

Spatial and temporal variability of immature green turtle abundance and somatic growth in Puerto Rico

Rita Patrício^{1,*}, Carlos E. Diez², Robert P. van Dam³

¹Centre for Ecology & Conservation, College of Life and Environmental Sciences, University of Exeter, Cornwall Campus, Penryn TR10 9EZ, UK

²Programa de Especies Protegidas, DRNA-PR, San Juan PR 00936, Puerto Rico

³Chelonia, PO Box 9020708, San Juan PR 00902-0708, Puerto Rico

ABSTRACT: Understanding conservation needs relies on robust estimates of key population parameters, such as survival, abundance and somatic growth. We investigated the somatic growth and abundance dynamics of 2 aggregations of immature green turtles, at Tortuga Bay and Puerto Manglar (Culebra, Puerto Rico), throughout 15 yr of capture-mark-recaptures. We used nonlinear models to investigate the effects of carapace length, sampling year, growth interval and the presence of fibropapillomas on growth rates, and used the size-specific growth rate function to estimate how long turtles remain at each bay. Abundances were estimated and compared with time-specific growth rate functions, to infer density-dependency effects on somatic growth rates, and trends in abundance were evaluated by fitting generalized linear models. We found foraging site specific growth rates and report the highest mean somatic growth rate for green turtles in the wild (6.1 ± 1.7 cm yr⁻¹, at Puerto Manglar). The size-specific growth rate function was monotonic at both sites, with growth rates declining continuously with increasing carapace length. We inferred minimum ages at maturity of 14 and 22 yr, for Puerto Manglar and Tortuga Bay turtles, respectively. Throughout the 15 yr of this study there was a positive trend in aggregation size at Puerto Manglar (mean annual increase of 10.9%), which was not observed at Tortuga Bay. Our study highlights the influence of geography and habitat quality on somatic growth rates, and delivers robust demographic estimates valuable for local and regional assessments of the conservation status of the green turtle.

KEY WORDS: Somatic growth · Abundance · Green sea turtle · Capture-mark-recapture · Puerto Rico · Linear and nonlinear models · Horvitz-Thompson estimator · *Chelonia mydas*

Resale or republication not permitted without written consent of the publisher

INTRODUCTION

Somatic growth and abundance are 2 key parameters of population dynamics essential for modeling long-term viability of populations and for the implementation of effective management strategies (Chaloupka & Limpus 2001, Chaloupka et al. 2004, Bjørndal et al. 2011). Long-term data sets are especially valuable for determining the current population status of endangered species and establishing baseline recovery values (Heppell et al. 2003, Hamann et al. 2010, Bjørndal et al. 2011).

The green turtle *Chelonia mydas* is listed as Endangered in the Red List of the International Union for the Conservation of Nature (IUCN 2012). Over recent years, however, conservation efforts have contributed to the recovery of several of the major populations worldwide (Broderick et al. 2006, Chaloupka & Balazs 2007, Chaloupka et al. 2008). For this reason, specialists are finding it unrealistic to list the species as endangered at a global level and suggest a more regional approach with appropriate criteria (Broderick et al. 2006, Godfrey & Godley 2008), so that local populations truly at risk of extinction, due

to persistent human exploitation, habitat destruction, bycatch or emerging diseases (Herbst et al. 2004, Epperly et al. 2007, Chaloupka et al. 2008, Varghese et al. 2010), can be correctly identified and preserved.

Green turtles are highly vagile, with a life cycle characterized by ontogenic habitat shifts and large-scale migrations (Heppell et al. 2003, Arthur et al. 2008). After emerging from their nests, hatchlings begin an oceanic period coupled with pelagic habitat and epipelagic feeding (Heppell et al. 2003), which may last ca. 3 yr in the Greater Caribbean (Bjorndal et al. 2005, Goshe et al. 2010). This post-hatchling stage is strongly influenced by oceanic currents (Lahanas et al. 1998) and is often referred to as the 'lost years' since the whereabouts of these small turtles remains unclear (Reich et al. 2007). At ca. 25 cm straight carapace length (SCL), juveniles recruit to shallow neritic areas and shift to benthic feeding (Bolten 2003, Heppell et al. 2003). Neritic zones are used as developmental habitats, and turtles may spend several years foraging in the same area until reaching a size or maturity stage that triggers them to migrate (Bjorndal et al. 2005, Patrício et al. 2011). Sexually mature individuals move periodically from foraging grounds to nesting beaches and mating areas, often separated by hundreds to thousands of kilometers (Bowen & Karl 2007, Bowen et al. 2007, Arthur et al. 2008).

Estimates of size-specific somatic growth rates of green turtles at the juvenile neritic phase allows assessment of the duration of this life stage, and hence contributes to the estimation of age at maturity (Balazs & Chaloupka 2004, Chaloupka et al. 2004, Krueger et al. 2011). Spatial and temporal variability in somatic growth dynamics, particularly when coupled with abundance estimates, make good indicators of the quality of foraging sites, as lower growth rates may imply less food availability (Balazs & Chaloupka 2004, Kubis et al. 2009), and declines in somatic growth rates coupled with higher abundance suggest a density-dependent effect (Bjorndal et al. 2000a, Kubis et al. 2009).

In Puerto Rico, the most-studied foraging grounds for green turtles are located at Puerto Manglar and Tortuga Bay, part of the Culebra Archipelago (Diez et al. 2010, Patrício et al. 2011). Green turtles as small as 23 cm SCL have been observed in these coastal bays, where they spend several years and then depart before the onset of sexual maturity (Patrício et al. 2011). Turtles with fibropapillomas (FP) were first observed at Puerto Manglar, with an initial prevalence of ~40% from 2000 to 2006, followed by a decrease in occurrence. At Tortuga Bay, FP were not

detected until 2009, but since then have been consistently observed, with a mean prevalence of 17% from 2009 to 2011. Tortuga Bay and Puerto Manglar foraging grounds are used by green turtles from multiple rookeries, as revealed by mitochondrial DNA analysis (Velez-Zuazo et al. 2010), pertaining to all 5 Atlantic and Caribbean Regional Management Units (Wallace et al. 2010). Movement of individuals between the 2 sites has very rarely been observed, suggesting that when turtles recruit to a specific bay they remain faithful to that area (Patrício et al. 2011).

Collazo et al. (1992) did a first assessment of the abundance and the somatic growth of green turtles at Culebra. They found a mean annual growth rate of 5.08 ± 0.83 cm SCL, and a higher abundance of turtles at Tortuga Bay compared to Puerto Manglar.

In this study, we investigated the somatic growth dynamics of the green turtles foraging at Tortuga Bay and Puerto Manglar through the analysis of 15 yr (1997 to 2011) of capture-mark-recapture (CMR) records. We used nonlinear models to fit the relationship between growth rates and 4 growth predictors: body size (SCL), sampling year, growth interval, and the occurrence of FP. The size-specific growth rate function was used to estimate the duration of the juvenile neritic phase at each site. Abundances were estimated and compared with the time-specific growth rate functions to infer the effects of density on somatic growth rates. Abundance trends in the last 15 yr were assessed using generalized linear models.

The analyses of our long-term data set allowed us to estimate important population parameters, imperative for a better understanding of the regional conservation status of green turtles. Additionally, we generated baseline information in somatic growth and abundance indispensable to assess future trends.

MATERIALS AND METHODS

Study site

Puerto Manglar and Tortuga Bay are foraging grounds for immature green turtles, and are located on the islands of Culebra and Culebrita, respectively. These islands lie east of the main island of Puerto Rico (Fig. 1). The coastal waters surrounding these islands are a critical habitat for green turtles, as designated by the Endangered Species Act 1998 (NMFS-NOAA 1998). Puerto Manglar (18.30°N, 65.25°W) is a mangrove-lined bay surrounded by wetlands and minor residential development. The

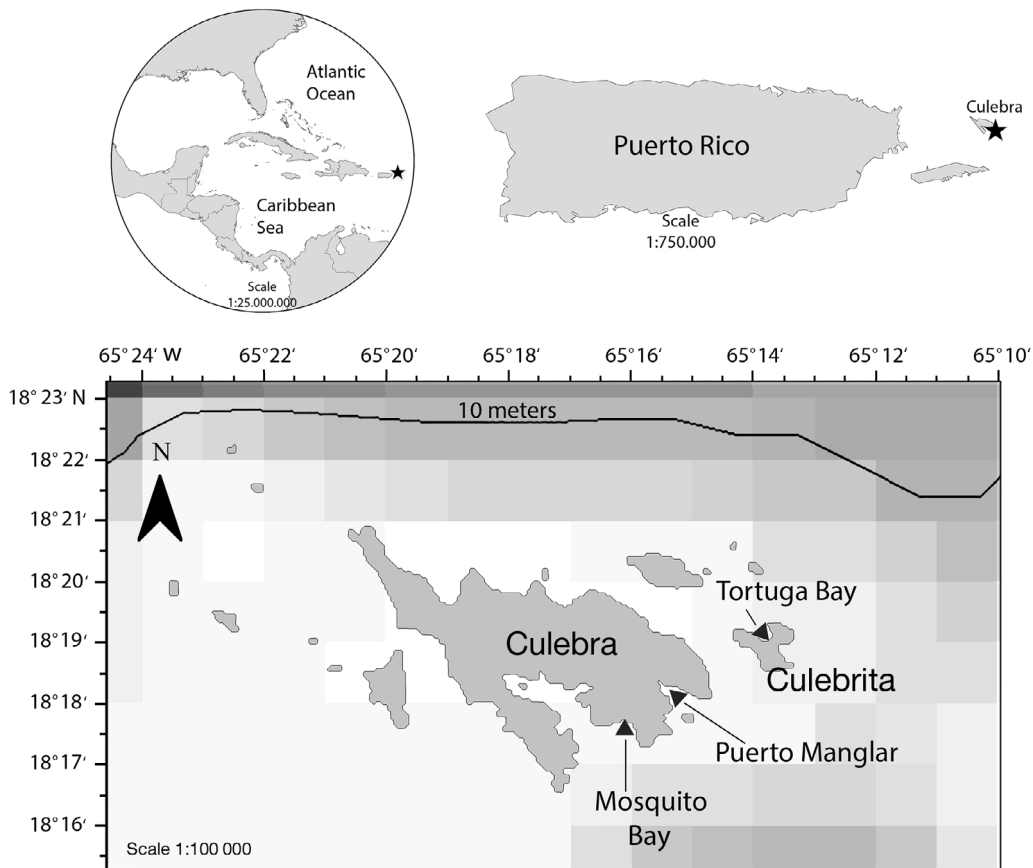


Fig. 1. Location of the green turtle *Chelonia mydas* foraging grounds surveyed for this study: Puerto Manglar and Tortuga Bay, Puerto Rico. Shades of grey represent different bathymetries. (Map created using www.seaturtle.org/maptool)

inner shores are bordered by *Rhizophora mangle* (red mangrove) and the submerged vegetation is dominated by the seagrass *Thalassia testudinum* and macroalgae (Diez et al. 2010). Depths range from 0.5 to 5 m and the water has high turbidity (Diez et al. 2010).

Tortuga Bay (18.32° N, 65.23° W) is on the uninhabited island of Culebrita, which is managed by the US Fish and Wildlife Service as part of the Culebra National Refuge. A sandy beach surrounds the bay, and underwater vegetation is more sparse than at Puerto Manglar. The seagrasses *Syringodium filiforme* and *Halodule wrightii* and corals are the main organisms colonizing the sea floor (Diez et al. 2010). Water transparency is greater than at Puerto Manglar, and depths range from 0.5 to 12 m (Diez et al. 2010).

Sampling methods

Turtles were captured with a 200 m long and 5 m deep entanglement net (nylon twine, 25 cm stretch

mesh), deployed for ~1 h and set in areas <5 m deep using a 7 m motor boat. An average of 6 swimmers snorkeled continually along the net to extract entangled turtles.

At Puerto Manglar, the net was set at a constant location, enclosing the inner portion of the bay. At the wider Tortuga Bay, the net was set at 3 different sites: at the east side, west side and the center of the bay. Due to the 25 cm stretch mesh size of the net, turtles <30 cm SCL can traverse the net without becoming entangled. Superior visibility at Tortuga Bay allowed some small turtles to be captured by hand when encountered away from the net. Turtles were tagged in the front flippers with 2 external tags (inconel and/or plastic tag) plus 1 internal passive integrated transponder (PIT) tag. Multiple tagging plus photo identification of each captured turtle assured correct identification of all recaptured individuals (Reisser et al. 2008, Schofield et al. 2008). As tag loss typically leaves identifiable scars in the flippers, we are confident that no previously tagged individual was misidentified as a new capture. SCL

(from the nuchal notch to the posterior-most tip) was measured to 0.1 cm using Haglof tree calipers. The presence of cutaneous or conjunctival FP was noted. To reduce stress to the turtles, we kept them covered with wet towels and minimized handling time to an average of 15 min per individual. Turtles were released near their capture location.

Capture sessions were conducted between 1997 and 2011 and, where possible, twice a year at each site, during 'summer' (May to October) and during 'winter' (November to April), to account for any seasonality effect associated with a change of ca. 3°C in water temperature from 'summer' to 'winter'. Due to rough sea conditions, there was no sampling during the summer season in 2008 and 2010, and no sampling during the winter season in 2002 and 2009. No sessions were carried out in 1999. Capture sessions lasted from 1 to 7 d. We pooled the data per calendar year since there was no evidence for inter-seasonal differences for either of our study areas. Sampling effort ranged from 5 to 16 net sets yr⁻¹, with 5.9 ± 3.5 net sets yr⁻¹ (mean ± SD) in Tortuga Bay and 6.6 ± 3.6 net sets yr⁻¹ (mean ± SD) in Puerto Manglar.

Data set and statistical approach

For the abundance estimation, we recorded 665 captures of green turtles from 1997 to 2011: 286 at Tortuga Bay, corresponding to 122 unique turtles, and 379 at Puerto Manglar, involving 183 ind. A total of 211 growth rate increments, 98 from Tortuga Bay, matching 56 ind., and 113 from Puerto Manglar, matching 66 ind., were used for the growth dynamics analyses. Minimum recapture intervals were set to 9 mo, to minimize measurement error in growth estimation, and maximum recapture intervals were set to 3.5 yr, as very long intervals tend to diverge from the linear growth assumed here between capture and subsequent recapture.

Somatic growth dynamics

Our sampling design was mixed-longitudinal, through time with partial replacement, with 53.6% of green turtles from Tortuga Bay and 45.5% from Puerto Manglar adding to 2–5 growth rate records. Therefore, we used generalized additive mixed modeling (GAMM), since it enables robust analysis of regression models with: (1) parametric or fixed effects (e.g. having FP or not), (2) nonparametric or nonlinear covariates (e.g. SCL, sampling year and

growth interval) and (3) random effects on predictors, to account for unobserved heterogeneity or correlation between observations inherent to mixed-longitudinal data sets (Chaloupka & Balazs 2005). GAMMs were fitted to the data using the packages *mgcv* (Wood 2001) and *nlme* (Pinheiro et al. 2011) in R v.2.13.2 (R Development Core Team 2008). Different GAMMs were tested, including different combinations of the following covariates or growth predictors: mean SCL, mean sampling year, growth interval and presence of FP. The importance of accounting for individual heterogeneity was also tested. Models were selected based on corrected Akaike's information criteria (AIC_c) (Sugiura 1978) and likelihood ratio tests (Neyman & Pearson 1933). All models had default Gaussian error distribution and identity link. Smoothing selection was performed with restricted maximum likelihood estimation (REML, Corbeil & Searle 1976). Models were examined for validity through residual checking, smoothing basis dimension choice checking and evaluation of the smoothness selection (Wood 2001).

Mean sampling year was calculated as the arithmetic mean between the year of capture and the year of subsequent recapture. It accounts for the variability in growth rates that can be attributed to environmental factors, although it can be confounded with unknown cohort effects in this analysis, since the age of individuals is unknown, as in most sea turtle studies. The year effect is also inexact since growth intervals were not always equal to 1 yr (growth intervals ranged from 0.8 to 3.5 yr), but it serves as a proxy for calendar year in the growth rate estimate. Mean SCL was calculated as the arithmetic mean between the SCLs at time of capture and subsequent recapture. This covariate describes the size-specific growth function well (Bjørndal et al. 2000b, Chaloupka et al. 2004, Krueger et al. 2011), assuming a linear growth function through the time interval between release and re-encounter. Growth interval was included in the model to account for possible biases associated with variable sampling intervals, in particular with longer intervals, which often lead to deviations in the linear growth (Casale et al. 2009). FP has been observed in our study areas with medium to high prevalence, so we included this covariate in the models to test for an effect of the presence of FP on somatic growth. We could not use FP as a quantitative covariate due to insufficient data, since for most years, FP was only identified as present or absent in our data set, regardless of the number of tumors. Therefore, it was included in the GAMMs as a binomial covariate.

The expected size-specific growth rate functions were extracted from the original data derived from the GAMMs, using cubic smooth splines, and numerically integrated to estimate the time in years that a turtle spends from recruitment, i.e. ~25 cm SCL, until a maximum size of 80 cm SCL at each foraging ground.

Aggregation abundances and abundance trends

A Cormack-Jolly-Seber (CJS) model (Lebreton et al. 1992) was fitted for each aggregation, using the program MARK v6.1 (White & Burnham 1999) to obtain maximum-likelihood estimates of the annual recapture probabilities for green turtles at Tortuga Bay and Puerto Manglar (see Patrício et al. 2011 for a detailed explanation of the selection of CJS models and model assumptions). Recapture probabilities from the CJS models were then applied to a Horvitz-Thompson type (HT) estimator to estimate annual abundance (Seber 1982):

$$N_i = (n_i/\rho_i) \quad (1)$$

where n_i is the number of turtles captured in the i th year, N_i is the number of turtles in the aggregation in the i th year and ρ_i is the estimated recapture probability in the i th year. It should be noted that the CJS model does not retrieve an estimation of recapture probability for the first year (1997), so we only estimated abundances from 1998 onwards. Approximate 95% confidence intervals were calculated using:

$$N_i \pm 1.96 \times SE(N_i) \quad (2)$$

$$SE(N_i) = [(n_i/\rho_i)^2 \times (\text{var}(\rho_i)/(\rho_i)^2)]^{0.5} \quad (3)$$

where $SE(N_i)$ is the conditional standard error and $\text{var}(\rho_i)$ is the estimated recapture probability variance in i th year (Loery et al. 1997, Chaloupka & Limpus 2001). The HT estimator is based on few assumptions (Seber 1982) and is especially applicable to long-term CMR studies where the emphasis is on robust statistical modeling of the recapture probability as an informative ecological process rather than a secondary parameter resulting from survival probability analysis (Chaloupka & Limpus 2001).

The long-term linear trends in green turtle abundance at each foraging ground were assessed using generalized least squares (GLS) models, with REML (Chaloupka & Limpus 2001), implemented through the nlme package (Pinheiro et al. 2011) in R v.2.13.2 (R Development Core Team 2008). Models were vari-

ance weighted, to account for measurement uncertainty, with log link and first order moving average error, to account for temporal correlation, since there was substantial overlap of individual turtles between successive years (Bjørndal et al. 2005). The response variable was the natural log form of the HT annual abundance estimates, so that the slope of the regression (i.e. the parameter estimate for year in the GLS models) was an estimate of the instantaneous rate of abundance change, assuming constant rate of change over the time interval (Chaloupka & Limpus 2001, Bjørndal et al. 2005).

RESULTS

The size distributions were similar between foraging grounds (Fig. 2). At Tortuga Bay, SCLs ranged from 22.8 to 84.2 cm, averaging 50.5 ± 11.8 cm (mean \pm SD), and the subset data for somatic growth analysis covered all size classes (25.1 to 83.6 cm SCL). At Puerto Manglar, SCLs ranged from 29.6 to 83.1 cm, with a mean of 52.5 ± 11.5 cm, but the growth data did not encompass the lowest and highest size classes (range of data: 34.0 to 73.2 cm SCL). Somatic growth rates ranged from 0.4 to 7.3 cm yr⁻¹, with a mean of 4.2 ± 1.6 cm yr⁻¹, at Tortuga Bay, and from 1.6 to 10.3 cm yr⁻¹, with a mean of 6.1 ± 1.7 cm yr⁻¹, at Puerto Manglar.

Somatic growth dynamics

Table 1 presents the GAMMS tested with respective AIC_c and likelihood ratio (L-ratio) tests. At both sites, GAMMs were significantly improved by the inclusion of random effects to test for individual heterogeneity (Table 1). The significantly best fitting GAMM for both sides excludes 'growth interval' from the growth predictors (Table 1). For Puerto Manglar data, we opted to use the second best fitting GAMM, since there is no significance lost in model fit by including 'sampling year' as covariate, and it provides us with a spline to visually compare results with Tortuga Bay. It is also important to note that our results did not vary, regardless of the GAMMs used.

The GAMM for Tortuga Bay was a good fit ($r^2 = 0.488$); however, the fit of the GAMM for Puerto Manglar was low ($r^2 = 0.199$), suggesting that there is significant variability in the growth data not attributable to the modeled covariates. For both aggregations, the models indicate a significant effect

Table 1. Corrected AIC (AIC_c) and likelihood ratio tests (L-ratio) of generalized additive mixed models (GAMMs) fitted to growth data from 15 yr of capture-mark-recaptures of immature green turtles *Chelonia mydas* at Tortuga Bay and Puerto Manglar foraging grounds, Puerto Rico. df: degrees of freedom; SCL: straight carapace length; FP: fibropapillomas; –: not applicable. **Bold** indicates significant values ($p < 0.05$) in L-ratio tests, as well as the smallest, AIC_c values, which indicate the best fit model

No. GAMMs		Tortuga Bay					Puerto Manglar				
		df	AIC_c	Test	L-ratio	p-value	df	AIC_c	Test	L-ratio	p-value
1	Growth rate ~ SCL + year + interval + FP + individual heterogeneity	10	326.9835	–	–	–	10	437.8288	–	–	–
2	Growth rate ~ SCL + year + interval + FP	9	339.2955	1 vs. 2	14.7952	0.0001	9	441.9154	1 vs. 2	6.4958	0.01
3	Growth rate ~ SCL + year + interval + individual heterogeneity	9	327.9021	1 vs. 3	3.4018	0.0651	9	435.3707	1 vs. 3	0.0488	0.8252
4	Growth rate ~ SCL + year + FP + individual heterogeneity	8	320.8085	1 vs. 4	1.2683	0.5304	8	432.0513	3 vs. 4	0.9565	0.3281
5	Growth rate ~ mean SCL + FP + individual heterogeneity	6	331.2138	4 vs. 5	15.1043	0.001	6	426.8039	4 vs. 5	0.6553	0.7206

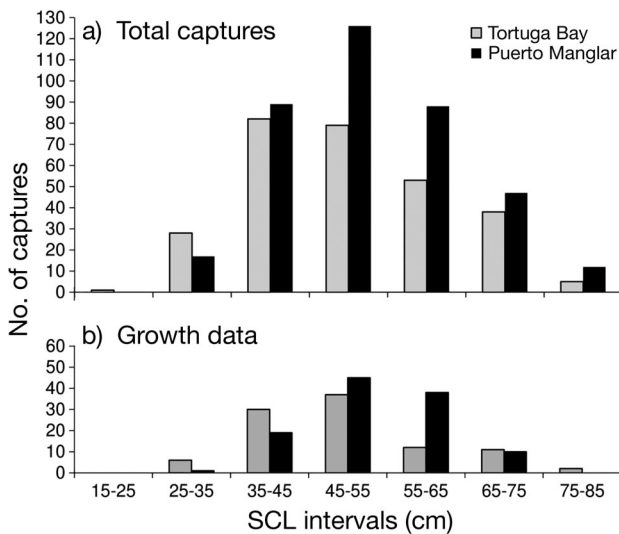


Fig. 2. *Chelonia mydas*. Straight carapace length (SCL) distributions of (a) total green turtle captures, used for abundance estimation ($n = 665$), and (b) green turtle captures used for somatic growth analyses ($n = 233$), throughout 15 yr of capture-mark-recaptures (1997 to 2011) at Tortuga Bay and Puerto Manglar foraging grounds, Culebra, Puerto Rico

of size on somatic growth, with monotonic size-specific growth rates declining continuously with increasing SCL (Fig. 3a,b). At Tortuga Bay, somatic growth rates declined faster at approximately ≥ 55 cm SCL, whereas at Puerto Manglar, the size-specific growth rate function was linear. At Tortuga Bay, there was also a significant effect of sampling year (Fig. 3c, Table 2) on somatic growth, with 2 minima in 2004 and 2009. The presence of FP had no significant effect on growth rates at either site (Table 2).

From the numerical integration of the expected size-specific growth rate functions (Fig. 4a), we obtained empirical estimates of the expected time in years spent by green turtles at each foraging ground, from recruitment (25 cm SCL) until a maximum size of 80 cm SCL was reached. This period is about 17 yr at Tortuga Bay and about 10 yr at Puerto Manglar (Fig. 4b).

Aggregation abundances and abundance trends

Mean annual abundance at each site, along with 95% confidence limits, and respective time-specific growth rate functions derived from the GAMM models were plotted jointly (Fig. 5) to look for any indication of density-dependent effects on somatic growth. We fitted 4 new GAMMs to the Tortuga Bay. Data set including abundance data as a covariate we used abundance in the same year as growth increment, and abundance 1, 2 and 3 years before each growth increment, to test for lag effects of density on growth. There was no significant effect of abundance on somatic growth using either GAMM, nor did either of these GAMMs improve model fit compared to the best model used for growth analyses shown in Table 1 (data not shown). The GLS model detected a positive trend in the abundance of green turtles at Puerto Manglar throughout the 15 yr of study, with a mean annual increase of 10.9% (Table 3). At Tortuga Bay, the abundance seems to have been decreasing since 2001 (Fig. 5a); however, the GLS model detected no significant trend throughout the sampling period (Table 3). We fitted a new GLS model to the Tortuga Bay abundance data, starting in 2001, and again no significant trend was found (data not shown).

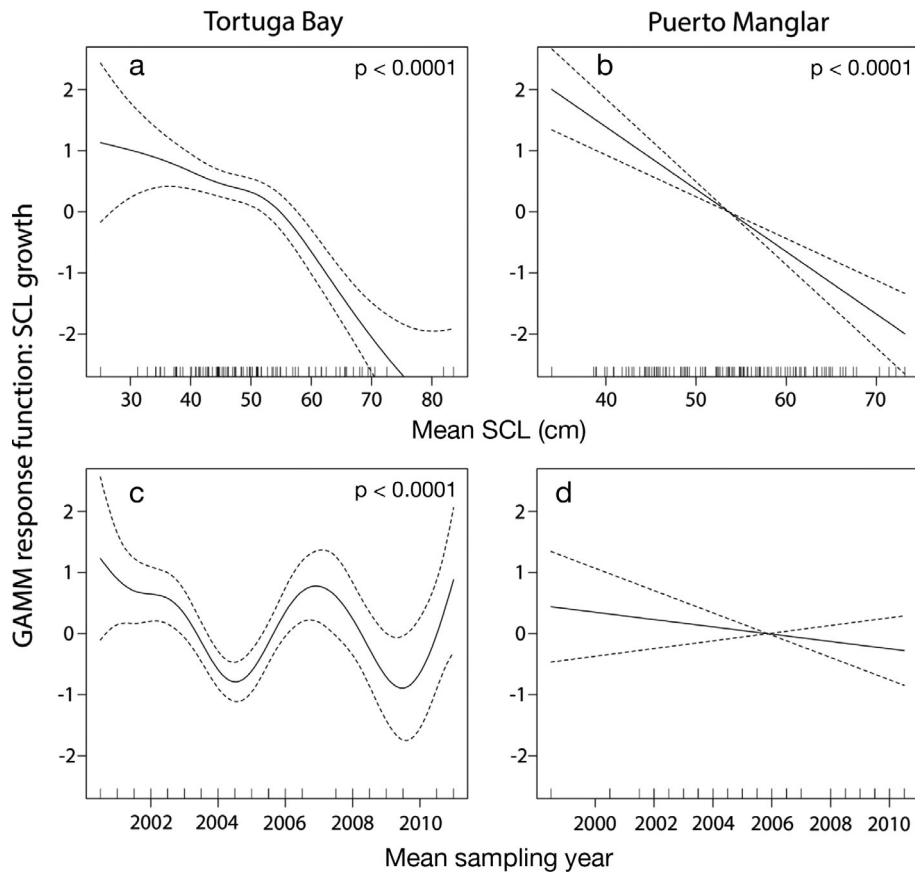


Fig. 3. Graphical summary of generalized additive mixed models (GAMM) fitted to the 15 yr capture-mark-recapture data set. Response variable: annual growth rates of immature green turtles *Chelonia mydas* from Puerto Manglar and Tortuga Bay foraging grounds, Culebra, Puerto Rico. Predictor variables (covariates): (a,b) mean straight carapace length (SCL); (c,d) mean sampling year. Solid lines are cubic smoothing spline fits for each continuous covariate conditioned on all other covariates in the GAMM and dotted curves are pointwise 95% confidence curves around the fits. p-values are displayed where there is a significant effect of the covariate on annual growth rates

Table 2. Summary of generalized additive mixed modeling (GAMM) analyses to model the relationships between annual growth rates of immature green turtles *Chelonia mydas* from Puerto Manglar and Tortuga Bay foraging grounds, Culebra, Puerto Rico (response variables) and mean straight-carapace-length (SCL), mean sampling year and presence of fibropapillomas (FP) (predictor variables or covariates). SE: standard error, df: estimated degrees of freedom of smooth term (1 = linear); -: not applicable; significant values ($p < 0.005$) are shown in **bold**

Term	Tortuga Bay				Puerto Manglar			
	Estimate	SE	<i>t</i>	<i>p</i>	Estimate	SE	<i>t</i>	<i>p</i>
Parametric								
Intercept	5.0083	0.4305	11.633	<0.0001	6.1465	0.3001	20.484	0.0001
FP status	-0.8429	0.4293	-1.964	0.0528	-0.0790	0.3774	-0.209	0.869
		df	<i>F</i>	<i>p</i>		df	<i>F</i>	<i>p</i>
Non-parametric								
Mean SCL (cm)	-	3.398	17.462	0.0001	-	1	36.661	0.0001
Mean sampling year	-	6.610	6.593	0.0001	-	1	0.949	0.332

DISCUSSION

Our study revealed important insights into the biology of the green turtles around Culebra and the

importance of geography and foraging site ecology for somatic growth and abundance. We report the highest mean somatic growth rate for green turtles in the wild and we estimate a minimum age at maturity

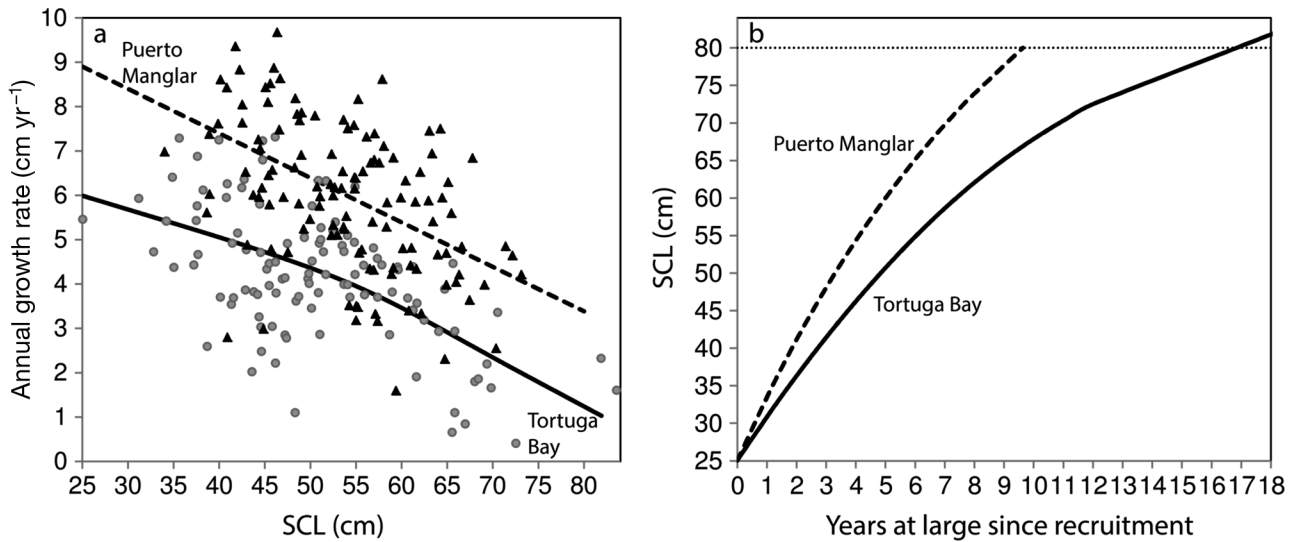


Fig. 4. (a) Expected size-specific growth rate functions and absolute somatic growth rates, and (b) years at large since recruitment until a maximum size of 80 cm straight carapace length, SCL (dotted line) for immature green turtles *Chelonia mydas*, at Puerto Manglar (dashed line, black triangles) and Tortuga Bay (solid line, grey circles) foraging grounds, Culebra, Puerto Rico

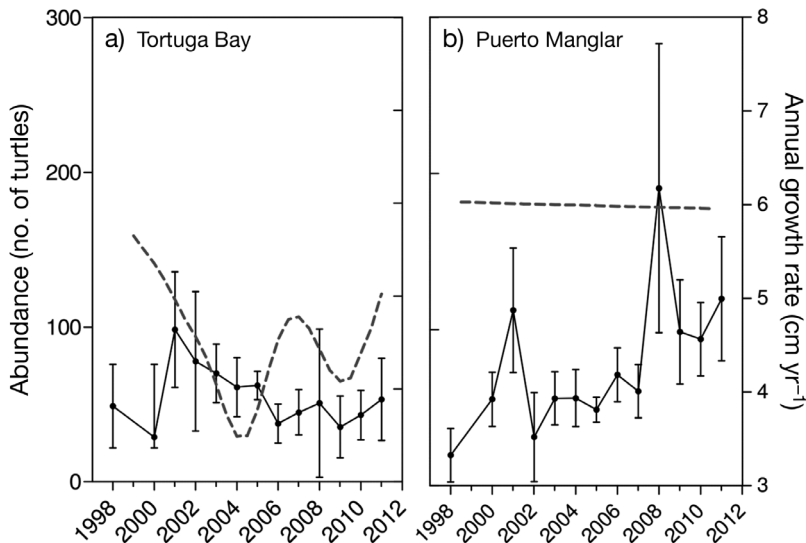


Fig. 5. Abundance (solid line) and expected size-specific growth rate functions (dashed line) of immature green turtles *Chelonia mydas* at (a) Tortuga Bay and (b) Puerto Manglar foraging grounds, Culebra, Puerto Rico, from 1998 to 2011

lower than that widely cited in the literature. (Bjorndal et al. 2000a, Balazs & Chaloupka 2004, Chaloupka et al. 2004, Goshe et al. 2010). This is one of the first of the few analyses of somatic growth of immature green turtles in the Caribbean Sea (see also Bell et al. 2005). Reasonably, our estimates may well be more comparable to other foraging aggregations from the Caribbean than other previously published estimates from less tropical areas.

Early age at maturation

The mean (\pm SD) somatic growth rate at Puerto Manglar was $6.1 \pm 1.7 \text{ cm yr}^{-1}$, significantly higher than that at Tortuga Bay, estimated to be $4.2 \pm$

Table 3. Summary of trend regression analysis (generalized least squares/restricted maximum likelihood) of immature green turtles *Chelonia mydas* from distinct aggregations at Culebra, Puerto Rico. Estimate: parameter estimate for year, equivalent to instantaneous growth rate; SE: standard error of predictor estimate; RSE: model residual standard error; -: not applicable. Mean annual aggregation growth = (estimate - 1) \times 100. LCL and UCL are lower and upper 95% confidence limits for aggregation growth, calculated as (estimate \times 1.96SE - 1) \times 100. Significant values ($p < 0.05$) shown in **bold**; ns: non-significant p-value (at $\alpha = 0.05$)

Foraging ground	Sampling period	Year predictor					Aggregation growth (%)		
		Estimate	SE	t-ratio	p-value	RSE	Mean	LCL	UCL
Tortuga Bay	1997–2011	-0.0160	0.0284	-0.5520	ns	0.1786	0	-	-
Puerto Manglar	1997–2011	0.1036	0.0246	4.2072	0.0015	0.2112	10.9120	5.6873	16.3960

1.6 cm yr⁻¹. Consequently, it likely takes immature green turtles resident at Tortuga Bay ca. 7 yr longer to reach 80 cm SCL than those of Puerto Manglar, although their habitats are only 3 km apart. If we consider that it may take about 3 yr for juvenile green turtles in the Greater Caribbean to recruit to shallow water habitats (Bjorndal et al. 2005, Goshe et al. 2010), green turtles from Tortuga Bay will be around 20 yr old at 80 cm SCL, whereas Puerto Manglar green turtles will only be 13 yr old at that size. No adults have ever been observed at our study areas, hence age at maturity cannot be definitively estimated. However, if we consider a minimum size of 83.2 cm SCL observed for nesting green turtles at Costa Rica and Mexico (Goshe et al. 2010), 2 of the most likely origins for green turtles from our study sites (Velez-Zuazo et al. 2010), we can infer minimum ages at maturity of 22 and 14 yr for Tortuga Bay and Puerto Manglar turtles, respectively. These values are similar to estimates from head-started green turtles from the Cayman Islands (15 to 19 yr, Bell et al. 2005), and much lower than estimates for green turtles from a Bahamian aggregation (over 30 yr, Bjorndal et al. 2000a) and for green turtles stranded along the southeastern US coast (28 yr, Goshe et al. 2010). These differences highlight the potential importance of geographic variability on somatic growth, possibly triggered by higher and constant year-round sea water temperatures. A recent study at St. Joseph Bay, Florida, however, estimated 17 to 20 yr for a juvenile stage comparable to that of this study (18.1 to 78.5 cm SCL, Avens et al. 2012), which is similar to our estimate for Tortuga Bay (17 yr). We hypothesize that the inferior habitat quality of Tortuga Bay (see next section) limits high rates of somatic growth, which may be more typical of warmer tropical waters.

Foraging site specific growth and abundance trends

At a local scale, previous studies have found foraging site specific growth rates, likely as a consequence of habitat quality and availability of food resources (Balazs & Chaloupka 2004, Kubis et al. 2009). The differences observed here between foraging aggregations are also likely attributable to habitat rather than to genetic stock (Velez-Zuazo et al. 2010) or to size distributions, as neither of these aspects differ significantly among sites. Ecologically, the most striking differences between the 2 foraging grounds is the dominance in percent cover of algae and of *Thalassia testudinum* at Puerto Manglar (Diez et al. 2010). Al-

though the seagrasses *Syringodium filiforme* and *Halodule wrightii* are more abundant in Tortuga Bay, this bay has a higher mean percent cover of open sand (Diez et al. 2010). Epiphytes are also more common in Tortuga Bay (Diez et al. 2010), and have been regularly observed here since 2009, sometimes smothering patches of seagrass. Furthermore, Tortuga Bay is a hot spot for recreational boaters that tie up to mooring buoys or anchor on the seagrass beds. Visitors are aware of the sea turtles, which are often the purpose of their visit. Arguably, this bay is a more stressful environment for the green turtles compared to Puerto Manglar, both in terms of potential anthropogenic impacts and of food abundance, which could partly explain the observed differences in somatic growth rates. The GAMM for Tortuga Bay supported a significant impact of mean sampling year on somatic growth rates. We tried to relate the year effect on somatic growth to abundance, and found no significant density-dependent effects (c.f. Bjorndal et al. 2000a). Additional years of CMR data are needed to enable an assessment of the carrying capacity of this foraging ground. Meanwhile, law reinforcement with respect to illegal 'turtle watching' activities and destruction of seagrass beds by continuous anchoring is needed at Tortuga Bay, as well as further monitoring to understand why numbers are staying, at best, stable at this site, despite the increase of green turtles locally and across the Caribbean. At Puerto Manglar, there was a positive trend in aggregation abundance throughout the 15 yr of this study, but no significant fluctuation in somatic growth rates through time was observed. This, along with the high somatic growth rates found, suggests that there is enough food to maintain current mean somatic growth rates at the present aggregation size.

Shifts in the geographic distribution of green turtles in Culebra

Collazo et al. (1992) carried out CMR studies of green turtles at 7 foraging grounds in Culebra from 1987 to 1989. They reported a mean somatic growth rate of 5.08 ± 1.47 cm yr⁻¹ for all surveyed sites, which is similar to our findings. Most surprising was the shift observed in the geographic distribution of green turtles. From 1987 to 1989, Mosquito Bay had the highest abundance of green turtles, with a catch per unit effort (CPUE, expressed as number of turtles caught per net set) of 2.16, followed by Tortuga Bay with a CPUE of 2.04, and Puerto Manglar with a CPUE of 0.86 (Collazo et al. 1992). Mosquito Bay (18.29° N, 65.26° W) is an open bay, located near

Puerto Manglar, facing the mouth of Ensenada Honda, the major bay of Culebra. The seafloor is colonized by abundant seagrass beds. We also surveyed Mosquito Bay during our CMR program, using the same methods as described above, yet green turtle captures at this site were very low throughout the sampling period and insufficient for statistically robust analysis. No green turtles tagged at Mosquito Bay were recaptured at either of our study sites. Why green turtle numbers increased at Puerto Manglar and severely decreased at Mosquito Bay is unknown, as the area does seem suitable for foraging.

Effect of FP on somatic growth

We included FP as a covariate for the somatic growth analyses as FPs are commonly observed at our study sites, and a study at the Hawaiian Archipelago has shown an inverse effect of tumor severity on somatic growth (Chaloupka & Balazs 2005). The fact that neither of the GAMMs supported an effect of FP on somatic growth in this study may result from the case that the majority of turtles with visible FP were only mildly affected. In the future, we hope to collect adequate quantitative data to categorize FP severity and compare results. It is interesting to note, however, that the 2 lowest growth rates in our data set (0.4 and 0.6 cm yr⁻¹) matched 2 turtles severely affected with several FPs.

Comparison with other green turtle aggregations

Somatic growth dynamics found here were similar to those of immature green turtles from the Bahamas (Bjorndal et al. 2000b), with monotonic size-specific growth rates decreasing with SCL. Absolute somatic growth rates are comparable, albeit higher, to those of green turtles from Atlantic foraging grounds at Union Creek, Bahamas (mean somatic growth of 4.2 cm yr⁻¹; Bjorndal et al. 2000a) and from the East Central coast of Florida (range of somatic growth rates of -0.2 to 7.3 cm yr⁻¹; Kubis et al. 2009), while much higher than those found for Pacific green turtles in the Gulf of California, Mexico (mean somatic growth of 1.4 cm yr⁻¹; Seminoff et al. 2002), the Hawaiian Archipelago (range of somatic growth rates of 0 to 2.5 cm yr⁻¹; Balazs & Chaloupka 2004) and the southern Great Barrier Reef, Australia (range of somatic growth rates of 0.5 to ~3.5 cm yr⁻¹; Chaloupka et al. 2004), supporting a difference in somatic growth for the species between these ocean basins.

Conclusions and implications

The conservation status of marine turtles is currently a matter of debate (Broderick et al. 2006, Godfrey & Godley 2008, Seminoff & Shanker 2008). The present classification of the green turtle as globally Endangered by the IUCN Red List (IUCN 2012) seems inadequate, as major rookeries both in the Atlantic and the Pacific Oceans are stable or increasing (Broderick et al. 2006, Chaloupka et al. 2008) and the global population is over 2 million individuals (Broderick et al. 2006). Granting more protection for the species may prove counterproductive, as raising conservation awareness based on the dogmatic statement that the green turtle is near extinction may seem absurd, particularly in high abundance areas. Furthermore, generalizing the conservation status of the green turtle implies that all regions deserve equal conservation efforts, potentially deviating attention from more critical areas (Broderick et al. 2006, Godfrey & Godley 2008). The foraging grounds of green turtles at Puerto Manglar and Tortuga Bay in the Culebra Archipelago are amongst the few areas in Puerto Rico where green turtles are observed in high numbers. Our long-term data set has allowed us to make robust estimates of vital population parameters (Patrício et al. 2011, present study), essential for the local and regional assessment of the conservation status of green turtles. The estimates and trends found here are also of great importance for evaluating the future impact of predicted environmental change.

Finally, the early age at maturity estimated for Puerto Manglar green turtles (14 yr), together with policy decisions concerning major feeding, mating and nesting grounds in the Caribbean (e.g. Nicaragua, Panama and Costa Rica; Troëng & Rankin 2005), could explain the rapid recovery, over the last 3 decades, of the main source populations, Tortuguero, Costa Rica, and Yucatan Peninsula, Mexico (Seminoff 2004), which likely also depend on other similarly productive and warm water developmental areas in the Caribbean.

Acknowledgements. The long-term study at Culebra was achieved thanks to the help of numerous field assistants and volunteers. We especially thank A. Alvarez, C. Carrion, N. Jimenez, G. Olivera, R. Soler, and Y. Vargas. We are also grateful for the constructive commentaries of M. Godfrey, B. Godley and 3 anonymous referees. Research support was provided by the Department of Natural and Environmental Resources of Puerto Rico (DNER), US National Marine Fisheries Service (NMFS-NOAA, Section 6, grant no. NA08-NMF4720436), US Fish and Wildlife Service, Chelonia, and WIDECAST. Work was conducted under permits from the NMFS-NOAA (permit nos. 1253 and 1518-01) and DNER (06-EPE-016).

LITERATURE CITED

- Arthur KE, Boyle MC, Limpus CJ (2008) Ontogenetic changes in diet and habitat use in green sea turtle (*Chelonia mydas*) life history. *Mar Ecol Prog Ser* 362:303–311
- Avens L, Goshe LR, Harms CA, Anderson ET and others (2012) Population characteristics, age structure, and growth dynamics of neritic juvenile green turtles in the northeastern Gulf of Mexico. *Mar Ecol Prog Ser* 458: 213–229
- Balazs GH, Chaloupka M (2004) Spatial and temporal variability in somatic growth of green sea turtles (*Chelonia mydas*) resident in the Hawaiian Archipelago. *Mar Biol* 145:1043–1059
- Bell CDL, Parsons J, Austin TJ, Broderick AC, Ebanks-Petrie G, Godley BJ (2005) Some of them came home: the Cayman Turtle Farm headstarting project for the green turtle *Chelonia mydas*. *Oryx* 39:137–148
- Bjorndal KA, Bolten AB, Chaloupka MY (2000a) Green turtle somatic growth model: evidence for density dependence. *Ecol Appl* 10:269–282
- Bjorndal KA, Bolten AB, Martins HR (2000b) Somatic growth model of juvenile loggerhead sea turtles *Caretta caretta*: duration of pelagic stage. *Mar Ecol Prog Ser* 202: 265–272
- Bjorndal KA, Bolten AB, Chaloupka MY (2005) Evaluating trends in abundance of immature green turtles, *Chelonia mydas*, in the Greater Caribbean. *Ecol Appl* 15:304–314
- Bjorndal KA, Bowen BW, Chaloupka M, Crowder LB and others (2011) Better science needed for restoration in the Gulf of Mexico. *Science* 331:537–538
- Bolten AB (2003) Variation in sea turtle life history patterns: neritic versus oceanic developmental stages. In: Lutz PL, Musick JA, Wyneken J (eds) *The biology of sea turtles*, Book 2. CRC Press, Boca Raton, FL, p 243–257
- Bowen BW, Karl SA (2007) Population genetics and phylogeography of sea turtles. *Mol Ecol* 16:4886–4907
- Bowen BW, Grant WS, Hillis-Starr Z, Shaver DJ, Bjorndal KA, Bolten AB, Bass AL (2007) Mixed-stock analysis reveals the migrations of juvenile hawksbill turtles (*Eretmochelys imbricata*) in the Caribbean Sea. *Mol Ecol* 16:49–60
- Broderick AC, Frauenstein R, Glen F, Hays GC and others (2006) Are green turtles globally endangered? *Glob Ecol Biogeogr* 15:21–26
- Casale P, Mazaris AD, Freggi D, Vallini C, Argano R (2009) Growth rates and age at adult size of loggerhead sea turtles (*Caretta caretta*) in the Mediterranean Sea, estimated through capture-mark-recapture records. *Sci Mar* 73:589–595
- Chaloupka M, Balazs G (2005) Modelling the effect of fibropapilloma disease on the somatic growth dynamics of Hawaiian green sea turtles. *Mar Biol* 147:1251–1260
- Chaloupka M, Balazs G (2007) Using Bayesian state-space modelling to assess the recovery and harvest potential of the Hawaiian green sea turtle stock. *Ecol Model* 205: 93–109
- Chaloupka M, Limpus C (2001) Trends in the abundance of sea turtles resident in southern Great Barrier Reef waters. *Biol Conserv* 102:235–249
- Chaloupka M, Limpus C, Miller J (2004) Green turtle somatic growth dynamics in a spatially disjunct Great Barrier Reef metapopulation. *Coral Reefs* 23:325–335
- Chaloupka M, Bjorndal KA, Balazs GH, Bolten AB and others (2008) Encouraging outlook for recovery of a once severely exploited marine megaherbivore. *Glob Ecol Biogeogr* 17:297–304
- Collazo JA, Boulon R Jr., Tallevast TL (1992) Abundance and growth patterns of *Chelonia mydas* in Culebra, Puerto Rico. *J Herpetol* 26:293–300
- Corbeil RR, Searle SR (1976) Restricted maximum likelihood (REML) estimation of variance components in the mixed model. *Technometrics* 18:31–38
- Diez CE, van Dam RP, Velez-Zuazo X, Torres F, Scharer M, Molina M (2010) Habitat and population assessment of Caribbean green turtle aggregations inhabiting the Culebra Archipelago's coastal waters. In: Dean K, Lopez-Castro MC (eds) *Proc 28th Annu Symp Sea Turtle Biol Conserv*, 2008, NOAA Tech Memo NOAA NMFS-SEFSC, US Department of Commerce, Miami, FL; p 272
- Epperly SP, Braun-McNeill J, Richards PM (2007) Trends in catch rates of sea turtles in North Carolina, USA. *Endang Species Res* 3:283–293
- Godfrey MH, Godley BJ (2008) Seeing past the red: flawed IUCN global listings for sea turtles. *Endang Species Res* 6:155–159
- Goshe L, Avens L, Scharf F, Southwood A (2010) Estimation of age at maturation and growth of Atlantic green turtles (*Chelonia mydas*) using skeletochronology. *Mar Biol* 157: 1725–1740
- Hamann M, Godfrey MH, Seminoff JA, Arthur K and others (2010) Global research priorities for sea turtles: informing management and conservation in the 21st century. *Endang Species Res* 11:245–269
- Heppell SS, Snover ML, Crowder LB (2003) Sea turtle population ecology. In: Lutz PL, Musick JA, Wyneken J (eds) *The biology of sea turtles*, Book 2. CRC Press, Boca Raton, FL, p 275–306
- Herbst L, Ene A, Su M, Desalle R, Lenz J (2004) Tumor outbreaks in marine turtles are not due to recent herpesvirus mutations. *Curr Biol* 14:R697–R699
- IUCN (International Union for the Conservation of Nature) (2012) IUCN Red List of threatened species. Version 2012.2. www.iucnredlist.org (accessed 20 May 2013)
- Krueger BH, Chaloupka MY, Leighton PA, Dunn JA, Horrocks JA (2011) Somatic growth rates for a hawksbill turtle population in coral reef habitat around Barbados. *Mar Ecol Prog Ser* 432:269–276
- Kubis S, Chaloupka M, Ehrhart L, Brette M (2009) Growth rates of juvenile green turtles *Chelonia mydas* from three ecologically distinct foraging habitats along the east central coast of Florida, USA. *Mar Ecol Prog Ser* 389:257–269
- Lahanas PN, Bjorndal KA, Bolten AB, Encalada SE, Miyamoto MM, Valverde RA, Bowen BW (1998) Genetic composition of a green turtle (*Chelonia mydas*) feeding ground population: evidence for multiple origins. *Mar Biol* 130:345–352
- Lebreton JD, Burnham KP, Clobert J, Anderson DR (1992) Modeling survival and testing biological hypothesis using marked animals: a unified approach with case-studies. *Ecol Monogr* 62:67–118
- Loery G, Nichols JD, Hines JE (1997) Capture-recapture analysis of a wintering Black-capped Chickadee population in Connecticut, 1958–1993. *Auk* 114:431–442
- Neyman J, Pearson ES (1933) On the problem of the most efficient tests of statistical hypotheses. *Philos Trans R Soc Lond B Biol Sci* 231:289–337
- NMFS-NOAA (1998) Designated critical habitat; green and hawksbill sea turtles. *Fed Reg*: 63 FR 46693, p 46693–46701

- Patrício AR, Velez-Zuazo X, Diez CE, van Dam R, Sabat AM (2011) Survival probability of immature green turtles in two foraging grounds at Culebra, Puerto Rico. *Mar Ecol Prog Ser* 440:217–227
- Pinheiro JC, Bates D, DebRoy S, Sarker D (2006) nlme: linear and nonlinear mixed effects models. R package version 3.1-98. R Foundation for Statistical Computing, Vienna. <http://cran.r-project.org/web/packages/nlme/index.html>
- R Development Core Team (2008). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. www.r-project.org
- Reich KJ, Bjørndal KA, Bolten AB (2007) The 'lost years' of green turtles: using stable isotopes to study cryptic lifestages. *Biol Lett* 3:712–714
- Reisser J, Proietti M, Kinas P, Sazima I (2008) Photographic identification of sea turtles: method description and validation, with an estimation of tag loss. *Endang Species Res* 5:73–82
- Schofield G, Katselidis KA, Dimopoulos P, Pantis JD (2008) Investigating the viability of photo-identification as an objective tool to study endangered sea turtle populations. *J Exp Mar Biol Ecol* 360:103–108
- Seber GAF (1982) The estimation of animal abundance and related parameters, 2nd edn. Griffin, London
- Seminoff JA (Southwest Fisheries Science Center, US) (2004) *Chelonia mydas*. In: IUCN 2012. IUCN Red List of threatened species, Version 2012.2. www.iucnredlist.org (accessed 10 May 2013)
- Seminoff JA, Shanker K (2008) Marine turtles and IUCN Red Listing: A review of the process, the pitfalls, and novel assessment approaches. *J Exp Mar Biol Ecol* 356:52–68
- Seminoff JA, Resendiz A, Nichols WJ, Jones TT, Guyer C (2002) Growth rates of wild green turtles (*Chelonia mydas*) at a temperate foraging area in the Gulf of California, México. *Copeia* 2002:610–617
- Sugiura N (1978) Further analysis of the data by Akaike's information criterion and the finite correction. *Comm Statist Theory Methods* 42:713–726
- Troëng S, Rankin E (2005) Long-term conservation efforts contribute to positive green turtle *Chelonia mydas* nesting trend at Tortuguero, Costa Rica. *Biol Conserv* 121: 111–116
- Varghese SP, Varghese S, Somvanshi VS (2010) Impact of tuna longline fishery on the sea turtles of Indian seas. *Curr Sci* 98:1378–1384
- Velez-Zuazo X, Diez CE, van Dam RP, Torres-Velez FJ (2010) Genetic structure and origin of a juvenile aggregation affected by fibropapillomatosis: potential impact on adult recruitment. In: Dean K, Lopez-Castro MC (eds) *Proc 28th Annu Symp Sea Turtle Biol Conserv*, 2008, NOAA Tech Memo NOAA NMFS-SEFSC, US Department of Commerce, Miami, FL, p 272
- Wallace BP, DiMatteo AD, Hurley BJ, Finkbeiner EM and others (2010) Regional Management Units for marine turtles: a novel framework for prioritizing conservation and research across multiple scales. *PLoS ONE* 5: e15465
- White GC, Burnham KP (1999) Program MARK: survival estimation from populations of marked animals. *Bird Study* 46:S120–S139
- Wood SN (2001) mgcv: GAMs and generalised ridge regression for R. *R News* 1:20–25

Editorial responsibility: Matthew Godfrey, Beaufort, North Carolina, USA

*Submitted: February 7, 2013; Accepted: October 11, 2013
Proofs received from author(s): January 9, 2014*