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Recovery of the South Atlantic's largest green turtle nesting population

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Abstract Although many species of marine mega-vertebrates are threatened as a result of human activity, some populations are showing promising signs of recovery following decades of protection. In this study, we report on the status of the South Atlantic's largest green turtle (*Chelonia mydas*) nesting aggregation at Ascension Island, 70 years after legal protection and the cessation of commercial turtle harvesting that decimated the population. Using a monitoring dataset spanning 36 years, we modelled long-term trends in nesting activity at both a rookery level and across individual nesting beaches and beach clusters. Since monitoring began in 1977, the average number of green turtle clutches deposited annually at Ascension Island has increased sixfold, from approximately 3,700 to 23,700; a trend that has been accompanied by a significant decrease in the average size of nesting females. Interestingly, however, rates of increase in nesting activity have varied dramatically among nesting beaches, ranging from 0.4 to 6 % growth per annum. More than 97 % of this variation could be explained by distance from the main human settlement of Georgetown—the historic centre of turtle harvesting—with beaches closer to Georgetown

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experiencing the most rapid growth. More rapid population growth close to human centres seems counterintuitive, but may reflect the more intensive depletion of these accessible, local stocks during the harvesting era. Overall, the Ascension Island green turtle population appears to be recovering strongly, mirroring positive trends for this species across many parts of its geographic range. While not a cause for complacency, these trends are encouraging and demonstrate the capacity of marine megafauna to rebound when anthropogenic pressures are alleviated through conservation action.

Keywords Marine turtle · Population trend · Population size · Demographic unit · Conservation status · Female size

Introduction

Marine mega-vertebrates, including elasmobranchs, sea turtles and cetaceans, have long histories of human exploitation that have driven global declines in numerous species, and continue to threaten the survival of many (Jackson et al. 2001). Conservation efforts for such species are often complicated by long lifespans and migratory lifecycles that carry them across jurisdictional boundaries and international waters. Nevertheless, some once-depleted stocks are currently rebounding as a result of effective protection and management, raising hopes that further extinctions and population collapses can be averted (e.g. Stevick et al. 2003; Chaloupka et al. 2008).

Since prehistory, marine turtles have been subject to multiple anthropogenic pressures that have seen global populations reduced to a fraction of their former sizes (McClenachan et al. 2006). Exploitation for shells, meat and eggs, along with more recent threats from habitat degradation and commercial fisheries bycatch have all contributed to these losses, resulting in the extirpation of some populations (McClenachan et al. 2006; Kittinger et al. 2013) and the continuing decline of others (Spotila et al. 2000). Fortunately, however, marine turtles have also proven to be responsive to relatively simple but sustained conservation measures, such as the protection of females and eggs at nesting beaches and changes in fishing practices (Troëng and Rankin 2005; Dutton et al. 2005; Heppell et al. 2005). As a result, many depleted populations are now recovering worldwide (Troëng and Rankin 2005; Dutton et al. 2005; Heppell et al. 2005; Chaloupka et al. 2008; Stewart et al. 2011; Mortimer et al. 2011), with interesting implications for the ecosystems they inhabit (Lal et al. 2010; Kelkar et al. 2013). This wide variation in population trajectories has led many to question the value of global status assessments, such as the *IUCN Red List*, for marine turtles and to advocate a greater emphasis on local and regional assessments of trends (Seminoff and Shanker 2008; Godfrey and Godley 2008).

Like many long-lived species, marine turtle populations fluctuate in size over long timescales and abundances at individual monitoring sites may vary significantly among years due to environmental factors (e.g. Broderick et al. 2001). Long-term monitoring is therefore essential to establish population trends with any certainty (Jackson et al. 2008; National Research Council 2010). The demographic units chosen for trend analysis are also important (National Research Council 2010). Marine turtles have complex population structures, characterised by female nest site fidelity, male-mediated gene flow, and migratory overlap between stocks at feeding and developmental habitats, which confound straightforward definitions of "populations" (see Bowen and Karl 2007 for a review). In

practice, the difficulties of quantifying cryptic and widely-dispersed marine turtles at sea mean that most long-term studies of abundance are based on adult females at nesting sites. But delineating nesting populations can itself be challenging because the precision of female natal philopatry (and thus the degree of demographic connectivity among nesting sites) is often unknown and is difficult to measure (National Research Council 2010). Indeed, the boundaries of nesting populations are frequently revised as methods for detecting demographic divisions advance (Browne et al. 2010; Shamblin et al. 2012). Population trends can also vary substantially among individual nesting beaches within a rookery (Witherington and Koeppel 2000; Stewart et al. 2011; Mortimer et al. 2011). Trend analyses that are too coarse in scale therefore risk overlooking local demographic realities that may be of particular relevance to conservation managers.

In this study, we report on the status of the South Atlantic's largest green turtle (*Chelonia mydas*) nesting aggregation at Ascension Island—one of the IUCN Index sites for this species (Seminoff 2004)—and compare 36-year trends in nesting activity across the Island's multiple nesting beaches and beach clusters (see Fig. 1). Green turtles nesting at this rookery migrate from foraging grounds along the tropical Atlantic coast of South America (Hays et al. 2002a) and are estimated to account for 40–70 % of individuals at feeding aggregations throughout the region (Naro-Maciel et al. 2012). Nesting trends at Ascension Island are therefore a good indicator of the regional status of this species. Following the discovery of the island in the sixteenth century, the green turtle population was subjected to several centuries of exploitation for meat. This intensified to a commercial scale following permanent settlement by the British in 1815, resulting in a severe depletion of the population (Huxley 1997, 1999; Broderick et al. 2006). Harvesting had largely ceased by the 1930s when the operation became uneconomical, and green turtles were legally protected in 1944 (Huxley 1997, 1999). At the last (and only) status assessment in 2004 the population was showing promising signs of recovery (Broderick et al. 2006). Here, we contribute an additional 9 years of monitoring data and assess contemporary trends against a historical baseline of abundance estimated from harvesting records (see Broderick et al. 2006). In addition, we present the first fine-scale analysis of nesting trends at individual sites, using beach-level covariates to explain observed differences. There are several motivations for this. Firstly, owing to the high annual level of nesting at Ascension Island, population monitoring has been based on surveys of a limited number of index beaches in many years. This is a common approach in marine turtle monitoring (e.g. Witherington et al. 2009; Stewart et al. 2011) but assumes that trends at index beaches are representative of all sites, which requires testing. Secondly, recent work has suggested significant divergence between turtles nesting in different areas of the island, which may warrant consideration as separate management units (Weber et al. 2012). An evaluation of trends at individual nesting sites is therefore timely and needed to refine future monitoring and management strategies.

Methods

Population monitoring

Ideally, assessments of marine turtle abundance and trends at nesting sites are based on recaptures of individually-marked females (e.g. Balazs and Chaloupka 2004a). However, in most large rookeries this is not practical and it is common to use counts of nests, or of the tracks left by nesting females ("nesting emergences"), as proxies (e.g. Troëng and

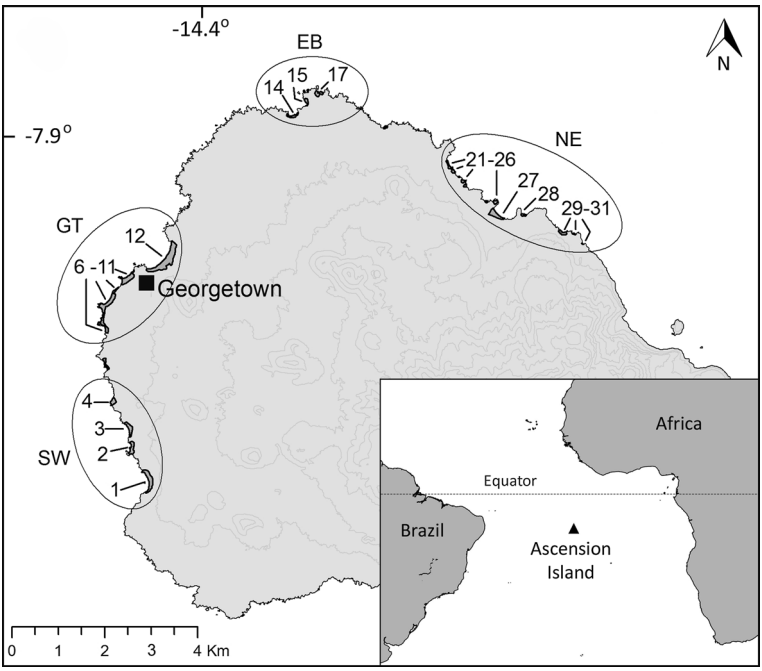

Fig. 1 Locations of green turtle nesting beaches and beach clusters at Ascension Island. Major nesting beach clusters are *circled* (*SW* South Western Cluster; *GT* Georgetown Cluster; *EB* English Bay Cluster; *NE* North Eastern Cluster). The location of the main human settlement of Georgetown, which served as the base for historic turtle harvesting operations, is also shown

Rankin 2005; Witherington et al. 2009). Monitoring of green turtle abundance at Ascension Island began in 1977–1978 when Mortimer and Carr (1987) conducted the first counts of nesting emergences on all of the Island's beaches. Intermittent surveys of a subset of nesting beaches were continued by the Island Administrator's Office (1981–1982 and 1990 nesting seasons) until 1999 when an annual monitoring programme was established that has run until the present day (Godley et al. 2001; Broderick et al. 2006). Annual monitoring has consisted of two types of survey depending on staffing constraints: "full surveys", during which nesting emergences on all 31 beaches were monitored (1999–2001, 2006, 2008 and 2012), and "index surveys" focussing on two primary nesting beaches (Beaches 1 and 12; Fig. 1) which together support approximately 40–50 % of total nesting emergences (all other years). Counts were conducted on two consecutive days each week for the two index beaches, and on one or two consecutive days every 2 weeks for other beaches. Prior to each survey, all existing tracks were removed using a landscape rake to allow fresh emergences to be quantified on the following morning. Monitoring began in November/December and continued until zero counts were obtained in two consecutive surveys (normally June/July). Counts of successful nests (identified from distinctive 'cover-ups': see Troëng and Rankin 2005) were included in routine surveys of index beaches from 2007 onwards, and extended to all beaches in the 2012 nesting season. Prior to this, estimates of nesting success were based on the outcome of a sample of nesting emergences during some surveys (Godley et al. 2001).

Besides estimates of abundance, other demographic parameters can also provide useful insights into population status and functioning (Seminoff and Shanker 2008). Therefore, in addition to synthesising available beach monitoring data, we also collated all existing data on female size (curved carapace length; CCL) collected between 1973 and 2012 to investigate potential relationships between long-term trends in abundance and the average size of nesters. Data were available for the following years: 1973 and 1974 ($n = 240$ and 478, respectively; from Simon and Parkes 1976), 1992 ($n = 43$; from Hays et al. 1993), 1999 ($n = 105$), 2000 ($n = 49$), 2007 ($n = 62$), 2008 ($n = 60$) and 2012 ($n = 80$; 1999–2012 authors' unpublished data). In addition, the mean CCL of females in 1931 was estimated by inputting the average mass of turtles reported in harvesting records for that year (180 kg; Huxley 1997) into the regression equation relating body mass and female size for the Ascension Island population (Hays et al. 2002b).

Estimating annual numbers of nests

Total annual nesting emergences for each beach in each year were estimated from weekly and biweekly count data using *phenology v3.40* for R (Girondot 2010). *Phenology* fits negative binomial models to seasonal nesting data and integrates observations with model predictions for days that were not surveyed to estimate annual totals and associated confidence intervals. The approach is therefore robust against variation in survey effort among beaches and years (Girondot 2010). Raw count data were not available for the 1977 and 1978 nesting seasons, so in this case we used published values that were derived using a similar curve-fitting approach (Mortimer and Carr 1987). Count data for closely-adjacent, minor nesting beaches were pooled prior to the *phenology* analysis to allow direct comparison with the annual totals for these clusters reported by Mortimer and Carr (1987). In addition, numbers of emergences recorded on minor nesting beaches were often too low to allow robust models to be fitted individually. In full survey years the estimated total annual nesting emergences for each beach or beach cluster were summed to obtain an overall total for Ascension Island. In index survey years, annual totals for index beaches were adjusted to give an overall total using the proportion of emergences that occurred at these sites during full surveys. Since the spatial distribution of nesting has changed significantly over the course of the study (see "Results" section), a logistic regression of the proportion of nesting emergences on index beaches against time was used to estimate the appropriate scaling factor for each year (Fig. S1). Confidence intervals for annual totals were calculated using a Monte Carlo procedure (10,000 iterations) to integrate uncertainty in counts for individual beaches and in the estimated scaling factors for index survey years.

Estimated total nesting emergences for each year were converted to an estimate of total nests using the mean nesting success for the whole island from the 2012 nesting season (0.34, 95 % CI 0.31–0.37), as this represents the only comprehensive survey of both tracks and successful nests on all beaches. This approach assumes that nesting success averaged across the whole island has not varied systematically over the course of the study. Insufficient data exist to formally test this assumption; however a similar mean value of 0.39 reported for the 1999 nesting season (Godley et al. 2001) suggests that the extrapolation is reasonable. Nesting success on Long Beach, for which the most complete records are available, has also not changed significantly since 1999 (linear regression, $F_{1,8} = 0.83$, $p = 0.38$). Confidence intervals for estimated total nests were calculated Monte Carlo-style using the probability distributions of nesting success and annual nesting emergences.

Trend analysis

Long-term trends in total annual nests and mean female CCL were analysed using generalized additive models (GAMs) implemented using the *mgcv* library for R v2.15.0 (Wood 2004). GAMs fit non-parametric smoothing splines that are defined by the data, and thus make no a priori assumptions about the functional form of the trend (e.g. Balazs and Chaloupka 2004a; Witherington et al. 2009). Smoothing parameter estimation used the generalized cross-validation (GCV) method (Wood 2004). A negative binomial error distribution was used for the analysis of the nester abundance time series, and a Gaussian error structure was used for the analysis of female size. Significant data gaps and uneven sampling intervals prior to 1999 meant that autoregressive time series models were inappropriate for analysis of 36-year trends. However, an analysis of the 15-year continuous time series between 1999 and 2013 using a GAM with an AR(1) autocorrelation structure produced a near identical fit to an independent errors model (see Fig. S2) suggesting that the trend estimated for the full monitoring period is reliable.

In addition to assessing overall trends, we also fitted separate models to annual counts of nesting emergences for individual beaches and beach clusters to examine long-term spatiotemporal patterns in nesting activity. This analysis was restricted to full survey years when all nesting beaches were monitored. When analysing this reduced dataset, GAMs indicated linear fits in all cases. We therefore replicated fits using negative binomial regressions (with a log-link function), as these allow the estimation of slope coefficients that are interpretable as the percentage annual population growth rate for each beach (Chaloupka et al. 2008). Nesting beach characteristics that might explain observed differences in annual population growth rates were then evaluated using multiple regression models. Explanatory variables tested included beach size, female nesting success (mean proportion of emergences resulting in a nest), hatching success (mean proportion of eggs in a clutch producing emergent hatchlings), mean sand temperature during the nesting season, and coastal distance from the main human settlement of Georgetown (data and sources are available in Table S1). Other beach characteristics such as sand colour and vegetation cover (which is largely absent from nesting beaches on Ascension Island) were not considered as they are proximate and influence population growth through one of the variables tested. Models were simplified by stepwise deletion of non-significant terms ($\alpha = 0.05$) to derive a minimum adequate model.

Historical baseline

Historical baselines of abundance are essential for the interpretation of contemporary population trends and can provide benchmarks for modern conservation efforts (McClenachan et al. 2006; Kittinger et al. 2013). Establishing baselines for marine turtle populations is challenging and often relies upon historical anecdotes. Fortunately, because the green turtle harvest on Ascension Island was rigorously controlled following permanent settlement—first by the British Navy and subsequently by the Eastern Telegraph Company—detailed harvesting records exist for many years between 1822 and 1944 (Huxley 1999; Broderick et al. 2006). Broderick et al. (2006) used these records coupled with an age-class-structured population matrix model to estimate the minimum number of females that must have nested at Ascension Island in 1822 in order for the population to have avoided extirpation. The model uses an iterative approach, starting from a range of initial population sizes and subtracting harvests for each year, to estimate the minimum number of females needed for the population be greater than zero in 1944 (see Broderick et al. 2006

for a full explanation). To parameterise the fecundity elements of the population matrix, Broderick et al. (2006) used a species average of three clutches/female/season that has recently been shown to substantially underestimate the annual fecundity of this population (Weber et al. 2013). We therefore re-ran the analysis using the more reliable, recent estimate of 6 clutches per female (all other parameters were as described in Broderick et al. 2006). Uncertainty in the model output was also evaluated using Monte Carlo simulation. Probability density functions for each parameter were randomly sampled and propagated into the model over a suite of 10,000 simulations to derive a probability distribution for the minimum estimated population size.

Results

Since monitoring began in 1977, the average number of green turtle clutches deposited annually at Ascension Island has increased sixfold, from 3,752 (95 % CI 3,598–3,907) nests per annum in years surveyed between 1977 and 1982, to 23,724 (95 % CI 22,510–24,938) nests per annum in the period between 2010 and 2013 (Fig. 2a). Total estimated numbers of emergences and nests for all surveyed years between 1977 and 2013 are available in Table S2. Assuming that each female lays an average of six clutches per season (Weber et al. 2013) and nests on average every 3.75 years (95 % CI 3.5–4; Mortimer and Carr 1987), there are currently estimated to be around 3,950 green turtles nesting annually at Ascension Island (95 % CI 3,752–4,158), with an overall population size of approximately 14,840 adult females (95 % CI 13,525–16,149). This compares to a minimum estimated population size of 17,660 ± 6,365 (95 % CI) adult females in 1822 in order for the population to have survived the recorded harvesting regime until 1944 when it was formally protected (see Fig. 3).

Interestingly, the upward trend in nesting at Ascension Island over the past 36 years has been mirrored by a significant decline in the average size of nesting females, from a mean carapace length of 116.0 ± 0.51 (s.e.) cm in 1973–1974 (range = 102–131) to a mean of 111.5 ± 0.83 cm (range = 97–124) in 2012 (Fig. 2b; approximate significance of GAM smooth: $F = 10.47$, $p = 0.01$, estimated d.f. = 2.8). This equates to a 10 % reduction in average body mass according to the allometric relationship established by Hays et al. (2002b) for this population (from 179 to 160 kg). Although data prior to 1999 are lacking, the forms of the nesting and body size trends are similar, with a period of relative stability until the mid-1990s followed by a phase of rapid change that has lasted until the present day (Fig. 2).

Although nesting is increasing rapidly at an island-level, a finer-scale analysis of trends at individual beaches and beach clusters revealed marked spatial variation in rates of increase in nesting activity over the past 36 years (Figs. 4, 5). Growth has been most rapid in the Georgetown Cluster (5.5 % increase per annum), slower in the South Western and English Bay Clusters (3.4 and 3.9 % per annum, respectively) and slowest in the North Eastern Cluster (1.3 % p.a.; Fig. 4). These growth rates are broadly consistent with those reported by Chaloupka et al. (2008) for other recovering green turtle rookeries in Japan, Australia, Costa Rica and the USA (range 3.8–13.9 % p.a.). Across individual nesting beaches and minor beach clusters rates of growth varied even more substantially, ranging from 0.4 to 5.9 % p.a. (equivalent to 36-year increases in nesting activity ranging from 17 to 700 %). Coastal distance from Georgetown (defined as Long Beach Turtle Ponds) explained the majority of this variance (multiple regression: $r^2 = 0.974$, $F_{1,8} = 304.9$, $p < 0.0001$), with beaches further from Georgetown exhibiting significantly slower rates of growth (Fig. 5). Other beach-level covariates including length, mean sand temperature,

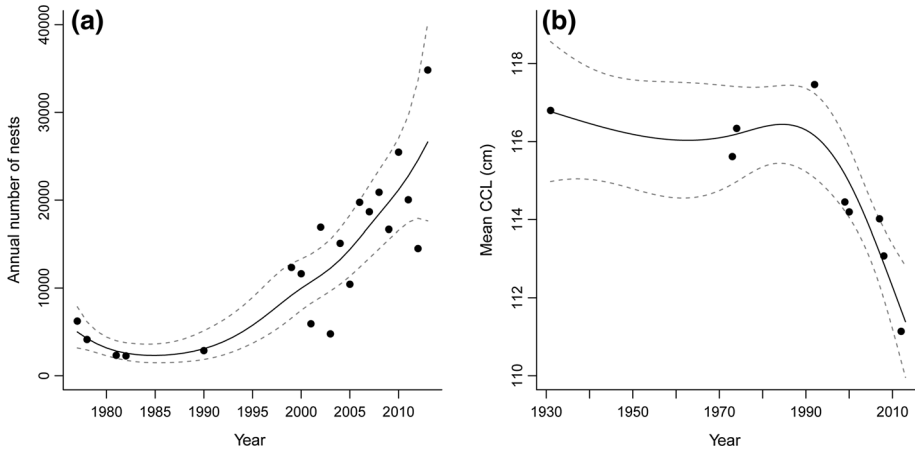

Fig. 2 Long-term trends in **a** the annual number of green turtle nests at Ascension Island, and **b** the average curved carapace length (CCL) of nesting females. Trend lines are cubic smoothing splines fitted using generalized additive models (GAMs). Broken lines show the 95 % confidence envelopes for the smoothes

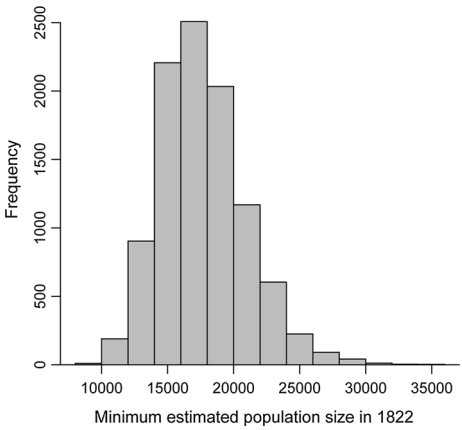

Fig. 3 Probability distribution of the estimated minimum number of adult females in the Ascension Island green turtle population in 1822. Estimates were derived from Monte Carlo sampling of an age class-structured population matrix model and historical harvesting time series over 10,000 trials (see "Methods" section for details)

female nesting success and hatching success were not retained in the minimum adequate model (all $p \geq 0.40$; Table S3). These results were qualitatively unchanged when restricting the analysis to recent data collected by the authors since 1999: distance from Georgetown continued to explain most of the variance in annual population growth rates ($F_{1,8} = 26.0$, $p = 0.001$, $r^2 = 0.76$), while other variables were not retained (all $p \geq 0.09$).

The current distribution of green turtle nesting activity at Ascension Island is shown in Table 1. Over 70 % of nesting currently occurs on just 3 beaches (Beach 1: Pan-Am Beach; Beach 12: Long Beach; Beach 27: North East Bay), and 47 % on a single beach (Long Beach). When combined with overall population trends, we therefore estimate that there are currently around 13,300 nests per annum on average in the Georgetown cluster (56 %), 5,930 in the South Western cluster (25 %), and 3,560 in the North Eastern Cluster (15 %).

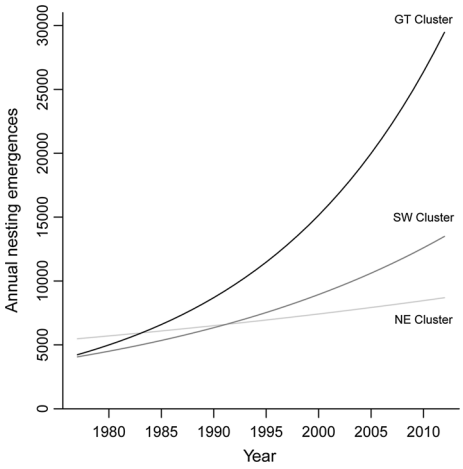

Fig. 4 Thirty-six-year trends in nesting activity at Ascension Island's three major nesting beach clusters (*GT* Georgetown Cluster, *SW* south western cluster, *NE* north eastern cluster; see Fig. 1). Trend lines were fitted by negative binomial regression. The trend for the smaller English Bay Cluster which accounts for <8 % of total annual nesting emergences is not shown

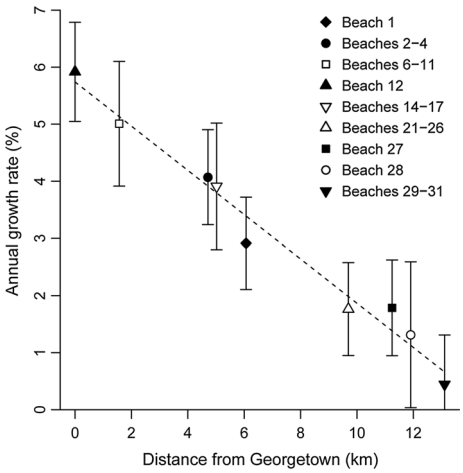

Fig. 5 Relationship between annual rates of increase in nesting activity and coastal distance from Georgetown (Long Beach Turtle Ponds) for individual beaches and minor beach clusters (see Fig. 1). Growth rates were estimated as the slopes of negative binomial regressions fitted to annual counts of nesting emergences in full survey years (data are plotted ±1 SD)

Discussion

The Ascension Island green turtle population has been legally protected at its nesting grounds for almost 70 years, and has benefitted from improving legislative protection and enforcement across its Brazilian foraging range since the mid-1970s (Marcovaldi and Marcovaldi 1999). The cumulative impact of these conservation measures has been profound. Since monitoring began in 1977, the average number of green turtle clutches deposited annually at Ascension Island has increased by almost 500 %, from approximately 3,700 to more than 23,700 (Fig. 2a), with a current estimated population size of around 14,800 adult females. This confirms the status of Ascension Island as the second largest green turtle rookery in the Atlantic Ocean (see Almeida et al. 2011 for a recent review).

As with many long-lived vertebrates, a lack of historical baselines of abundance for most marine turtle populations means that contemporary trends must be interpreted with

Table 1 Spatial distribution of green turtle nesting at Ascension Island based on the 2012 full survey

Cluster	Beach(es)	Emergences (%)	Nesting success	Nests (%)
SW	1	12.5 (11.2–13.8)	0.45 (0.38–0.52)	16.3 (14.5–18.1)
	2–4	11.1 (9.7–12.5)	0.28 (0.21–0.35)	9.1 (7.4–10.8)
GT	6–11	18.8 (16.9–20.7)	0.17 (0.13–0.22)	9.5 (7.6 –11.4)
	12	33.8 (31.4–36.2)	0.47 (0.42–0.53)	46.5 (43.7–49.3)
EB	14–17	7.8 (6.6–9.0)	0.16 (0.10–0.22)	3.6 (2.5–4.8)
NW	21–26	2.6 (1.8–3.4)	0.23 (0.06–0.42)	1.7 (0.6–2.9)
	27	6.7 (5.6–7.7)	0.51 (0.38–0.63)	9.8 (8.1–11.6)
	28	2.0 (1.5–2.6)	0.22 (0.09–0.36)	1.3 (0.6–2.0)
	29–31	4.8 (3.4–6.1)	0.15 (0.04–0.27)	2.1 (0.7–3.5)

95 % confidence intervals are shown in parentheses. Beach notations follow Fig. 1

caution (McClenachan et al. 2006; Seminoff and Shanker 2008; Kittinger et al. 2013). To provide an historical context for the Ascension Island green turtle, Broderick et al. (2006) used an age-class-structured population matrix model coupled with harvesting records to estimate the minimum number of adult females in the population at around the time of human settlement. We re-ran this analysis, using the most recent and reliable estimates of annual fecundity for the Ascension Island population to parameterise the model (Weber et al. 2013). Although there is considerable uncertainty in the model predictions, we estimate that there must have been at least 17,660 adult females in the population in 1822 for it to have avoided extirpation. This estimate is a minimum and inevitably underestimates pre-human population size because it does not account for harvesting between 1501 (discovery of the island) and 1822, which was not quantified but is known to have occurred (Huxley 1999). Thus, the current population of approximately 14,800 adult females is still somewhat lower than even the most conservative estimate of pre-human abundance, but is continuing to grow.

Reinstating marine turtles to pre-human population sizes may not be possible because ecosystems have been substantially altered. But restoring populations to levels of abundance at which they can fulfil their ecological roles remains a realistic goal (Bjorndal and Bolten 2003). For example, as the dominant megaherbivores in many tropical coastal ecosystems, green turtles play a vital role in structuring seagrass and algal communities (Lal et al. 2010; Kelkar et al. 2013). According to mixed stock analyses, the Ascension Island rookery is currently the source of 40–70 % of green turtles at foraging habitats along a 6,000 km stretch of South American coastline, from northern Argentina to north-eastern Brazil (Bjorndal et al. 2006; Naro-Maciel et al. 2012; Prosdocimi et al. 2012). It seems likely, therefore, that the resurgence of the population has had, and will continue to have, significant impacts on coastal ecosystem functioning in the tropical south-western Atlantic. In this respect, it is potentially relevant that the recent, rapid population growth at Ascension Island has been mirrored by a significant decline in the average size of females nesting at both Ascension (Fig. 2b) and at least one other regionally-important rookery that shares the same foraging grounds (Rocas Atoll; Bellini et al. 2013). Increasing competition for resources is one possible explanation for these trends. Indeed, density-dependent

somatic growth has been documented previously in green turtles (Bjorndal et al. 2000), including in another rapidly recovering stock (Balazs and Chaloupka 2004b). An alternative explanation is that the increasing recruitment of younger females into the rapidly expanding Ascension Island nesting population may have driven the reduction in average body size (marine turtles continue to grow, albeit slowly, after maturity, e.g. Broderick et al. 2003). Although we cannot rule this out, the parallel decrease in female size at the Rocas Atoll rookery has occurred despite a lack of any discernible trends in abundance (Bellini et al. 2013). Thus, while there is no evidence that the population is yet approaching carrying capacity (see Fig. 2a), it seems possible that the recovery of the Ascension Island green turtle could be increasingly affecting demographic processes in the region through competition effects.

Overall, the Ascension Island green turtle population is rebounding strongly. However, this general trend masks significant variation in rates of population growth at a local level. Indeed, annual rates of increase in nesting activity have varied among individual beaches by an order of magnitude, with 97 % of the variation explained by proximity to the main human settlement of Georgetown (Figs. 4, 5). Contrary to what might be expected, beaches closer to Georgetown have experienced the most rapid population growth (Fig. 5). Given that rates of population growth are determined by the balance of births, deaths and migration, these results indicate that at least one of the fundamental population dynamic rates has varied among sites as a function of distance from Georgetown. A similar linear trend in population growth rates along a distance gradient has been described in leatherback turtles (*Dermochelys coriacea*) nesting in Florida, which the authors attributed to differences in habitat quality (Stewart et al. 2011). One possibility, therefore, is that there has been a continuous net immigration of individuals into the Georgetown cluster beaches, and a net emigration from more distant sites, as a result of a gradient in nesting habitat quality. However, none of the correlates of "beach quality" that we tested (including size, female nesting success, sand temperature and hatching success) vary linearly with distance from Georgetown or explained the observed differences in population trajectories. Other less easily quantified factors could also be involved. For example, Witherington and Koeppel (2000) suggested that avoidance of heavily-illuminated, developed areas could explain spatial variation in green turtle population trends in Florida. Shifts in the distribution of marine turtle nesting have also been described in relation to broad-scale changes in coastal geomorphology (Pritchard 2004). However, beaches in the Georgetown cluster - which have experienced the most rapid growth in nesting activity - are currently the only nesting areas affected by anthropogenic light pollution (at a low level) and are the only sites where beach conformation is known to have been altered within the timeframe of this study (as a result of sand mining for construction; Fletemeyer 1986). Hence, it is unlikely that directional migration in response to variation in habitat quality or coastal change explains the observed gradient in population trajectories.

It is therefore worth considering a second possibility: that female survival has historically varied among nesting sites. Although it is known from harvesting records that turtles were taken on most beaches (Huxley 1999), given the logistical difficulties of extracting turtles from more remote sites (there were no roads, and sea conditions were often treacherous: see Huxley 1999 for an account) it is reasonable to assume that harvesting was most intense in the vicinity of Georgetown, which at the time was the only major human settlement and the site of the port, turtle storage ponds, and other infrastructure. Thus, current rates of recovery may reflect the extent to which localised nesting populations were depleted in the past. Indeed, a correlation between historical levels of exploitation and contemporary population growth has been suggested in at least one other green turtle

rookery (Mortimer et al. 2011), as well as in a comparison across rookeries (Chaloupka et al. 2008). This mechanism requires a degree of demographic independence among local nesting sites, but is consistent with evidence of strong within and among-season nest site fidelity at Ascension Island (Mortimer and Portier 1989) and divergence between turtles nesting at eastern and western beaches (Weber et al. 2012). Further studies using high resolution genetic markers (e.g. Shamblin et al. 2012) may help to clarify the degree of demographic structure at this rookery. Although we cannot conclusively assign a cause, the fine-scale variation in population trajectories that we report has significant implications for local monitoring and management. For example, abundance estimates in many years have been based on two west coast index beaches with annual growth rates of 6 % (Beach 12) and 3 % (Beach 1), which are not representative of slower growth in the North Eastern Cluster (1.3 % per annum). If not taken into account, this shift in nesting distribution would lead to overall population trends being overestimated. Moreover, slower population growth in the NE Cluster combined with evidence of local adaptation of turtles nesting in this area (Weber et al. 2012) makes a strong case for this being considered as a separate management unit. We therefore recommend that North East Bay (Beach 27 in Fig. 1), the most important nesting beach in the NE Cluster, is included as a routine monitoring site in all future index surveys.

Although global declines of marine megafauna are continuing at an alarming rate, sustained conservation efforts are beginning to reverse declines for some species (e.g. Stevick et al. 2003). The green turtle is one such example. Following centuries of exploitation for meat that eliminated many rookeries (McClenachan et al. 2006; Kittinger et al. 2013), green turtle populations are now increasing across many parts of the species global range (this study, Troëng and Rankin 2005; Chaloupka et al. 2008; Mortimer et al. 2011). These trends are encouraging and demonstrate the capacity of marine turtle stocks to rebound when anthropogenic pressures are eliminated or alleviated through effective management. But they are also not a cause for complacency. Even well-protected populations may decline unexpectedly (e.g. Witherington et al. 2009) and many threats remain. Climate change in particular looms as a future challenge for marine turtles, particularly for insular nesting populations with no possibility for adaptation through range shifts (Hawkes et al. 2009). The consequences of climate warming may not be felt for decades, but are likely to be experienced first at nesting beaches where incubation temperatures are already close to the thermal limits of development, such as those in Ascension Island's more slowly-recovering North Eastern cluster (Weber et al. 2012). Ongoing monitoring at multiple spatial scales is therefore essential.

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