



Unveiling loggerhead turtles size decline at a major Brazilian nesting ground

Josiele Alves Pereira¹ · Agnaldo Silva Martins² · Alexsandro Santana dos Santos³ · Ana Cláudia J. Marcondes³ · Wilian Vaz-Silva^{1,4}

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Abstract

Brazil's second-largest reproductive colony of loggerhead turtles (*Caretta caretta*) has a long history of overexploitation, with its temporal ecological dynamics still unknown. This study investigates changes in the average size of females and post-maturity somatic growth rates in marked and recaptured loggerhead turtles at a breeding site over a 33-year period (1982–2014). Loggerhead curved carapace length (CCL) was evaluated over the course of the study using a generalized additive model (GAM) with a Gaussian family distribution and time smoothed. Includes the nesting year and the CCL for a total of 2,359 female loggerhead turtles. The overall average length of females was 99.4 cm ± 5.8 (mean ± SD). The results suggest that the CCL of females in the nesting area is decreasing. From 1982 to 1998, the mean CCL was 102.6 cm; from 1999 to 2014, the average length was 98.7 cm. There were no statistically significant differences in post-maturity growth rates among recaptured females, supporting the hypothesis of increased recruitment. The GAM results showed significant differences in the size structure changes of reproductive site females over time. The study highlights how a population parameter can be influenced by long-term conservation of feeding and nesting areas for sea turtles, resulting in a higher number of recruits. The curved carapace length serves as an important metric to describe population changes and raise awareness about future conservation challenges.

Keyword Atlantic Ocean. Conservation. Temporal series. Population trends analysis. Espírito Santo

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✉ Josiele Alves Pereira
josielepereira@discente.ufg.br

Agnaldo Silva Martins
agnaldo.martins@ufes.br

Alexsandro Santana dos Santos
alex@tamar.org.br

Ana Cláudia J. Marcondes
ana.marcondes@tamar.org.br

Wilian Vaz-Silva
herpetovaz@gmail.com

¹ Programa de Pós-Graduação em Biodiversidade Animal, Universidade Federal de Goiás, Goiânia, Goiás, Brasil

² Departamento de Oceanografia e Ecologia, Universidade Federal do Espírito Santo, Vitória, Espírito Santo, Brasil

³ Fundação Projeto TAMAR, Linhares, Espírito Santo, Brasil

⁴ Centro de Estudos E Pesquisas Biológicas, Escola de Ciências Médicas e da Vida, Pontifícia Universidade Católica de Goiás, Goiânia, Goiás, Brasil

Introduction

Loggerhead turtle populations (*Caretta caretta*; Linnaeus 1758) have undergone a long process of overexploitation along the Brazilian coast, with intensive use of their eggs, meat, and carapace throughout the region (Da Silva et al. 2016; López-Mendilaharsu et al. 2020). Excessive exploitation (e.g., overfishing, hunting, and poaching; Bugoni et al. 2001; Monteiro et al. 2016), coupled with issues arising from coastal development (e.g., artificial lighting, gradual increase in waste, chemical contamination from domestic, agricultural, and industrial runoff; Wilcox et al. 2018), have historically posed threats to this species, resulting in population declines (Jackson et al. 2001). Implementing environmental public policies and developing sea turtle conservation programs have reduced global impacts and enabled the recovery of several populations (Mazaris et al. 2017). Conservation efforts have also included the protection of the nesting and foraging sites (Marcovaldi and Marcovaldi 1999), regulation of hunting and bycatch (Brasil 1998), and

the establishment of the South Atlantic Sea Turtle Network (redasotortugas.com). The network focuses on the interaction between sea turtles and fishing activities (López-Mendilaharsu et al. 2020), and the establishment of protected areas (Hamann et al. 2010). As a result, loggerhead turtle populations in the Western South Atlantic have shown signs of recovery, reflected in their change in conservation status from “Endangered” to “Vulnerable” in 2022 (Casale and Tucker 2017; ICMbio 2022). In a global study, 95 of 130 study sites showed an increase in nesting abundance (Mazaris et al. 2017) showing independent global growth. But little is known about the impact this has on nesting female size.

In general, body size comparisons of recovering sea turtle populations are under studied (Hays et al. 2022). The increase in smaller females may indicate higher recruitment rates or lower growth rates; however, smaller individuals typically lay fewer eggs per clutch (Mortimer et al. 2022), impacting population productivity. On the other hand, increased protection of adults not only enhances annual survival rates but also the number of eggs laid, resulting in long-term recruitment increase (Piacenza et al. 2016; Hays et al. 2022). Furthermore, size structure analyses can indicate changes in growth rates (Bjørndal et al. 2017), represent the distribution of stranded animals (Monteiro et al. 2016; Herren et al. 2018), or indicate size variations to attain sexual maturity (Phillips et al. 2021). Long-term monitoring of sea turtle populations can detect issues in resource stability early, thus providing managers better data for conservation.

The second-largest population of loggerhead turtles nesting on the eastern coast of Brazil has been continuously monitored since 1982 (Marcovaldi and Chaloupka 2007; Colman et al. 2019). Due to the philopatric behavior of females (returning where they were emerged; Reis et al. 2010), long-term monitoring can yield valuable insights into the demographic structure of the reproductive population (Baltazar-Soares et al. 2020). Population surveys in the area have described temporal patterns of nests, reproductive success of females (Baptistotte et al. 2003), and indicated an increase in relative abundance during the early years of monitoring (Marcovaldi and Chaloupka 2007). However, no attempt has been made to identify loggerhead female size variation in this nesting population.

Given the importance of size structure in demonstrating population patterns, we analyzed capture-mark-recapture (CMR) records from the initial 33 years of monitoring conducted by the Sea Turtle Project (TAMAR) to identify variations in curved carapace lengths (CCL) and post-maturity growth of females. The CCL was employed as a biological indicator to monitor long-term demographic changes; we explored the hypothesis of an annual gradual decrease in CCL due to an increase in the number of smaller

recruits each year. If confirmed, our findings could yield new insights into population trends of loggerhead turtles in northern Espírito Santo. These additional data are pertinent to the conservation and management of loggerhead turtles, offering insights into how long-term conservation efforts can benefit local nesting colonies of marine turtles.

Materials and methods

Study area

The study area encompasses a stretch of 194 km of beaches on the northern coast of the State of Espírito Santo, southeastern Brazil, between latitudes 19° 50' and 18° 36' S (Fig. 1). Of the 194 km, approximately 78 km of the nesting beaches are consistently monitored for the marking and recapture of females (from km 0 to km 78; Fig. 1), while the remaining kilometers are monitored intermittently for marking. The beaches of the Northern region of Espírito Santo are characterized by dynamic beaches with coarse sand in the south, and low-energy beaches with fine sand in the north, adjacent to the estuaries of the Riacho, Doce, São Mateus, Itaunas, and Mucuri rivers (Baptistotte et al. 2003).

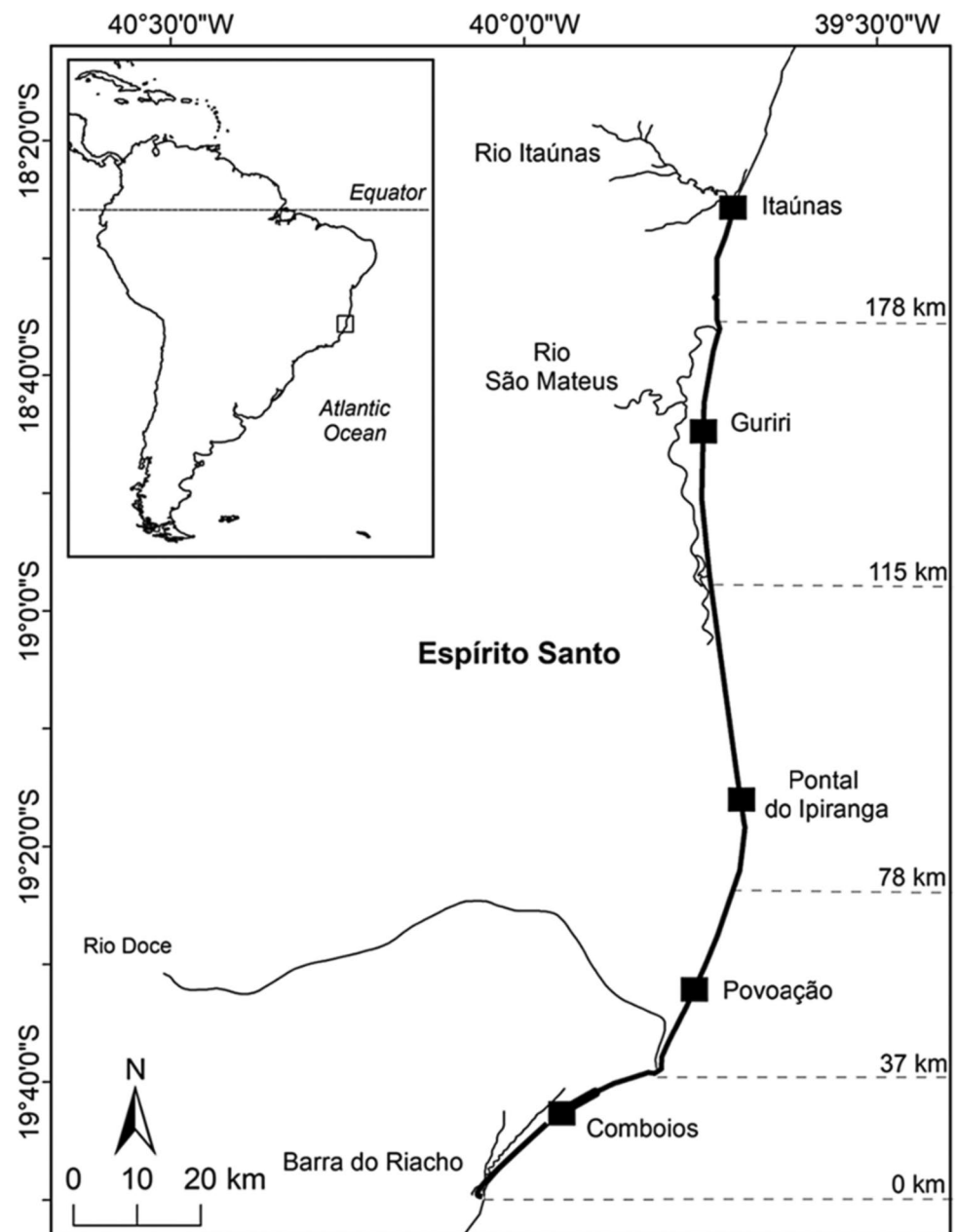
Female biometrics

Nightly monitoring was conducted by the TAMAR project occurred during the peak of nesting activity (September 1–March 31; hours of 18:00 and 05:00) from 1982 to 2014 (Santos et al. 2011). When detecting turtle tracks, the team carefully searches for the female and the nest, avoiding startling the animal. During the nesting process, they mark the nest and, taking advantage of the female’s resting period, perform marking and measurements. Patrols multiple were conducted using vehicles, with a team comprising approximately eight individuals. Monitoring during the 1997 to 2003 seasons encountered logistical difficulties due to budget constraints, resulting in a shortage of field personnel and irregular monitoring, typically occurring around three times a week.

Adult females were measured from the anterior nuchal notch to the posterior tip of the carapace using a flexible measuring tape (Bolten 2003; Thomé et al. 2007) and tagged on the front flippers with Inconel tags (Style 681, National Band Compan, Kentucky USA; Almeida et al. 2011). Before the marking process, barnacles and epibionts are removed. Females were marked during the resting period following nest closure. The presence of calluses and scars were checked, which could indicate previous tag loss (Hughes 1996).

Measurement records of nesting females were only used once per reproductive season to avoid pseudoreplication.

Fig. 1 Location of the nesting beaches of the loggerhead turtle (*Caretta caretta*) on the northern of State of Espírito Santo, east coast of Brazil. The dark line indicates the kilometers of the beaches where the monitoring of female took place. Black boxes represent the names of the beaches. Operational sections monitored, in the south-north direction: Comboios (0–37 km), Povoação (38–78 km), Pontal do Ipiranga (79–115 km), Guriri (116–178 km), and Itaunas (179–194 km)



However, for cases of females recaptured in the same reproductive season, we calculated a mean CCL following the approach of Phillips et al. (2021). We made no distinction between recruited females (first-time nesters) and remigrants (nesters recaptured in subsequent seasons) when conducting the statistical tests.

Baptistotte et al. (2003) identified that CCL of nesting loggerhead females range from 83 to 123 cm in this breeding population. We divided this range into three groups (83–96 cm; > 96–110; > 110 cm) for recruitment size thresholds. A single size determinant (96 cm) is limiting, however it is a reasonable assumption for recruitment in this population.

Growth variability

To verify if there were changes in growth rates over the monitoring period, we used the average CCL at first tagging ($x\text{CCL}_{\text{first}}$) and the last average CCL from the subsequent season ($x\text{CCL}_{\text{last}}$) divided by the number of years between these records Le Gouvello et al. (2020). The number of years corresponds to the difference between the first and last observation (> 1 year; Le Gouvello et al. 2020). The growth rate was estimated using the following formula (Le Gouvello et al. 2020):

$$\text{Growth rate} = \frac{CCL_{\text{last}} - CCL_{\text{first}}}{\text{Number of years}}$$

Data analysis

We utilized the years of monitoring as an predictor variable and CCL as response variable, as the reproductive site underwent significant overexploitation, which was subsequently mitigated. The normality and homogeneity of the residuals were assessed before creating the model. The main generalized additive model (GAM) ($CCL \sim \text{year}$) was fitted to the Gaussian family distribution. The GAM, was used to test the hypothesis of an increase in smaller females over the reproductive seasons (Table S1). The second GAM model (ranges $CCL \sim \text{year}$) was fitted to the Scat family due to the residual distribution exhibiting long tails (heavy-tailed distribution; Wood et al. 2016). This model was designed for three different size ranges. Time variable was smoothed in both models due to previous statistical tests. Analysis was performed using the R software (R Core Version 4.1.0, Team 2017) with the ‘mgcv’ (Wood 2017), and visualized using the ‘ggplot2’ (Arnold 2019), and ‘ggthemes’ packages (Wickham 2016).

We compared post-maturity growth rates estimated between 1982 and 2004 with those of distinct females marked and recaptured between 2005 and 2014. The post-maturity growth rates were categorized into three CCL intervals (99 to 107 cm) with replicates for statistical testing. The Mann–Whitney U test was employed to assess whether there were differences in post-maturity growth rates (response variable) over time (predictor variable).

Results

Patterns of curved carapace length

Biometric records of 2,359 females were collected between 1982 and 2014 during nightly monitoring at the peak of nesting activity (Table S2). The overall mean CCL of females throughout the monitoring period from 1982 to 2014 was 99.4 cm \pm 5.8 (mean \pm SD), with a range of 81.2–136.4 cm.

There was an increase in the frequency of smaller-sized females over time (Fig. 2a). The GAM model’s results indicated that time was a significant predictor in the CCL structure of nesting females ($\chi^2 = 18.79$; $df = 1$; $P < 0.001$; pseudo $-R^2 = 0.556$ and deviance = 58%; Fig. 2b; Table 1).

Due to the low number of females observed in some seasons, we graphically represented the temporal pattern of size variations only for 14 reproductive seasons that had a minimum number ($N = 50$ females). The annual reproductive

population exhibited an increase from 4.83% of females with $CCL < 96$ cm in the early years of monitoring to 45.26% in the final years. Conversely, the percentage of “larger” females, classified as > 96 –110 cm and > 110 cm, was higher in the early years (95.16 and 19.44%), decreasing in subsequent years to 53.68 and 1.05%, respectively (Fig. 3). The size distribution revealed an asymmetry between the monitored periods, with an increased frequency of CCL values for females smaller than 96 cm, a pattern that became more evident from 2004 onwards compared to previous seasons (Fig. 3; Fig S1 and Table S3).

The results of the GAM analyses regarding changes in the three size ranges can be observed in Fig. 4 (Table 2). The percentage of females with $CCL \leq 96$ cm increased between reproductive seasons, with a more pronounced pattern after the year 2000 ($\chi^2 = 69.51$; $df = 1$; $p < 0.001$; pseudo $-R^2 = 0.657$ and deviance = 65%; Fig. 4a). However, the percentages of the larger CCL ranges $> 96 < 110$ cm and > 110 cm showed a decrease throughout the reproductive seasons ($\chi^2 = 16.09$ and $\chi^2 = 8.91$; $df = 1$; $P < 0.001$; pseudo $-R^2 = 0.323$ and 0.185; deviance = 37 and 15% respectively; Figs. 4b, c).

Post-maturity growth rates

Post-maturity growth rates of females in the nesting area ranged from 0 to 3.81 cm/year, with a mean of 0.56 ± 0.65 cm/year (Fig. S1). The highest post-maturity growth rates were recorded within the first 3 years after following initial sightings (3.81, 3.52, 3.51 cm/year; Fig. S2). Post-maturity growth rates by CCL can be visualized in Fig. 5. There were no statistically significant differences between the growth rates and CCLs across the reproductive seasons of 1989–2004 and 2005–2014 ($P > 0.05$; Fig. 5).

Discussion

The results presented here provide evidence of recruitment to a recovering loggerhead nesting population. Smaller females tend to be younger (Richardson et al. 2006; Hays et al. 2022; Turner Tomaszewicz et al. 2022) and the biometric evidence supports this assertion. The analysis of CCL variation has been suggested as an alternative method to provide demographic information at various life stages of marine turtles (Piacenza et al. 2016; Hays et al. 2022). However, this type of approach requires years of monitoring and the capture, tagging, and recapture of these animals.

We have demonstrated the first reduction in the average size of loggerhead turtles females at the second-largest nesting site in Brazil. While there may be potential reasons for this reduction, we propose that this result is linked to the proportional increase in female recruitment in the breeding

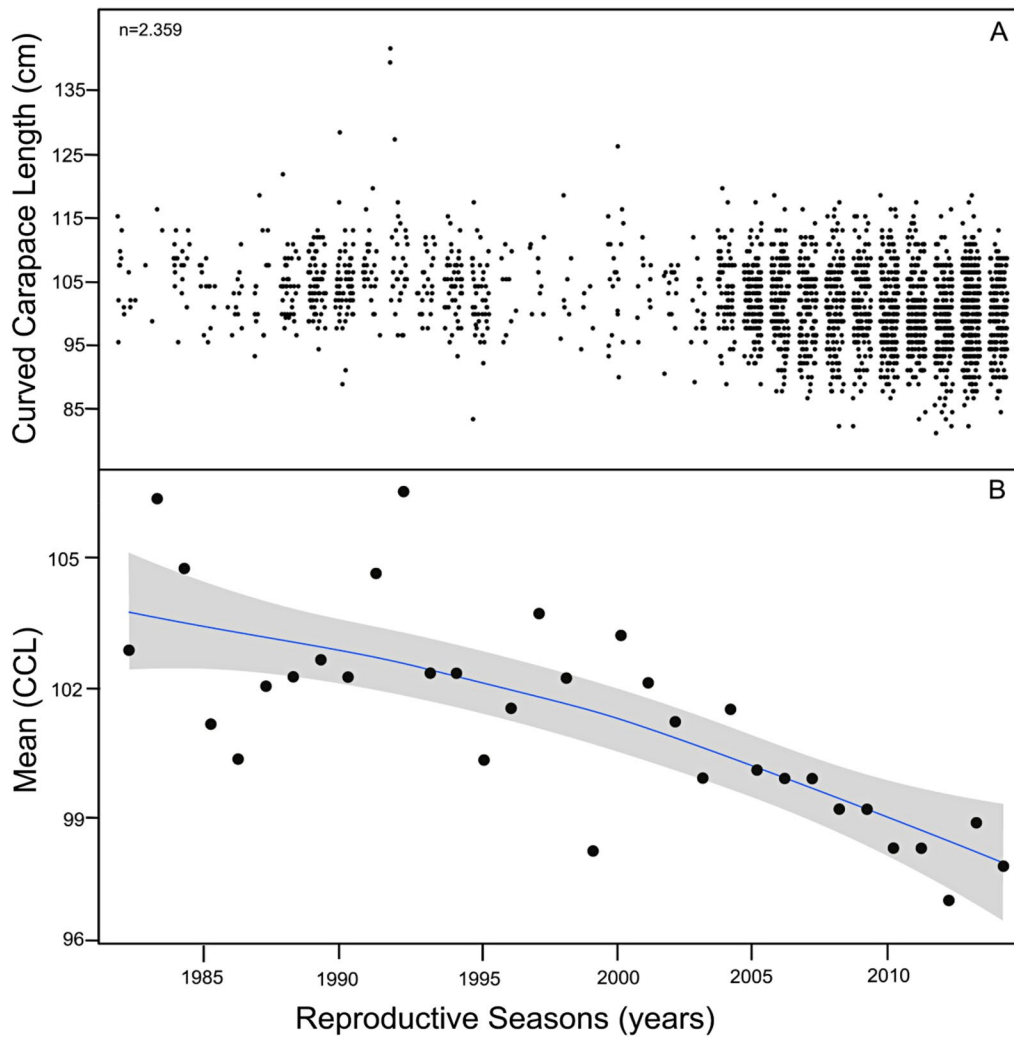


Fig. 2 **A** Full presentation of curved lengths **B** Average curved carapace length (CCL) variation (line) indicated by the generalized additive model (GAM) (line) and standard deviation indicating $p < 0.001$ (shaded area in gray). The dots represent the mean values of CCL

Table 1 Results of the analysis of deviance applied to the generalized additive model fit to describe the curved carapace length (CCL) off females throughout the study

	Estimate β	Std.error	Z	P
Intercept	101.28	0.2706	374.3	<0.001
Smooth term	Edf	Ref.Df	χ^2	P
Year	1.753	2.185	18.79	<0.001

area, which has shown signs of recovery. The increase in recruitment in a breeding population can lead to a decrease in the average size of females (Hays et al. 2022).

Female size decreases imply an increase in recruitment which is due to the cumulation of 30 + years of conservation efforts. Offspring from nests within the early monitoring period will have reached sexual maturity

(28–32 years Piovano et al. 2011; Petit et al. 2012; Avens et al. 2015). Increased recruitment shows high survival rates in various life stages for these animals (Chaloupka 2002; Bellini et al. 2013; Lopez-Mendilaharsu et al. 2020).

To reinforce our hypothesis of increased recruitment, we must consider the history of overexploitation of loggerhead turtles on the Brazilian coast, where hunting and collection were the main threats (Fontinelli and Creato 2020). The TAMAR project, established in 1980, has contributed to the species’ preservation by involving local communities and developing viable economic alternatives for populations that relied on these animals (Liles et al. 2015; Da Silva et al. 2016). In addition to the boosting of environmental laws, such as the prohibition of hunting, the inclusion of marine turtles in the list of endangered species, use of Turtle Excluder Devices, and increased penalties for

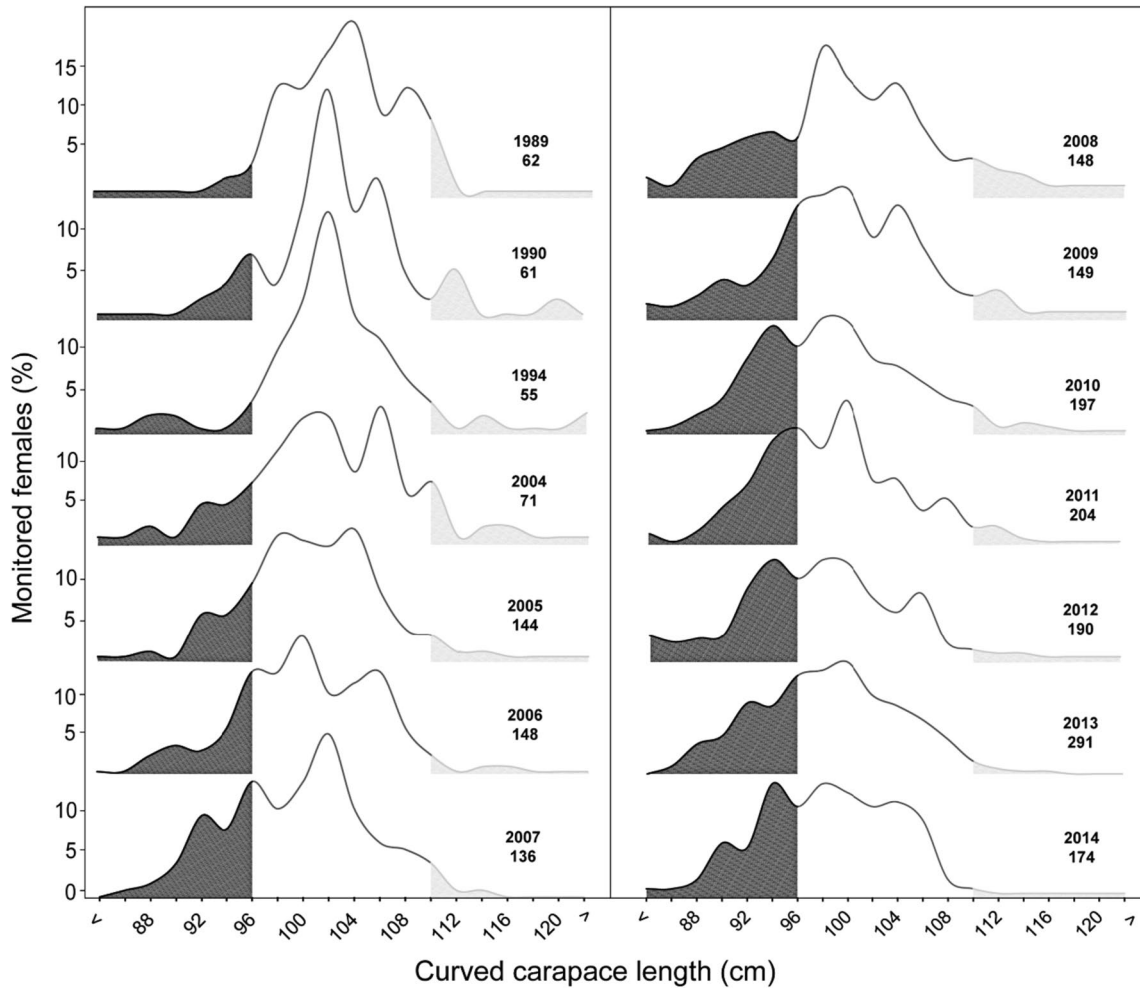


Fig. 3 Frequency distribution of curved carapace length of loggerhead females, organized by reproductive seasons. Areas shaded in black delimit the proportion of smaller individuals (“recruits”) in the

population (80–96 cm). Areas shaded in light gray delimit the proportion in the population of the largest individuals in the population (110 to 136 cm CCL)

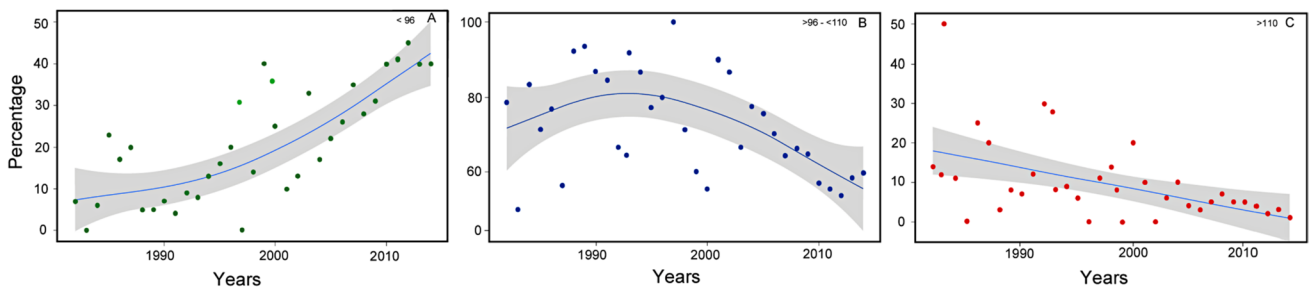


Fig. 4 Variation of the percentage of mature loggerhead turtle females with respect to the lengths indicated by the generalized additive model line with standard deviation (shaded gray area). **A** Green points represent CCL ≤ 96 cm with an intercept of 19.57%. **B** Blue

points represent CCL between >96 and <110 cm with an intercept of 73.0%. **C** Red points represent CCL >110 cm with an intercept of 7.71%

Table 2 Results of the analysis of deviance applied to the generalized additive model fit to describe CCL ≤ percentages 96 cm throughout the study

CCL		Estimate β	Std.Error	Z	P
< 96 cm	Intercept	19.57	1.33	14.63	<0.001
	Smooth term	Edf	Ref.Df	χ^2	P
	Year	2.33	2.914	69.51	<0.001
> 96–< 110	Intercept	73.0	1.958	37.28	<0.001
	Smooth term	Edf	Ref.Df	χ^2	P
	Year	2.522	3.141	16.09	<0.001
> 110 cm	Intercept	7.71	1.006	7.66	<0.001
	Smooth term	Edf	Ref.Df	χ^2	P
	Year	1	1	8.915	<0.001

and model fit to describe CCL percentages > 96–< 110 cm throughout the study. To the generalized additive model fit to describe CCL percentages > 110 cm throughout the study

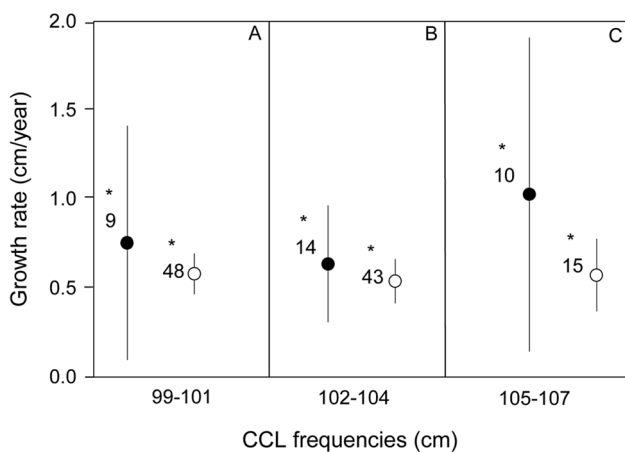


Fig. 5 Median annual curved carapace growth rate (CCL) (circles) and standard deviations (vertical bars) post-maturity for loggerhead females that nesting in northern Espírito Santo State, east coast of Brazil. Black circles indicate females that were tagged and returned between 1982 and 2004. White circles indicate females that were tagged and returned in 2005–2014. **A** represents the post-maturity growth of females with CCL between 99 and 101. **B** represents the post-maturity growth of females with CCL between 102 and 104. **C** represents the post-maturity growth of females with CCL between 105 and 107. Equal numbers of asterisks indicate non-significant differences with the test *U* Mann–Whitney

capture, collection, killing, and disturbances. These are important measures for species conservation.

Despite observing lower recruitment rates (with a small presence of smaller females) until the reproductive season of 2004, it should be noted that there was less monitoring effort between 1997 and 2003. This may have led to reduced species protection during the initial period of the TAMAR Project implementation. For instance, the first foraging area base was only built in 1991 (Gallo et al. 2006). In 1994, only 31.5% of the nests were protected, and human egg predation

occurred along the entire coast (Da Silva et al. 2016). Currently, 80% of marine turtle nests are protected due to the establishment of bases in feeding and nesting areas and the enforcement of environmental laws (Lopez et al. 2014).

Adult and subadult mortality, mainly due to interactions with fishing activities and plastic ingestion (Rizzi et al. 2019; Cantor et al. 2020), may have masked the potential of recruitment. This is shown by the increase in abundance, but the reduction of larger females after 2005. In the region, 71% of strandings overlap with fishing activities during the nesting season (Lopes-Souza et al. 2015; Monteiro et al. 2016). Further, 45% of loggerhead bycatch between Brazil and Uruguay are within loggerhead foraging grounds (Giffoni et al. 2014). With these animals spending a significant part of their time offshore, their protection will be a challenge to be faced in the coming decades.

The post-maturity growth rates of females in relation to CCL remained stable for over a decade, indicating that the decline in mean curved carapace length (CCL) is not associated with this metric, supporting the hypothesis of increased recruitment. Although some females exhibit lower growth rates, the overall population has remained stable, indicating that this isolated fact does not explain the increase in smaller-sized females in a reproductive site that has been showing indications of recovery. The post-maturity growth (0 to 3.81 cm/year) of females from the northern region of Espírito Santo exceeds that of other populations in the South Atlantic, ranging from 0.63 to 2.71 cm/year (Lenz et al. 2016). External factors such as habitat degradation, intraspecific competition, temperature, or food variation influence growth (Ramirez et al. 2020).

From 1982 to 1998, nesting females were identified as the largest amongst studied populations (Fig. 6), but from 1999 to 2014, the opposite is true. An increase in smaller females could imply fewer nests with reduced egg quantities (Brost et al. 2015; Mortimer et al. 2022). Baptistotte and colleagues (2003) determined that the average number of eggs per nest in this population was 119.7 and the average hatch success rate was 68.3%. If this trend of smaller females continues, there could be less hatchlings resulting in long-term population losses. However, the reproductive population has shown signs of recovery with an increasing number of nests at a rate of 1.9% each season (Marcovaldi and Chaloupka 2007; Da Silva et al. 2016; López-Mendilaharsu et al. 2020). Furthermore, it is expected that these females will age and the pattern of average size will return to initial levels (Hays et al. 2022). This was observed in a long-term study of green turtles in a reproductive site in Hawaii (Piacenza et al. 2016).

In summary, this study highlights the importance of analyzing size structure to demonstrate population recoveries influenced by increased recruitment and the significance of long-term conservation programs involving capture, tagging, and recapture. We also conclude that the reproductive female

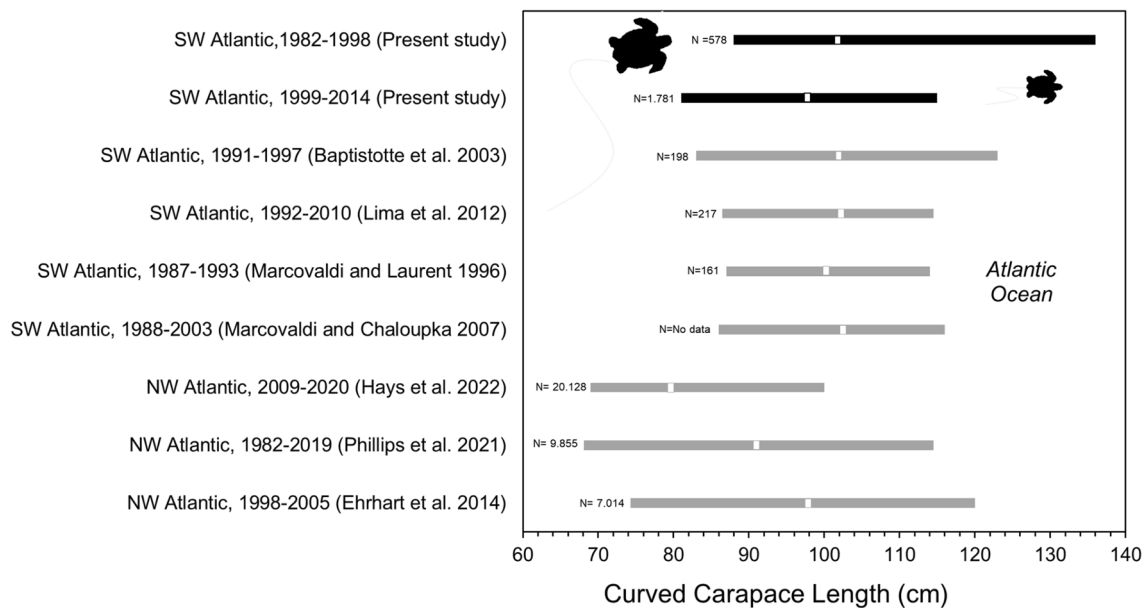


Fig. 6 Range of the curved carapace lengths (cm) recorded for loggerhead females that nest on the northern coast of Espírito Santo State with other nesting sites. The mean CCL of all populations is represented in White

population structure of loggerhead turtles in the northern region of Espírito Santo has changed, with a gradual increase in smaller-sized females as a result of conservation efforts. As this study focuses on the same reproductive site, it can serve as a reference for future research following the Mariana disaster in 2015. We suggest conducting future studies on population abundance to assess the effectiveness of recruitment in population growth, as well as developing a metric using stranding data related to mortality by CCL.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00227-024-04408-3>.

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Author contributions All authors contributed to the conception and design of the study. Conceptualization, methodology, formal analysis, investigation, data curation, writing, and visualization were conducted by JAP, ASM, and WVS participated in conceptualization, process, writing, and supervision. Resources, writing, and methodology were carried out by ASS and ACM. The initial manuscript draft was written by JAP, and all authors provided comments on previous versions of the manuscript. All authors have read and approved the final manuscript.

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Data availability The dataset analyzed during the current study is not publicly. However, the data are available from Projeto TAMAR upon reasonable request. For more information contact Gustavo Stahelin (Advisor to the National Directorate of Research and Conservation; gustavo@tamar.org.br).

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All procedures performed in studies involving animals were in accordance with the ethical standards of the Centro TAMAR-ICMbio and conducted under SISBIO permit 28938–3 from the Brazilian Ministry of the Environment.

References

- Almeida AP, Moreira LMP, Bruno SC, Thomé JCA, Martins AS, Bolten AB, Bjorndal KA (2011) Green turtle nesting on Trindade island, Brazil: Abundance, trends, and biometrics. *Endanger Species Res* 14:193–201. <https://doi.org/10.3354/esr00357>
- Avens L, Goshe LR, Coggins L, Snover ML, Pajuelo M, Bjorndal KA, Bolten AB (2015) Age and size at maturation and adult-stage duration for loggerhead sea turtles in the western North Atlantic. *Mar Biol* 162:1749–1767. <https://doi.org/10.1007/s00227-015-2705-x>
- Baltazar-Soares M, Klein JD, Correia SM, Reisching T, Taxonera A, Roque SM, Passos L, Durão J, Lomba JP, Dinis H, Cameron SJK, Stiebens VA, Eizaguirre C (2020) Distribution of genetic diversity reveals colonization patterns and philopatry of the loggerhead sea turtles across geographic scales. *Sci Rep* 10:18001. <https://doi.org/10.1038/s41598-020-74141-6>

- Baptistotte C, Thomé JCA, Bjorndal KA (2003) Reproductive Biology and Conservation Status of the Loggerhead Sea Turtle (*Caretta caretta*) in Espírito Santo State. Brazil Chelonian Conserv Biol 4:3
- Bellini C, Santos A, Grossman A, Marcovaldi M, Barata P (2013) Green turtle (*Chelonia mydas*) nesting on Atol das Rocas, north-eastern Brazil, 1990–2008. J Mar Biol Assoc UK 93:1117–1132. <https://doi.org/10.1017/S002531541200046X>
- Bjorndal KA, Bolten AB, Chaloupka M, Saba VS, Bellini C, Marcovaldi MAG, Meylan PA (2017) Ecological regime shift drives declining growth rates of sea turtles throughout the West Atlantic. Glob Change Biol 23:4556–4568. <https://doi.org/10.1111/gcb.13712>
- Bolten AB (2003) Active swimmers – passive drifters: the oceanic juvenile stage of loggerheads in the Atlantic System. In: Bolten AB, Witherington BE (eds) Loggerhead sea turtles. Smithsonian Books, Washington DC
- Bugoni L, Krause L, Petry MV (2001) Marine debris and human impacts on sea turtles in Southern Brazil. Mar Pollut Bull 42:1330–1334. [https://doi.org/10.1016/S0025-326X\(01\)00147-3](https://doi.org/10.1016/S0025-326X(01)00147-3)
- Brasil. Lei Federal N° 9.605, fevereiro de 12, (1998) Dispõe sobre as sanções penais e administrativas derivadas de condutas e atividades lesivas ao meio ambiente, e dá outras providências. http://www.planalto.gov.br/ccivil_03/leis/L9605.htm. Accessed 15 Jun 2022
- Brost B, Witherington B, Meylan A, Leone E, Ehrhart L, Bagley D (2015) Sea turtle hatchling production from Florida (USA) beaches, 2002–2012, with recommendations for analyzing hatching success. Endang Species Res 27:53–68. <https://doi.org/10.3354/esr00653>
- Cantor M, Barreto AS, Taufer RM, Giffoni B, Castilho PV, Maranhão A, Beatriz C, Kolesnikovas C, Godoy D, Rogério DW, Dick JL, Groch KR, Rosa L, Cremer MJ, Cattani PE, Valle RR, Domit C (2020) High incidence of sea turtle stranding in the southwestern Atlantic Ocean. ICES J Mar Sci 77:1864–1878. <https://doi.org/10.1093/icesjms/fsaa073>
- Casale P, Tucker AD (2017) *Caretta caretta* (amended version of 2015 assessment). IUCN Red List Threat Species. <https://doi.org/10.2305/IUCN.UK.2017>
- Chaloupka M (2002) Stochastic simulation modelling of southern Great Barrier Reef green turtle population dynamics. Ecol Model 148:79–109. [https://doi.org/10.1016/S0304-3800\(01\)00433-1](https://doi.org/10.1016/S0304-3800(01)00433-1)
- Colman LP, Thomé JCA, Almeida AP, Baptistotte C, Barata PCR, Broderick AC, Ribeiro FA, Vila-Verde L, Godley BJ (2019) Thirty years of leatherback turtle *Dermochelys coriacea* nesting in Espírito Santo, Brazil, 1988–2017: Reproductive biology and conservation. Endanger Species Res 39:147–158. <https://doi.org/10.3354/esr00961>
- Da Silva VR, Mitraud SF, Ferraz ML, Lima EH, Melo MTD, Santos AJ, Dei Marcovaldi MÁG (2016) Adaptive threat management framework: integrating people and turtles. Environ Dev Sustain 18:1541–1558. <https://doi.org/10.1007/s10668-015-9716-0>
- Fontinelli DS, Creado ESJ (2020) From food to offspring: engagement between humans and sea turtles in two communities on the north coast of Espírito Santo. Vibrant Virtual Braz Anthropol. <https://doi.org/10.1590/1809-43412020v17a351>
- Gallo BM, Macedo S, Giffoni BDB, Becker JH, Barata PC (2006) Sea turtle conservation in Ubatuba, southeastern Brazil, a feeding area with incidental capture in coastal fisheries. Chelonian Conserv Biol 5:93–101. [https://doi.org/10.2744/1071-8443\(2006\)5\[93:STCIUS\]2.0.CO;2](https://doi.org/10.2744/1071-8443(2006)5[93:STCIUS]2.0.CO;2)
- Giffoni B, Leite JRN, Miller P, Pons M, Sales G, Domingo A (2014) Captura incidental de tortugas marinas por las flotas de palangre pelágico de Brasil y de Uruguay (1998–2010). Collectiv Vol Sci Pap ICCAT N 5(70):2217–2225
- Hamann M, Godfrey M, Seminoff J, Arthur K, Barata P, Bjorndal K, Bolten A, Broderick A, Godley BJ (2010) Global research priorities for sea turtles: informing management and conservation in the 21st century. Endanger Species Res 11:245–269. <https://doi.org/10.3354/esr00279>
- Hays GC, Taxonera A, Renom B, Fairweather K, Lopes A, Cozens J, Laloë JO (2022) Changes in mean body size in an expanding population of a threatened species. Proc R Soc B 289:1976–20220696. <https://doi.org/10.1098/rspb.2022.0696>
- Herren RM, Bagley DA, Bresette MJ, Holloway-Adkins KG, Clark D, Witherington BE (2018) Sea Turtle abundance and demographic measurements in a marine protected area in The Florida Keys, USA. Herpetol Conserv Biol 13:224–239
- Hughes GR (1996) Nesting of the Leatherback Turtle (*Dermochelys coriacea*) in Tongaland, KwaZulu-Natal, South Africa, 1963–1995. Chelonian Conserv Biol 2:153–158
- ICMbio Chico Mendes Institute for Biodiversity Conservation (2022) Red Book of the Brazilian Fauna Threatened with Extinction, IV – Reptiles.
- Jackson JBC, Kirby MX, Berger WH, Bjorndal KA, Botsford LW, Bourque BJ, Warner RR (2001) Historical overfishing and the recent collapse of coastal ecosystems. Science 293:629–637. <https://doi.org/10.1126/science.1059199>
- Le Gouvello DZM, Giron dot M, Bachoo S, Nel R (2020) The good and bad news of long-term monitoring: an increase in abundance but decreased body size suggests reduced potential fitness in nesting sea turtles. Mar Biol 167:8. <https://doi.org/10.1007/s00227-020-03736-4>
- Lenz AJ, Avens L, Campos Trigo C, Borges-Martins M (2016) Skeletochronological estimation of age and growth of loggerhead sea turtles (*Caretta caretta*) in the western South Atlantic Ocean. Austral Ecol 41:580–590. <https://doi.org/10.1111/aec.12347>
- Liles MJ, Peterson MJ, Lincoln YS, Seminoff JA, Gaos AR, Peterson TR (2015) Connecting international priorities with human wellbeing in low-income regions: lessons from hawksbill turtle conservation in El Salvador. Local Environ 20:1383–1404. <https://doi.org/10.1080/13549839.2014.905516>
- Lopez GG, Lara PH, Salies E (2014) Pursuing coastal conservation in Northeast Brazil as a shared responsibility. State World's Sea Turt SWOT Rep 9:42–43
- Lopes-Souza A, Schiavetti A, Álvarez MR (2015) Analysis of marine turtle strandings (Reptilia: Testudine) occurring on coast of Bahia State, Brazil. Lat Am J Aquat Res 43:675–683. <https://doi.org/10.3856/vol43-issue4-fulltext-6>
- López-Mendilaharsu M, Giffoni B, Monteiro D, Prosdociami L, Vélez-Rubio GM, Fallabrino A, Estrades A, Santos AS, Lara PH, Pires T, Tiwari M, Bolten AB, Marcovaldi MA (2020) Multiple-threats analysis for loggerhead sea turtles in the southwest Atlantic Ocean. Endanger Species Res 41:183–196. <https://doi.org/10.3354/esr01025>
- Mortimer JA, Appoo J, Bautil B, Betts M, Burt AJ, Chapman R, Hays GC (2022) Long-term changes in adult size of green turtles at Aldabra Atoll and implications for clutch size, sexual dimorphism and growth rates. Mar Biol 169(1–10):123. <https://doi.org/10.1007/s00227-022-04111-1>
- Marcovaldi MA, Marcovaldi GG (1999) Marine turtles of Brazil: the history and structure of Projeto TAMAR-IBAMA. Biol Cons 91:35–41. [https://doi.org/10.1016/S0006-3207\(99\)00043-9](https://doi.org/10.1016/S0006-3207(99)00043-9)
- Marcovaldi MA, Chaloupka M (2007) Conservation status of the loggerhead sea turtle in Brazil: an encouraging outlook. Endanger Species Res 3:133–143. <https://doi.org/10.3354/esr003133>
- Mazaris AD, Schofield G, Gkazinou C, Almpantidou V, Hays GC (2017) Global Sea turtle conservation successes. Sci Adv 3(9):e1600730. <https://doi.org/10.1126/sciadv.1600730>
- Monteiro DS, Estima SC, Gandra TBR, Silva AP, Bugoni L, Swimmer Y, Seminoff JA, Secchi ER (2016) Long-term spatial and

- temporal patterns of sea turtle strandings in southern Brazil. *Mar Biol* 163:247. <https://doi.org/10.1007/s00227-016-3018-4>
- Petit R, Secchi ER, Avens L, Kinas PG (2012) Age and growth of loggerhead sea turtles in southern Brazil. *Mar Ecol Prog Ser* 456:255–268. <https://doi.org/10.3354/meps09681>
- Phillips KF, Stahelin GD, Chabot RM, Mansfield KL (2021) Long-term trends in marine turtle size at maturity at an important Atlantic rookery. *Ecosphere* 12(7):e03631. <https://doi.org/10.1002/ecs2.3631>
- Piacenza SE, Balazs GH, Hargrove SK, Richards PM, Heppell SS (2016) Trends and variability in demographic indicators of a recovering population of green sea turtles *Chelonia mydas*. *Endanger Species Res* 31:103–117. <https://doi.org/10.3354/esr00753>
- Piovano S, Clusa M, Carreras C, Giacoma C, Pascual M, Cardona L (2011) Different growth rates between loggerhead sea turtles (*Caretta caretta*) of Mediterranean and Atlantic origin in the Mediterranean Sea. *Mar Biol* 158:2577–2587. <https://doi.org/10.1007/s00227-011-1759-7>
- R Core Team (2017) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna Austria. <https://www.R-project.org/>
- Ramirez MD, Avens L, Goshe LR, Snover ML, Cook M, Haas HL, Heppell SS (2020) Regional environmental drivers of Kemp's ridley sea turtle somatic growth variation. *Mar Biol* 167:1–20. <https://doi.org/10.1007/s00227-020-03754-2>
- Reis EC, Soares LS, Vargas SM, Santos FR, Young RJ, Bjorndal KA, Lôbo-Hajdu G (2010) Genetic composition, population structure and phylogeography of the loggerhead sea turtle: colonization hypothesis for the Brazilian rookeries. *Conserv Genet* 11:1467–1477. <https://doi.org/10.1007/s1052-009-9975-0>
- Richardson JI, Hall DB, Mason PA, Andrews KM, Bjorkland R, Cai Y, Bell R (2006) Eighteen years of saturation tagging data reveal a significant increase in nesting hawksbill sea turtles (*Eretmochelys imbricata*) on Long Island, Antigua. *Anim Conserv* 9:302–307. <https://doi.org/10.1111/j.1469-1795.2006.00036.x>
- Rizzi M, Rodrigues FL, Medeiros L, Ortega I, Rodrigues L, Monteiro DS, Proietti MC (2019) Ingestion of plastic marine litter by sea turtles in southern Brazil: abundance, characteristics and potential selectivity. *Mar Pollut Bull* 140:536–548. <https://doi.org/10.1016/j.marpolbul.2019.01.054>
- Santos AS, Soares LS, Marcovaldi MÂ, Monteiro DS, Giffoni B, Almeida AP (2011) Avaliação do estado de conservação da tartaruga marinha *Caretta caretta* Linnaeus, 1758 no Brasil. *Revista Biodiversidade Brasileira* ano I, 1:3–11. Disponível em: https://tamar.org.br/publicacoes_html/pdf/2011/2011_avaliacao_caretta.pdf
- Thomé JC, Baptistotte C, Moreira LMP, Scalfoni JT, Almeida AP, Rieth DB, Barata PC (2007) Nesting biology and conservation of the leatherback sea turtle (*Dermochelys coriacea*) in the state of Espírito Santo, Brazil, 1988–1989 to 2003–2004. *Chelonian Conserv Biol* 6:15–27
- Turner Tomaszewicz CN, Avens L, LaCasella EL, Eguchi T, Dutton PH, LeRoux RA, Seminoff JA (2022) Mixed-stock aging analysis reveals variable sea turtle maturity rates in a recovering population. *J Wildl Manag* 86:4–e22217. <https://doi.org/10.1002/jwmg.22217>
- Wickham H (2016) GGPlot2: Elegant Graphics for Data Analysis. Springer-Verlag New York. ISBN 978–3–319–24277–4. Available from <https://ggplot2.tidyverse.org> (accessed October, 2021).
- Wilcox C, Puckridge M, Schuyler QA, Townsend K, Hardesty BD (2018) A quantitative analysis linking sea turtle mortality and plastic debris ingestion. *Sci Rep* 8:12536. <https://doi.org/10.1038/s41598-018-30038-z>
- Wood SN, Pya N, Saefken B (2016) Smoothing parameter and model selection for general smooth models. *J Am Stat Assoc* 111:1548–1575. <https://doi.org/10.1080/01621459.2016.1180986>

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