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3 **Demography of endangered juvenile green turtles in face of environmental**
4 **changes: 10 years of capture-mark-recapture efforts in Martinique**

5

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78 Damien Chevallier conceptualized the study, searched the fund required for the research
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1 **Demography of endangered juvenile green turtles in face of environmental**
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3

4 **Abstract**

5 Estimating demographic parameters is key for unraveling the mechanisms governing the
6 population dynamics of species of conservation concern. Endangered green sea turtles navigate
7 vast geographical ranges during their life cycle and face various pressures in coastal areas,
8 especially during their juvenile life-stage. Here, we investigated survival, abundance,
9 recruitment and emigration of juvenile green turtles on two developmental grounds in
10 Martinique, French West Indies, using a capture-mark-recapture dataset of 658 captures over
11 10 years. We detected increasing abundances of green turtles, likely attributed to the continuous
12 recruitment of new individuals, low mortality and low rate of emigration from these two
13 developmental sites. Local recruitment slightly decreased with small turtles densities while
14 emigration strongly increased with large turtles densities. These results associated with known
15 food availability and size-dependent diet preference of local green turtles suggest that the
16 expansion of invasive seagrass *H. stipulacea* may facilitate the settlement of small juveniles,
17 however it also limits the capacity of seagrass beds to sustain large juveniles. Boat anchorage,
18 pollution and *H. stipulacea* invasion reduced the availability of native seagrass species. This
19 could intensify competition between large turtles, trigger earlier emigration, therefore
20 modifying the structure of the green turtle populations in Martinique. Measures to protect native
21 seagrass beds are essential to maintain their capacity to sustain the entire green turtle
22 developmental stage. This study will help to connect sea turtle life-stages and to set up efficient
23 regional conservation measures. Moreover, results shown here provided clues to understand
24 demography of endangered megaherbivores in context of pasture degradation.

25 **1. Introduction**

26 Recruitment (through birth or immigration), emigration and mortality are demographic
27 parameters that drive population size (Williams et al., 2002). Capture-Mark-Recapture (CMR)
28 models are useful to estimate these demographic parameters and explain their variations in
29 response to environmental factors or individual traits (Amstrup et al., 2005). Through the
30 estimation of survival rates, emigration, recruitment or abundance, CMR models allow to detect
31 or predict trends in populations of species of conservation concern, as well as to determine risk
32 factors (Williams et al., 2002; e.g. Chevallier et al., 2020; Fujiwara and Caswell, 2001;
33 Chaloupka and Limpus, 2001; Monadjem et al., 2014) and can thus guide relevant management
34 actions to be implemented (e.g. Warret Rodrigues et al., 2021). This method is therefore crucial
35 to define efficient conservation measures for species whose recovery rates is slow, such as
36 marine megafauna, a third of which are threatened with extinction (Pimiento et al., 2020).

37 Sea turtles are members of the marine megafauna threatened by human activities (Wallace et
38 al., 2011). Population viability of all the seven extant sea turtle species is usually estimated
39 from samples of nesting female (Wildermann et al., 2018). Nonetheless, studies tend to
40 demonstrate that the juvenile life-stage is also an important determinant of population viability
41 in several long-lived marine species (Heppell et al., 1999), as it could be for marine turtles
42 (Crowder et al., 1994; Wildermann et al., 2018). All species of sea turtles, at the exception of
43 the leatherback turtle (*Dermochelys coriacea*), may use neritic habitat during their juvenile life-
44 stage (Lutz et al., 2003), where they are exposed to several risks induced by human activities
45 and degraded coastal environments (Domiciano et al., 2017; Lotze et al., 2006). Investigating
46 vital rates of juvenile sea turtles is therefore critical.

47 The green turtle (*Chelonia mydas*), classified as “Endangered” by the IUCN Red List
48 (Seminoff, 2004; <https://www.iucnredlist.org/species/4615/247654386>; accessed 27/12/2023),

49 recruits in shallow coastal waters at around 30 cm carapace length after a post-hatchling pelagic
50 phase called the “lost years” (Lutz et al., 2003). Several studies have focused on immature green
51 turtle demography, mostly on survival rates and abundance (Chaloupka and Limpus, 2005;
52 Colman et al., 2015; Kameda et al., 2023; Mollenhauer et al., 2022; Patricio et al., 2011).
53 Nonetheless, few studies investigated the emigration rates of juvenile green turtles from their
54 development grounds (Bjorndal et al., 2003; Seminoff et al., 2003) and, to the best of our
55 knowledge, none described recruitment rates. Consequently, factors that could drive the global
56 population dynamics of green turtles remain unclear.

57 Juvenile green turtles recruiting in coastal waters of Martinique, French West Indies, originate
58 from various Caribbean and Atlantic nesting sites (Chambault et al., 2018). There they spend
59 several years, feeding on seagrass beds located in shallow sheltered bays. Once they reach a
60 size around 80 cm curved carapace length (CCL), they embark on a major post-developmental
61 migration, and they join Caribbean and Atlantic breeding populations (Chambault et al., 2018).
62 During their developmental phase in Martinique, juvenile green turtles show high fidelity to
63 highly touristic areas (Siegwalt et al., 2020) making them vulnerable to local anthropic
64 pressures such as bycatch and boat collision (Louis-Jean et al., 2008; Siegwalt et al., 2020).
65 Moreover, coastal pollution might also enhance disease risk in green turtles, especially the
66 development of fibropapillomatosis (Jones et al., 2016), a deadly neoplastic disease that has
67 been observed in the green turtle population on the coast of Martinique (Bonola et al., 2019;
68 Roost et al., 2022). Green turtles primarily graze on seagrass beds composed of varying
69 proportions of three marine phanerogams species: the turtle grass *Thalassia testudinum*, the
70 manatee grass *Syringodium filiforme*, and the exotic *Halophila* seagrass originating from the
71 Red Sea, *Halophila stipulacea*. This last seagrass species was first documented in coastal waters
72 of Martinique in 2006 (Maréchal et al., 2013) and is currently the most widespread of the three
73 phanerogams consumed by turtles in Martinique, but it has the lowest nutritional value

74 (Siegwalt et al., 2022). *H. stipulacea* invasion and native seagrass meadows loss by boat
75 anchoring could both have an impact on the fitness of juvenile green turtles (Siegwalt et al.,
76 2022) and are therefore likely to affect their demography. All these factors present in the coastal
77 area of Martinique, mainly due to human activity, can have an impact on the development of
78 green turtles. Considering the important contribution of Martinique juvenile green turtle
79 population to the Atlantic breeder population (Chambault et al., 2018), it is necessary to assess
80 their demographic parameters to ensure their conservation.

81 Here we estimated apparent survival, abundance and recruitment of green turtles using a Multi-
82 State Jolly-Seber (MSJS) model structure. This analysis was based on a decade-years dataset
83 of CMR collected from two sites in the Lesser Antilles renowned for their high concentration
84 of juvenile green turtles. Our study had two main objectives: 1) to identify internal and external
85 drivers of juvenile demography at their foraging grounds, and 2) to establish conservation
86 guidelines aimed at mitigating the primary threats to juvenile demography.

87 **2. Material and Methods**

88 **2.1. Study location and Capture-Mark-Recapture data collection**

89 The present study takes place in three bays of Les Anses d'Arlet (Martinique, French West
90 Indies (14°30'9.64"N, 61°5'11.85"W, Fig. A1): Grande Anse d'Arlet (GA), Anse du Bourg
91 d'Arlet and Anse Chaudière. During the analyses, the latter two sites were combined and
92 denominated as Anse du Bourg d'Arlet/Chaudière (ABAC), since there is no geographical
93 barrier between these. Importantly, in these two sites, no poaching is known and natural
94 predators (*i.e.* sharks) are absent (Chevallier & Lelong, pers. obs.).

95 Between 2013 and 2023, at the exception of 2014 and 2021, primary capture sessions have
96 taken place yearly for one-week periods (Fig. A2). They occurred typically in the month of
97 October excepted for 2013 (September), 2015 (additional session in June), 2022 and 2023

98 (February). These yearly sessions were complemented by multiple irregular capture sessions of
99 less than one day occurring throughout the year, with the exception of 2014, when no such short
100 capture sessions took place (Fig. A2). During these capture sessions, immature green turtles
101 were captured by free-divers at maximum depths of 25 m and lifted on a boat to carry out all
102 the following protocols. Animals were identified by a Passive Integrated Transponder (ID-100,
103 TROVAN). Capture and tagging procedures are described in Bonola et al. (2019). Carapace
104 dimensions, including central curved carapace length (CCL), were measured using a flexible
105 fiber glass tape at 0.1 cm precision (see Bonola et al., 2019 for details). Fibropapillomatosis
106 tumors (if present) on the body of turtles were photographed next to a metal ruler. These
107 photographs were later used to count and measure the tumors during animal data post-
108 processing. Body condition of the animals was estimated visually with carapace and plastron
109 concavity and carapace shape (Bonola et al., 2019). Flipper tissue, scale, claw and blood
110 samplings were performed when animal (stress, health) and environmental (waves) conditions
111 allowed them.

112 All fieldwork, captures and samplings were performed in accordance with the French legal and
113 ethical requirements. The protocol was approved by the Conseil National de la Protection de la
114 Nature and the French Ministry for Ecology (permit numbers: 2013154-0037, 201710-0005 and
115 R02-2020-08-10-006) and followed the recommendations of the Police Prefecture of
116 Martinique. Fieldwork was carried out under the certification of Damien Chevallier (prefectural
117 authorizations' owner) under strict compliance of the Police of Martinique's recommendations
118 to minimize animal disturbance.

119 **2.2. Data analysis**

120 We considered a total of 412 marked individual green turtles captured between September 2013
121 to February 2023 (Fig. A2). The green turtle is a long-lived species with an expected high
122 survival rate and they experience little environmental seasonality in Martinique. Consequently,

123 the data from primary and punctual capture sessions between June of year i and February of
124 year $i+1$ were grouped on October of year i . For instance, February 2023 is grouped with
125 October 2022 and analysis were then performed between 2013 and 2022. If an individual was
126 captured multiple time among grouped capture sessions, only the first capture was retained for
127 the analysis.

128 We analyzed this CMR dataset using Multi-State Jolly-Seber models (MSJS; Dupuis and
129 Schwarz 2007) fitted in MARK software v6.2 (White and Burnham, 1999). We defined six
130 states which combine the information of capture locations (two sites: GA and ABAC) and size
131 classes (SC; three size classes: SC1: $25 \text{ cm} \leq \text{CCL} < 59 \text{ cm}$, SC2: $59 \text{ cm} \leq \text{CCL} < 73 \text{ cm}$; SC3:
132 $73 \text{ cm} \leq \text{CCL}$). We thus obtained estimations of: ϕ the apparent survival, p the capture
133 probability considering the animal is available in the study area, Ψ the transition probability
134 between states, $pent$ the probability of the year when an individual enters the study area
135 considering his initial state, and π the probability of recruitment in a given initial state.

136 During the analyses, we controlled for the effect of capture effort on capture probabilities by
137 including the log-transformed half-days of prospection (logCE) in the models, with one half-
138 day equivalent to 4 hours. In addition, we controlled for the effect of water turbidity on capture
139 probabilities with a binary variable (1: turbid, 0: not turbid) since high rainfall in 2018 and 2020
140 clouded water and increased difficulty to catch turtles. Capture probability p was fixed to 0 for
141 2014 to account for the absence of capture session this year. To note, this missing year had
142 implications for the estimation of Φ and $pent$ when modeled as time-dependent. In that case,
143 specific estimates for these parameters in 2013 and 2014 were not separately obtainable;
144 instead, the estimates pertain to the combined duration spanning these two years *i.e.*, the
145 probability of staying available in the study area for the years 2013 and 2014 ($\Phi_{2013} * \Phi_{2014}$)
146 and the probability of entering the study area in 2013 or 2014 ($pent_{2013} + pent_{2014}$).

147 In order to detect any potential capture heterogeneity or transient behavior, a general goodness-
148 of-fit (GoF) test for multi-state models (Pradel et al., 2003) was performed on the global time-
149 dependent model using UCARE v3.3 (Choquet et al., 2009).

150 The most general model included state-specific and time-dependent survival probability Φ ; site-
151 specific, log(CE) and turbidity effects on capture probability p , size-class-specific and time-
152 dependent entrance probabilities $pent$ and state-specific π . To avoid over-parametrization, Ψ
153 was classified according to transition possibilities: SSI/SSC = same site/same size class,
154 SSI/CSC = same site/change size class, CSI/SSC = change site/same size class, CSI/CSC =
155 change site/change size class, $CSI/C2SC$ = change site/skip one size class, $SSI/C2SC$ = same
156 site/skip one size class (Fig. B1). Transition to a smaller size-class were set to 0. Models were
157 then simplified by step, starting by p and following, in this order, by Φ , Ψ , $pent$ and then π .
158 Time-dependent effect, when present, was removed first. Then, state-specific effect was
159 reduced to size-class-specific effect, then site effect and finally to constant estimates. Ψ was
160 only simplified to constant. Selected model for a given step was used as general one for the
161 next step. Model selection was based on the comparison of AICc. When $\Delta AICc > 2$, model with
162 the lowest AICc is kept. Otherwise, a Likelihood Ratio Test (LRT) was used to determine which
163 model to keep.

164 **2.3. Structural parameter estimates**

165 The best model selected was re-run using Monte-Carlo Markov Chain (MCMC) procedure
166 implemented in MARK software with 50000 iterations, 4000 tuning samples and 1000 burn-in
167 samples, with uninformative prior on each parameter (Normal(0,1.75)). The output was
168 processed in R v4.2.2 (R Core Team, 2022) using the ‘coda’ package (Plummer et al., 2006) to
169 calculate the estimate and precision of each parameter with the median, the variance and the
170 95% highest posterior density intervals (HPDI_{95%}) of the posterior distribution.

171 **2.4. Abundance, density, recruitment and trends**

172 Derived parameters provided by the MSJS were the super-population size N^* corresponding to
173 the overall number of individuals that used the sampled area during the study, the annual
174 abundance per state s $N_{i,s}$ and the global annual abundance N_i .

175 Annual abundance per site $N_{i,site}$ was estimated using an Horwitz-Thompson (HT) type
176 estimator (Seber, 1982). $N_{i,site}$ was then converted in density, *i.e.*, the number of turtles per
177 hectare $D_{i,site}$ using the area of each site (Seber, 1982).

178 For the present study, annual recruitment in each size class $E_{i,sc}$ was defined as the number of
179 immigrant individuals which settled on one of the two sites between i th and $i+1$ th year in a
180 given size class sc . Formula described in Dupuis and Schwarz (2007) was adapted as follows:

$$181 \quad E_{i,sc} = \pi_{sc} \cdot \text{pent}_{i,sc} \cdot N^*$$

182

183 Abundance and recruitment estimates, along with their associated precision, were calculated
184 with the median, the variance and 95% credible intervals. Variance-weighted trend analyses
185 were performed on site and size-class specific abundance and on total number of new entrants
186 using generalized least squared (GLS) method with the package ‘nmls’ (Pinheiro et al., 2022)
187 and following the method described in Chaloupka and Limpus (2001).

188 **2.5. Relationship between apparent survival, recruitment and density of turtles**

189 Relationship between recruitment E , apparent survival ϕ and density of turtles D was studied
190 using Pearson correlation tests on MCMC output. Correlation tests were performed: 1) between
191 D_i and ϕ_i and between D_i and E_i in order to test density-dependence of recruitment and
192 emigration, 2) between D_{i+1} and ϕ_i and between D_{i+1} and E_i to test the effect of emigration and
193 recruitment on density. For each test, significance was assessed by whether its HPDI_{95%}
194 involved the value “0”.

195 Diet and habitat usage of green turtles vary depending of their size (Bjorndal, 1980; Madeira et
196 al., 2022) and stable isotopes analysis confirm diet differences in Martinique (Siegwalt, 2021).
197 Competition would therefore be more likely size-specific and correlation tests were then
198 performed using state-specific density and size-class specific apparent survival and recruitment.

199 **3. Results**

200 **3.1. Site prospection and captured turtles**

201 Sampling effort was variable across years and the success of turtle capture by the free-divers
202 depended on water turbidity. Sampling effort was summarized in Table A1.

203 A total of 413 captures were performed in GA (Table A1) corresponding to 237 different
204 immature green turtles (Fig. A2). Individuals were captured one to five times during the study
205 (Fig. A3). CCL ranged 29.5 – 100.7 cm (mean CCL \pm SD: 64.9 \pm 15.5 cm; Fig. A4). In ABAC,
206 245 captures were performed (Table A1) from a total of 181 different immature green turtles
207 (Fig. A2). Individuals were captured one to three times during the study (Fig. A3). In this site,
208 CCL ranged 26 – 94.6 cm (mean CCL \pm SD: 66.0 \pm 13.7 cm; Fig. A4). Turtle size distribution did
209 not differ between sites (Student t-test; $p > 0.05$).

210 **3.2. Goodness of Fit results and model selection**

211 The Goodness of Fit procedure for Jolly Movement (JMV) model was not significant
212 ($\chi^2 = 49.669$, $df = 93$, $p = 1$) indicating no capture heterogeneity and no transience in our
213 dataset. According to AICc selection (Table B1), ϕ was size-class- and time-dependent. p varied
214 between site and depended of log(CE) and turbidity. Ψ varied among defined categories. $Pent$
215 was size-class- and time-dependent and π varied among size-classes.

216 **3.3. Structural parameter estimates**

217 Apparent survival probabilities ϕ had a mean estimate of 0.95 (HPDI_{95%}: 0.90 – 0.99) for SC1
218 and 0.84 (HPDI_{95%}: 0.76 – 0.91) for SC2, noticeably higher than those of SC3 0.64 (HPDI_{95%}:
219 0.57 – 0.70).

220 The modeled recapture probabilities p accounting for turbidity and sampling effort varied
221 among years and sites. Specifically, p ranged from 0.32 (HPDI_{95%}: 0.24 – 0.39) to 0.56
222 (HPDI_{95%}: 0.50 – 0.64), for GA; and from 0.04 (HPDI_{95%}: 0.02 – 0.07) to 0.42 (HPDI_{95%}: 0.34
223 – 0.51) for ABAC.

224 **3.4. Derived parameter estimates**

225 In SC1, there were between 6.9 (HPDI_{95%}: 0.1 – 17.7) and 44.2 (HPDI_{95%}: 26.6 – 62.5)
226 individuals that settled yearly in each bay. For SC2 and SC3, yearly number of new entrants
227 ranged from 0.3 (HPDI_{95%}: 0 – 1.9) to 2.6 (HPDI_{95%}: 0 – 7.3) and from 0.7 (HPDI_{95%}: 0 – 2.3)
228 to 4.8 (HPDI_{95%}: 1.5 – 8.9) respectively (Fig.1, details in Table C1).

229 Relatively similar abundances were observed between the two sites. Annual abundance of
230 turtles varied between 64.7 (HPDI_{95%}: 55.2 – 74.4) and 141.8 (HPDI_{95%}: 110.8 – 178.9)
231 individuals in GA and between 73.4 (HPDI_{95%}: 59.6 – 90.0) and 138.5 (HPDI_{95%}: 112.6 – 169.0)
232 individuals in ABAC throughout the study (resulting density per size-classes in Fig.1, details
233 in Table C2).

234 **3.5. Trends in annual abundance and annual recruitment**

235 Trend analysis revealed that the green turtle population increased in GA at a rate of 9.99% per
236 year ($p = 0.018$), largely driven by SC1 abundance growth (22.96% per year, $p = 0.01$, Table
237 C3). At ABAC, the green turtle abundance remained stable throughout the study ($p = 0.092$)
238 despite an increase of SC1 turtle abundance of 14.08% per year ($p = 0.004$, Table C3). No
239 significant trend was detected for SC2 and SC3 abundance, nor for the yearly number of new
240 entrants ($p > 0.05$, Table C3).

241 3.6. Relationship between apparent survival, recruitment and density of turtles

242 We used $\phi_{2013/2014}$ in correlation tests since $\phi_{2013/2014}$ was high across all size-classes (mean =
243 0.94, HPDI_{95%}: 0.88 – 1), which indicated a high survival rate in 2013 and 2014. For E , we
244 excluded $E_{2013/2014}$ since the mean yearly number of new entrants for the two years combined
245 (2013 and 2014, $E_{2013/2014} / 2$) could be different from the real yearly number of new entrants.

246 Most of the recruitment occurred in SC1 (Fig.1) while most of the emigration occurred in SC3.
247 Thus, state-specific correlation tests were only performed on SC1 for recruitment E_i and on SC3
248 for apparent survival ϕ_i (Fig.2). Relationship between ϕ_i and D_i was stronger in ABAC (-0.84,
249 HPDI_{95%}: -0.97 – -0.61, Fig. D1) than GA (-0.49, HPDI_{95%}: -0.78 – -0.02, Fig. D1). The
250 relationship between E_i and D_i was only significant in GA (-0.39, HPDI_{95%}: -0.66 – -0.04, Fig.
251 D1). ϕ_i was not related to D_{i+1} while E_i was positively related to D_{i+1} both in GA (0.81, HPDI_{95%}:
252 0.57 – 0.96, Fig. D1) and ABAC (0.61, HPDI_{95%}: 0.24 – 0.88, Fig. D1).

253

254 4. Discussion

255 Using wild-derived CMR data, this study provides key demographic results for a long-term
256 investigation focusing on immature green turtle population dynamics in the Lesser Antilles.
257 Importantly, we provide data on recruitment rates of juveniles at their foraging grounds, a key
258 component of the population dynamics of this endangered reptile. Altogether, results presented
259 can serve as basis for future investigations and enables us to formulate specific hypotheses
260 about the internal and external factors that could influence the recruitment and emigration from
261 the juvenile aggregations on the Martinique coasts, therefore providing a solid basis to support
262 their conservation.

263 4.1. Dynamics of juvenile green turtle aggregations in Martinique

264 Apparent survival did not differ between Anse du Bourg d'Arlet/Chaudière (ABAC) and
265 Grande Anse d'Arlet (GA) despite a higher prevalence of fibropapillomatosis in ABAC (Roost
266 et al., 2022), suggesting that there is no effect of the disease on survival as observed in Patrício
267 et al. (2011). Nonetheless, further studies should consider fibropapillomatosis severity in order
268 to assess its impacts on green turtles. High ϕ estimates for SC1 (0.95, HPDI_{95%}: 0.90 – 0.99,
269 25 cm \leq CCL < 59 cm) and SC2 (0.84, HPDI_{95%}: 0.76 – 0.91, 59cm < CCL < 73cm) are similar
270 to apparent survival estimated on turtle of same size in Puerto Rico (0.83, CI_{95%}: 0.79 – 0.87;
271 Patrício et al., 2011) and South Great Barrier Reef (0.88, CI_{95%}: 0.84 – 0.93; Chaloupka and
272 Limpus, 2005) and to the true survival of the first 3 cohort classes in Bahamas (0.89; Bjorndal
273 et al., 2003). This suggests low mortality and limited emigration of small turtles probably due
274 to favorable developmental conditions in areas where poaching and natural predators (*i.e.*
275 sharks) are absent, unlike foraging grounds in Baja California (true survival = 0.58, CI_{95%} :
276 0.36 – 0.78; Seminoff et al., 2003). Considering that true survival increases with sea turtle age
277 (Chaloupka and Limpus, 2005), difference in apparent survival observed between SC1/SC2 and
278 SC3 could then be attributed to definitive emigration expected at large sizes. Indeed, the
279 developmental migration of individuals over 78.5 cm CCL in the juvenile foraging ground of
280 Martinique (Chambault et al., 2018) is thought to be the responsible for a lower apparent
281 survival, as suggested by other CMR studies on immature green turtles (Bjorndal et al., 2003;
282 Colman et al., 2015; Kameda et al., 2023; Patrício et al., 2011). Considering the structure of the
283 model used in this study, apparent survival variations presented here seem therefore to be a
284 proxy of emigration variations.

285 Settlement of new individuals predominantly took place in SC1. However, there were
286 occasional instances of settlement of turtles belonging to SC3. These arrivals could originate
287 from sites in Martinique not covered by this study or from feeding grounds on other islands.
288 Earlier emigration of juvenile turtles at smaller sizes than expected has been observed under

289 unfavorable environmental conditions, as reported in green turtles by Meylan et al. (2022) and
290 Pillans et al. (2021). This behavior has been linked to turtles that exhibit slower growth rates in
291 the Bahamas, potentially indicating an adaptive strategy to optimize their development by
292 relocating to other feeding grounds offering more abundant or higher-quality resources
293 (Bjorndal et al., 2019). Settlement of new large individuals, as well as the presence of resident
294 turtles from 27 cm up to 100 cm CCL (Fig. A4), demonstrate that the two sites studied are
295 currently able to support the entire developmental stage of juvenile green turtles in the area.

296 Our study highlights increasing abundances of juvenile green turtles during the study period.
297 The link between increasing abundances of juveniles and nesting trends has been mentioned by
298 Bjorndal et al. (2005) and Kameda et al. (2023). Nonetheless, constant recruitment trends
299 prevent us from hypothesizing that positive abundance trends observed in Martinique are linked
300 to increasing nesting trends in the contributing Caribbean rookeries (Mazaris et al., 2017). The
301 constant recruitment trends could then be explained by low hatchling success as observed in
302 the Gulf of Mexico (Lasala et al., 2023). Indeed, low hatchling success effects on population
303 growth could take a long time to be detected in nesting trends (Mazaris et al., 2017), however
304 it is therefore likely to affect within a few years recruitment in juvenile foraging grounds,
305 considering the ‘lost years’ phase duration (Lutz et al., 2003). This hypothesis needs to be taken
306 carefully since no data on nesting rookeries has been included in this study.

307 **4.2. Effect of density on juvenile green turtle population dynamics**

308 Drivers of variations of demographic parameters could be multiple, especially those affecting
309 emigration, as this parameter is highly sensible to local environmental factors (Mollenhauer et
310 al., 2022; Pillans et al., 2021). Our analysis demonstrated that the local density significantly
311 and negatively influenced apparent survival in large turtles (SC3, Fig.2). The most likely
312 explanation is an effect on the probability of emigration, as discussed earlier, with a more
313 pronounced effect observed in ABAC (Fig.2). Consequently, our results suggest that dispersal

314 in older juveniles could be triggered by high densities, a phenomena commonly observed in
315 population dynamics (Harman et al., 2020). In parallel, yearly recruited number of small turtles
316 seems to have low density-dependence. This difference of sensitivity to density between small
317 and large turtles suggests that the carrying capacity of the environment could be size-dependent.
318 Indeed, green turtles exhibit size-specific diet and habitat use in juvenile foraging grounds
319 (Bjorndal, 1980; Madeira et al., 2022). In Martinique, large turtles consume *T. testudinum* and
320 *S. filiforme* (Siegwalt, 2021) which are less digestible resources (Siegwalt et al., 2022) while
321 new recruits mainly consume highly digestible resources such as *H. stipulacea* and macroalgae
322 (Siegwalt et al., 2021, 2022).

323 The high availability of *H. stipulacea* and macroalgae at the studied sites in Martinique
324 (Siegwalt et al., 2022) may mitigate density-dependence in the recruitment of juveniles and
325 contribute to low emigration rates. This hypothesis is also consistent with the observed effect
326 of recruitment variations on density and lack of effect of apparent survival on density, which
327 seems to indicate that there is a higher number of turtles entering the study sites than leaving
328 them.

329 In contrast, it appears that the density of large turtles is approaching the maximum number that
330 the environment can support. This maximum capacity is strongly linked to the health of the
331 seagrass beds (Williams, 1988). In Martinique, native seagrass meadows face pressures from
332 recreational boat anchoring and from eutrophication (Roost et al., 2022; Siegwalt et al., 2022).
333 The rapid growth of *H. stipulacea* enables this species to colonize disturbed patches of sand
334 (e.g. those cleared by anchors), and to outcompete native species such as *S. filiforme* and *T.*
335 *testudinum* (Smulders et al., 2017). Moreover, under eutrophic conditions, *H. stipulacea* tends
336 to form dense meadows, thus preventing the development of native seagrass species (Van
337 Tussenbroek et al., 2016). The scarcity of native seagrass meadows, which are preferred by
338 large turtles, results in an increased density of turtles on these native patches (Siegwalt et al.,

339 2022). Native seagrasses are consequently more likely to suffer from overgrazing, exacerbating
340 the decline of their available biomass (Gangal et al., 2021) and associated density-dependent
341 mechanisms. This reduction in the surface area and the scarcity of remaining native patches
342 could lead to several interconnected consequences such as the need to expend more energy to
343 locate suitable food sources (Meylan et al., 2022) and exposure to increased competition for
344 food. This context could thus explain these density-dependent emigration peaks, observed in
345 our study.

346 Ultimately, the reduced quality of their diet, also by including the less energetic *H. stipulacea*
347 (Siegwalt et al., 2022), could trigger earlier definitive emigration (*i.e.* below ~60cm straight or
348 curved carapace length; Bjorndal et al., 2019; Pillans et al., 2021). In this context, multiple
349 consequences are expected: slower growth rate, delayed maturation (Girondot et al., 2021),
350 negative abundance trends (Gangal et al., 2021), or modified juvenile population structure
351 (Meylan et al., 2022) with negative effect on Atlantic green turtle population recovery
352 (Chambault et al., 2018). In Martinique, similar high apparent survival rates between SC2 and
353 SC1 suggests that there is no significant earlier emigration yet. Nonetheless, without
354 conservation measures on green turtle foraging habitat, such consequences are expected.

355 Complementary approach will be required to study turtles diet (stable isotope analysis), spatial
356 use of the habitat and interaction between turtles (biologgers; Jeantet et al., 2020) according to
357 their size and will expand knowledge on density-dependent mechanisms demonstrated here.

358 **4.3. Conservation implications**

359 Here, we discuss potential threats faced by large juvenile green turtles on their foraging grounds
360 in Martinique. High pressures observed on seagrass meadows may lead to anticipate negative
361 impact on the structure of juvenile green turtle populations.

362 Given the significant role played by the juvenile green turtle population of Martinique in
363 supporting the Atlantic breeder population (Chambault et al., 2018), it is imperative to preserve
364 favorable environmental conditions to ensure the viability of the entire Atlantic green turtle
365 regional population. Conservation measures may need to focus on preventing native seagrass
366 depletion and invasive seagrass expansion and on factors associated with these biotic changes.
367 For instance, damages promoted by boat anchors and classic mooring could be avoided by the
368 installation of sustainable mooring in foraging areas of green turtles (Luff et al., 2019).
369 Moreover, sources of pollution should be identified and measures limiting pollutants emission
370 in coastal waters should be implemented. The protection of the last areas of native seagrass is
371 therefore a priority that must be implemented as quickly as possible, even if it is not enough to
372 stop their disappearance (Siegwalt et al., 2022). Seagrass restoration is perhaps a
373 complementary solution to consider on long-term, as it has been shown worldwide, specifically
374 in the Caribbean (Thorhaug et al. 2020). Foraging habitat conservation has been similarly
375 proposed for terrestrial herbivores, since their demography is affected by grassland and
376 savannah degradation (Lima et al., 2018). Complementary monitoring studies will be essential
377 to understand seagrass bed dynamics under anthropic pressures and to assess the effectiveness
378 of restoration measures in improving the demography of green turtles and the overall health of
379 these critical ecosystems.

380 **5. Conclusion and perspectives**

381 Here we provided results supporting the hypothesis that native seagrass beds depletion could
382 1) lead to a restructuration of juvenile green turtle aggregations and 2) impede the capacity of
383 Martinique foraging grounds to support the entire juvenile life-stage. Considering the
384 worldwide decline of seagrass beds, results and conservation measures outlined in this study
385 could prove highly valuable in the management of other juvenile green turtle foraging areas.

386 Moreover, these measures could benefit other species, also threatened by seagrass bed depletion
387 such as manatees, fishes and birds species (Thorhaug et al., 2020).

388 Estimating both recruitment, survival and emigration of juvenile sea turtle aggregations
389 represents a critical step to fill the knowledge gaps regarding this crucial life-stage (Wildermann
390 et al., 2018). This is paramount given the vast geographical range of sea turtle life cycles and
391 their vulnerability to anthropogenic threats in each of their life-stages, underscoring the
392 necessity for conservation measures that transcend regions and life-stages. To further advance
393 our knowledge and conservation efforts, future studies should consider the following
394 objectives: (1) Quantify the presence of pollutants in the coastal environment and their effect
395 on seagrass bed depletion. (2) Extend the knowledge about juvenile demography by exploring
396 somatic growth rate in function of habitat/food quality and turtles diet; this could be useful to
397 determine time of residency of turtles in the foraging grounds and to investigate potential
398 density-dependent effects on growth rates. (3) Pursue the juvenile green turtle demography
399 monitoring with yearly CMR sessions in Martinique, mainly focused on Grande Anse and Anse
400 du Bourg/Chaudière, to enable the detection of decline in abundance or survival rates, and
401 facilitate the assessment of the effectiveness of local conservation measures. (4) Extend the
402 investigations to related nesting rookeries, such as French Guiana, to establish connections
403 between the demography of the different life-stages and develop efficient regional conservation
404 measures that encompass the entire range of sea turtle habitats. These future studies will be
405 crucial for the ongoing conservation and protection of sea turtles throughout their entire life
406 cycle.

407 **6. Conflict of interest**

408 The authors declare no conflict of interest.

409

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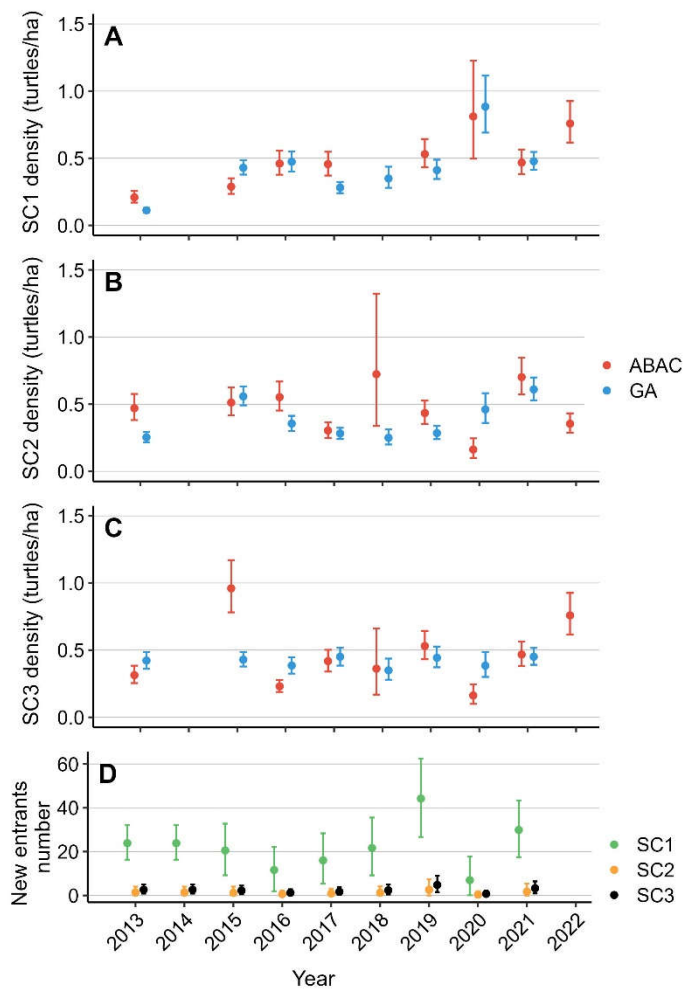
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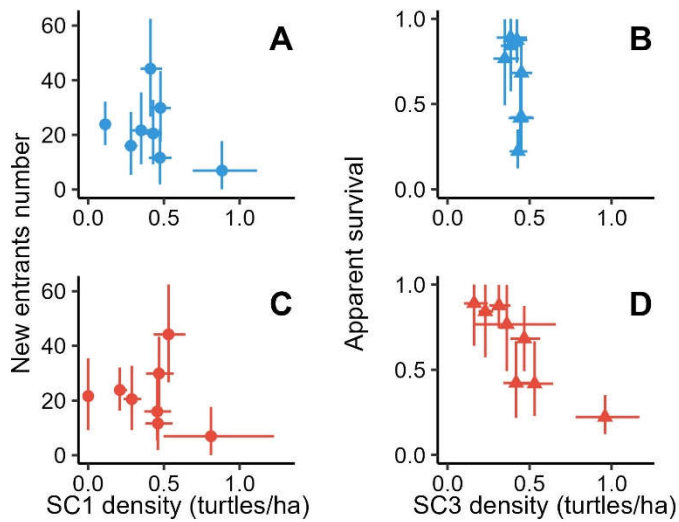
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640 Fig.1: Annual green turtle density in GA (blue dots) and ABAC (red dots) for (A) size-class 1,
 641 (B) size-class 2 and (C) size-class 3 and (D) size-class-specific number of new entrants with
 642 HPDI_{95%} from the best model.



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644 Fig.2: (A, C) Yearly recruitment in SC1 as function of density of SC1 turtles (dots) and (B, D)
 645 apparent survival of SC3 as function of density of SC3 turtles (triangles) for (A, B) Grande
 646 Anse d'Arlet (blue) and (C, D) Anse du Bourg d'Arlet/Chaudière (red). Estimates of
 647 recruitment, apparent survival and density with HPDI_{95%} were obtained from the best model.

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651 Fig 1 : One column width

652 Fig 2 : One column width

Supplementary materials

Appendix A: Study sites and dataset characteristics

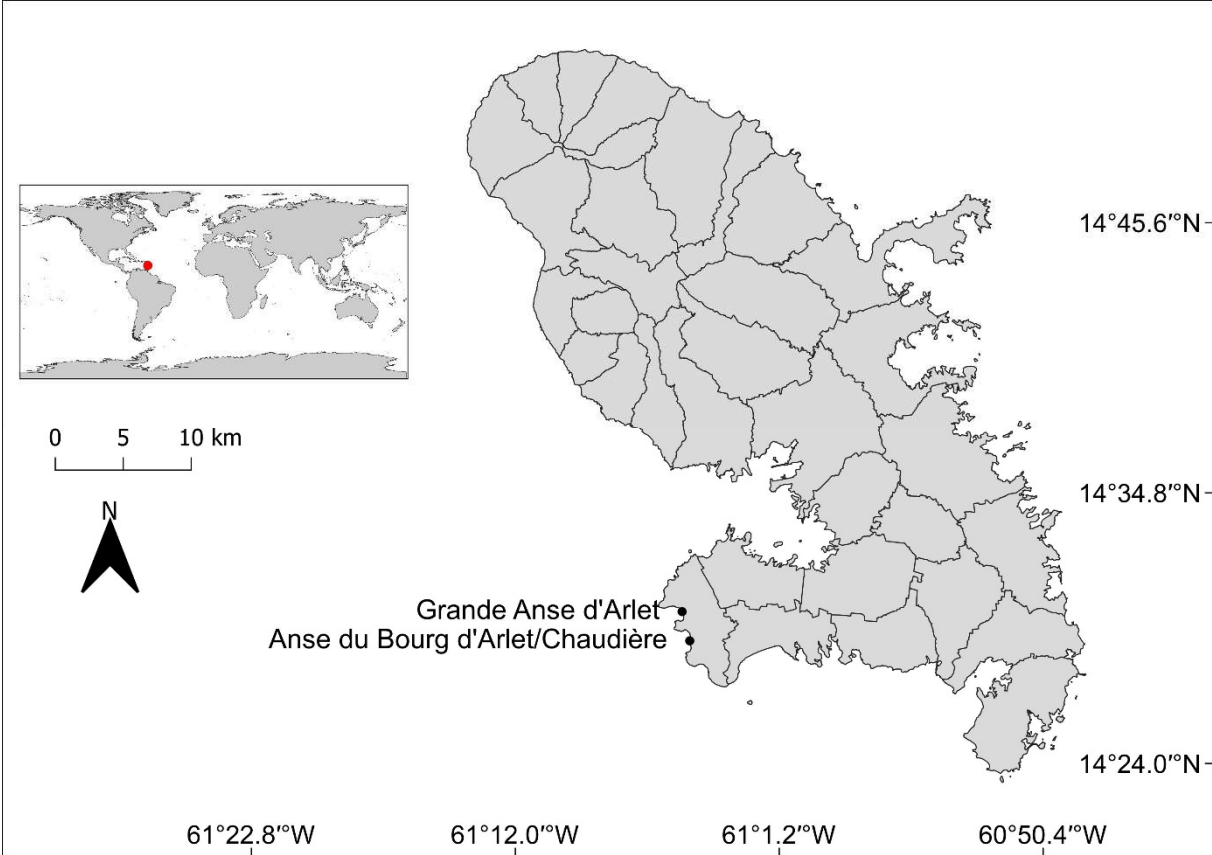


Figure A1: Location of Martinique Island in the world map (red dot) and location of the two sampled sites in Martinique (black dots).

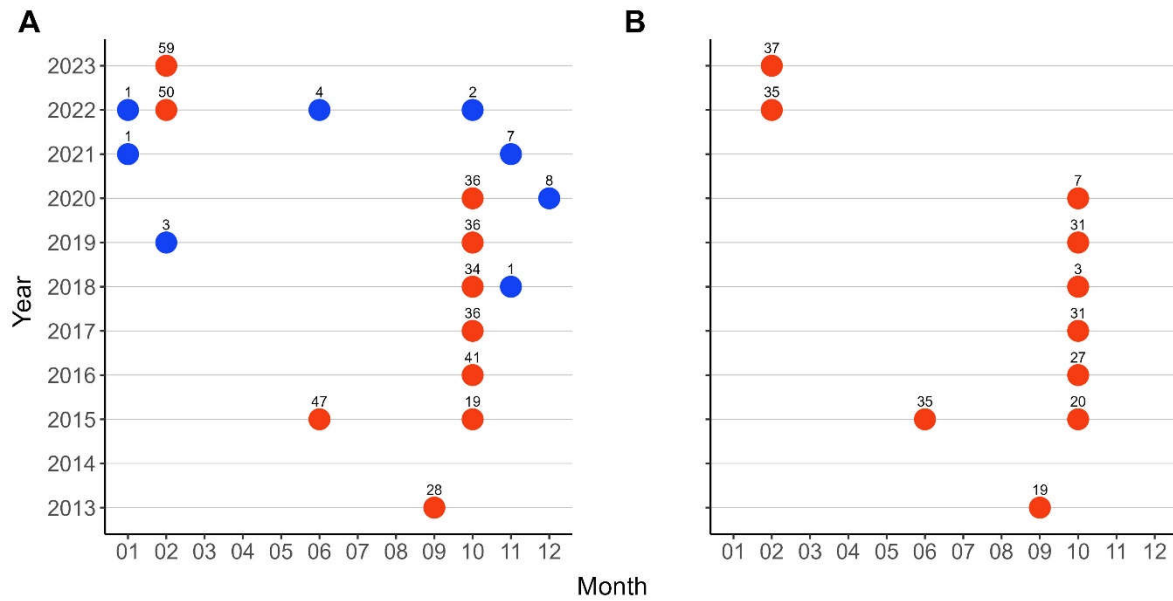


Figure A2: Calendar of capture occasions in (A) Grande Anse d'Arlet and (B) Anse du Bourg d'Arlet/Chaudière between 2013 and 2023. Number of capture per session are indicated above each dot. Primary and irregular sessions are symbolized by red and blue dots respectively.

Table A1: Sampling effort (half-day) and number of individuals captured by year and by sampled site from 2013 to 2022. ABAC = Anse du Bourg/Chaudière and GA = Grande Anse d'Arlet.

Year	Capture effort		Number of captures	
	ABAC	GA	ABAC	GA
2013	2.11	3.49	19	28
2015	4.58	6.18	55	66
2016	2.53	3.16	27	41
2017	3.4	3.49	31	36
2018	0.4	8.55	3	38
2019	2.33	2.83	31	36
2020	0.97	3.96	7	45
2021	2.43	3.89	35	58
2022	2.19	4.25	37	65
Total	20.94	39.8	245	413

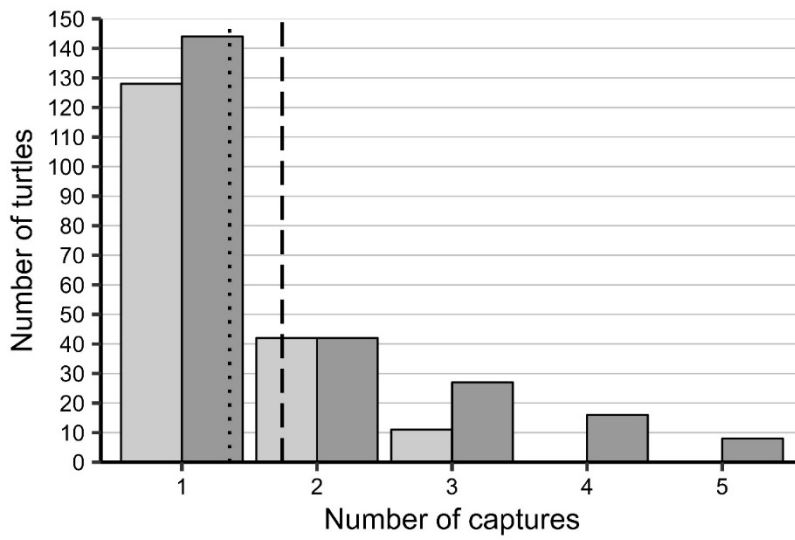


Figure A3: Frequency of individual-specific number of captures on Anse du Bourg/Chaudière (light grey) and Grande Anse d'Arlet (dark grey). Mean numbers of captures per turtle were represented for Grande Anse d'Arlet (dashed vertical line, 1.74 ± 1.11 captures) and Anse du Bourg/Chaudière (dotted vertical line, 1.35 ± 0.59 captures).

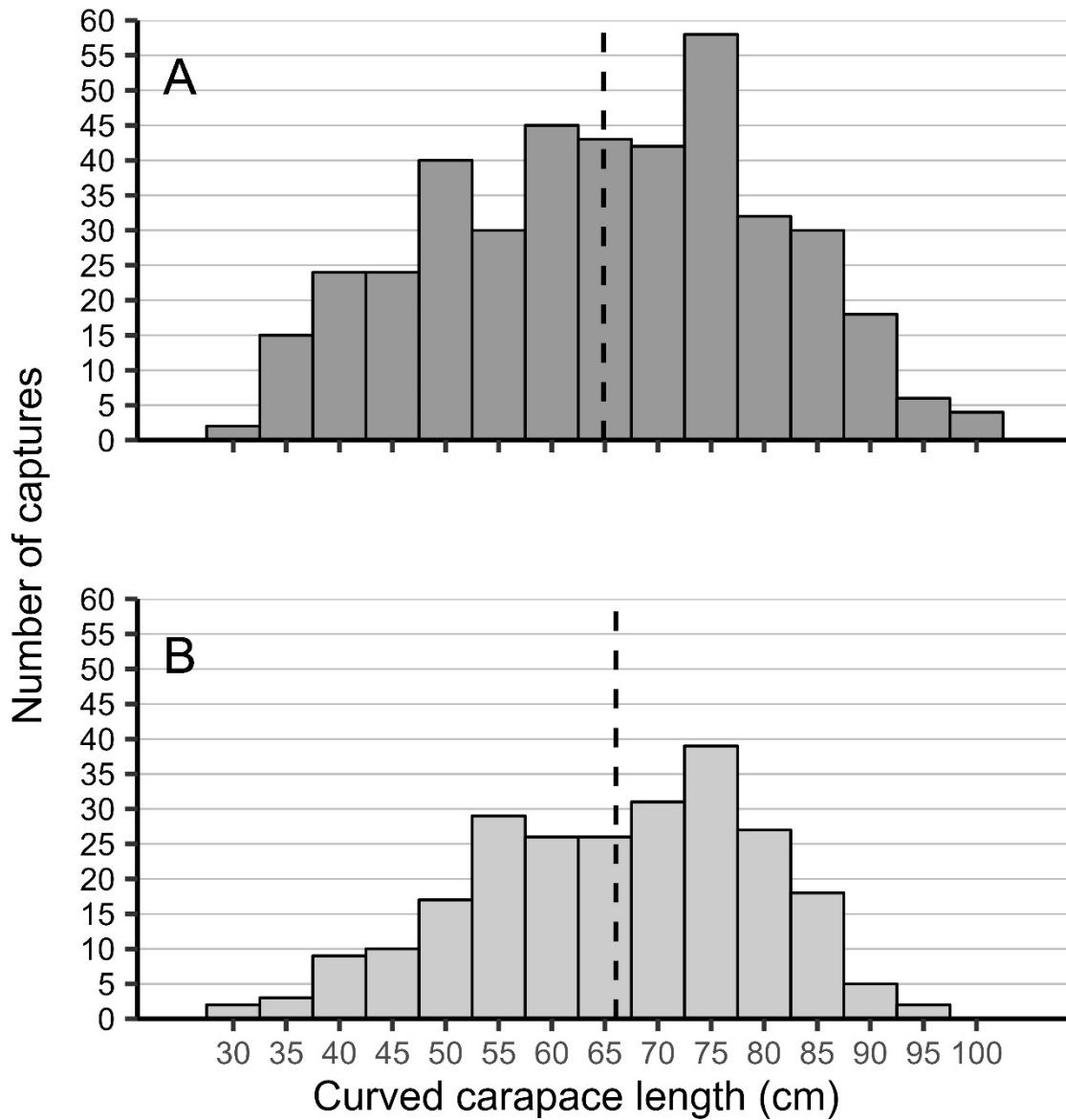


Figure A4: Central curved carapace length (CCCL, cm) distribution in Grande Anse d'Arlet (A, dark grey, n=413) and Anse du Bourg/Chaudière (B, light grey, n=245) of captures used by the MSJS model with mean CCL represented by dashed line for each site.

Appendix B : Model structure and selection

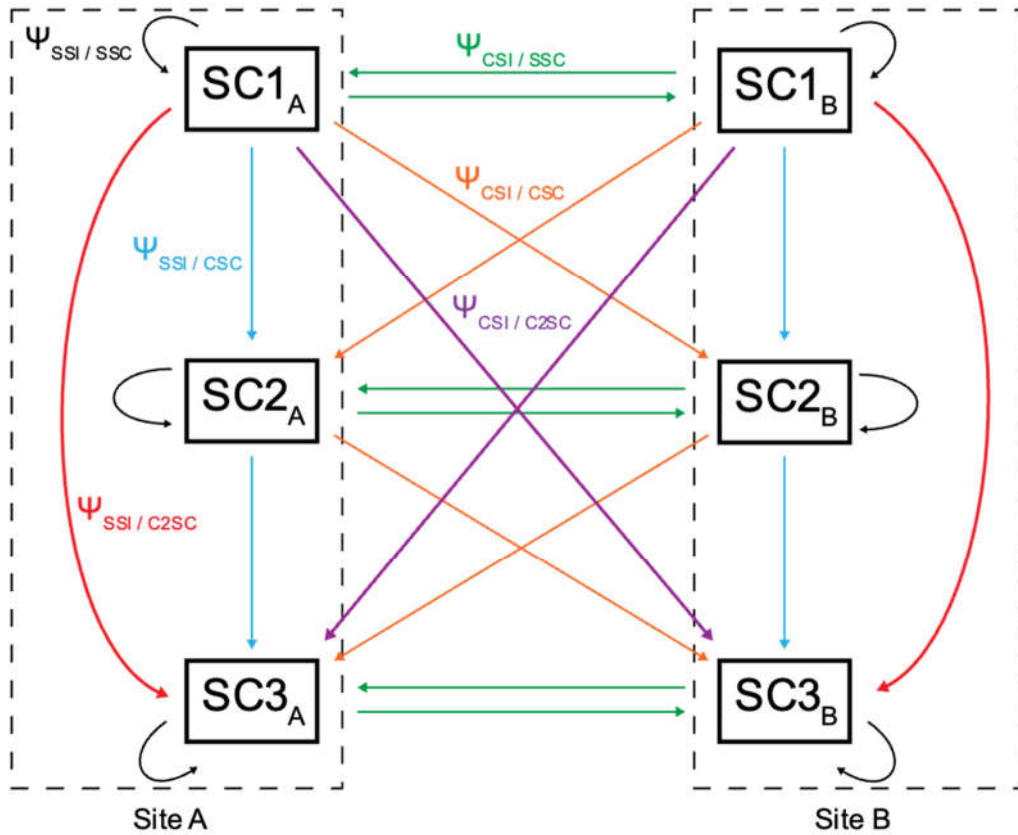


Figure B1: Transitions between three size classes (from the smaller to the larger : SC1, SC2 and SC3) on two sites (Site A and Site B) and associate probabilities Ψ . *SSI/SSC* = Same site/same size class (black), *SSI/CSC* = same site/change size class (blue), *CSI/SSC* = change site/same size class (green), *CSI/CSC* = change site/change size class (orange), *CSI/C2SC* = Change site/skip one size class (purple), *SSI/C2SC* = Same site/skip one size class (red).

Table B1: Selection of models built using green turtle CMR dataset collected in Martinique with estimation of apparent survival probability (ϕ), recapture probability (p), transition probability (Ψ), probability of entry between 2 occasions ($pent$) and initial probability of recruitment (π). Selected model for each step is in **bold**, and best model is in **bold and red**. LR Test **Mod 10** vs Mod 3 : $\chi^2 = 5.424$, $df = 3$, $p = 0.1432$ | LR test **Mod10** vs Mod16 : $\chi^2 = 16.088$, $df = 7$, $p = 0.0243$ | LR test **Mod17** vs Mod18 : $\chi^2 = 15.965$, $df = 7$, $p = 0.0254$ | LR test **Mod20** vs Mod17 : $\chi^2 = 3.722$, $df = 2$, $p = 0.1555$. No.= model number, AICc = corrected Akaike Information Criterion, Dev = Deviance, Npar = number of estimable parameters.

Step	No.	Model	AICc	Delta AICc	Num. Par	Deviance
p	1	$\Phi(St+t) p(St+t+\log EC+Turb) \Psi(T_type) pent(St+t) \pi(St)$	4633.0198	47.5585	53	697.88
	2	$\Phi(St+t) p(St+\log EC+Turb) \Psi(T_type) pent(St+t) \pi(St)$	4625.8660	40.4047	45	709.44
	3	$\Phi(St+t) p(\text{Site}+\log EC+Turb) \Psi(T_type) pent(St+t) \pi(St)$	4593.6900	8.2287	41	686.44
	4	$\Phi(St+t) p(CT+\log EC+Turb) \Psi(T_type) pent(St+t) \pi(St)$	4640.4592	54.9979	38	740.01
	5	$\Phi(St+t) p(\text{Site}+Turb) \Psi(T_type) pent(St+t) \pi(St)$	4628.1546	42.6933	40	723.18
	6	$\Phi(St+t) p(\text{Site}+\log EC) \Psi(T_type) pent(St+t) \pi(St)$	4600.5669	15.1056	40	695.59
	7	$\Phi(St+t) p(\text{Site}) \Psi(T_type) pent(St+t) \pi(St)$	4645.7901	60.3288	39	743.08
	8	$\Phi(St+t) p(.) \Psi(T_type) pent(St+t) \pi(St)$	4655.7060	70.2447	38	755.26
ϕ	9	$\Phi(St) p(\text{Site}+\log EC+Turb) \Psi(T_type) pent(St+t) \pi(St)$	4614.0845	28.6232	34	722.60
	10	$\Phi(CT+t) p(\text{Site}+\log EC+Turb) \Psi(T_type) pent(St+t) \pi(St)$	4592.3118	6.8505	38	691.86
	11	$\Phi(SC1./SC2./SC3+t) p(\text{Site}+\log EC+Turb) \Psi(T_type) pent(St+t) \pi(St)$	4599.2155	13.7542	38	698.77
	12	$\Phi(CT) p(\text{Site}+\log EC+Turb) \Psi(T_type) pent(St+t) \pi(St)$	4614.5751	29.1138	31	729.75
	13	$\Phi(\text{Site}) p(\text{Site}+\log EC+Turb) \Psi(T_type) pent(St+t) \pi(St)$	4657.9420	72.4807	31	773.11
	14	$\Phi(.) p(\text{Site}+\log EC+Turb) \Psi(T_type) pent(St+t) \pi(St)$	4653.8433	68.382	29	773.41
Ψ	15	$\Phi(CT+t) p(\text{Site}+\log EC+Turb) \Psi(.) pent(St+t) \pi(St)$	4829.7719	244.3106	33	940.52
$pent$	16	$\Phi(CT+t) p(\text{Site}+\log EC+Turb) \Psi(T_type) pent(St) \pi(St)$	4592.7805	7.3192	31	707.95
	17	$\Phi(CT+t) p(\text{Site}+\log EC+Turb) \Psi(T_type) pent(CT+t) \pi(St)$	4586.1946	0.7333	35	692.48
	18	$\Phi(CT+t) p(\text{Site}+\log EC+Turb) \Psi(T_type) pent(CT) \pi(St)$	4586.6900	1.2287	28	708.45
	19	$\Phi(CT+t) p(\text{Site}+\log EC+Turb) \Psi(T_type) pent(.) \pi(St)$	4638.3805	52.9192	26	764.50
π	20	$\Phi(CT+t) p(\text{Site}+\log EC+Turb) \Psi(T_type) pent(CT+t) \pi(CT)$	4585.4613	0	33	696.21
	21	$\Phi(CT+t) p(\text{Site}+\log EC+Turb) \Psi(T_type) pent(CT+t) \pi(.)$	4657.3236	71.8623	31	772.49

Abbreviations: SC = Size-class-dependent, t = Time-dependent, Site = Site-dependent, logCE = $\log(\text{Capture effort})$, Turb = Turbidity, Cat = Transition type, St = State-dependent., . = constant

Appendix C: Abundance, recruitment and trends in abundance

Table C1: Median (E), associated variance (Var) and credible interval (HPDI_{95%}) from the high posterior distribution of recruitment estimates.

Sizeclass	Year	E	Var	HPDI _{95%}	
SC1	2013	23.9	16.3	16.3	32.1
	2014	23.9	16.3	16.3	32.1
	2015	20.5	36.3	9.2	32.7
	2016	11.6	28.3	1.9	22.2
	2017	16.0	35.4	5.3	28.3
	2018	21.6	45.6	9.2	35.5
	2019	44.2	83.1	26.7	62.5
	2020	6.9	27.4	0.1	17.7
	2021	29.9	44.7	17.5	43.3
SC2	2013	1.4	1.5	0.0	4.0
	2014	1.4	1.5	0.0	4.0
	2015	1.2	1.6	0.0	4.0
	2016	0.6	0.5	0.0	2.2
	2017	0.9	1.0	0.0	3.1
	2018	1.2	1.7	0.0	4.1
	2019	2.6	5.0	0.0	7.3
	2020	0.3	0.5	0.0	1.9
	2021	1.8	2.9	0.0	5.4
SC3	2013	2.6	1.2	0.9	5.0
	2014	2.6	1.2	0.9	5.0
	2015	2.2	1.1	0.5	4.5
	2016	1.2	0.6	0.1	2.8
	2017	1.7	1.0	0.3	3.8
	2018	2.3	1.6	0.5	5.0
	2019	4.8	3.8	1.5	8.9
	2020	0.7	0.5	0.0	2.3
	2021	3.3	2.2	0.9	6.4

Table C2: Median (N), variance (Var) and credible interval (HPDI_{95%}) from the high posterior distribution of size-class- and site-specific annual abundance of turtles. Abundances were not estimated for 2014 because capture were not performed this year, and no estimation was provided for SC1 in ABAC for 2018 since no turtles belonging to SC1 were captured.

Sizeclass	Year	Grande Anse				Anse du Bourg/Anse Chaudière			
		N	Var	HPDI _{95%}		N	Var	HPDI _{95%}	
SC1	2013	9.2	0.5	7.9	10.6	15.5	2.7	12.5	19.0
	2015	35.2	5.2	31.0	39.9	21.3	5.0	17.3	26.0
	2016	38.9	10.0	32.8	45.2	34.1	11.8	27.9	41.2
	2017	23.1	3.1	19.7	26.6	33.8	11.4	27.5	40.5
	2018	28.7	11.2	22.9	35.8	0.0	0.0	0.0	0.0
	2019	33.7	9.0	28.3	40.1	39.3	16.1	32.0	47.6
	2020	72.5	81.2	56.6	91.4	60.0	210.3	36.8	90.9
	2021	39.1	7.8	33.9	44.8	34.6	12.2	28.2	41.8
	2022	54.0	13.7	47.2	61.7	56.1	34.3	45.6	68.5
	SC2	2013	20.8	2.5	17.7	23.9	34.8	13.6	28.2
2015		45.7	8.7	40.3	51.8	37.9	15.9	30.8	46.2
2016		29.2	5.6	24.6	33.9	40.9	16.9	33.5	49.5
2017		23.1	3.1	19.7	26.6	22.5	5.1	18.3	27.0
2018		20.5	5.7	16.4	25.6	53.5	424.4	25.0	97.9
2019		23.3	4.3	19.6	27.8	32.1	10.8	26.2	38.9
2020		37.8	22.1	29.5	47.7	12.0	8.4	7.4	18.2
2021		50.0	12.7	43.4	57.3	51.9	27.5	42.4	62.7
2022		29.1	4.0	25.4	33.2	26.2	7.5	21.3	32.0
SC3		2013	34.6	7.0	29.6	39.9	23.2	6.1	18.8
	2015	35.2	5.2	31.0	39.9	71.0	55.8	57.8	86.6
	2016	31.6	6.6	26.7	36.7	17.0	2.9	14.0	20.6
	2017	37.0	7.9	31.5	42.5	30.9	9.6	25.2	37.2
	2018	28.7	11.2	22.9	35.8	26.8	106.1	12.5	49.0
	2019	36.3	10.5	30.5	43.2	39.3	16.1	32.0	47.6
	2020	31.5	15.4	24.6	39.8	12.0	8.4	7.4	18.2
	2021	37.0	6.9	32.1	42.4	34.6	12.2	28.2	41.8
	2022	51.9	12.6	45.4	59.3	56.1	34.3	45.6	68.5
	All	2013	64.7	24.2	55.2	74.4	73.4	60.8	59.6
2015		116.1	56.3	102.2	131.6	130.2	187.6	106.0	158.7
2016		99.6	65.4	84.1	115.8	92.0	85.7	75.4	111.3
2017		83.1	40.1	70.9	95.7	87.2	76.2	70.9	104.7
2018		77.8	82.8	62.2	97.3	80.3	954.8	37.5	146.9
2019		101.2	81.2	85.0	120.3	110.7	127.8	90.1	134.1
2020		141.8	311.0	110.8	178.9	84.0	412.1	51.5	127.3
2021		137.0	95.3	118.8	157.0	121.1	149.8	98.9	146.4
2022		135.0	85.5	118.0	154.2	138.5	208.8	112.6	169.0

Table C3: GLS model outputs for Grande Anse d’Arlet (GA) all size classes confounded, Anse du Bourg /Chaudière (ABAC) all size classes confounded, and for size class 1 (SC1), size class 2 (SC2) and size class 3 (SC3) on each site.

Model	Model Summary					Population Growth (%)			
	Slope	SE	t	p	RSE	Df	Mean	LCI	UCI
GA	0.10	0.03	3.09	0.0175	0.11	9	9.99	3.55	16.84
ABAC	0.04	0.02	1.77	0.1202	0.09	9	-	-	-
GA(SC1)	0.21	0.06	3.52	0.0097	0.36	9	22.96	9.60	37.96
GA(SC2)	0.05	0.04	1.30	0.2336	0.27	9	-	-	-
GA(SC3)	0.02	0.02	1.24	0.2557	0.10	9	-	-	-
ABAC(SC1)	0.13	0.03	4.54	0.0039	0.15	8	14.08	7.77	20.76
ABAC(SC2)	-0.04	0.04	-1.04	0.3348	0.28	9	-	-	-
ABAC(SC3)	0.00	0.03	0.04	0.9696	0.33	9	-	-	-

Population growth was estimated when the slope was significant using the formula $(e^{\text{slope}}-1) \times 100$ with associated 95% confidence intervals using $(e^{\text{slope} \pm 1.96\text{SE}}-1) \times 100$ (Bjorndal et al., 2005). Significant models and associated p-values are in bold.

Appendix D: Correlation tests

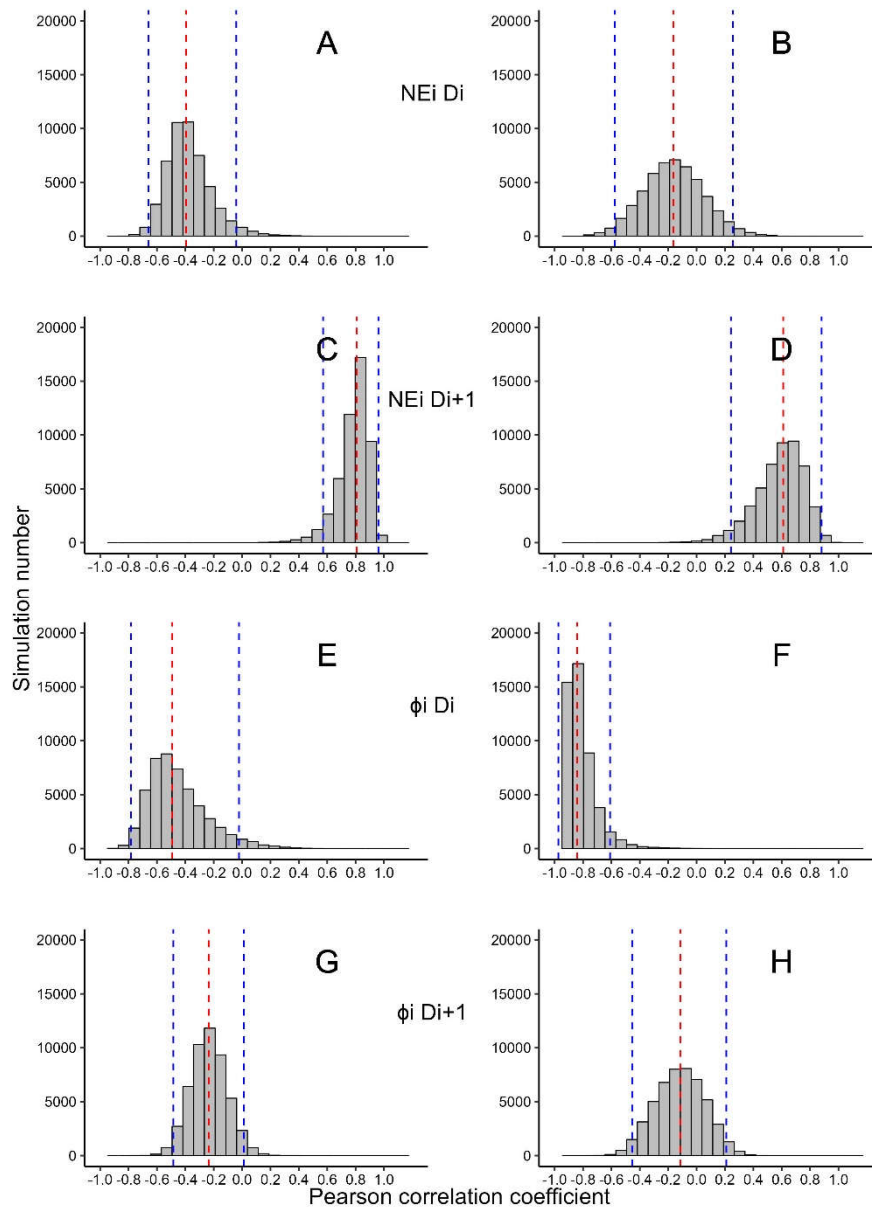


Figure D.1: Posterior distribution with median (dashed red line) and 95% highest posterior distribution interval (dashed blue lines) of Pearson correlation coefficients between : number of new recruit between year i and $i+1$ and density at year i ($NE_i D_i$); number of new recruit between year i and $i+1$ and density at year $i+1$ ($NE_i D_{i+1}$); apparent survival between year i and $i+1$ and density of turtles at year i ($\phi_i D_i$) and apparent survival between year i and $i+1$ and density of turtles at year $i+1$ ($\phi_i D_{i+1}$). Results for Grande Anse d'Arlet are on the left column (A, C, E, G) and for Anse du Bourg/Chaudière on the right column (B, D, F, H).

Appendix references

Bjorndal, K.A., Bolten, A.B., Chaloupka, M.Y., 2005. Evaluating Trends in Abundance of Immature Green Turtles, *Chelonia mydas*, in the Greater Caribbean. *Ecological Applications* 15, 304–314.