CCL}/\Delta t) \times 365$, where ΔCCL was the CCL variation between captures and Δt was the number of days elapsed since initial capture. Only recapture intervals greater than 10 months were included in the analysis (van Dam 1999; Rees et al. 2012).

GAM and age at maturity

We modelled somatic growth using a generalised additive model (GAM; Hastie and Tibshirani 1990). The GAMs were fitted using the package 'mgcv' (Wood 2001) in the software R 2.8.1 (R Core Team 2012). The response variable (absolute growth rate) was determined as a function of four potential growth covariates. Three covariates were continuous (median size, median sampling year and recapture interval) and one was categorical (site). The median size is the median CCL between the capture and subsequent recapture, the latter being the next chronological recapture of the individual, after a minimum of 10 months, which could be recaptured on more than one occasion.

This midpoint is believed to be more representative of the turtles' size during the time interval for which the growth rate was calculated than using the CCL at the first or last capture (Limpus and Chaloupka 1997; Casale et al. 2009). The recapture interval was included in the analysis to account for any bias from variable durations of these intervals. The median sampling year was assigned as the midpoint between the year of capture and subsequent recapture. The expected size-specific growth rate function was extracted from the GAM model using cubic smooth splines and numerically integrated to estimate the time in years that a turtle would spend in Fernando de Noronha from recruitment—ca. 30 cm CCL—until reaching a maximum size of 87 cm CCL, which was the maximum size of a turtle in this population on its first capture. The expected size-specific growth rate function resulting from the loess regression was extracted and numerically integrated using the difference equation: $y(\text{CCL}_i) = y(\text{CCL}_{i-1}) + (\text{CCL}_i - \text{CCL}_{i-1})/r(\text{CCL}_i)$, where y stands for years at large since recruitment, CCL_i is the curve carapace length for which the years at large are being estimated, CCL_{i-1} is the preceding CCL value and r is the growth rate from the loess regression.

Sampling design

The sampling design in this study was mixed longitudinal sampling, with 50 % of individual green turtles being recaptured one or more times. As age is unknown, as in most sea turtle studies, this sampling design confounds cohort and year effects (Limpus and Chaloupka 1997; Bjørndal et al. 2000).

Survival

Individual capture history profiles were gathered over the 12-year sampling period from 2001 to 2012. This time interval was more representative of an equally distributed capture effort throughout the period. The Cormack–Jolly–Seber (CJS) model was used following Lebreton et al. (1992) and implemented in Program MARK v6.1 (White and Burnham 1999). Goodness of fit (GoF) of the general time-dependent model was evaluated using the programme RELEASE. GoF tests were used to determine whether the model fitted the data and to evaluate the CJS assumptions (Lebreton et al. 1992). In particular, the TEST 2.C was used to verify the assumption of equal catchability and TEST 3.SR to evaluate the effect of handling or of presumed transients on survival probabilities. Transients are considered individuals that are not residents in the sampling area but rather are in transit, so they are captured once and never seen again, having zero probability of recapture although they are still alive (Cormack 1993; Pradel et al. 1997). This represents an operational definition of transience, since it was not based on any assessment of local dispersion to identify true individual transients (Chaloupka and Limpus 2001) and thus constitute an apparent transience.

The global CJS model $\{\Phi(t)p(t)\}$ fitted the data poorly (TEST 2 + TEST 3: $X^2 = 159.775$, $df = 49$; $p < 0.001$). Failure of GoF TESTS 2 and 3 led us to use a time-since-marking model structure to account for transient behaviour (Chaloupka and Limpus 2002), and a recently developed random effects CJS model approach to account for capture heterogeneity in survival and/or recapture probabilities (Gimenez and Choquet 2010). There are no established procedures for assessing a random effects CJS model GoF (Gimenez and Choquet 2010). We used the median c-hat estimate (1.2) to adjust the model selection metric [Akaike's information criterion (AIC)] used for the random effects CJS model fits. The best-fit model chosen was the one with the lowest AIC value, which was used to estimate apparent survival and recapture probabilities. Since the recovery of dead turtles was scarce (1.3 %; $n = 16$), we proceeded with the analysis using a live-captures-only model. This model generates estimates of apparent survival probability (Φ), which is the probability that a turtle has neither died nor emigrated from the study area, and the

recapture probability (p), which is the probability that a turtle that is available for capture in the study population is caught (Bjorndal et al. 2003).

Abundance

The calculated recapture probabilities derived from the best-fit CJS model were then applied in a Horwitz–Thompson (HT) type estimator: $N_i = (n_i/\rho_i)$ (Seber 1982) to estimate annual abundance, where n_i is the number of captured turtles in the i th year, N_i is the number of turtles in the area in the i th year and ρ_i is the recapture probability in the i th year. The approximate 95 % confidence intervals were calculated as $N_i \pm 1.96 \times \text{SE}(N_i)$, where $\text{SE}(N_i) = \text{conditional standard error}$ ($\text{SE}(N_i) = [(n_i/\rho_i)^2 \times (\text{var}(\rho_i)/(\rho_i)^2)]^{0.5}$), where $\text{var}(\rho_i)$ is the estimated recapture probability variance in i th year (Loery et al. 1997; Chaloupka and Limpus 2001). The underlying trend in the population abundance series was estimated using a generalised least squares (GLS) model with restricted maximum likelihood estimation (REML) (Chaloupka and Limpus 2001). The GLS models were fitted using the package ‘nmls’ (Pinheiro et al. 2006) in the software R 2.8.1 (R Core Team 2012). The model was variance weighted, with log link and first-order moving average error to account for temporal correlation, since there was a substantial overlap of individual turtles in successive years (Bjorndal et al. 2005).

Results

Captured turtles and size distribution

From 1988 through to February of 2013, 1,279 individual green turtles were captured in a total of 2,979 capture events. Of these, 640 turtles (50.0 %) were recaptured from between one ($n = 276$) to seventeen ($n = 2$) times. Curved carapace length at first capture ranged from 27 to 87 cm (mean $\pm$ SD 47.9 ± 11.4 cm, median 45.5 cm, IQ range 39–55 cm, $n = 1,279$; Fig. 2). Only one turtle was found in Noronha bearing tags applied at another Projeto TAMAR station in Brazil. It was caught 11 years after being tagged 2.8 km away, in Ubatuba, southeast Brazil (23°40'S, 45°03'W). Its CCL was 39 cm at first capture and 69 cm at recapture.

Differences among sites

There was a significant difference in the size of the turtles on their first capture across the three different sites within our study area ($K = 103.39$, $df = 2$, $p < 0.001$). A post hoc Kruskal–Wallis multiple comparisons test showed that median size at all sites was significantly different from each other. Turtles at Sueste were larger (52.5 cm) than

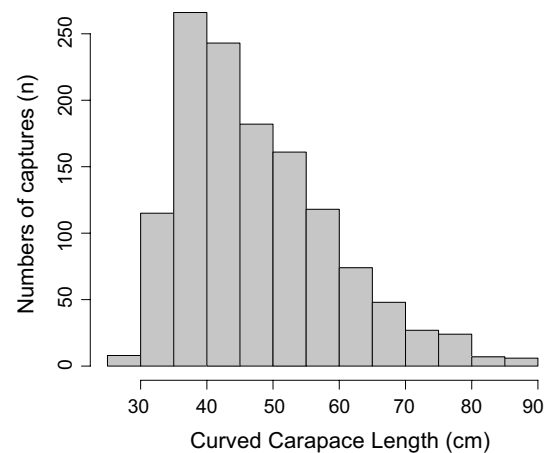


Fig. 2 Green turtles *Chelonia mydas* curved carapace length at first capture in Fernando de Noronha ($n = 1,279$)

those at Ilhas Secundárias (46.5 cm) and Mar de Dentro (43.4 cm). The size of captured turtles was, however, relatively constant across years, when considering the overall mean (Supplemental Fig. 1).

Median time of residency and distance between captures

The interval between recaptures ranged from one day to 11.2 years ($n = 637$; Supplemental Fig. 2a) with a median of 2.4 years (IQ range 1.2–4.2 year). The mean minimum swimming distance between captures was 1.0 ± 3.0 km (range 0–14.3 km, $n = 637$; Supplemental Fig. 2b), with 84.1 % of the turtles recaptured <500 m from where they were originally captured.

Growth rates

Recapture intervals varied between 10 months and 10.6 year, with a median of 1.2 year. We recorded 1,022 growth increments from 542 individual turtles. Overall, the mean growth rate for juvenile green turtles in Fernando de Noronha was 2.6 ± 1.6 cm year⁻¹ (range -0.9 to -7.9 cm year⁻¹). The growth rate function was, however, non-monotonic, with a peak in growth rates for the 50–60 cm CCL size class (Supplemental Fig. 3 and Table 1). The GAM model of growth rates explained only 27.6 % of the variance, suggesting that there is significant variability in the growth data that is not attributable to the modelled covariates (median size, median sampling year, recapture interval and site). The model indicated that size, site and median sampling year had significant effects on somatic growth, while the recapture interval had no significant effect on growth rates (Fig. 3). The GAM results for each site are shown in Supplemental Fig. 4. From the numerical integration of the size-specific growth rate function, we

Fig. 3 Graphical summary of GAM model fits for growth rates ($n = 1,022$). Covariates are shown on the x-axis: **a** median curved carapace length, **b** recapture interval in years, **c** median sampling year and **d** site. The response variable (growth rate in cm year^{-1}) is shown on the y-axis in each panel as a centred smoothed function scale to ensure a valid pointwise 95 % confidence interval (ILH Ilhas Secundárias, MDD Mar de Dentro, SWT Sueste)

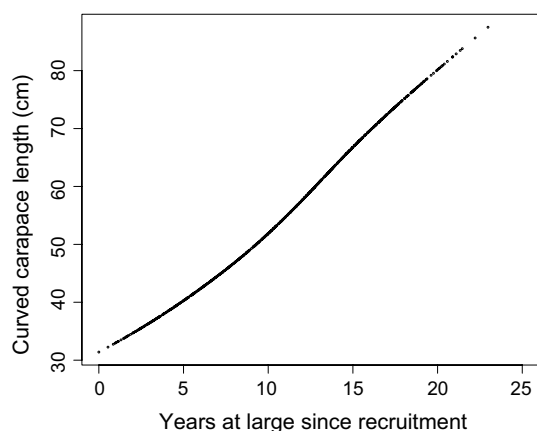
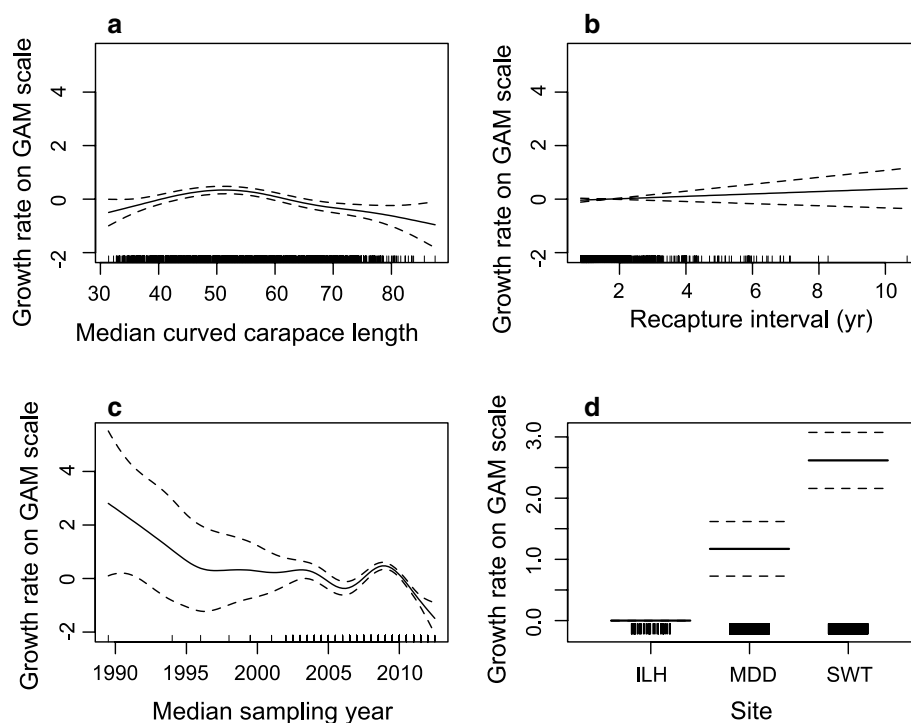


Fig. 4 Numerical integration of the expected size-specific growth function for immature green turtles at Fernando de Noronha, shown in Fig. 5, to derive the expected size-at-age function, where age is in years at large since recruitment, as the age of recruits is unknown. CCL curved carapace length

obtained empirical estimates of the expected time in years necessary for a typical green turtle in Fernando de Noronha to grow from ca. 30 cm to 87 cm CCL, which was ca. 22 years (Fig. 4).

Survival

The dataset comprised 1,194 individual CMR profiles. Extensions to the CJS model, as the Burnham (1993) and

the Barker (1997) models, integrate data from tag recoveries (i.e. from animals found dead) or from both tag returns and re-sight occasions, allowing estimations of true survival and emigration rates. However, dead recoveries of marked individuals are often too sparse to include in the models (Bjorndal et al. 2003). In our study site, we recovered only 1.3 % of the tagged individuals ($n = 16$), and when a Burnham model was run, it returned biased estimates of survival (~ 1.0). We therefore proceeded with the analysis using a live-captures-only model. This model generates estimates of apparent survival probability (Φ), which is the probability that a turtle has neither died nor emigrated from the study area, and the recapture probability (p), which is the probability that a turtle that is available for capture in the study population is caught (Bjorndal et al. 2003).

The best-fit model according to the AIC value comprised (1) time-dependent 2-age-class-specific (time-since-marking) survival and (2) time-dependent 2-age-class-specific (time-since-marking) recapture probabilities accounting for individual capture heterogeneity (Table 1). The estimated annual apparent survival probability derived from the best-fit model (Table 1) for the previously marked or “resident” turtles was 0.85 (95 % CI 0.59–1). The mean annual recapture probability was 0.29 (95 % CI 0.09–0.6).

Abundance estimates and trends

The recapture probabilities were used to estimate the annual green turtle population in the study area over the

Table 1 Summary of the Cormack–Jolly–Seber models built in Mark v6.1 for the Fernando de Noronha capture-mark-recapture data set from 2001 to 2012

Model	QAICc	Delta QAICc	QAICc weight	Model likelihood	Number of parameters	Deviance
1. {Phi (tsm) p (tsm)} random effects}	3,864.42	0	1	1	35	476.36
2. {Phi(tsm) p (tsm)}	3,924.01	59.58	0	0	38	529.73
3. {Phi(t) p (t)}	3,962.89	98.46	0	0	22	601.57
4. {Phi(.) p (t)}	3,981.17	116.75	0	0	12	640.19
5. {Phi(tsm) p (t)}	4,056.04	191.62	0	0	20	698.81
6. {Phi(t) p (.)}	4,080.11	215.69	0	0	11	741.16
7. {Phi(.) p (.)}	4,156.64	292.21	0	0	2	835.80

tsm time-since-marking (2 age-classes), *t* time, *Phi* survival, *p* recapture)

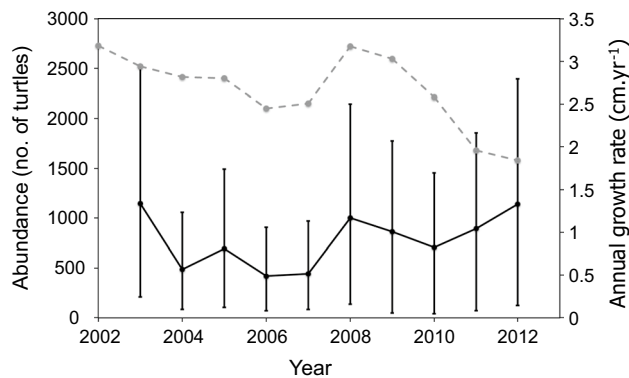


Fig. 5 Annual estimates of abundance (N_t) and expected size-specific growth rate function of juvenile green turtles in Fernando de Noronha, Brazil. Black dots represent mean annual abundance estimates derived from the Horvitz–Thompson estimator presented with the 95 % confidence intervals. Grey dots represent the expected size-specific growth rate function according to median sampling year derived from the GAM model

sampling period. The Horvitz–Thompson estimates of abundance (N_t) ranged from 420 to 1,148 individuals per year (Supplemental Table 2). The GLS model detected no significant trend in the abundance throughout the 12-year period although confidence around estimates was quite large. There was no correlation between the estimated mean annual abundance and the time-specific growth rates (Spearman's correlation $\rho = 0.187$, $p > 0.05$). The mean annual abundance, along with the 95 % confidence limits, and respective time-specific growth rate function derived from the GAM model are plotted together in Fig. 5.

Discussion

This study provides valuable information regarding the biology of green turtles in the southwest Atlantic and highlights the importance of maintaining long-term monitoring studies to better understand the dynamics of populations in

different foraging areas. Major insights obtained are five-fold: (1) size at recruitment, (2) patterns of residency, (3) growth rates and years at large spent in the study area, (4) temporal trends in abundance and (5) survival. The linkages between the latter three aspects are of particular conservation concern and broadly discussed.

Green turtles in Fernando de Noronha recruit to the neritic habitat at a similar size to that reported for other populations in the Caribbean (Bjorndal 1997; Bjorndal et al. 2005; Patrício et al. 2011). The continued capture of small and unmarked juveniles, coupled with the constant size distribution of the captured turtles throughout the years, indicates that new turtles are constantly being recruited to the area. The median time interval between the first and last captures of ca. 2.4 years indicates that Fernando de Noronha is a long-term developmental area for some green turtles, with some individuals remaining for up to 11.2 year. The turtles exhibited site fidelity to a certain extent, with 84 % of those recaptured, re-encountered <500 m from initial capture.

Research has shown a tendency towards a slowing of growth as maturity approaches (Green 1993), when resource allocation shifts from somatic investment to reproductive outputs (Bjorndal et al. 2013a, b). The growth rate function varies among species and populations, and for green turtles in the Caribbean, the growth rates decrease with increasing size (Bjorndal and Bolten 1988; Boulon and Frazer 1990; Collazo et al. 1992; Patrício et al. 2014), as also described for other marine turtle species such as Western Atlantic loggerheads (Scott et al. 2012; Bjorndal et al. 2013a, b). The non-monotonic pattern exhibited in Fernando de Noronha, with a peak in growth rates (around 50–60 cm CCL) followed by a decrease, has mainly been reported for conspecific green turtle populations in the Pacific (Limpus and Chaloupka 1997; Seminoff et al. 2002; Balazs and Chaloupka 2004; Chaloupka et al. 2004). In the Atlantic, Kubis et al. (2009) described this pattern for the first time on a green turtle population in Florida. Green turtles in Fernando de Noronha also showed slower

growth than most other Atlantic populations in the Caribbean (Boulon and Frazer 1990; Bjørndal et al. 2000; Patrício et al. 2014), being closer to rates described in the North Atlantic (Bresette and Gorham 2001; Kubis et al. 2009; Goshe et al. 2010). It is likely that variability in growth rates will be driven at least in part by the quality and abundance of the diet. Juvenile green turtles at most aggregations on the northeast and southeast Brazilian coast have a diet dominated by macroalgae (Ferreira 1968; Mendonça 2009; Guebert-Bartholo et al. 2011), while in the Caribbean they are known for feeding on pastures of the seagrass *Thalassia testudinum* (Mortimer 1982; Bjørndal 1997).

The spatial variability observed within our study site indicates that on a small scale, growth rates are likely to vary depending on where the turtles are and how much fidelity to a particular site they show. The within-site variability in foraging-site growth rates is likely to be a consequence of habitat quality and resource availability (Balazs and Chaloupka 2004; Kubis et al. 2009). The higher growth rates observed at Sueste could also be related to the ecological characteristics of this bay. Shallow and sheltered waters, protected from wave action, could provide a warmer microhabitat selected by turtles (Schofield et al. 2009; Fossette et al. 2012). Additionally, sheltered waters are a lower energy environment that could be energetically beneficial for turtles, since they do not have to battle currents or dive deeply for access to benthic resources, such as what happens in the Mar de Fora, an open ocean site. This could possibly explain the significant size difference among subregions. It is important to highlight that the covariates used in this study may not be the only factors influencing growth rates, and other aspects, which were not considered due to lack of data, such as sex and rookery of origin, might also play an important role in somatic growth.

Slow growth rates could be associated with high mean annual abundance, suggesting density-dependent effects may be occurring. However, the abundance confidence intervals were relatively large and no trends were detected during the study period. The recovery of several green turtle nesting populations, including the major source rookery for this foraging aggregation (Ascension Island), has been reported as a result of conservation efforts from the 1940s on Ascension and since the 1980s in Brazil (Broderrick et al. 2006; Chaloupka et al. 2008; Weber et al. in press). This suggests recovery on the feeding grounds would have happened many years before. Significant year effects on growth rates, as observed in this study, have also been related to density-dependence effects (Bjørndal et al. 2000). Observed growth rates have generally been declining since we started monitoring in the early 1990s (Supplemental Fig. 5). Data for abundance, however, are more temporally constrained, and further studies to investigate the carrying capacity, measures of productivity, algae and

seagrass abundance and growth in the study area would be valuable to explore this possibility.

Given that it might take ca. 3–5 years until green turtles recruit to neritic habitats (Bjørndal et al. 2005; Reich et al. 2007; Goshe et al. 2010), it would take approximately 25 years for a green turtle in Fernando de Noronha to reach a size of 87 cm CCL, and even longer to reach sexual maturity (considering 97 cm CCL, the minimum size for a nesting female on Ascension Island (Weber et al. in press)). It is reasonable, however, that it would take at least three decades to reach maturity if they remain in the Archipelago or if growth rates are similar at other Brazilian foraging areas. The delayed maturity on green turtles has been previously described, and it has been suggested that they may take 25 years or more to reach sexual maturity (Bjørndal et al. 2000; Goshe et al. 2010). However, recent studies have suggested shorter time intervals for Caribbean green turtles, such as 15–19 years described by Bell et al. (2005), for turtles with live tags from the Cayman Turtle Farm, and 14–22 years estimated for turtles resident in Culebra Island, Puerto Rico (Patrício et al. 2014). In the Pacific, age at maturity was estimated as being as long as 35–40 years in Hawaii (Balazs and Chaloupka 2004), 50 years in the southern Great Barrier Reef (Chaloupka et al. 2004) and up to 92 years in the Galápagos Islands (Green 1993).

Estimated apparent survival for juveniles in Fernando de Noronha was in the upper range of those reported for green turtles on studies conducted in the Caribbean (Bjørndal et al. 2003; Patrício et al. 2011) and in the Pacific (Chaloupka and Limpus 2005; Table 2). Survival probabilities can vary among populations and life stages in response to different environmental conditions and causes of mortality (Bjørndal et al. 2003). Fernando de Noronha is an environmentally protected area, with fishing restrictions and no direct take of sea turtles. The relatively low level of anthropogenic threats is in accordance with the high apparent survival. During the study period, only 24 green turtles were found with evidence of fishery interactions or boat collisions, only six of them were dead. The incorporation of data from dead recoveries would improve the CJS models capacity to allow the estimation of the true survival (S) and emigration rates. However, dead recoveries were too scarce to be included in this study.

The relatively high proportion of transients, which must be considered when analysing mark-and-recapture data (Pradel et al. 1997; Sasso et al. 2006), was 50 % in our study, indicating that Fernando de Noronha is possibly an interim foraging area for turtles that are *en route* to other feeding grounds. Stopover areas, where turtles recruit to after a pelagic phase, spending some time recovering from the previous oceanic phase and storing resources before travelling to other developmental habitats, have also been seen in the Eastern Pacific (Amorochio et al. 2012). In

Table 2 Estimates of apparent survival (ϕ) and recapture probabilities (ρ) for different juvenile and sub adult green turtle (*Chelonia mydas*) aggregations worldwide, expressed as a point estimate or mean (95 % CI), unless noted

Life stage	Carapace length	Location	ϕ	ρ	Method	References
Juveniles	(SCL 25–84)	Union Creek, Bahamas	(0.510–0.814)	0.549 (0.262–0.884)	B	Bjorndal et al. (2003)
	(SCL 22–64)	Conception Creek, Bahamas	0.68 (0.631–0.725)	0.590 (0.328–0.940)	CJS	Bjorndal et al. (2003)
	(CCL 24–65)	Culebra, Puerto Rico	0.832 (0.787–0.869)	0.359 (0.310–0.410)	CJS	Patricio et al. (2011)
	(CCL 40–65)	sGBR, Australia	0.880 (0.835–0.927)	0.276 (0.078–0.634)	CJS	Chaloupka and Limpus (2005)
Juveniles and subadults	(CCL 27–87)	Fernando de Noronha, Brazil	0.85 (0.59–1.00)	0.29 (0.09–0.6)	CJS	Current study
Subadults	(CCL 65–90)	Culebra, Puerto Rico	0.529 (0.385–0.668)	0.359 (0.310–0.410)	CJS	Patricio et al. (2011)
	(CCL 65–90)	sGBR, Australia	0.847 (0.790–0.908)	0.169 (0.049–0.449)	CJS	Chaloupka and Limpus (2005)

CCL curved carapace length, *SCL* straight carapace length, *sGBR* southern Great Barrier Reef, *CJS* Cormack–Jolly–Seber model, *B* Burnham model

Fernando de Noronha, apart from one individual that was recaptured at Atol das Rocas, another important feeding ground located nearby (and after that recaptured in Fernando de Noronha again), the destination of those transients is currently not known, however, is likely to be in neritic waters of Brazil, where large numbers of adults are known to reside (Hays et al. 2002). Considering other Brazilian feeding grounds, in northeast Brazil, juvenile green turtles are believed to exhibit different behaviour patterns, from residency with a high level of site fidelity, to extended home ranges (Godley et al. 2003). In Ubatuba, however, it is suggested that turtles would have a low residency time and a high number of individuals are never seen again after the initial tagging (Gallo et al. 2006). A similar pattern of low residency time was also found on an aggregation of juvenile green turtles inside the effluent discharge channel of a steel plant located in the coast of Espírito Santo State, eastern Brazil (Torezani et al. 2010). The ecological attributes that would make Fernando de Noronha a feeding ground with high incidence of transients are unknown, but could be related to its location, as it is an off shore island that could be reached by individuals through the Equatorial Current from Ascension Island or Africa. Also, the relatively slow growth rates observed could indicate a sub-optimal habitat, where some of the turtles would not settle for long periods.

The importance of monitoring juvenile life stages has been recognised (Bjorndal and Bolten 2000; Bjorndal et al. 2005) and studies such the one presented here help to fill a key knowledge gap (Hamann et al. 2010). By monitoring juveniles, changes in population abundance and trends can be detected earlier, leading to more effective conservation measures (Bjorndal et al. 2005). The temporal and spatial variability in growth rates demonstrates the complexity of sea turtle population dynamics. Supplementary

investigation of the ecological conditions of this habitat is needed to understand the observed patterns. More research into the movements of turtles from this aggregation and genetic studies developed with larger sample sizes would help to clarify the connectivity among South Atlantic feeding grounds and between this aggregation and the major green turtle rookeries.

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