

Population parameters of green turtle adult males in the mixed ground of Atol das Rocas, Brazil

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ABSTRACT: While there is an established and expanding body of literature on population trends of sea turtle nesting females, studies focusing on male sea turtles are only recent (although they have increased over the past 10 yr). Filling this gap is important for understanding sea turtle population dynamics. We provide the first estimates of demographic parameters of adult males from the mixed ground of Rocas Atoll, an important breeding and feeding ground for green turtles in the South Atlantic. Abundance estimates were obtained from a 5 yr mark-recapture effort between 2003 and 2007 using open-population models. Annual abundance estimates varied from 86 to 146, and the total estimated number of males that used the area within the study period was 294 individuals (superpopulation). Differences among estimates indicate a transient pattern (i.e. marked individuals that were never recaptured) and highlight open population dynamics, where there is a mix of transient and resident animals using the area for breeding and/or feeding. Most recaptures occurred in consecutive years or in 2 yr intervals, indicating some level of site fidelity. A similar pattern also influenced apparent survival estimates, with annual survival varying between 0.47 and 0.51 when considering transients and residents, and between 0.78 and 0.80 when considering only residents. It was not possible to evaluate population trends based on the 5 yr mark-recapture data, as robust projections would require 18 yr of monitoring with comparable effort. Therefore, understanding the open dynamic of this population requires a long-term monitoring effort, and is critical for understanding the role of Rocas Atoll in the conservation and management of green turtles in the South Atlantic.

KEY WORDS: Mark-recapture · Population modeling · Breeding ground · South Atlantic

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1. INTRODUCTION

Many sea turtle populations have declined to critical sizes in the last decades (Jackson 1997) due to global threats related to human activities, such as habitat degradation, direct harvest, incidental mortalities from fishing by-catch and marine pollution (e.g. Carranza et al. 2006, Wallace et al. 2010), stressing the urgent need for conservation and manage-

ment actions (Mazaris et al. 2014). Most of these efforts, however, have focused on nesting beaches and their adjacencies around the world (e.g. Frazer 1992), protecting primarily nesting females and their eggs (e.g. Marcovaldi & Marcovaldi 1999, Trøng et al. 2005, Bellini et al. 2013). Studies on foraging grounds and migratory routes have also enhanced our understanding of habitat use and the link between breeding and foraging sites, and helped to

identify critical conservation areas, either for resident populations or to maintain connectivity among populations and protected areas (Makiwski et al. 2006, Schofield et al. 2013, Pendoley et al. 2014, Dujon et al. 2018). Combining these strategies has led to successful conservation outcomes (Mazaris et al. 2014, 2017) with long-term increases in the abundance of females and the number of nests (Hays 2004, Chaloupka et al. 2008). On the other hand, in addition to the well known overexploitation in breeding grounds since prehistory, fishing activities overlapping with feeding and breeding areas have also caused population declines (Spotila et al. 2000, Lewison et al. 2004).

Sea turtles, such as *Chelonia mydas* (green turtle), are typical migratory species, traveling between their breeding and feeding areas (Hawkes et al. 2011, Pendoley et al. 2014). After numerous cases of historical overexploitation (Chaloupka et al. 2008), many populations are considered relictual (McClenachan et al. 2006). Life history traits such as longevity, slow growth, and delayed sexual maturity drive concern and require long-term effort to assess the status of the populations and evaluate the effectiveness of conservation programs (e.g. Marcovaldi & Chaloupka 2007). The migratory dynamic of marine turtles also jeopardizes a proper identification of populations, especially in feeding grounds—requiring the application of mixed stocks analyses, which are increasingly common and accessible (e.g. Proietti et al. 2009, Read et al. 2015, Shamblin et al. 2018). Individuals within populations can use multiple foraging sites or overlap with other feeders from different genetic stocks (Hays et al. 2002, Godley et al. 2003, Naro-Maciel et al. 2007, 2012, Proietti et al. 2009, Schofield et al. 2013, Shamblin et al. 2015). Fidelity to nesting grounds is well known in the literature, but recent studies also indicate high levels of fidelity to migratory corridors and key foraging sites (Broderick et al. 2007, Schofield et al. 2013, Pendoley et al. 2014, Bradshaw et al. 2017).

Natal philopatry is widely recognized for female sea turtles (Karl et al. 1992) and a recent study comparing mtDNA of green turtles from Rocas Atoll, Southwestern Atlantic, suggests that males may also have some level of natal philopatry (Naro-Maciel et al. 2012). However, because turtles can mate during migration (Encalada et al. 1996, FitzSimmons et al. 1997), adult males may have a major role in the gene flow within and among different reproductive areas (Karl et al. 1992, FitzSimmons 1998, Roberts et al. 2004, Schofield et al. 2010). If this is a valid assumption, then monitoring the trends of adult males can be

as critical as understanding the dynamic of females. While there is a massive body of literature describing population trends of nesting female sea turtles (e.g. Bjørndal et al. 1999, Balazs & Chaloupka 2004, Bellini et al. 2013, Mazaris et al. 2017), for adult males, recent literature has only covered migratory routes, reproductive periodicity, survival, and abundance (e.g. Schofield et al. 2010, 2013, Arendt et al. 2012, Hays et al. 2014).

Precise estimates of abundance and survival rates are critical for conservation goals (Sutherland 2000), and modern mark-recapture models allow the elucidation of multiple population aspects, such as the tendency to return to a previously occupied location (site fidelity, sensu Switzer 1993), migration, and habitat effect (Williams et al. 2002). Mark-recapture sampling is an effective and widely used approach to assess multiple population parameters of various species (e.g. O'Hara et al. 2009, Rowat et al. 2009, Sharma et al. 2010, Cantor et al. 2012), including sea turtles, despite the unexpectedly few examples in the scientific literature (e.g. Chaloupka & Limpus 2001, Chaloupka & Balazs 2007, Eguchi et al. 2010, Colman et al. 2015). For most of the existent studies, logistical challenges regarding species home range, life cycle, use of remote areas, and long-distance migrations are among the main constraints affecting the development of robust mark-recapture studies (e.g. Chaloupka & Limpus 2001, Hays et al. 2010, Cantor et al. 2012).

Rocas Atoll is the only atoll in the South Atlantic. It is a foraging ground for juveniles and figures as the second largest breeding colony of *Chelonia mydas* in Brazilian waters (mean annual number of nests = 335, range = 136–563; Bellini et al. 1996, 2013). With a unique coralline-algal formation, the Biological Reserve of Rocas Atoll was the first Marine Protect Area in Brazil. It was established in the late 70s but has been effectively enforced since the 90s (Bellini et al. 1996, 2013, Gherardi & Bosence 2001, Longo et al. 2015). The local complexity presents a challenge for understanding the dynamics of the green turtle population, but also an opportunity to gain novel insights into regional subpopulations since this remote oceanic area may be visited by sea turtles coming from different breeding grounds. This complex scenario, which is allied to constant loss (emigration and deaths) and addition (immigration and births) to the green turtle population, constrains the assessment of precise population parameters and explains the lack of effort that has been made in this direction. Filling this gap is critical for monitoring the trend of this local subpopulation effectively and for

making inferences about regional stocks of this species in the South Atlantic. Rocas Atoll is a privileged natural laboratory allowing assessment of adult green turtle populations and exploration of several aspects of their ecology and behavior, including breeding events. In contrast to juvenile sea turtles that are commonly observed in the Atoll during the entire year, adult males and females are only abundant during the breeding season (December to January; M. B. Silva pers. obs.).

We applied the Cormack-Jolly-Seber (CJS) and Jolly-Seber (JS) open population models—based on the POPAN formulation—to explore a 5 yr mark-recapture database of adult male green turtles at Rocas Atoll. The POPAN Jolly-Seber model (Arnason & Schwarz 1999) has been used to estimate abundance of migratory species because the ‘super-population’ estimate considers both resident individuals in the breeding or feeding ground and transient individuals on a migratory route (e.g. Carroll et al. 2011). We modeled abundance estimates for each year and the entire period, also assessing survival and entrance probabilities, reproductive periodicity and site fidelity. Monitoring green turtles at Rocas Atoll may offer valuable insights into the species dynamics in the South Atlantic.

2. MATERIALS AND METHODS

2.1. Study area

Rocas Atoll is located 144 miles off the Brazilian coast (03° 52' S, 33° 49' W) and 80 miles west of the Fernando de Noronha Archipelago (Fig. 1), a region influenced by the South Equatorial Current that originates in Africa (Stramma & England 1999). The Atoll is on top of the east–west chain of submarine mountains, which define the fracture zones of Fernando de Noronha, rising from a depth of 1000 m to the surface. The Biological Reserve covers an area of 36 000 ha, and the atoll ring consists primarily of calcareous algae and mollusks (Kikuchi & Leão 1997). The ellipsoidal structure (reef ring) forms pool systems (see Longo et al. 2015 for details) surrounded by 2 permanent islands of 7.2 km² covered by natural vegetation and divided by 2 channels connecting the internal reef lagoon with the sea. The proximity with

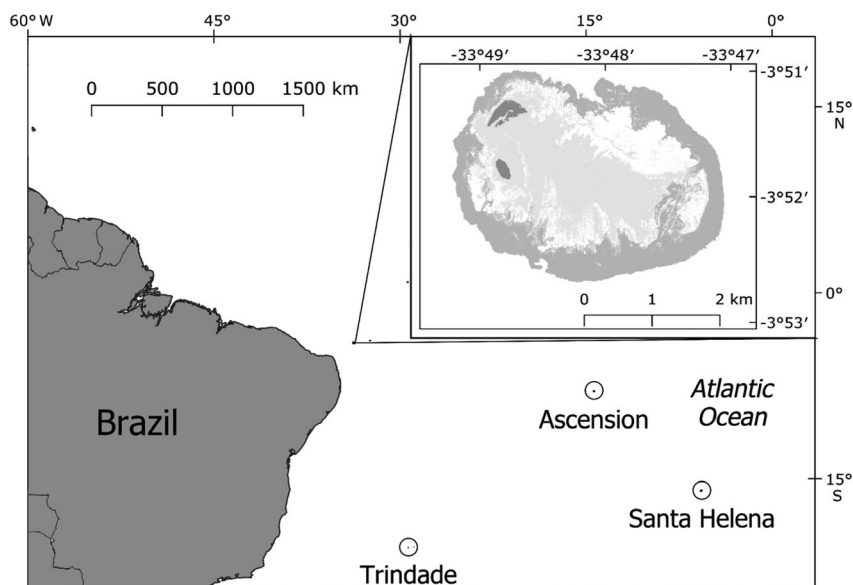


Fig. 1. The main green turtle *Chelonia mydas* rookeries in the South Atlantic (circles), with Rocas Atoll (Atol das Rocas) in detail

the equator promotes large tidal fluxes of up to 4 m between high and low spring tides (Kikuchi & Leão 1997).

2.2. Field procedures

From 2003 to 2007, we conducted 28 d research expeditions every year during December and January, which is the breeding season and when mating pairs of adult green turtles can be observed in the Atoll (Bellini et al. 1996, 2013). We conducted systematic dives at different depths inside (from 0.5 to 7 m) and outside the Atoll (from 5 to 25 m) to capture male green turtles by ‘turtle rodeo’ (Limpus 1993). The sampling effort was evenly distributed spatially (same sites every year) and seasonally (same number of days) and was conducted by the same number of trained divers (3 out of the 4 divers in the fieldwork team participated together every year). We identified adult males as all individuals with minimum carapace size around 100 cm and with developed secondary sexual characteristics (i.e. longer nails and tail; see Limpus 1993). For each capture, we took morphometric data such as curved carapace length (CCL) and width (CCW), and weight when possible (see Grossman et al. 2007). All animals captured for the first time were double marked with 2 Inconel flipper tags (Balazs 1999), while recaptured animals were recognized based on these uniquely coded tags. For each sampling campaign (year), we added a colorful ribbon to the flipper tag to indicate the animals

previously captured in that year. Thus, we did not recapture an animal twice within a year.

2.3. Modeling procedures

We applied mark-recapture models to our 5 yr database of adult male green turtles in Rocas Atoll (2003 to 2007). Field effort was grouped in a calendar year and each year corresponds to a capture occasion. To evaluate the sampling effort and speculate on the open or closed population dynamic, a cumulative curve based on the number of individuals captured was generated using the rarefaction method (Gotelli & Colwell 2001), resampling (1000 iterations) the capture occasions using the Monte Carlo randomization approach. The expected curve was a function of the number of samples (Mao Tau) and built using the software EstimateS (<http://purl.oclc.org/estimates>). Considering the local dynamic, we used open population models, such as CJS to evaluate model assumptions and to estimate apparent survival probabilities (ϕ) and capture probabilities among years (p) (Lebreton et al. 1992). Each year represented a single capture occasion. Additionally, we estimated abundance (N) and entrance probability (pent) for each year using the POPAN JS formulation (Schwarz & Arnason 1996). This approach considers the 'superpopulation' concept, where N_T corresponds to the total number of animals that occurred in the study area between the first and last capture occasion (Williams et al. 2002). Thus, the parameter pent represents the likelihood of an individual from the 'superpopulation' returning to the study area.

Considering the species biology and our sampling effort, we built a set of models to evaluate the following effects on the parameters estimated: (1) time effect (t) and 'time-since-marking' (tsm) effect on the survival (ϕ) and capture probabilities (p); and (2) cohort effect (cohort) on capture probabilities (p). The 'time-since-marking' (tsm) models incorporate transience effects in the model structure, by estimating survival for the year after the initial capture occasion and between the second and following years of sampling (Evans et al. 2015). Therefore, 'tsm' models estimate survival probabilities for 2 classes: (1) the whole population (combining transients and residents), which is biased by the proportion of transient individuals in the population—confounding death and emigration; and (2) only for individuals seen more than once in the area (residents), which is the true survival rate for the population. For POPAN models, we also evaluated the time effect (t) and 'tsm'

effect on the survival (ϕ) and capture probabilities (p), but only time effect (t) on entrance probabilities (pent). The absence of effect was notated as (.).

2.4. Model assumptions

The main assumptions for open population models (e.g. CJS and JS) include: (1) every marked animal present in the population at period x has the same recapture probability; (2) every marked animal present at period x has the same probability of surviving to period $x + 1$; (3) marks are not lost during the study; (4) all migrations are permanent; (5) individuals are immediately released after capture and the sampling procedure is instantaneous; (6) the fate of marked and released animals is independent of the fate of any individual (Williams et al. 2002). Violation of these assumptions causes extra-binomial noise (overdispersion) and generates biased estimates (Williams et al. 2002). We measured overdispersion to investigate the violation of assumptions (1) and (2) using the goodness-of-fit (GOF) test (TEST 2 and TEST 3 in the program RELEASE; Burnham et al. 1987). The variance inflation factor (\hat{c})—an extra-binomial noise measure—was then estimated by bootstrapping with 1000 iterations (White & Burnham 1999). Where \hat{c} was >1 , we used the estimated value to adjust the models. For the POPAN formulation, we estimated \hat{c} using the GOF chi-square divided by the degree of freedom.

2.5 Model selection procedures

We used the Akaike's Information Criterion (AIC) values to select the most parsimonious models (Anderson et al. 1994). Because AIC behaves poorly in overdispersion cases (Anderson et al. 1994), where the variance inflation factor (\hat{c}) has been adjusted due to extra-binomial noise, we used the Quasi-likelihood Akaike's Information Criterion (QAIC), which is an adaptation for overdispersion cases (Burnham & Anderson 2002). The Likelihood Ratio Test (LRT) was used to test specific biological hypotheses among nested models. When there was uncertainty in the selection of the most appropriate model, we used the average of the parameter estimates across all models based on the AIC weights (Burnham & Anderson 2002). All analyses and modeling of population estimate parameters were performed using the software MARK (White & Burnham 1999).

2.6. Trends and the monitoring program evaluation

We fitted a linear model to evaluate trends in the abundance estimates over the 5 yr. Because sea turtles have a long lifespan, late sexual maturity, and migratory behavior, and most adults use Rocas Atoll as a temporary breeding area, we expected that our 5 monitoring years would not be enough to detect significant trends. Therefore, we used the software Trends (Gerrodette 1993) to conduct a power analysis to assess the sensitivity of our monitoring effort to detect changes in abundance of animals using the area. For this analysis we assumed a probability of Type I and II errors of 5% and 20%, respectively (the value routinely used by managers), used a 1-tailed test (the focus here is a decreasing trend); used a coefficient of variance (CV) proportional to the square root of abundance (as recommended for mark-recapture data, Gerrodette 1987), used an exponential model, and assumed a Student's *t*-distribution. As the CVs were constant when plotted against the square root of abundance (see Gerrodette 1987), we used an overall CV for the whole study period, averaging the annual CVs (0.32).

3. RESULTS

3.1. Descriptive data

There were 181 capture events during which 136 individuals were tagged and 30 recaptured. The CCL and CCW of males at initial capture were 105 ± 5 cm (mean \pm SD; $N = 129$) and 97 ± 5 cm ($N = 127$), respectively, while their weight was 133.86 ± 16.10 kg ($N = 37$; see Grossman et al. 2007). The mean number of captures per year was 35.8 ± 9.58 , varying from 47 in 2003 to 26 in 2006 (Fig. 2a). Even though no clear pattern was evident in the capture number over the years, there was a slight increase in recapture. Most recapture events occurred over consecutive years (60%) or with a 1 yr interval in-between (33%). The sample-based rarefaction curve for species accumulation (Mao Tau) considering new individuals in each year did not stabilize, indicating an open population dynamic (Fig. 2b).

3.2. CJS models

The GOF test result suggested extra-binomial noise from our data (cumulative result of TEST 3; $p = 0.03$), showing the violation of assumption (2), or

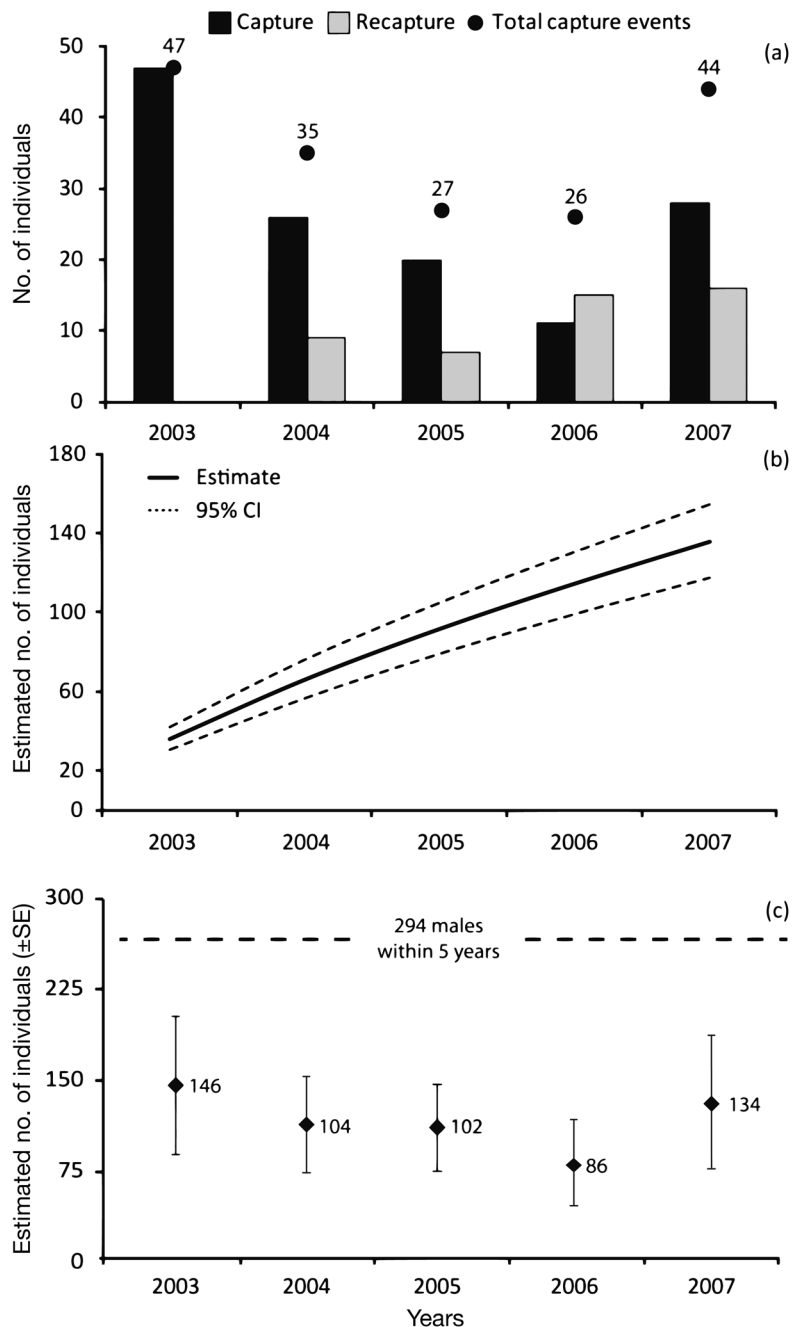


Fig. 2. (a) Captures (black bars), recaptures (gray bars) and total capture (black circles) events of adult male green turtles *Chelonia mydas* in each field trip to Atol das Rocas Marine Biological Reserve. (b) Sample-based rarefaction curve (Mao Tau) of cumulative individual captures. The Mao Tau estimates (black curve) and the 95% confidence intervals (dashed curves) are shown. (c) Estimated number of individuals per year based on POPAN Jolly-Seber formulation for males

unequal survival probabilities. From evaluating the details in TEST 3, we observed a significant variation between the fourth and fifth occasions (year). In contrast, assumption (1) of equal capture probability was not violated (TEST 2 not significant). The \hat{c} value estimated by bootstrapping was 1.90. Although this value indicates non-substantial overdispersion, we used it to adjust the models.

According to $QAIC_c$, the most parsimonious CJS model indicated a 'tsm' effect on survival rates ($\varphi(\text{tsm})$) and constant capture probabilities ($p(\cdot)$; Table 1). However, the 'tsm' effect was not confirmed by the LRT test ($p > 0.05$), which combined with the $\Delta QAIC_c$ (i.e. differences in $QAIC_c$ scores) values may suggest uncertainty in model selection. Therefore, we used the averaging approach to estimate the parameters of interest. Considering the average of the models, the survival probability (φ) for the first class (likely combining transient and resident individuals) varied from 0.47 ± 0.11 (mean \pm SE) to 0.51 ± 0.13 . For the second class (likely resident individuals), the survival estimate varied from 0.78 ± 0.13 to 0.80 ± 0.14 . The capture probability ranged from 0.34 ± 0.11 to 0.14 ± 0.13 .

3.3. JS models

The GOF test for POPAN models showed a similar result to that of the CJS models (Table 2). We therefore fitted the models using the same \hat{c} value (1.90) estimated previously. The most parsimonious model was fitted by the 'tsm' effect in survival probability ($\varphi(\text{tsm})$), and constant capture-probability ($p(\cdot)$). The parameters were adequately identified only when we fixed the time effect in the entrance probability ($\text{pent}(t)$). Even though Model 2 also supports the data, the best-fitted model was 2-fold more parsimonious ($\Delta QAIC_c < 3$; according to Burnham & Anderson 2002). Therefore, we used the averaging approach to estimate the parameters of interest.

Survival probability (φ) varied significantly between 'tsm' classes, being 0.47 ± 0.13 (mean \pm SE) for the first (likely combining transients and residents) and from 0.72 ± 0.12 to 0.75 ± 0.13 for the second (likely residents). Capture probability (p) was constant, from

Table 1. Selection of Cormack-Jolly-Seber candidate models for survival probability (φ) and capture probability (p). Models are ranked by the corrected Quasi-likelihood Akaike's Information Criterion ($QAIC_c$) values. $QAIC_c$ weight indicates how much support the selected model has over the others. N. Par: no. of parameters. Notation: (\cdot) constant; (t) time-dependence; (tsm) time-since-marking effect; (cohort) cohort effect

ID	Model	$QAIC_c$	$\Delta QAIC_c$	$QAIC_c$ weight	Likelihood	N. Par
1	$\{\varphi(\text{tsm})p(\cdot)\}$	132.101	0.000	0.457	1.000	3
2	$\{\varphi(\cdot)p(\cdot)\}$	133.823	1.722	0.193	0.423	2
3	$\{\varphi(\text{tsm})p(\text{cohort})\}$	134.436	2.335	0.142	0.311	6
4	$\{\varphi(\text{tsm})p(t)\}$	135.325	3.224	0.091	0.200	6
5	$\{\varphi(t)p(\cdot)\}$	136.354	4.254	0.054	0.119	5
6	$\{\varphi(t)p(t)\}$	137.327	5.227	0.033	0.073	7
7	$\{\varphi(\cdot)p(t)\}$	137.574	5.474	0.030	0.065	5

Table 2. Selection of POPAN (formulation) candidate models for survival probability (φ), capture probability (p) and entrance probability (pent). Models are ranked by the corrected Quasi-likelihood Akaike's Information Criterion ($QAIC_c$) values. $QAIC_c$ weight indicates how much support the selected model has over the others. N. Par: no. of parameters. Notation: (\cdot) constant; (t) time-dependence; (tsm) time-since-marking

ID	Model	$QAIC_c$	$\Delta QAIC_c$	$QAIC_c$ weight	Likelihood	N. Par
1	$\{\varphi(\text{tsm})p(\cdot)\text{pent}(t)\}$	163.87	0.00	0.53	1.00	8
2	$\{\varphi(\cdot)p(\cdot)\text{pent}(t)\}$	164.99	1.12	0.31	0.57	7
3	$\{\varphi(t)p(\cdot)\text{pent}(t)\}$	167.54	3.67	0.09	0.16	10
4	$\{\varphi(\text{tsm})p(t)\text{pent}(t)\}$	168.49	4.62	0.05	0.10	12
5	$\{\varphi(\cdot)p(t)\text{pent}(t)\}$	171.07	7.20	0.01	0.03	11
6	$\{\varphi(t)p(t)\text{pent}(t)\}$	172.72	8.85	0.01	0.01	14

0.32 ± 0.09 to 0.37 ± 0.09 , while the entrance probability (pent) ranged from 0.03 ± 0.06 to 0.24 ± 0.07 (Table 3). The total number of individuals that used the study area during the monitoring years ('super-population') was estimated to be 287 ± 56 .

3.4. Abundances and trends

The derived parameter B_i , which represents the number of males that returned in each period, varied from 9 individuals to 70 (occasions 4 and 5, respectively). The estimated abundance of males for each

Table 3. Summary of the parameters estimated from the POPAN formulation for each year. φ : survival probability; p : capture probability; pent : entrance probability

Year	φ estimate (\pm SE)	p estimate (\pm SE)	pent estimate (\pm SE)
2003		0.37 ± 0.09	
2004	0.47 ± 0.13	0.35 ± 0.10	0.11 ± 0.09
2005	0.72 ± 0.12	0.32 ± 0.09	0.09 ± 0.08
2006	0.75 ± 0.13	0.32 ± 0.09	0.03 ± 0.06
2007	0.73 ± 0.14	0.33 ± 0.10	0.24 ± 0.07

Table 4. Summary of the derived parameters estimated from the POPAN Jolly-Seber formulation for each year. B_i : number returned; N_i : abundance; LCI: lower confidence interval; UCI: upper confidence interval

Year	B_i estimate	SE	LCI	UCI	N_i estimate	SE	CV	LCI	UCI
2003					146	48	0.33	35	257
2004	33	27	-26	93	104	33	0.32	33	175
2005	27	23	-25	79	102	30	0.29	40	164
2006	9	17	-28	46	86	28	0.32	28	143
2007	70	29	11	129	134	46	0.34	38	229

year varied from 86 individuals on occasion 4 to 146 on occasion 5 (Table 4; Fig. 2c), showing a fluctuation without any defined trend (Fig. 2c). The fact that the 'super-population' estimate for the 5 yr was much higher than the estimates obtained for each year, suggests a high flux in this population (immigration and emigration) and a highly transient pattern. This pattern is corroborated by the rarefaction curve which indicates an open population dynamic (Fig. 2b). This open dynamic generated imprecise abundance estimates, indicating that longer-term efforts are needed to identify significant trends. Indeed, the negative trendline from our regression analysis for the abundance estimates was not significant ($r^2 = -0.24$, $p = 0.66$; Fig. 2c). The power analysis indicates that if we continue with our standard monitoring program, it will require 18 yr of data to detect a decrease/increase of 10 % yr^{-1} with 80 % statistical power.

4. DISCUSSION

This study provides the first estimates of demographic parameters for adult male green turtles from the isolate mixed ground of Rocas Atoll, highlighting: (1) the open population dynamic likely formed by a combination of migrant and resident individuals; (2) the abundance fluctuation among years; and (3) the variability in the survival rates indicating transient and resident individuals. In addition, it provides a monitoring evaluation for further efforts. Although our results show the occurrence of individuals with distinct visit periodicity in the area, indicating a subset of residents and another of transients, our 5 yr study elucidates only part of the system dynamic. Robust projections of population trends would require 18 yr of monitoring with comparable effort. Therefore, the maintenance of similar monitoring effort and, in particular, intensifying effort may clarify population dynamics and the role of Rocas Atoll in migratory events at a regional scale.

4.1. Resident and transient individuals

The occurrence of a time-since-marking (tsm) effect on survival probability, added to the evidence of assumption (2) violation, confirmed that the studied population is an open system, compounded by transient and resident individuals. In such cases, the use of 'tsm' models is recommended to account for the effect promoted by these transient individuals on the estimates (Pradel et al. 1997). A combination of evidence corroborates the hypothesis of a resident subset of individuals.

This subset of individuals are not necessarily year-round residents but may comprise individuals with breeding site fidelity. The same individuals were recorded at the Atoll with a 1 to 2 yr interval between capture events, which has also been observed in a green turtle population in Australia (e.g. Chaloupka & Limpus 2001). There were multiple captures of the same males at the same site in different seasons, which has also been reported by similar studies (Balazs 1980, Limpus 1993, Hays et al. 2014). Previous opportunistic captures of adult males at Rocas Atoll (since 1990) have indicated that at least 8 individuals were recaptured 7 to 10 yr after the first capture (A. Grossman pers. obs.). In fact, a recent study indicated that male and female green turtles at Rocas Atoll share similar haplotypes, suggesting male philopatry (Naro-Maciel et al. 2012). The absence of large aggregations of males during non-breeding seasons, as observed at Rocas Atoll, can be interpreted as evidence of breeding site fidelity (Balazs 1980), as males may be migrating to adjacent areas after the breeding season (e.g. Arendt et al. 2012). In contrast, the cumulative curve of capture indicates that several new individuals are captured in each year, likely using the area temporally. Such a transient pattern may be due to the subset of individuals that occasionally visit the area as a route for migration and feeding. We emphasize that these transients can also visit the area multiple times, at longer intervals than our 5 yr effort can detect.

The high incidence of short remigration events and high rate of males returning to the area in consecutive years may indicate an annual reproductive activity of males. Similar results were previously reported for male green turtles in different grounds (e.g. Limpus 1993; Balazs, 1983, Hays et al. 2014), while females seem to return with a periodicity of 2 to 4 yr (Mortimer & Portier, 1989), including at Rocas Atoll, where the mean observed remigration period is around 3.5 yr (Bellini et al. 2013). Recent evidence, based on satellite telemetry, indicates that males

breed more frequently than females, likely because their body condition is less affected during breeding seasons, in contrast to females that invest a lot of energy in producing and releasing eggs (Hays et al. 2014). This short periodicity of males in the area may be a combination of the residency pattern of some individuals, the high frequency of transient individuals, or resident males who do not breed every year. Differences in reproductive periodicity between males and females generate more balanced operational sex ratios, which may be an important strategy for adapting to the female-skewed offspring predicted for sea turtle populations given climate changes (Hays et al. 2014). Indeed, males are also philopatric to natal regions in their choice of breeding grounds (FitzSimmons et al. 1997). The mtDNA haplotype frequencies of males and females are similar at feeding grounds within the Great Barrier Reef (FitzSimmons et al. 1997) and the mixed ground of Rocas Atoll (Naro-Maciel et al. 2012), suggesting that male behavior has strong parallels to that of females regarding natal philopatry. Likewise, males and females may commonly overlap feeding grounds and migratory behaviors, which potentially results from selective pressures to ensure their co-occurrence in mating grounds (FitzSimmons et al. 1997).

4.2. Survival and abundance estimates

The annual survival estimates varied between classes of a 'time-since-marking' model, indicating the effect of transient and resident patterns. The lower estimate (0.47) is surely biased by individuals captured in the study during temporary visits of migratory events, confounding mortality with permanent emigration. In contrast, the higher estimates (0.72 to 0.75) represent the survival probability for just the subset of resident individuals. Even so, these higher survival probabilities are considerably lower than the estimates for other areas (e.g. Bahamas: 0.89, Bjornndal et al. 2003; Great Barrier Reef: 0.95, Chaloupka & Limpus 2005; Tortuguero: 0.85, Troëng et al. 2005; San Diego Bay: 0.87, Eguchi et al. 2010). Two hypotheses may explain these survival estimates for the green turtles in Rocas Atoll. Even when the effect of transient individuals (tsm models) is included in survival estimates, different degrees of residency and site fidelity patterns may influence survival negatively, confusing temporary emigration, or individuals with low periodicity in the area, with mortality. This study period, for example, may not have been long enough to detect entire reproductive cycles of

adult males. However, biological effects on survival, such as high mortality promoted by natural causes or by anthropogenic factors in adjacent breeding or feeding grounds, as well as during their migratory routes, must also be considered. Because adult male green turtles from Rocas Atoll may have originated from multiple breeding sites, monitoring these survival rates in the future may provide critical information on green turtles in the South Atlantic. For further monitoring efforts, however, incorporating the probability of temporary emigration in modeling procedures (a Robust Design approach; see Kendall et al. 1997) is strongly recommended to generate more reliable survival estimates and a better understanding of the local dynamic (see Eguchi et al. 2010).

The abundance estimates fluctuated from 86 to 146 adult males and our 5 yr monitoring effort did not have enough power to detect a significant trend—18 yr of monitoring with comparable effort are required to detect population changes. The open system dynamic and the modeling approach we used produced relatively imprecise estimates in comparison to other studies (e.g. Eguchi et al. 2010), and yet highlight some biological patterns. The fluctuation among years may be the result of variation in the probability of entry and not a direct response to mortality processes (as observed in 2006). The probability of entry is a combination of the probability of occasional visits of transient animals on migratory routes and the probability of the return of individuals with site fidelity. The high periodicity and the high number of new individuals each year confirm this dynamic of a local stock composed of a mix of transient and resident animals using the area for breeding and/or feeding. As nesting events and migratory behaviors are influenced by environmental conditions—such as rainfall, sea-surface temperature, marine currents, and the El Niño South Atlantic Oscillation (Limpus & Nicholls 1994)—the number of mating males and migratory visitors might also be related to these factors, potentially explaining the abundance fluctuation throughout the study.

4.3. Future perspectives and conservation implications

Our research provides baseline data needed to fill the information gap on adult male green turtles in mixed breeding and foraging grounds in Brazilian waters. Further monitoring efforts should move towards: (1) the maintenance or intensification of the mark-recapture effort (monthly instead of yearly) to

produce longer time series—but using a Robust Design approach (e.g. Eguchi et al. 2010) to generate precise abundance estimates and clarify the temporary emigration process; (2) the inclusion of juveniles, males and females in mark-recapture efforts; (3) the identification of resident and migrant individuals; (4) the assessment of male genetic structure over time; and (5) the use of satellite telemetry on adult males to understand residency and migratory patterns. Clarifying the population dynamics is a key element for the maintenance of conservation and management plans for this species in the South Atlantic.

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