

1 **Long-term changes in body size of green turtles nesting on Trindade Island, Brazil:**
2 **Signs of Recovery?**

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26 **Abstract**

27 Trindade Island is an important wildlife refuge in the South Atlantic Ocean and hosts the largest
28 nesting population of green turtles (*Chelonia mydas*) in Brazil, about which temporal
29 ecological dynamics are still not well understood. The present study examines 23 years of
30 nesting for green turtles at this remote island to evaluate annual mean nesting size (MNS)
31 changes and post-maturity somatic growth rates. Our results show a significant decrease in
32 annual MNS over the study; Whereas MNS during the first three consecutively monitored years
33 (1993-1995) was 115.1 ± 5.4 cm, during the last three years (2014-2016) it was 111.2 ± 6.3
34 cm. There was no significant change in post-maturity somatic growth rate over the course of
35 the study; the mean annual growth rate was 0.25 ± 0.62 cm/year. These findings suggest an
36 increase in the relative proportion of smaller, presumptive neophyte nesters appearing in
37 Trindade during the study period.

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39 **Keywords:** Conservation; mean nesting size; population ecology; body size; Southwestern
40 Atlantic Ocean; time-series; monitoring.

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51 1. Introduction

52 Oceanic islands often host high species richness and biodiversity, and due to their
53 remoteness, such areas, when pristine, have the potential to offer refugia for sensitive and
54 conservation-dependent wildlife populations (Fonseca et al., 2006). Yet approximately one-
55 third of all currently endangered vertebrates are associated with oceanic islands (Fonseca et al.,
56 2006), and many insular species are already extinct (Heinen et al., 2018). Therefore,
57 understanding ecological and demographic changes in island wildlife populations is
58 fundamental for determining their population status and recovery potential, and for identifying
59 potential drivers of ecological change.

60 Trindade is a remote oceanic island in the Southwest Atlantic Ocean (SWAO),
61 considered one of the most important refuges for marine fauna in this region (Almeida, 2001),
62 and highlighted by the Convention on Biological Diversity (1992) as an ecologically and
63 biologically relevant area (Dutra et al., 2012). The island hosts the largest nesting assemblage
64 of green turtles (*Chelonia mydas*) in Brazil and the second largest rookery in the SWAO,
65 making the protection of this site crucial for the conservation of the species (Almeida et al.,
66 2011a). Trindade Island was discovered by colonial explorers in 1501 or 1502, marking the
67 beginning of four centuries of anthropic impacts that ultimately resulted in substantial negative
68 impacts on local biodiversity (Gasparini, 2004; Morh et al., 2009; Alves and Silva, 2016).
69 Perhaps the most devastating event was the introduction of pigs (*Sus* sp.) and goats (*Capra* sp.)
70 in 1700 by the astronomer Edmond Halley (Copeland, 1882; Alves, 1998; Duarte and Horta,
71 2012). It is believed that soon after their introduction, pigs became voracious predators of green
72 turtle eggs deposited in nests along the beaches of Trindade (Barth, 1958). This chronic
73 depredation of eggs was considered an important factor in the decrease in abundance of the
74 local nesting population of green turtles (Barth, 1958).

75 Like most sea turtles, green turtles have late sexual maturation and a long lifecycle
76 (Bolten, 2003). Atlantic green turtles reach maturity at curved carapace lengths (CCLs) ranging
77 from 89.7 cm to 108.0 cm (Almeida et al., 2011a; Colman et al., 2015), which equates to 15–
78 28 years in age based on skeletochronology and the known-year marking of young turtles and
79 their recapture as adults (Zug et al., 2002; Bell et al., 2005; Colman et al., 2015). This slow
80 maturation creates distinct conservation challenges for the species, as it reduces the likelihood
81 that an individual can survive the myriad of human threats to reach reproductive age (Mazaris
82 et al., 2017). Coupled with the fact that adult females nest only every ca. 3 years in the SWAO
83 (Almeida et al., 2011b), delayed sexual maturity in green turtles contributes to the species’
84 vulnerability because it requires that conservation efforts must be undertaken for decades or
85 more for populations to recover from human-induced reductions in population size (Gosh et
86 al., 2016). In the SWAO, including Brazilian waters, green turtle conservation status was
87 recently updated to ‘least concern’ on the IUCN Red List (IUCN, 2019) and to ‘almost
88 threatened’ in the Red Book of Brazilian Fauna (ICMbio, 2022).

89 The TAMAR Project started monitoring green turtles nesting on Trindade in 1982.
90 Since then, the project has estimated between 558 to 3559 visits per annum by green turtles to
91 the island (Marcovaldi and Marcovaldi, 1987; Medeiros et al., 2022). The Trindade Island
92 green turtle nesting population is thought to be relatively stable based on ongoing monitoring
93 efforts (Medeiros et al., 2022), contrasting the widespread increasing trends for green turtle
94 nesting populations in the Atlantic (García-Cruz et al., 2015; Mazaris et al., 2017). However,
95 this apparent stable status was inferred from a comparison of past (Almeida et al., 2011b) and
96 present (Medeiros et al., 2022) studies that used different techniques, thus presenting a major
97 caveat to this finding. Considering that the Trindade Island green turtle nesting population was
98 thought to suffer extreme losses due to an introduced predator (i.e. pigs) more than a century
99 ago (Alves et al., 2011), and in light of the eradication of this predator in the more recent past,

100 it is possible that Trindade green turtles are in a not yet described recovery phase due to higher
101 survival rates of eggs and neonates on the island during recent decades.

102 Determining long-term trends in abundance for sea turtle nesting populations typically
103 requires consistent on-beach monitoring, and robust counting of nesting individuals, over many
104 decades (National Research Council, 2010). However, there may be demographic
105 measurements other than annual abundance that can yield inferences, albeit indirectly, about
106 population trends. For example, Hays et al. (2022) show that a decrease in mean body size of
107 about 2.4 cm—from 83.2 to 80.8 cm—for loggerhead turtles (*Caretta caretta*) nesting in the
108 Cape Verde Islands was due to an influx of first-time nesters as the annual population size
109 expanded. A similar mean body size decrease was found for green turtles nesting at Ascension
110 Island in the South Atlantic, as the population underwent a significant increase in abundance
111 from 1973 to 2012 (Weber et al., 2014). Yet despite these examples and the potential for body
112 measurements to reveal demographic shifts indicative of population growth and recovery, so
113 far the have been no efforts to monitor changes in mean body size of nesting green turtles at
114 Trindade Island.

115 Here we analyze 23 season of nesting beach monitoring data for green turtles at
116 Trindade Island collected across a 32-year interval (1985–2016). Our goals were to evaluate
117 annual body size distributions and mean nesting sizes (MNSs), and adult female somatic
118 growth rates each year, to determine the extent to which these demographic parameters
119 changed over the course of the study. Using annual MNS as a simple biological indicator to
120 track long-term demographic changes, we hypothesized that if the population is in a recovery
121 phase, there would be a gradual decrease in annual MNS stemming from greater numbers of
122 smaller, neophyte nesters each year of the study. If so, our results can yield novel insights about
123 population trends for Trindade Island green turtles that were not previously considered despite
124 decades of monitoring at this remote nesting site. Our results also add relevant data for the

125 conservation and management of green turtles in Brazil and the SWAO, and provide a glimpse
126 as to how the eradication of a voracious island predator (i.e., pigs) may benefit local sea turtle
127 nesting colonies.

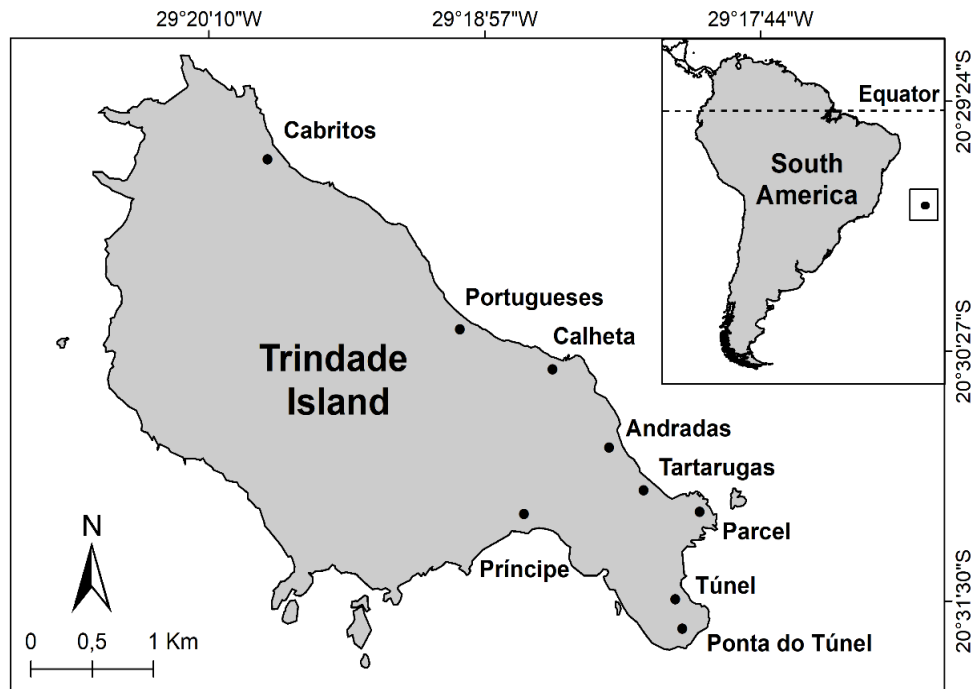
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129 **2. Methodology**

130 *2.1. Study Area*

131 Trindade Island (20°30'S, 29°20'W) is located 1160 km east of the Brazilian coast and
132 is part of the Vitória-Trindade oceanic island chain in the Southwestern Atlantic Ocean region
133 (Serafini et al., 2010; Fig. 1). Trindade is 13.5 km² in area, with interior terrain dominated by
134 rocky mountains, and coastal areas comprised of sand and pebble beaches (SECIRM, 2012).
135 Marine environments around the island are influenced by warm sea currents (Brazilian current;
136 Stramma, 1991) with a mean sea surface temperature of 27°C and mean wave heights between
137 1.0 and 2.0 meters (Pianca et al., 2010). The climate is tropical oceanic, with an average annual
138 air temperature of 25°C, with the warmest conditions usually in February (monthly mean =
139 30°C), and coolest periods in August (monthly mean = 17°C; Mohr et al., 2009).

140



141

142 **Figure 1.** Location of the nine green turtle nesting beaches monitored on Trindade Island,

143 South Atlantic Ocean. Data for this study are derived primarily from Andradas and

144 Tartarugas.

145

146 *2.2. Green Turtle Sampling*

147 This study assessed a green turtle nesting dataset spanning 32 years (1985–2016), with

148 body size data collected for 6132 nesting females across 23 reproductive seasons; 9 seasons

149 were not monitored due to logistic challenges. Nightly monitoring occurred from December to

150 February, primarily on the beaches of Andradas and Tartarugas, and sporadically (due to

151 logistic constraints) on seven other beaches (Fig. 1, Supplementary Table S1). Encountered

152 adult females were measured from the nuchal notch to the posterior-most edge of the carapace

153 (i.e., curved carapace length, CCL) using a flexible tape with 0.1-mm precision (Marcovaldi

154 and Marcovaldi, 1999). Each turtle was tagged on the first large proximal scale of each front

155 flipper (i.e. double-tagged) with Inconel tags (Style 681, National Band Company, Kentucky

156 USA; Almeida et al., 2011a). We note that tag loss can happen with green turtles, although

157 Colman et al. (2015) reports a tag loss rate of only 0.6% for loss of both tags during a study of
158 double-tagged adult green turtles. In the present study, green turtles that lost a single tag were
159 re-tagged in the appropriate front flipper.

160

161 *2.3. Body Size Distribution*

162 Each nesting turtle measured during a breeding season was represented only once in the
163 respective annual dataset. For individuals encountered more than once in a season, the mean
164 CCL was used (Phillips et al., 2021). With these data on individual size measurements, we
165 evaluated the annual body size distributions for each year of the study to gain an understanding
166 about changes in the body size structure for the population. Body size frequency distributions
167 were represented graphically (Kaps and Lamberson, 2004) for each of the 23 breeding seasons
168 to gauge potential long-term changes in the proportion of neophyte vs. experienced adult
169 nesters. For this exercise we used 108.0 cm CCL—the maximum size at maturation for SWAO
170 Atlantic green turtles (Almeida et al., 2011a; Colman et al., 2015)—as the putative threshold
171 for distinguishing between the neophytes and experienced nesters. We recognize the inherent
172 caveats of using a single size threshold for a dynamic population, due to the variability in
173 female maturation size for any given population (Turner Tomaszewicz et al., 2022); however,
174 without unequivocal knowledge about reproductive histories for each turtle we deem this size
175 threshold to be a reasonable approximation for the population.

176

177 *2.4. Mean Nesting Size*

178 Building off the inspection annual body size distributions, we also calculated the mean
179 body size of nesting females (i.e. mean nesting size, MNS) for each season. As with size
180 frequency calculations, for turtles that were captured on multiple occasions, we used the mean
181 of all measurements in analyses. To determine potential changes in annual MNS we used a

182 generalized additive model (GAM) (Hastie, 2020). Here, the GAM was used to test for changes
183 in mean CCL (response variable) across years (predictor variable). For this, we built the model
184 containing the variables “CCL ~ year”.

185

186 *2.5. Post-maturity Somatic Growth Rate*

187 To evaluate the effect of body size and year on post-maturity somatic growth rates for
188 the Trindade Island nesting population, first we calculated the annual growth rate (AGR) for
189 each individual observed during two or more nesting seasons following Le Gouvello et al.
190 (2020):

$$191 \quad AGR = \frac{CCL_{last} - CCL_{first}}{Number\ of\ Years}$$

192 where CCL_{last} and CCL_{first} are the curved carapace lengths (cm) of the turtle upon its
193 final and initial measurements, respectively, and *Number of Years* is the total ordinal days
194 between first and last measurement divided by 365 days.

195 Generalized linear models (GLMs) were used to test for differences in individual post-
196 maturity growth rates across all years of the study. We assumed a quasipoisson data
197 distribution, and used GLMs with growth rate as the response variable, and time and initial
198 body size (CCL) as predictor variables. We compared the null model “rate~1” with the model
199 containing the variables “rate~CCL + time”, “rate~CCL”, and “rate~time”. The best model
200 took into account the explanatory power residual deviance.

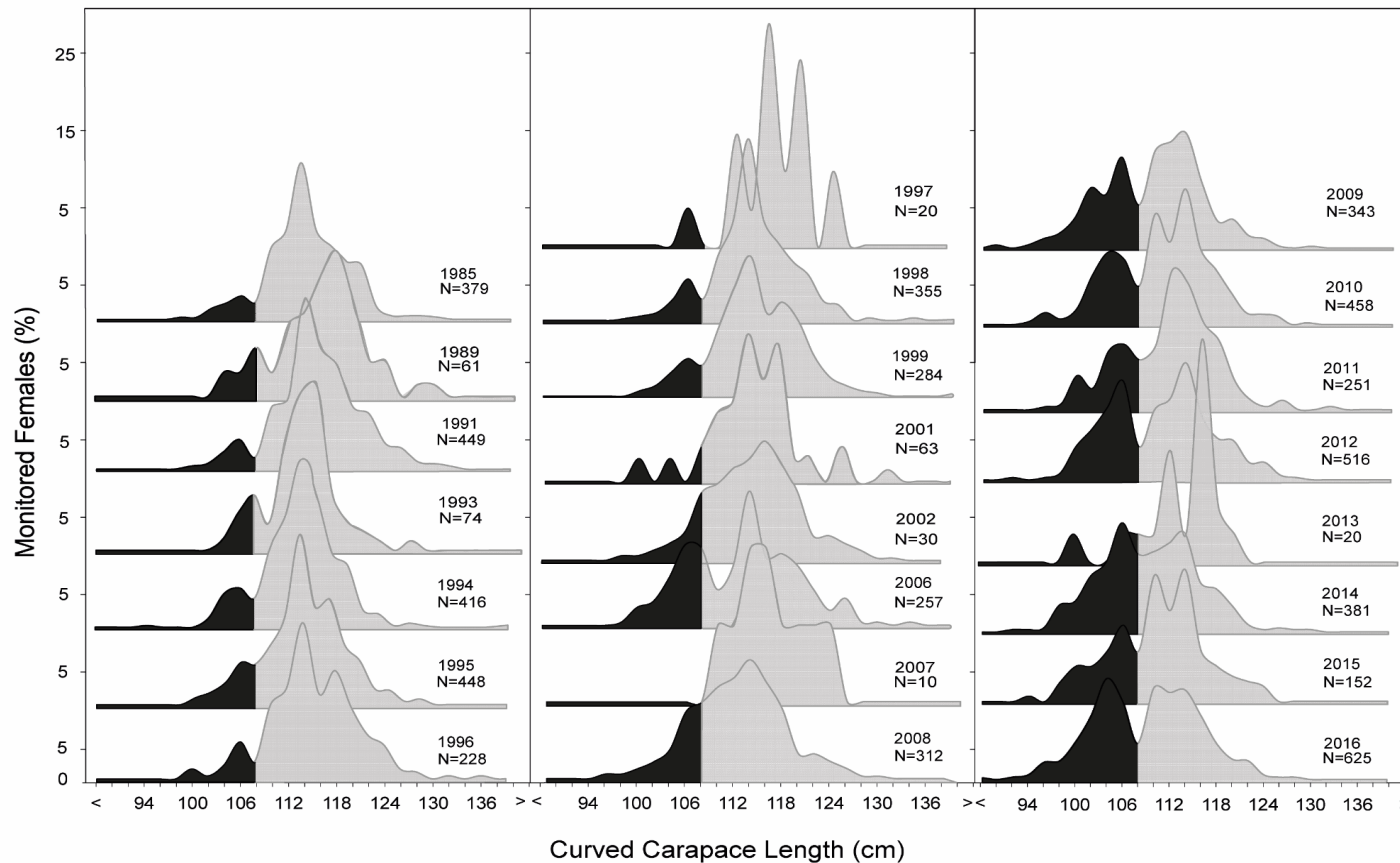
201 Modeling analyses were performed in R (R CORE TEAM, 2017), using the packages
202 'mgcv', 'ggplot2' and 'ggthemes' (Wickham, 2016).

203

204 **3. Results**

205 *3.1. Annual Body Size Distribution*

206 Overall, 6132 individual turtles were measured during this study, with an annual range
207 of 10–625 (mean = 267 ± 183) green turtles encountered. When examining the annual body size
208 frequency distributions for nesting green turtles we found a clear increase in the proportion of
209 smaller, putative neophyte nesters (black portion of graphs) as the years progressed. Annual
210 nesting populations had between 8% and 41.6% of females with CCL < 108 cm, our putative
211 threshold for distinguishing between the neophytes and experienced nesters, and there was a
212 gradual increase in the annual proportion of females with CCL < 108 cm as the study progressed
213 (Fig. 2). In turn, the proportion of ‘large’ females with CCL > 120 cm was greatest during the
214 initial years of monitoring, with observed maximum values of 36.7%, and decreased in later
215 years, to as low as 5% (2013) (Fig. 2). Reflective of these shifts in body size, we also observed
216 a gradually more-pronounced bi-modality in the CCL frequency distribution, with distinct
217 groups of smaller and larger nesting females (Fig. 2).



218

219 **Figure 2.** Curved carapace length frequency distribution for adult female *Chelonia mydas* on Trindade Island during 23 nesting seasons
 220 interspersed from 1985 to 2016. Black shading indicates CCL frequencies of the putative neophytes, based on a maximum recruitment size of 108
 221 cm CCL for the South Atlantic (Avens and Snover, 2013); Gray shading delimits the adult sizes considered to be post-recruits (i.e. experienced
 222 nesters). See ‘reproductive seasons’ in Figure 3B.

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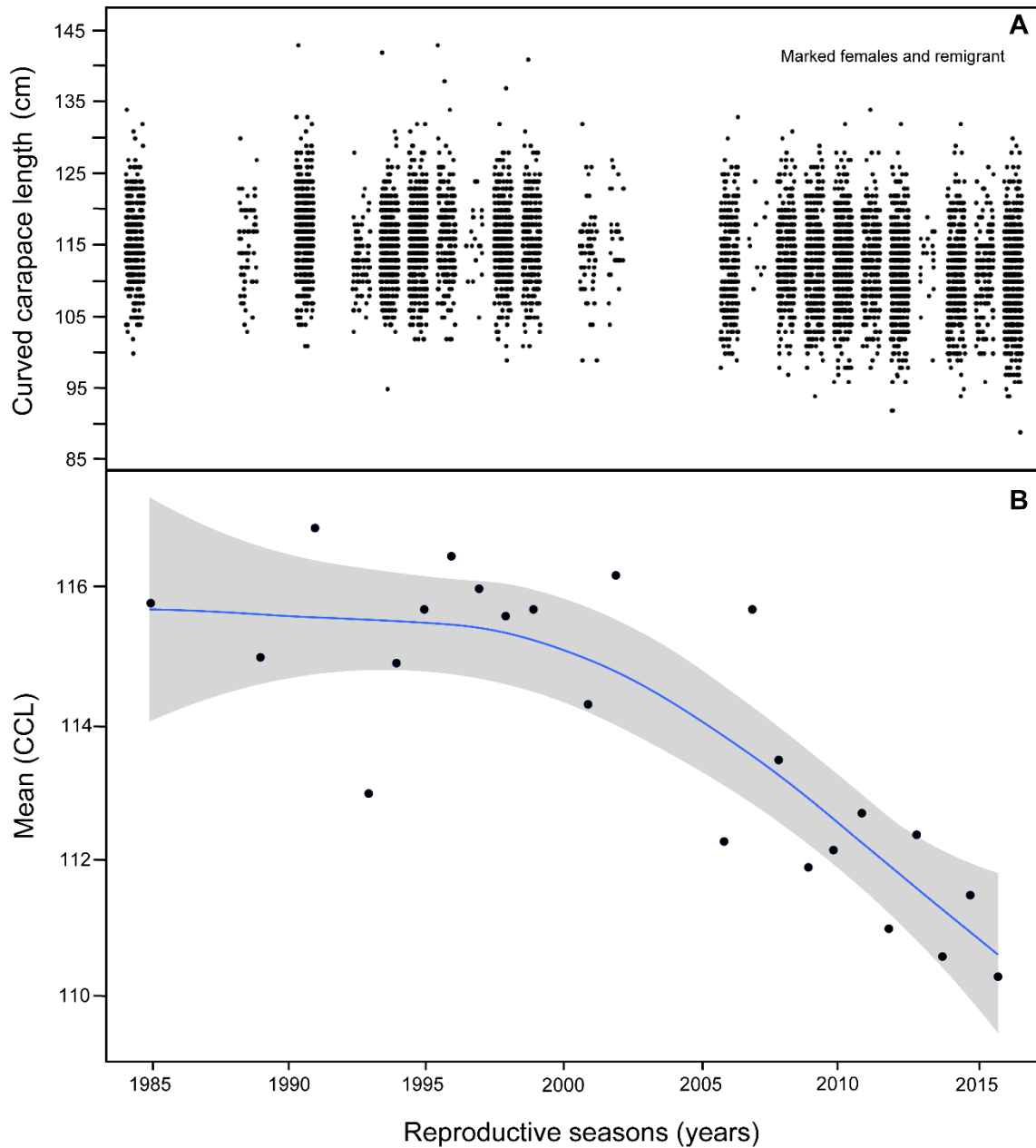
225 *3.2. Mean Nesting Size*

226 For the 23 years of monitoring results, GAM analyses identified significant differences
227 in annual CCL frequency structure and mean CCL of nesting females ($p < 0.0001$, with model
228 explanatory power [pseudo R^2] of 0.718 and deviance of 75%; Table 1, Fig. 3). The overall
229 mean CCL of measured females across all years was 113.3 cm ($n = 6132$, range = 89.1–144.2
230 cm; $SD = 6.3$). There was an evident increase in the proportion of smaller females as the study
231 progressed (Fig. 3A), which resulted in a monotonic declining trend in MNS among measured
232 female green turtles (Fig. 3B). The MNS during the first three consecutively monitored years
233 (1993–1995; = 1 nesting remigration interval, Almeida et al., 2011b) was 115.1 ± 5.4 cm CCL
234 (range = 95.2–143.5 cm, $n = 938$), and during the last three years of data (2014–2016), it was
235 111.2 ± 6.3 cm CCL (89.3–132.2 cm, $n = 1158$). It is interesting to note that, in addition to the
236 4-cm difference in MNS between these two periods, the maximum CCL of nesting females
237 during 1993–1995 (143.5 cm CCL) was more than 10 cm larger than the maximum CCL
238 recorded during 2014–2016 (132.2 cm CCL; Supplementary Table S2).

239

240 **Table 1.** Results of the analysis of deviance applied to the generalized additive model fit to
241 describe the variations in mean annual CCL throughout the study. Note: standard error
242 ‘Std.Error’, estimated degree of freedom ‘Edf’, reference degree of freedom ‘Ref.Df’, Z for
243 statistics, X^2 for Chi-square p for statistics.

	Estimate β	Std.Error	Z	P
Intercept	113.9	0.2314	492.1	<0.001
Smooth term	Edf	Ref.Df	X²	P
Year	2.5	3.152	56.92	<0.001



245

246 **Figure 3.** A, Curved carapace lengths (CCL) for green turtles (*Chelonia mydas*) nesting at
 247 Trindade during 23 nesting seasons interspersed from 1985 to 2016. B, variability in annual
 248 mean nesting size (CCL) tested using a generalized additive model with standard deviation
 249 analysis of female CCL ($p < 0.01$).

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253 3.3. Post-maturity Somatic Growth

254 A total of 570 female green turtles were measured during multiple nesting seasons
255 during the study. Of these females, 52 % (n=299) did not show post-maturity growth. The
256 interval between the first and last measurements for any single turtle ranged from 2 to 32 years.
257 Individual-based post-maturity annual somatic growth rate ranged from 0.02 to 9 cm/year, with
258 a mean of 0.25 ± 0.62 cm/year; there was no relationship with sampling year nor with female
259 CCL_{first} (Table 2). Moreover, there was no explanatory power between post-maturity annual
260 growth rates when compared to time (Model 3: $\beta = -0.166$; $p = 0.455$) and CCL (Model 2: $\beta =$
261 0.016 ; $p = 0.347$; Table 2). The null model showed the best explanatory power.

262

263 **Table 2.** Selection of generalized linear models in relation to post-maturity growth rates $p <$
264 $0,001$. Note: Df reference of degree of freedom and F for statistics.

Model selection	Resid. Df	Resid Dev	Df	Deviance	F	P value
Model null: rate ~1	569	372.75	—	—	—	—
Model 1: rate~ccl + time	567	371.02	2	1.728	0.583	0.558
Model 2: rate ~ ccl	568	371.45	1	-0.424	0.287	0.592
Model 3: rate ~ time	568	371.91	0	- 0.458		

265

266 4. Discussion

267 Our study reveals several important demographic parameters for Trindade green
268 turtles, including their annual mean nesting size (MNS) and range in body size across 23
269 different nesting seasons, as well as trends in somatic growth rates among turtles encountered
270 during two or more nesting seasons. These findings show the value of long-term tagging
271 programs at nesting beaches for studying sea turtle demography and population status. The
272 data also highlight the importance of mark-recapture records for understanding how sea turtle
273 status may change through time (e.g. Stokes et al., 2014).

274

275 4.1. Changes in Mean Body Size

276 We demonstrate a trend of reduced mean nesting size of reproductive green turtles at
277 Trindade Island, a remote location in the Southwestern Atlantic Ocean. In the early 1980s there
278 was a greater relative proportion of large females, with relatively few smaller-bodied new
279 recruits, although the proportion of smaller turtles increased in the later years of this study (Fig.
280 2). There are multiple potential reasons for this reduction in body size, although we suggest
281 this proportional increase in smaller turtles arriving at Trindade each year was due to increased
282 recruitment and the presence of greater numbers of neophyte (i.e. first time) nesters, which are
283 usually smaller than older females (Le Gouvello et al., 2020; Hays et al., 2022). Recovering
284 sea turtle populations elsewhere in the Atlantic as well as in the Pacific have shown similar
285 nesting female mean body size reductions, and these demographic shifts too have been
286 attributed to increases in the relative proportion of neophyte nesters (García-Cruz et al., 2015;
287 Piacenza et al., 2016; Hays et al., 2022). Moreover, the magnitude of the overall decrease in
288 annual mean CCL (-3.9 cm) found for Trindade Island green turtles is similar to the 4.5 cm
289 decrease found for a recovering green turtle population at Ascension Island in the South
290 Pacific. An increase in the proportion of smaller nesting females following significant
291 conservation efforts and population increase has also been reported for leatherback turtles
292 (*Dermochelys coriacea*) at Espirito Santo, Brazil (Colman et al., 2019).

293 While we suggest reductions in MNS and changes in body size frequency are
294 probably the result of increased neophyte nesters, additional considerations are warranted to
295 evaluate the efficacy of this theory. As noted above, there was a long history of pig depredation
296 of green turtle eggs and hatchlings at Trindade (Barth, 1958; Alves and Silva, 2016), which
297 likely reduced population sizes to all-time lows. A timeline taking into account pig eradication
298 efforts and green turtle maturation ages suggests that the pulse of putative neophyte nesters

299 was likely the result of pig eradication (Supplementary Fig. S1). Eradication efforts started in
300 1965 (Alves, 1998) and likely took several years, perhaps as long as a decade, to achieve a
301 complete removal of pigs. If we consider that the mean time from neritic recruitment (ca. 30
302 cm CCL) to adulthood is about three decades for green turtles at Fernando de Noronha, the
303 nearest neighboring major green turtle rookery in Brazil (Colman et al., 2015), then the initial
304 surviving cohorts of green turtles coinciding with eradication would have been expected to
305 show up as adult nesting females in the early-to-mid 2000s, which is consistent with our data
306 showing significantly smaller mean nesting sizes by 2006. We note that there is a slight
307 increase in the proportion of smaller females prior to 2006, which we attribute to variability in
308 maturation age (e.g. Bell et al., 2005; Patrício et al., 2014). In the eastern Pacific, for example,
309 Turner Tomaszewicz et al. (2022) found that some green turtles matured in as little as 17 years.

310 We acknowledge that increases in the proportion of smaller turtles at Trindade Island
311 may also be due to other factors besides the positive effects of conservation (Mazaris et al.,
312 2017; Hays et al., 2022). For example, one driver for such change could be differential at-sea
313 mortality from fisheries bycatch, with the larger green turtles interacting with fisheries at a
314 greater rate. Both artisanal and industrial fisheries are widespread throughout the region, and
315 green turtles are known to interact with a variety of gear types (Marcovaldi et al., 2006).
316 However, there is no evidence of a size bias among the turtles that interact with these fisheries.
317 Changes in female CCL frequency could also stem from extrinsic factors such as habitat
318 degradation (e.g. marine pollution, climate change) disproportionately impacting larger turtles,
319 reducing prey availability and/or increasing competition for resources (Bjorndal et al., 2000a,
320 Balazs and Chaloupka, 2004). This possibility seems less likely considering the lack of any
321 change in somatic growth rate partially related to habitat quality (Bjorndal et al., 2000).

322 While the exact drivers for the observed change in mean body size may be unclear,
323 the fact that nesting turtles have gotten smaller at Trindade Island has important implications

324 for the reproductive output of the population. Such changes in body size relative frequencies
325 may have important ecological consequences related to a population's reproductive output
326 potential (Shackell et al., 2010; Romanuk et al., 2011; Brost et al., 2015). For instance, larger
327 females may have greater potential reproductive output, due to increased internal space to
328 produce more eggs (Brost et al., 2015; Cameron et al., 2016; Mortimer et al., 2022), and in
329 turn, populations with increased proportions of neophyte nesters may have a net decrease in
330 per-individual fitness (Le Gouvello et al., 2020).

331

332 *4.2. Effects of Pig Eradication*

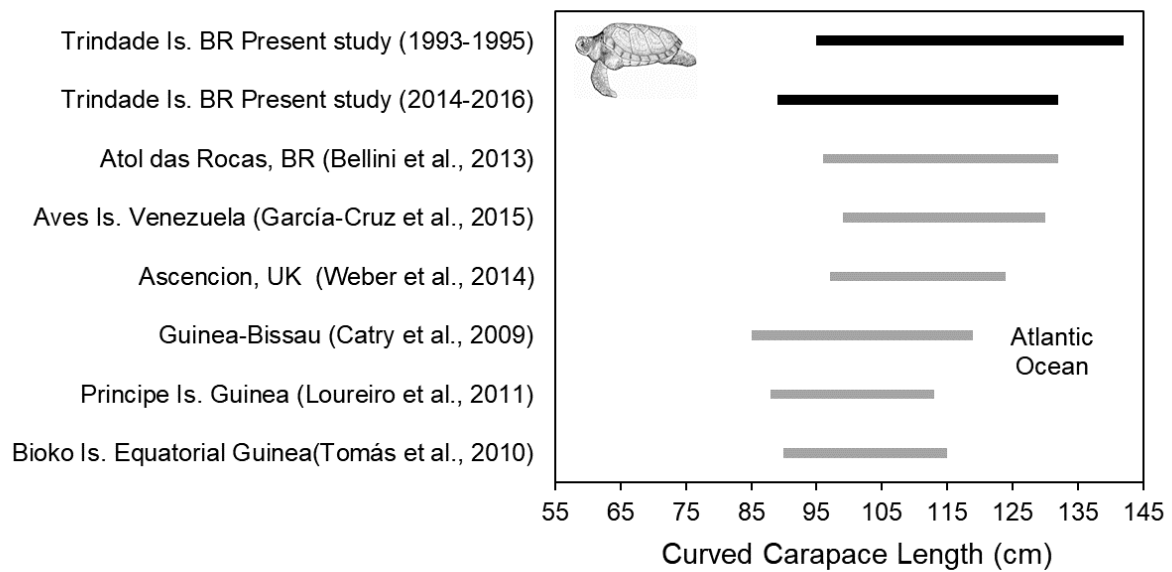
333 Whereas the true impact of introduced rats on Trindade Island green turtle survival
334 and population size are unknown due to the historic timeline of pigs introduction (prior to
335 record keeping or nesting beach monitoring), there is little doubt that the introduction of pigs
336 had a devastating negative impact on the green turtle population. Nest predation by pigs is
337 currently a significant conservation challenge for many sea turtle populations around the world
338 (Fowler, 1979; Engeman et al., 2005; Longo et al., 2009). For example, in Georgia (USA),
339 predation by introduced pigs was identified as having the greatest impact among egg predators
340 on loggerhead turtle nests (*Caretta caretta*, Butler et al., 2020). Similarly, pigs were the
341 primary culprit responsible for the loss of 89.6% of all nests deposited by flatback (*Natator*
342 *depressus*), olive ridley (*Lepidochelys olivacea*), and hawksbill (*Eretmochelys imbricata*)
343 turtles in Western Cape York Peninsula, Australia (Whytlaw et al., 2013). Moreover, and
344 consistent with our theory about the benefits of pig eradication on Trindade to local green
345 turtles, pig removal at Keewaydin Island (Florida, USA) resulted in a decrease from 41.6% to
346 27.7% in green turtle/loggerhead nest loss in just two years, and to 9.4% after four years
347 (Engeman et al., 2014, 2019). Such positive signs after the eradication of rats on other nesting
348 beaches suggests that the removal of rats on Trindade had a profound positive influence on the

349 local green turtle population. However, unfortunately there is no information about female
350 abundance prior to 1982, nearly two decades after the eradication of pigs (in 1965). To shed
351 light on this important topic, we recommend continued monitoring to ensure that future
352 changes in population size are well-understood, especially in relation to the first year of
353 monitoring in 1982.

354

355 *4.3. Maximum Body Size of Nesting Females*

356 Another interesting finding in the present study is that the maximum size of green
357 turtles encountered (143.5 cm CCL) is 10 cm larger than that largest female found nesting
358 elsewhere in the Atlantic Ocean (Fig. 4). The reasons for this substantial ‘maximum size’
359 disparity are unclear, but may relate to differing harvest histories among the different SWAO
360 nesting populations. Although Trindade Island green turtles were likely heavily impacted by
361 introduced pigs, which impacted egg and neonate survival, the remote nature of the island
362 perhaps lessened the access for turtle hunters, making it more difficult to actively target the
363 largest of individuals, which was often the case during historical directed take (Carr and
364 Caldwell, 1956; Pritchard, 1980). We note that this maximum size for our study population is
365 from the early portion of our study period (1991); nevertheless, such differences in harvest
366 history could still manifest today in some populations, considering the long-lived nature of sea
367 turtles. Alternative scenarios for this maximum size disparity be also relate to differences in
368 forage habitat quality and/or intraspecific competition in foraging areas among the different
369 nesting assemblages, since growth is dependent on density and availability of food (Bjorndal
370 et al., 2000).



372

373 **Figure 4.** Comparison of curved carapace length (cm) ranges (horizontal bars) for *Chelonia*
 374 *mydas* nesting at Trindade Island (black bars) and other locations (grey bars) in the Atlantic
 375 Ocean.

376

377 4.4. Somatic Growth

378 With a mean annual growth rate of 0.25 ± 0.6 cm/year, adult female green turtles at
 379 Trindade Island appear to grow slower than their counterparts at other nesting rookeries in the
 380 Atlantic Ocean (0.3–0.9 cm/year; Omeyer et al., 2017). The drivers for annual growth often
 381 relate to extrinsic factors such as habitat quality (Diez and Van Dam, 2002). However, green
 382 turtles nesting at Trindade use the same foraging areas as those from other nesting rookeries in
 383 the South Atlantic (Proietti et al., 2012), thus any negative influence of poor habitat on somatic
 384 growth likely would have affected these other nesting subpopulations as well. Instead, perhaps
 385 the location of Trindade Island requires that green turtles expend greater amounts of energy to
 386 access this offshore locality, such that greater nutrient proportions are routed for the production
 387 of eggs rather than somatic growth. Whatever the reason, it is apparent that the intrinsic and/or

388 extrinsic factors influencing growth were constant through time, as we demonstrated that post-
389 maturity female growth rates did not change over the 32-year duration of this study. In contrast,
390 Le Gouvello et al. (2020) found that the somatic growth of female loggerheads nesting in South
391 Africa did change over time. The reasons for the disparate adult growth patterns are unclear
392 and warrant further study

393

394 *4.5. Conservation Measures*

395 The TAMAR project has been protecting sea turtles at nesting and feeding areas
396 throughout Brazil for over four decades (Colman et al., 2019). People's greater awareness,
397 coupled with better protection of coastal and feeding environments, likely contributed to the
398 stabilization and putative recovery of the green turtle nesting population at Trindade. In
399 addition to pig eradication, important conservation actions that likely contributed to this
400 positive situation include increased sanctions and penalties for capture, killing, egg collection,
401 and habitat disturbance imposed by the Environmental Crimes Law n° 9.605, of 12 February
402 1998 (Brazil, 1998); the categorization of sea turtles as endangered species by IBAMA
403 Ordinance n° 1.522, of 19 December 1989 (Brazil, 1989); and the required mitigation of
404 incidental bycatch in fishing gear as stated in Law n° 31 of December 2004 (Brazil, 2004).
405 Along with this increased environmental oversight, outreach and education campaigns
406 developed by TAMAR were instrumental for the protection of green turtles and other sea turtle
407 species along the Brazilian coast.

408

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416

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