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Effect of body size on the long-term reproductive output of eastern Atlantic loggerhead turtles *Caretta caretta*

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ABSTRACT: We assessed the relationship between body size and several important life history parameters to understand the demographic significance of interpopulation variability in the body size of loggerhead turtles *Caretta caretta* nesting on Boa Vista Island (Cabo Verde). The adult growth rate (0.34 ± 0.60 cm yr^{-1}), annual mortality rate (0.13, 95% CI: 0.12–0.15) and remigration interval (3.1 ± 1.2 yr) were independent of curved carapace length (minimum curved carapace length [CCLmin]). Conversely, the body condition index decreased significantly with female CCLmin. The clutch size, mean egg mass, mean hatchling straight carapace length and mean hatchling mass increased significantly with female CCLmin. However, there was no relationship between female size and hatching success. Randomization and bootstrapping were used to incorporate variability when calculating the average individual fecundity over 20 yr, a period that accumulated, on average, 94% of the adult mortality. The overall fecundity during this period increased with carapace length at first maturity (71 cm CCLmin: 815 eggs, 95% CI: 653–863; 80 cm CCLmin: 906 eggs, 95% CI: 822–959; 90 cm CCLmin: 1089 eggs, 95% CI: 926–1415). However, only 8% of the adult females nesting on Boa Vista Island are larger than 90 cm CCLmin, and they produce less than 12% of the total annual egg production. The scarcity of large females might result from a shortage of high-quality foraging grounds where females may reach first sexual maturity at a large carapace length and from the combined effect of a small carapace length at first sexual maturity, low adult somatic growth and high adult mortality.

KEY WORDS: Cabo Verde · Fecundity · Foraging strategies · Intrapopulation variation · Loggerhead sea turtle · West Africa

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1. INTRODUCTION

Intrapopulation variability in foraging and reproductive patterns is widespread in wild animals and has important implications for population dynamics and evolutionary ecology (Charnov 1993, Araújo et al. 2011, Bolnick et al. 2015). Alternative life histories occur when a small group of individuals exploits a narrow subset of the population's ecological niche, or resource base, independently of factors such as age and sex class (Charnov 1993, Bolnick et al. 2003, Araújo et al. 2011). The fitness trade-offs associated

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with predator avoidance (Dingemanse et al. 2007), mate choice (Gross 1982, Charnov 1993) and foraging behaviour (Svanbäck & Bolnick 2007, Horswill et al. 2016) result in a frequency-dependent fitness advantage, usually leading to an evolutionary stable strategy with 2 alternative life histories (Charnov 1993). When this is true, intraspecific competition is the ultimate driver of intrapopulation variability (Vander Zanden et al. 2010, Araújo et al. 2011).

Intrapopulation variability in hard-shelled marine turtles has been suggested to result from both the genetic variability in growth rate (Bjorndal et al. 2013) and the phenotypic response to differences in the quality of adult foraging grounds (Hatase et al. 2002, Eder et al. 2012, Cardona et al. 2014). The post-hatchling juvenile stages of most species of hard-shelled marine turtles are oceanic, and their distribution is strongly determined by currents (Scott et al. 2014, Cardona & Hays 2018). Late immature sea turtles settle in the foraging grounds they will use through the rest of their lives, and the choice results from the interaction between the habitat knowledge gained during the juvenile stage, philopatry and the existence of a migratory ceiling impeding reproductive migrations longer than 2000 km (Hatase et al. 2002, Hays & Scott 2013). As the early juveniles from the same population may follow different drifting trajectories, and that experience determines the choice of the settlement habitat, populations of hard-shelled marine turtles are usually composed of a diversity of habitat and diet specialists (Hatase et al. 2002, Vander Zanden et al. 2010, Zbinden et al. 2011, Eder et al. 2012) with strong fidelity after settlement to foraging grounds (Broderick et al. 2007, Stokes et al. 2015) and foraging strategies (Hatase et al. 2002, Cardona et al. 2017). Nevertheless, foraging ground choice may have a fitness cost, as sea turtles using different foraging grounds may differ in body size (Hatase et al. 2002, Hawkes et al. 2006, Zbinden et al. 2011, Eder et al. 2012, Pikesley et al. 2015), clutch size (Hatase et al. 2002, Zbinden et al. 2011, Eder et al. 2012, Cardona et al. 2014, Ceriani et al. 2017) and hatchling quality (Hatase et al. 2002, Vander Zanden et al. 2010, Vieira et al. 2014).

The Cabo Verde archipelago supports the second-largest nesting aggregation of loggerhead sea turtles *Caretta caretta* in the Atlantic Ocean (Marco et al. 2012a, 2018b, Laloë et al. 2020), although the population has been classified as Endangered by the IUCN because its nesting habitat is concentrated in a small area (Wallace et al. 2011, Casale & Marco 2015). Females nesting in the archipelago exhibit a broad variability in carapace length (71–102 cm minimum curved carapace length [CCLmin]) and foraging strategies (Hawkes et al. 2006, Eder et al. 2012, Cardona et al. 2017, Cameron et al. 2019). Seminal studies using satellite tracking and stable isotope analysis revealed 2 distinct adult foraging strategies on Boa Vista Island, where most adults foraged in the oceanic area between the archipelago and mainland Africa and a smaller fraction of the adult population foraged in the coastal waters of mainland Africa (Hawkes et al. 2006, Eder et al. 2012, Varo-Cruz et al. 2013, Pikesley et al. 2015). More recently, Cameron et al. (2019) suggested that neritic foragers did not nest on the other islands of the archipelago and that oceanic foragers could be split into 2 groups on the basis of their C and N stable isotope ratios.

Independent of the causes for such diversity, clutch size correlates positively with carapace length in the Cabo Verde population (Eder et al. 2012), although females larger than 90 cm are scarce on Boa Vista Island (Hawkes et al. 2006, Eder et al. 2012, Cameron et al. 2019) and virtually missing from other islands (Cameron et al. 2019). The scarcity of large adults in the population is reasonable if the largest individuals were also the eldest or if the foraging grounds resulting in a larger carapace length were scarce (Eder et al. 2012). However, Cameron et al. (2019) challenged the hypothesis that larger sea turtles were neritic foragers and suggested that no relationship exists between foraging behaviour and carapace length. If so, the broad variability in adult carapace length and the scarcity of the individuals with the highest nesting potential are even more surprising. However, clutch size is not the only determinant of fecundity in marine turtles, and the number of nests (NN) per season and the remigration interval (RI) are also highly relevant (Rivalan et al. 2005, Vander Zanden et al. 2014, Ceriani et al. 2015). Nothing is known about the potential effect of carapace length on these parameters in the Cabo Verde population; hence, nothing is known about the potential hidden costs of migration to the more distant foraging grounds off mainland Africa. Survival rate is also a major determinant of the overall fecundity of females, but nothing is known about its relationship to carapace length in Cabo Verde.

This study aims to fill the above knowledge gaps by (1) characterizing the reproductive parameters and the rate of somatic growth of female loggerhead turtles nesting on Boa Vista Island (Cabo Verde archipelago; Fig. 1), (2) evaluating the relationship between female reproductive output and carapace length and (3) assessing the relevance of intrapopulation variability to population fecundity.

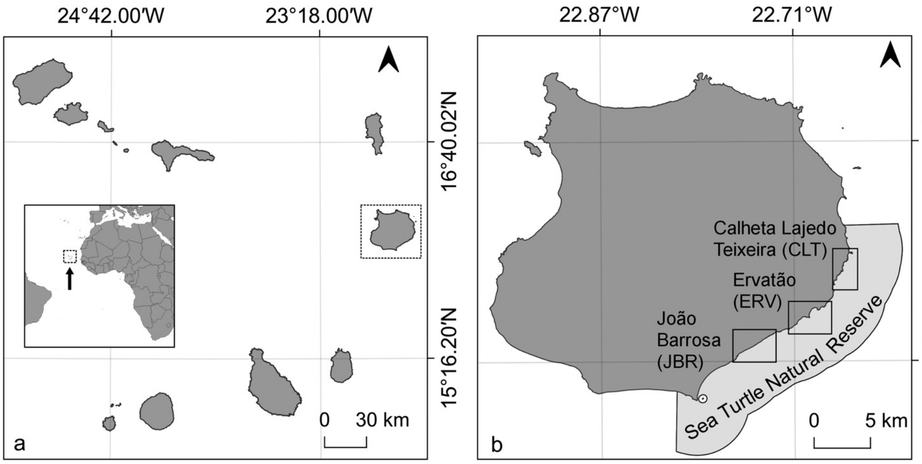

Fig. 1. (a) Cabo Verde islands, West Africa (inset shows the location of the Cabo Verde islands off the coast of West Africa), and (b) Boa Vista (indicated in [a] with dashed box). João Barrosa, Ervatão and Calheta Lajedo Teixeira beaches are in boxes. Light grey area shows the boundaries of the Sea Turtle Natural Reserve

2. MATERIALS AND METHODS

2.1. Study site and sample collection

The study was conducted at the Sea Turtle Natural Reserve (STNR; 16° 02′ N, 22° 45′ W), on the southeastern coast of Boa Vista Island, Cabo Verde archipelago, 450 km off the coast of Senegal (Fig. 1). The STNR is an important nesting area for the loggerhead turtle in the entire eastern Atlantic Ocean and supports more than 50% of total nesting activity of this regional management unit (Marco et al. 2012a, Laloë et al. 2020). The results reported here were collected from 2013 to 2018 at João Barrosa (JBR) Beach, which hosts approximately 25% of the nesting activity in the STNR (Marco et al. 2012a). To assess philopatry, data from a tagging program run from 2005 to 2007 at JBR and 2 other nearby beaches (Ervatão [ERV] and Calheta Lajedo Teixeira [CLT]) were also analyzed.

Every season, from 2013 to 2018, JBR Beach was monitored daily from mid-June to mid-October, coinciding with the loggerhead nesting season. Monitoring was conducted by an experienced supervisor supported by 2 to 4 volunteers; patrolling started at 20:00 h and lasted until around 08:00 h the next morning. When encountering a female, a team member hid behind the sea turtle and observed her behaviour. When the female started laying, a nesting event and the date were recorded. Female identity was checked with an Avid MiniTracker 3 scanner for passive integrated transponder (PIT) tags when she finished camouflaging the nest or started returning to the sea without laying eggs. Untagged females were tagged with an Avid FriendChip PIT tag in the right front flipper, according to the Cabo Verde tagging protocol (Marco et al. 2012b). CCLmin from the nuchal notch to the posterior notch (Bolten 1999) was measured with a flexible measuring tape (accuracy = 0.2 cm). Due to logistical constraints and because some sea turtles become disoriented during handling, only a small portion of the study females were weighed on a 300 kg capacity spring scale (accuracy = 0.1 kg). Body condition was assessed using Fulton's index ($\mathrm{BCI} = W \times \mathrm{CCLmin}^{-3}$, where BCI is body condition index, W is body weight and CCLmin is curved carapace length from notch to notch) (Bolten 1999) to characterize the well-being or fitness of the females (Peig & Green 2010).

Due to the difficulty of monitoring nest emergence onsite, some clutches were relocated to a beach hatchery in JBR to assess hatching success using protocols tested previously (Abella et al. 2007, Martins et al. 2021): $n_{(2013)} = 437$ (17.7% of the clutches laid on the beach), $n_{(2014)} = 443$ (33.9% of the clutches laid on the beach), $n_{(2015)} = 427$ (38.0% of the clutches laid on the beach), $n_{(2016)} = 705$ (18.6% of the clutches laid on the beach), $n_{(2017)} = 1005$ (21.4% of the clutches laid on the beach) and $n_{(2018)} = 1065$ (7.3% of the clutches laid on the beach). All these clutches were reburied in standardized hand-dug cavities that resembled natural nests in shape, size and sand characteristics at a depth of 50 cm, the average for this population (Abella et al. 2007, Marco et al. 2018a, Martins et al. 2021). The time between laying and clutch relocation was always less than 6 h.

Clutch size was assessed in 3 independent ways. First, the number of eggs laid during oviposition in each nest was counted by an observer lying on the ground behind the female. Second, the number of eggs in the clutches relocated to the hatchery was counted again when deployed in the artificial cavities. Third, the number of eggs in the clutches incubated on the beach and the hatchery was assessed after hatchling emergence, by counting the number of dead eggs remaining in the nest and the number of empty egg shells. We randomly selected 30 of the clutches transferred to the hatchery to compare the results of the 3 methods and detected no statistically significant difference in the average clutch size (ANOVA; $F_{2,87} = 0.602$, $p = 0.550$), thus assuming that results were comparable.

To minimize the impact the invasive handling required (drying and cleaning of the eggshell), subsamples of 20 eggs from each of 64 relocated clutches were selected randomly and weighed with a digital scale (Mission Quark Pocket Scales; ±0.1 g).

Hatching success was assessed only for nests translocated to the hatchery. All nests were marked with labelled sticks, and a circular plastic mesh was set on the sand surface above each nest the same night that the clutch was relocated to enable the counting and sampling of hatchlings by trapping them upon emergence. Hatchlings were counted when they emerged from the nest to the beach surface. Furthermore, all the nests were exhumed 3 d after the emergence of the last hatchling or when the incubation duration reached 60 d, following protocols previously tested (Abella et al. 2007, Marco et al. 2018a, Martins et al. 2021). Hatching success was calculated for the clutches relocated to the hatchery by dividing the number of hatchlings by the number of eggs relocated to the artificial cavity and for the clutches incubated on the beach by dividing the number of empty eggshells by the total number of initial eggs (Abella et al. 2007).

Twenty hatchlings from each nest (n = 358) were selected randomly for taking length and weight measurements. The straight carapace length notch to tip from the anterior point at the midline (nuchal scute) to the posterior tip of the supracaudal scute (distal border of the carapace closer to the tail) was measured using a digital calliper (Digital Vernier calliper, 150 mm [6 inch]; ±0.1 mm) (Bolten 1999). Total mass was measured with an electronic scale (Mission Quark Pocket Scales; ± 0.1 g). Handling time did not exceed 15 min, and hatchlings were immediately released.

The annual rate of somatic growth ($GR = (CCLmin_{final} - CCLmin_{initial})$/recapture interval in years) was calculated for 754 adult females measured in at least 2 different years (Chaloupka & Limpus 1997, Bjorndal et al. 2000). For females measured in more than 2 different years, data from the most distant years were used for this analysis. Negative and zero growth rates were included in the analyses to avoid bias linked to measurement error, which leads to overestimation of the growth rate (Chaloupka & Limpus 1997, Bjorndal et al. 2000, 2013, Casale et al. 2009, Omeyer et al. 2018). The effect of carapace abrasion (Bell & Pike 2012, Omeyer et al. 2018) was avoided by measuring CCLmin.

A nesting event was considered when a clutch was deposited. RI was calculated for 449 females as the number of years elapsed between 2 consecutive nesting seasons. The length of the internesting interval (IN) was calculated for 1052 tagged females as the number of days elapsed between 2 consecutive nesting events of each female within a single season (Broderick et al. 2003). Intervals ≥22 d were excluded, because it was assumed that clutches laid between 2 observed clutches had been missed. Sea surface temperature (SST) data downloaded from http://seatemperature.info were correlated with each IN.

The estimation of the egg biomass (EB, kg) produced by each female during the nesting season was calculated by multiplying the number of eggs registered for each female (NE) during the nesting season by the mean egg mass (g) estimated for 3 arbitrary size classes of females (CCLmin: <80, 80–89 and ≥90 cm). The reproductive effort (RE, %) was estimated for 100 females as the percentage of EB with respect to the female body mass during each nesting season (Rivalan et al. 2005, Ceriani et al. 2015).

Note that sea turtles were not tagged to saturation and that no female was instrumented with PIT tags at the beginning of the nesting season. As a result, the NN detected for each female was likely much lower than the actual NN laid in a season. For that reason, NE was calculated for 514 females that have been successfully tracked during at least 4 consecutive nesting events in the same season. NE was calculated by adding the clutch sizes of each of the clutches laid for every female during a given nesting season (Gerrodette & Taylor 1999, Varo-Cruz et al. 2007).

To estimate annual mortality (and survival) rates, we first attempted a capture–recapture analysis of all females encountered and tagged during the period 2013 to 2019. Initial Cormack-Jolly-Seber goodness of fit tests showed a transience effect (test3.sr, chi-squared = 22.66, $p < 0.001$) possibly attributable to a combination of tagging below saturation, imperfect detection, individual remigrations after 2019 and low-level true transience. We also found a trap awareness effect (test2.ct, chi-squared = 65.56, $p < 0.001$), likely due to the low probability of remigration in immediately consecutive years (i.e. few individuals with RI = 1 yr). We explored multiple recommended model structures to adequately account for these statistical effects and putative causes (e.g. but not limited to Genovart & Pradel 2019, Pradel & Sanz-Aguilar 2012), yet given the available data, we were unable to find a well-converged model that provided plausible estimates for all model parameters that required inclusion. Instead, to estimate mortality directly from our data set, we use a simpler method calculating mean annual mortality rate (AM) and instantaneous mortality rate (Z) for each of 3 size classes above reported (<80, 80–89 and ≥90 cm). Z was estimated as $Z = [\ln(N_0) - \ln(N_6)]/6$, where N_0 is the number of females of each size class tagged in 2013 and N_6 is the number of females still alive in 2019, and AM was estimated as $AM = 1 - e^{Z}$. As sea turtles do not nest every year and some of the turtles tagged in 2013 were not recaptured until 2019, all the females nesting at least once from 2014 to 2019 were considered to be alive at the end of the study period (2019). On the other hand, the probability that a female dispersed to a different nesting area was estimated using the data of the tagging program run in 2005 to 2007 simultaneously at JBR and 2 nearby beaches (ERV and CLT), located 4 and 8 km, respectively, to the east of JBR (Fig. 1). We computed both the proportion of turtles tagged at ERV and CLT shifting to JBR during the same season and in subsequent seasons. We focused on the turtles recaptured at JBR because sampling effort was much lower at ERV and CLT and the probability of recapture much lower. Bootstrapping of 1000 populations of each class size was used to assess the 95% CIs. The size of each simulated population was the same as that in the original sample (n = 99 for turtles <80 cm CCLmin, n = 400 for turtles 80–89 cm CCLmin and n = 44 for turtles ≥90 cm CCLmin), which resulted in looser credible intervals for the smaller and larger class sizes.

2.2. Data analysis

Generalized additive mixed model (GAMM) analysis was used to evaluate the non-linear relationship between the response variable (GR) and the covariates (recapture interval and CCLmin). Detailed descriptions of the GAMM application can be found in previous studies on sea turtle growth (Chaloupka & Limpus 1997, Casale et al. 2009, Bjorndal et al. 2013, Omeyer et al. 2018).

Two-way ANOVA was conducted to test the influence of year (2013–2018) and approximate fortnights (30 or 31 d in a month) within each year (data were grouped by fortnight with 6 levels: jul1 = first half of July, jul2 = second half of July, aug1 = first half of August, aug2 = second half of August, sep1 = first half of September and sep2 = second half of September). Pearson linear correlation (data with normal distribution) was used for the evaluation of the relationship between pairs of quantitative parameters. Prior to testing, all data were checked for normality using Shapiro-Wilk's test and for homogeneity of variance using Levene's test. Data were transformed as $\log(x + 1)$ to ensure normality when necessary.

All statistical analyses were conducted using the R packages tidyverse, gamm4, ggplot2, MuMIn, nlme and mgcv (Wood 2003, 2004, Wickham 2016, 2017, Wood & Scheipl 2017, Pinheiro et al. 2018, Barton 2019) in R v.3.5.0 software (R Core Team 2020).

Finally, the average fecundity of females reaching sexual maturity at 71, 80 and 90 cm CCLmin over a 20 yr period was computed to integrate the effect of mortality rate and clutch size. The 95% CI was assessed through bootstrapping. The first step was to simulate 1000 virtual populations of each class size composed of 100 turtles. The average RI was assumed to be 3.12 yr, which results in 6 nesting seasons in 20 yr. For simplicity, all the females in each population were expected to nest on years t_0, t_4, t_8, t_{12}, t_{15} and t_{19}. Other patterns are possible. All females were assumed to lay 5 nests per year, independently on carapace length (Varo-Cruz et al. 2007), and grow at the same rate (0.34 cm yr^{-1}). Contrarily, clutch size was assumed to increase with carapace length, as detailed in Fig. S1 in the Supplement at www.int-res.com/articles/suppl/n048p175_supp.pdf. In the third step, the number of nesting seasons over 20 yr was assigned to each turtle. Finally, life expectancy was assigned to each turtle, according to the mortality rate calculated for each size class (see Section 3). The 2.5% higher and lower estimates of the average fecundity over 20 yr of 1000 virtual samples of oceanic and neritic turtles were removed to calculate the average and the 95% CI of each group.

3. RESULTS

3.1. Body length and body condition

Data were compiled from 5438 different tagged loggerhead females detected while nesting at JBR Beach from 2013 to 2018 (Fig. 2). The annual number

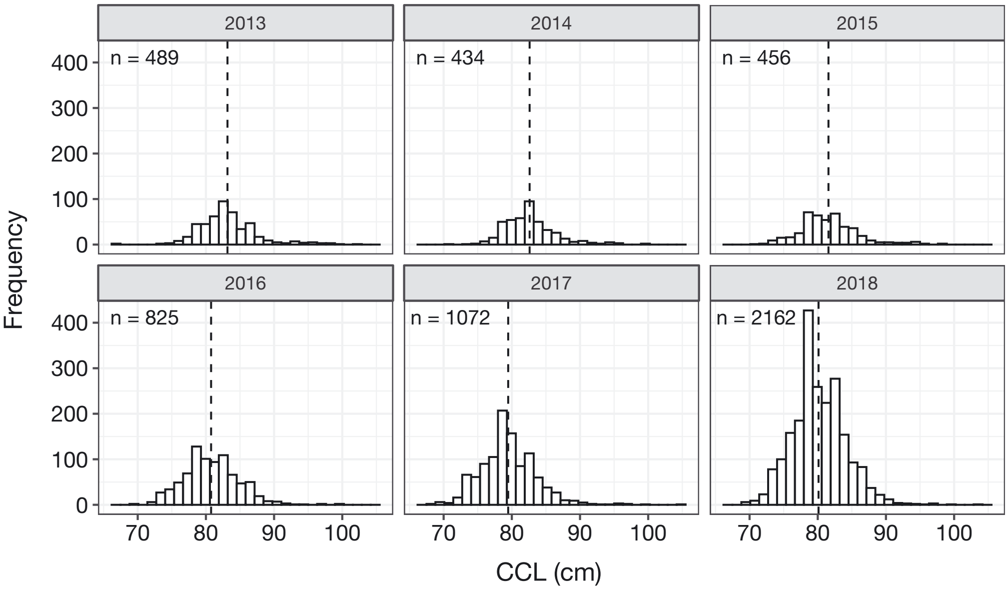

Fig. 2. Length–frequency distribution and number of female loggerhead turtles nesting at the Sea Turtle Natural Reserve at João Barrosa Beach (Boa Vista Island, Cabo Verde archipelago) from 2013 to 2018. Vertical dashed lines represent the mean. Sampling effort was similar every year, so changes in sample size reflect changes in nesting intensity. CCL: curved carapace length

Table 1. Summary statistics of ANOVA to assess changes in turtle body size (minimum curved carapace length) through the nesting season and across sampling years. The nesting season was split into 6 periods of 15 d each (fortnight)

	SS	df	MS	*F*	p
Intercept	797264.86	1	797264.86	49711.50	<0.001
Fortnight	525.86	5	105.17	6.56	<0.001
Year	1325.49	5	265.10	16.53	<0.001
Fortnight × year	798.25	25	31.93	1.99	0.002
Error	86636.38	5402	16.04		

of nesting females increased remarkably throughout the study period, although sampling effort was similar every year. The carapace length of the nesting females varied throughout the study period and throughout each nesting season, as revealed by the 3 statistically significant terms (fortnight, year and fortnight × year interaction) in the 2-way ANOVA (Table 1). Post hoc tests revealed a decreasing trend in the average carapace length of nesting females throughout the study period (Figs. 2 & 3) and during each individual nesting season, except in 2014 (Fig. 3).

The body mass of the nesting females ranged from 42 to 116 kg (mean = 64 kg, SD = 11.95, n = 464) and was strongly and positively correlated with CCLmin (r = 0.86, t = 36.04, df = 462, p < 0.001). However, BCI decreased significantly with CCLmin (r = −0.310; t = 6.076, df = 337, p < 0.001). Repeated measurements of body mass in the same female within the same year (n = 42) showed that BCI decreased significantly during the nesting season (t = 3.45, df = 24, p = 0.002; first capture = 1.19, SD = 0.08; recapture = 1.13, SD = 0.08). When the data (first capture and recaptures) of all the turtles sampled in 2014, 2015 and 2016 were pooled, BCI decreased from early July to late August and increased again in September (ANOVA test: $F_{5,458}$ = 7.70, p < 0.0001; Fig. 4). There was no statisti-

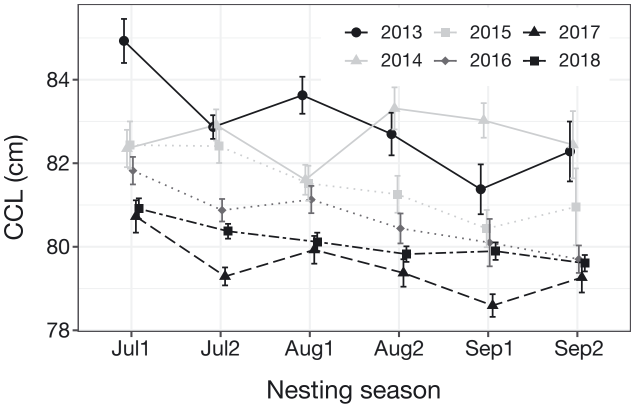

Fig. 3. Changes in loggerhead female mean curved carapace length (CCL) throughout the nesting season at the Sea Turtle Natural Reserve at João Barrosa Beach (Boa Vista Island, Cabo Verde archipelago) from 2013 to 2018. Jul1 = first half of July, Jul2 = second half of July, etc. Data from June and October were not included due to the small sample size. Error bars represent SE

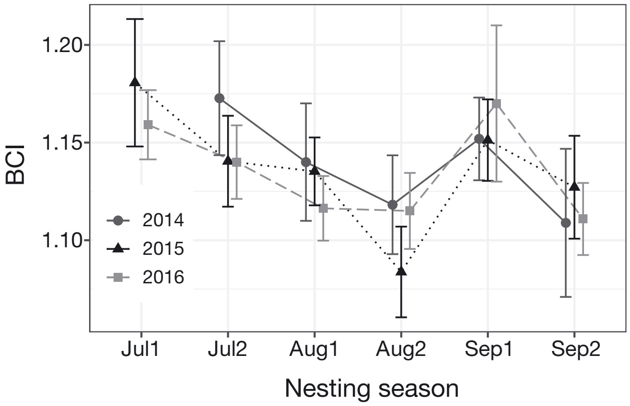

Fig. 4. Body condition index (BCI) throughout the nesting season of loggerhead females at the Sea Turtle Natural Reserve at João Barrosa Beach (Boa Vista Island, Cabo Verde archipelago). Nesting season designations as in Fig. 3. Error bars represent SE

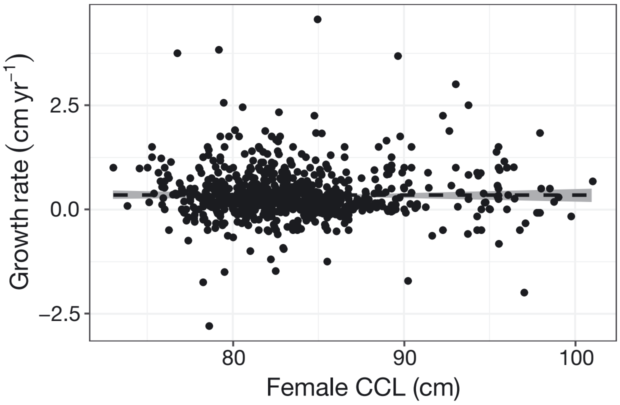

Fig. 5. Female curved carapace length (CCL) and annual growth rate of female loggerhead turtles at the Sea Turtle Natural Reserve (STNR) at João Barrosa Beach (Boa Vista Island, Cabo Verde archipelago). The dashed line shows the average and the grey area the 95% CI band, respectively

cally significant interaction between year and season (fortnight) on BCI when controlling for CCLmin ($F_{9,293}$ = 0.257, p = 0.985), thus suggesting that the seasonal pattern was year invariant.

3.2. Growth rate

Most of the females were recaptured only once (n = 691), with several turtles captured twice (n = 12), 3 times (n = 41), 4 times (n = 1) or 6 times (n = 1). The average mean growth rate was 0.34 cm yr^{-1} (SD = 0.60; range = −2.80 to 4.56 cm yr^{-1}). Growth rate was independent of body size and depended on the recapture interval (Table 2, Fig. 5).

3.3. Beach fidelity and survival rate

We tagged 1296 different adult females at ERV and CLT from 2005 to 2007, of which 233 were found nesting at JBR from 2005 to 2019. There were no significant differences across size classes in the level of beach fidelity (ERV-JBR: chi-squared test: χ^2 = 1.03, df = 2, p = 0.599; CLT-JBR: chi-squared test: χ^2 = 0.77, df = 2, p = 0.682); hence, the probability of moving to another beach for nesting was assumed to be independent of carapace length.

All the turtles tagged at JBR in 2013 and detected nesting at JBR from 2014 to 2019 (180 of 544 tagged females) were assumed to be alive at the end of the study period, because the RI can be as long as 6 yr (see below) and most turtles were detected only once. Any turtle tagged at JBR in 2013 and not detected from 2014 to 2019 could be dead or have shifted to another nesting beach. The probability of emigrating to other beaches for nesting was estimated from the beach fidelity data set described above. We first removed from the analysis the 91 turtles that moved to a distinct beach within the same nesting season of tagging. We later restricted the analysis to the 6 nesting seasons following tagging, as this is the length of the study period at JBR. This revealed that 10% of the turtles tagged on one beach migrated to a different beach over a period of 6 yr after tagging. Accordingly, 10% of the turtles tagged in 2013 at JBR had probably nested elsewhere from 2014 to 2019 and hence were alive but undetected at JBR. When these additional turtles were added to those observed nesting at JBR at least once, the AM of the whole population was 0.13 (95% CI: 0.12–0.15). When split

Table 2. Summary of generalized additive mixed model (with robust quasi-likelihood error term and cubic smoothing splines) fitted to minimum curved carapace length (CCLmin) growth rate (cm yr^{-1}) of adult females of loggerhead sea turtles *Caretta caretta* on Boa Vista Island, Cabo Verde Republic. Null deviance = 0.778, null df = 0.279, residual deviance = 1.483, residual df = 0.385, R^2 = 0.05. df: estimated degrees of freedom; RI: remigration interval

Parameter	Estimate	SE	*t*	p	Nonlinear effect		
					df	*F*	p
Intercept	0.318	0.017	18.764	<0.0001			
Mean CCLmin	−0.012	0.058	−0.201	0.235	2.206	1.594	0.219
RI	0.069	0.039	−1.777	0.023	1.003	3.163	0.008

by size classes, the AM was 0.12 (95% CI: 0.08–0.15) for turtles >90 cm CCLmin, 0.13 (95% CI: 0.12–0.15) for turtles 80–90 cm CCLmin and 0.13 (95% CI: 0.12–0.18) for turtles <80 cm CCLmin. Credible intervals were broad and encompassed the average of the 3 size classes. Thus, differences between size classes were not statistically significant, and only 6% of the turtles in each cohort were still alive 20 yr after first sexual maturity (95% CI: 5–9%).

3.4. Individual reproductive output

The average RI was 3.12 yr (SD = 1.15, range = 1–6). Body size and RI were uncorrelated (r = –0.05, p = 0.252, n = 447). Females nesting in 2 consecutive nesting seasons were on average 91.0 cm CCLmin (SD = 4.62, range = 84.0–98.0 cm, n = 12), whereas females nesting every 2, 3 and 4 yr did not differ in carapace length (2 yr: 83.0 cm CCLmin [SD = 5.71, range = 79.0–99.0 cm, n = 166]; 3 yr: 2.30 cm CCLmin [SD = 4.95, range = 75.5–100.5 cm, n = 104]; 4 yr: 83.7 cm CCLmin [SD = 5.25, range = 76.0–98.0 cm, n = 95]).

The observed average NN per female in a season was 1.44 (SD = 0.75, range = 1–6) and did not differ between size classes (Table 3). Nevertheless, this value clearly underestimates the actual NN due to the logistical challenges of detecting every nesting event. Previous research on Boa Vista Island reported 5 nests per female per season (Varo-Cruz et al. 2007), and this is the average NN per female per season used for calculations here.

The mean IN was 14.83 d (SD = 2.33, range = 9–21 d; n = 729; Fig. S2) and independent of CCLmin (ANCOVA: $F_{2,1096}$ = 0.123, p = 0.883) but decreased throughout the season (Fig. S2; ANCOVA: $F_{2,1096}$ = 19.51, p < 0.001). There was, however, a statistically significant interaction between year and fortnight ($F_{6\,1096}$ = 9.08, p < 0.001). This is because the duration of the IN decreased steadily from early July to early August and then stabilized in 2013, 2015, 2016 and 2017 but decreased steadily from early July to early September in 2014 and 2018. This might reveal inter-annual differences in SST, as the IN was strongly and negatively correlated with SST off Boa Vista Island (r = –0.94, R^2 = 0.88, *t* = –5.39, df = 4, p = 0.005).

The overall mean clutch size was 83 eggs (SD = 15.81, range = 22–151 eggs, n = 4979), but larger females laid significantly more eggs per clutch (r = 0.61, *t* = 7.02, df = 83, p < 0.001; Fig. 6a). Clutch size decreased throughout the nesting season, independently of female carapace length (Fig. S1). The estimated mean of the total number of eggs laid per season was 359 (SD = 11) for females <80 cm CCLmin, 418 (SD = 33) eggs for females 80–90 cm CCLmin and 477 (SD = 28) for females >90 cm CCLmin.

Mean egg mass showed a positive and statistically significant correlation with female CCLmin (Pearson correlation: r = 0.50, df = 62, p < 0.0001; Fig. 6b). Female body size (CCLmin) was also positively correlated with mean hatchling size (r = 0.50, *t* = 5.26, df = 83, p < 0.0001; Fig. 6c) and mean hatchling mass (r = 0.56, *t* = 6.19, df = 83, p < 0.0001; Fig. 6d). However, there was no relationship between female size and hatching success (67.5 ± 30.4%; r = –0.01, *t* = –0.43, df = 1094, p = 0.670).

3.5. Overall reproductive output

Only 6% (95% CI: 5–9%) of the turtles in each cohort survived for 20 yr after first sexual maturity, as reported in Section 3.3. On average, females observed nesting for the first time when they were 90 cm CCLmin laid 1089 eggs in 20 yr (95% CI: 926–1415), those observed nesting for the first time when 80 cm CCLmin laid 906 eggs in 20 yr (95% CI: 822–959) and those observed nesting for the first time when 71 cm CCLmin laid 815 eggs in 20 yr

Table 3. Summary statistic of ANOVA to assess differences between size classes in body mass, remigration interval (RI), number of nests (NN), egg mass and reproductive effort (RE). Means with differing superscript letters are significantly different at the p < 0.05 level, based on Tukey's HSD post hoc paired comparisons

Parameter	<80 cm		80–89 cm		≥90 cm		*F*	df	p
	Mean	SD	Mean	SD	Mean	SD			
Body mass (kg)	55.4^{A}	4.49	63.9^{B}	6.41	97.7^{C}	10.9	407.6	2,336	<0.0001
RI (yr)	2.96^{A}	1.01	3.26^{B}	1.18	2.55^{A}	1.18	10.1	2,446	<0.0001
NN (n)	1.37	0.67	1.45	0.76	1.54	0.84	1.73	2,137	0.179
Egg mass (g)	38.1^{A}	2.21	39.3^{A}	2.03	42.5^{B}	1.48	13.65	2,82	<0.0001
RE (%)	5.74	1.09	5.39	0.72	5.04	0.51	2.14	2,82	0.124

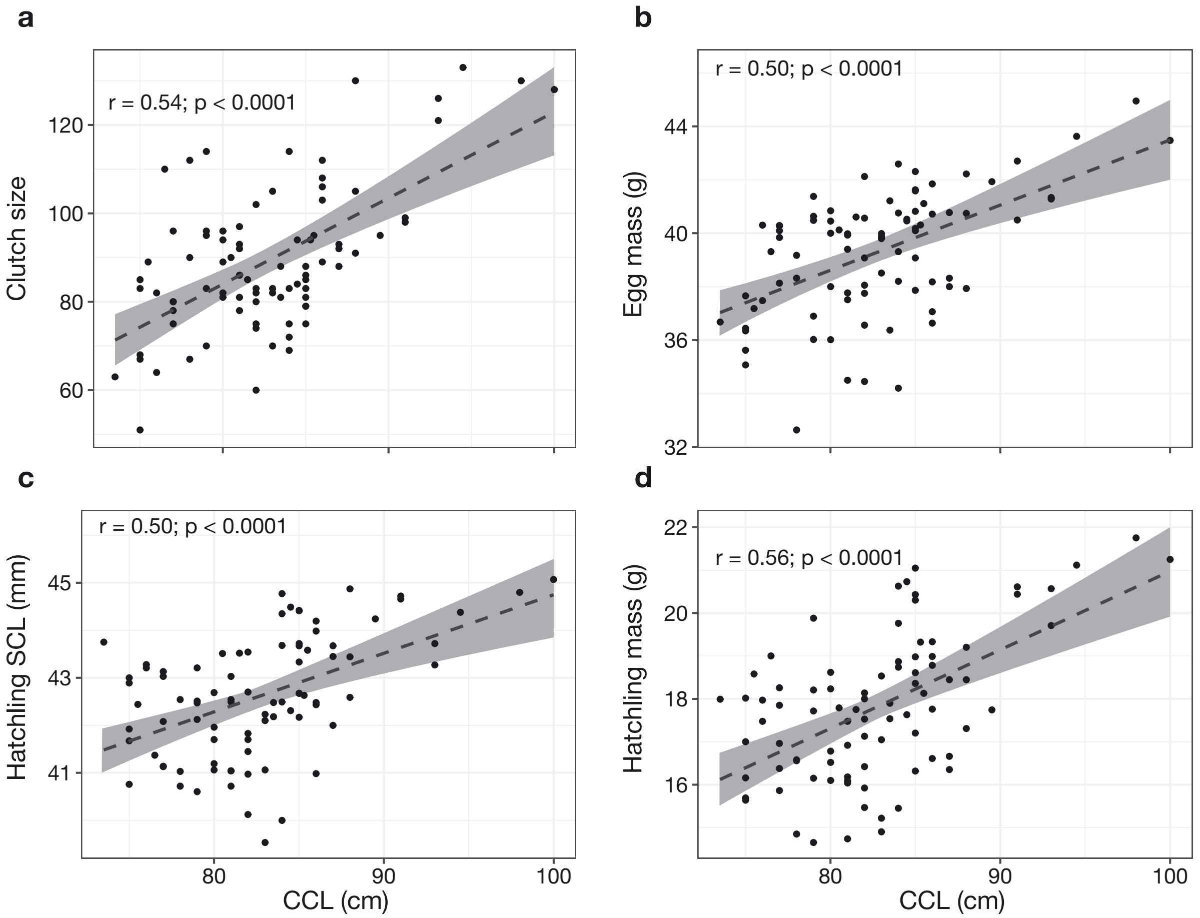

Fig. 6. Relationship between body length (curved carapace length [CCL]) and (a) clutch size, (b) egg mass, (c) hatchling straight carapace length (SCL) and (d) hatchling mass for female loggerhead turtles at Cabo Verde (northeastern Atlantic). Dashed line and grey areas correspond to regression line and 95% CI band, respectively

(95% CI: 653–863). Despite higher reproductive output, both during a single season and also during a 20 yr period, females >90 cm contribute less than 12% to the total egg production on Boa Vista, and contribution decreased from 2013 to 2018 (Table S1), as both the number and the proportion of turtles smaller than 90 cm CCLmin increased in the population (Fig. 2).

4. DISCUSSION

Here we present results from 6 yr of study characterizing the reproductive effort of loggerhead sea turtles nesting on Boa Vista Island and report the relationship between carapace length and several important life history parameters. The annual rate of somatic growth, BCI, mean AM, RI and hatching success were unrelated to female carapace length. However, clutch size, egg mass, hatchling size and hatchling mass increased with female carapace length. The actual NN per season was assumed to be constant across size classes but could not be assessed properly due to low recapture rates. The overall reproductive output over 20 yr increased significantly with female carapace length at first sexual maturity, which in turn was assumed to be determined by the quality of the foraging grounds used during the immature stage (Hatase et al. 2002, Vander Zanden et al. 2010, Zbinden et al. 2011, Eder et al. 2012). Considering the low somatic growth rate and the low annual survival probability of adult females reported here, size at first maturity is the major determinant of the overall reproductive output over the long term, as only 6% of the females survive for more than 20 yr after first reaching sexual maturity.

It is important to highlight that we were unable to monitor every female that came ashore to nest, which certainly resulted in the possibility of missing many females. Furthermore, some females switched nesting beaches during the same season and in subsequent nesting beaches, as reported in the present study and

Abella et al. (2013). RI, IN and mean AM are the parameters most affected by the aforementioned limitations, and longer RI and IN values may be a result of missing females (Tucker 2010, Hancock et al. 2019, Casale & Ceriani 2020). However, there is no reason to believe that females of different size classes differ in their detection probability, and the error in the estimates is expected to be the same for all size classes.

4.1. Growth rate

Marine turtles typically exhibit indeterminate growth, but the adult growth rate is less than 0.5 cm annually and often close to zero (Broderick et al. 2003, Hatase et al. 2004, Bjorndal et al. 2013, Rees et al. 2013, Omeyer et al. 2018). The growth rate reported here (0.34 cm yr^{-1}) fits that pattern. Multiple data collectors increase the risk of error estimation even when the same protocol is used during the study period (Braun-McNeill et al. 2008). This error may result in negative growth rates for certain individuals, but the inclusion of all the growth rates (positive and negative) in the analysis controls for that error and results in reliable estimates (Braun-McNeill et al. 2008, Bell & Pike 2012, Bjorndal et al. 2013, Omeyer et al. 2018).

Interestingly, no significant relationship was observed between growth rate and carapace length. This means that differences in adult size emerged before the onset of sexual maturity (Hawkes et al. 2006, Eder et al. 2012, Pikesley et al. 2015). This is because the growth rate of juvenile marine turtles is strongly determined by food availability and quality (Bjorndal et al. 2013). Differences are conserved through adulthood, when females allocate most of their available energy and resources to reproduction (Broderick et al. 2003, Hatase et al. 2004, Omeyer et al. 2018). Furthermore, the observed growth rate is so small that a female breeding for the first time with a CCLmin of 71 cm will have a curved carapace length (CCL) of only 77.5 cm after 20 yr, and a female breeding for the first time with a CCLmin of 80 cm will have a CCL of 86.5 cm after that time. Accordingly, she will not experience major changes in her reproductive output throughout her adult life.

4.2. BCI

Several indices have been proposed to assess the well-being or fitness of marine turtles, some based on morphological parameters (Bolger & Connolly 1989, Bjorndal et al. 2000) and others using biochemical parameters (Jessop et al. 2004, Goldberg et al. 2013, Vieira et al. 2014). Here we used Fulton's index, based on body mass and body size, as it is widely used in sea turtles and other vertebrates (Bolger & Connolly 1989, Bjorndal et al. 2000, Jessop et al. 2004, Peig & Green 2010, Goldberg et al. 2013) because it can be measured easily in a large number of individuals in field conditions.

The body condition of the nesting females decreased significantly throughout the nesting season due to successive clutch depositions and lack of food intake during the nesting season (Goldberg et al. 2013). A similar trend has been revealed by biochemical indices based on nucleic acid derived indices (RNA:DNA ratio) (Vieira et al. 2014). However, a substantial increase in the BCI was observed in September. Recovery of the BCI due to feeding during the late internesting period was ruled out by previous studies (Vieira et al. 2014). Alternatively, females foraging in distinct areas may differ in their nesting phenologies (Ceriani et al. 2017); the largest females nesting at JBR arrived and departed earlier in the nesting season, with only the smallest females remaining at the breeding grounds towards the end of the season. Accordingly, the increase in the body condition observed in September might result from the arrival of a new batch of small females with a higher condition index. However, the analysis of the recapture data shows very little consistency in the date of first arrival to the beach in subsequent years, thus suggesting that well-defined groups of females nesting at different times of the year probably do not exist. Further research is necessary to identify the actual cause of the increase in the body condition of females nesting in September.

4.3. Beach fidelity and survival

The accuracy of the survival rate estimate is highly dependent on the tag loss ratio, site fidelity and the possibility to monitor every female that came ashore to nest. Females were tagged in the front flippers with PIT tags, so the possibility of tag loss was close to zero and the probability of tag migration of other body parts was also negligible. Although some females shifted nesting beaches, both within the same season and across seasons, fidelity to the nesting beach was similar between size classes, and there is no reason to believe that detection probability is related to carapace length. Therefore, the error in the estimate of the survival rate is expected to be the same for all the size classes. In any case, we caution that the method used here likely slightly overestimates mortality compared to hidden Markov capture–recapture methods, which explicitly account for encounter probability. Unfortunately, statistical inference of the number of turtles dead is the only approach possible with the data set analyzed here, which clearly shows the difficulty of obtaining accurate estimates of life history parameters even after several years of intense field work.

Historically, loggerhead sea turtles in Cabo Verde suffered high mortality while nesting, because of the harvesting of adults for meat consumption (Marco et al. 2012a), but little was known about at-sea mortality. This study has been developed in the STNR, a protected area that has comprised several sea turtle camp vigilances for more than 2 decades. Therefore, at-beach mortality is thought to be low, and incidental bycatch at the foraging grounds is the most likely source of anthropogenic mortality.

The Canary Current upwelling system is one of the most productive regions in the Atlantic Ocean (Benazzouz et al. 2014, Gómez-Letona et al. 2017) and supports intense fishing (Pikesley et al. 2015). Information about sea turtle bycatch in the region has been traditionally scarce (Riskas & Tiwari 2013), and the foraging grounds used by the loggerhead turtles nesting at Cabo Verde were not identified as hot spots in previous global reports on sea turtle bycatch (Wallace et al. 2010, Lewison et al. 2014). Nevertheless, recent research has revealed broad overlap between fishing grounds and the habitat used by loggerhead turtles nesting at Cabo Verde (Pikesley et al. 2015), as well as significant levels of loggerhead turtle bycatch by longliners operating off the coast of Cabo Verde (Coelho et al. 2015). Bycaught turtles were usually released alive (Coelho et al. 2015), but experimental evidence reveals high levels of post-release mortality (Àlvarez de Quevedo et al. 2013). Conversely, industrial pelagic trawlers operating off the coast of mainland Africa captured much lower numbers of turtles (Zeeberg et al. 2006). Very little is known about the bycatch of loggerhead turtles by artisanal boats operating from mainland Africa, although Marco et al. (2019) observed that large females presented higher risk of amputation than small ones, which might be considered indicative of a higher bycatch risk with nets. In any case, experimental fishing demonstrated that the bycatch rate of loggerhead turtles by drifting longlines operating off the coast of Cabo Verde can be reduced by 50% by changing the hook type and using fish as bait instead of the traditional J-style hooks (Coelho et al. 2015). These gear modifications offer simple methods to greatly increase the survival rate of oceanic foragers.

Independent of the relevance of bycatch mortality, the numbers of adult females living more than 20 yr may seem extremely low (6%), but long-term tagging programs elsewhere have also reported low numbers (0.50%) of adults more than 20 yr old (Margaritoulis et al. 2020). An important consequence of such high mortality rates, combined with a very low growth rate, is that adult loggerhead turtles with a CCLmin greater than 90 cm cannot be simply and exclusively the oldest turtles.

The modal size of the adult females nesting on Boa Vista is close to 80 cm, and most adult females are 75 to 85 cm CCLmin. If we assume that 75 cm CCLmin is the length at first maturity, growing to 90 cm CCLmin would take 44 yr; hence, only 1 of 1000 turtles in each cohort would live long enough to reach 90 cm CCLmin. However, turtles larger than 90 cm CCLmin represent approximately 2.5% of the population in the 2013–2018 period, and their contribution to the populations was even larger in 2013 to 2016. Accordingly, large turtles cannot be just old turtles but probably sea turtles that grew faster before they reached adulthood due to favourable environmental conditions, such as higher food availability (Hatase et al. 2002, Hawkes et al. 2006, Zbinden et al. 2011, Eder et al. 2012, Pikesley et al. 2015).

4.4. Long-term reproductive output and conservation implications

The results reported here revealed that more than 80% of the reproductive output of the population results from the contribution of turtles less than 90 cm CCLmin, due to their high prevalence in the population. The relative abundance of small turtles nesting at JBR increased throughout the study period and resulted in a drop of the average carapace length. Neophytes are usually smaller than remigrants in marine turtles (Lamont et al. 2014, Stokes et al. 2015); hence, increasing numbers of small nesting females might suggest improved recruitment to the adult population (Arendt et al. 2013, Omeyer et al. 2021). Nest counts have increased recently across the archipelago, and during the 2018 nesting season, the number of nesting loggerhead turtles at Cabo Verde tripled in comparison to the previous year (2017), which was a record year for the NN registered (Marco et al. 2012a, 2018b, Laloë et al. 2020, Patino-Martinez et al. 2022). This could be interpreted as evidence of an increased population size, but caution is needed because increased NN might also result from changes in the RI and the total number clutches laid per season, even if population size remains unmodified (Hays et al. 2022). Actually, the loggerhead turtles nesting on Boa Vista forage in the Canary Current upwelling region (Hawkes et al. 2006, Pikesley et al. 2015), one of the most productive ecosystems in the world (Benazzouz et al. 2014, Gómez-Letona et al. 2017) but also subject to major interannual cycles of primary productivity (Gómez-Letona et al. 2017). These cycles likely influence the availability of food for the loggerhead turtles and may explain the considerable interannual variability observed in the RI, BCI and even in the size structure of the population. Interannual fluctuations in food availability may also explain the variability observed in nest counts. Furthermore, interannual differences in SST may also have a strong influence in parameters such as the duration of the IN, because high ambient temperatures accelerate egg maturation and shorten INs (Sato et al. 1998, Hays et al. 2002, Valverde-Cantillo et al. 2019). The IN values reported here ranged from 9 to 21 d, are similar to those reported elsewhere (Sato et al. 1998, Hays et al. 2002, Valverde-Cantillo et al. 2019) and are strongly correlated with SST. In any case, a longer study period is necessary to confirm the observed trend in nest counts, which is always necessary before inferring changes in the population size of long-lived species (Mazaris et al. 2017).

Independent of the reason for the recent increase in the numbers of small nesting females, the results reported here revealed a very small contribution of the largest turtles to the fecundity of the population. This small contribution is due to their scarcity, despite an observed positive increase of clutch size with turtle carapace length. The reasons for the variability in body size across adult female loggerhead turtles nesting at Cabo Verde and the scarcity of turtles >90 cm CCLmin are poorly known, and 2 contrasting hypotheses have been proposed (Eder et al. 2012, Cameron et al. 2019). On the one hand, the scarcity of turtles larger than 90 cm CCLmin in the population could be the result of early sexual maturity, low somatic growth and high mortality. This hypothesis would also explain why female loggerhead turtles >90 cm CCLmin nesting on Boa Vista are usually older than small conspecifics (Eder et al. 2012). On the other hand, the size of adult loggerhead females has been suggested to be determined by the quality of foraging habitat (Hatase et al. 2002, Vander Zanden et al. 2010, Zbinden et al. 2011, Eder et al. 2012). The intrapopulation variability in female body size may reveal the diversity in the quality of their foraging grounds. Further research is necessary to determine the real cause of such variability.

5. CONCLUSIONS

At a first glance, reducing the bycatch of large adult females should be a conservation priority for the loggerheads nesting on Boa Vista, due to the largest potential reproductive output. However, the results reported here reveal that most of the offspring production depends on the survival of small adult females, the prevalent size class in the population. The AM of adult female loggerhead turtles is independent of carapace length, but there is a possibility that adult turtles of different size classes are exposed to contrasting sources of mortality due to differences in habitat use and hence exposure to different fishing gears. There is an urgent need to identify anthropogenic causes of at-sea mortality for different size classes of adult loggerhead turtles and reduce them to ensure the viability of the Cabo Verde population.

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